Dispersal and biotic interactions shape butterfly metacommunity structure

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Abstract

Dispersal and biotic interactions are key processes that structure communities, yet the ways in which these processes may act in parallel or interactively to alter diversity and composition remain unclear. In this thesis, I used butterflies as a study system to investigate how biotic interactions, dispersal, and landscape connectivity interact to shape butterfly metacommunities. In Chapter 2, I asked how interactions with predators and floral mutualists, as well as habitat size and connectivity, impact alpha diversity in a butterfly metacommunity. Only floral mutualist diversity and richness directly impacted butterfly diversity and richness, suggesting that small and isolated sites, and sites with high predation pressure, may nevertheless be valuable for conservation if mutualist diversity is maintained. In Chapter 3, using the same study system, I asked whether dispersal mediates species' interactions with predators, floral mutualists, and the landscape. I found that strong dispersers occurred at higher density in isolated sites with low floral density and predation, while poor dispersers occurred at a higher density in more connected sites with higher floral density and predation. These findings demonstrate that, while alpha diversity may not change with site isolation and predation (Chapter 2), species composition does. In Chapter 4, I asked what drives alpha and beta diversity along a gradient of naturalized to urban metacommunities. I found that alpha diversity was driven by local scale biotic interactions with host plants and other flowering plants, while beta diversity was driven by biotic and abiotic factors at different scales. These findings highlight that species are being filtered out of landscapes with high impervious surface area, but small, urban sites with rich host plant communities can support high butterfly diversity. This thesis furthers our understanding of metacommunity dynamics, with implications for both our understanding of ecological patterns and processes and our ability to conserve species in increasingly fragmented and urbanized landscapes.

Résumé

La dispersion et les interactions biotiques sont des processus clés qui structurent les communautés, mais les façons dont ces processus peuvent agir en parallèle ou de manière interactive pour modifier la diversité et la composition restent incertains. Dans cette thèse, j'ai utilisé les papillons comme système d'étude pour étudier comment les interactions biotiques, la dispersion et la connectivité du paysage interagissent pour former les métacommunautés de papillons. Dans le chapitre 2, je me suis demandé comment les interactions avec les prédateurs et les mutualistes floraux, ainsi que la taille et la connectivité de l'habitat, influence la diversité alpha dans une métacommunauté de papillons. Seules la diversité et la richesse des mutualistes floraux ont eu un impact direct sur la diversité et la richesse des papillons, ce qui suggère que les sites isolés et de petite taille, ainsi que les sites soumis à une forte pression de prédation, peuvent néanmoins être précieux pour la conservation si la diversité des mutualistes est maintenue. Dans le chapitre 3, en utilisant le même système d'étude, j'ai cherché à savoir si la dispersion médiait les interactions des espèces avec les prédateurs, les mutualistes floraux et le paysage. J'ai constaté que les forts disperseurs étaient plus nombreux dans les sites isolés où la densité florale et la prédation étaient faibles, tandis que les faibles disperseurs étaient plus nombreux dans les sites plus connectés où la densité florale et la prédation étaient plus élevées. Ces résultats démontrent que, si la diversité alpha ne change pas en fonction de l'isolement et de la prédation des sites (chapitre 2), la composition des espèces, elle, change. Dans le chapitre 4, je me suis demandé ce qui déterminait la diversité alpha et bêta le long d'un gradient de métacommunautés naturalisées à urbaines. J'ai constaté que la diversité alpha était déterminée par les interactions biotiques à l'échelle locale avec les plantes hôtes et les autres plantes à fleurs, tandis que la diversité bêta était déterminée par des facteurs biotiques et abiotiques à différentes échelles. Ces résultats soulignent que les espèces sont filtrées des paysages à forte surface imperméable, mais que les petits sites urbains avec de riches communautés de plantes hôtes peuvent soutenir une grande diversité de papillons. Cette thèse approfondit notre compréhension de la dynamique des métacommunautés, avec des implications à la fois pour notre compréhension des modèles et processus écologiques et pour notre capacité à conserver les espèces dans des paysages de plus en plus fragmentés et urbanisés.

Official statement of work

All research presented in this thesis is my own work, produced with invaluable input from co-authors. I led the design, analysis, interpretation, and writing of all chapters, with support from my supervisor Dr. Jeremy Kerr. Dr. Julien Martin made vital contributions to the analysis of Chapter 3.

For fieldwork at Burnt Lands Provincial Park (Chapters 2 and 3) I received approval to conduct research from the Ontario Ministry of the Environment, Conservation, and Parks. I received approval from the University of Ottawa Animal Ethics and Compliance to use modeling clay models of butterflies which were designed to mimic butterflies for visual predators, including birds.

For fieldwork in the Ottawa Greenbelt and National Capital Commission properties within the city of Ottawa I received approval to conduct research from the National Capital Commission (Chapter 4). I received permission from the City of Ottawa to survey city parks within Ottawa. I also received permission from 19 private landowners to conduct fieldwork on their properties in the Centrepointe, Westboro, and Sandy Hill/Overbrook neighborhoods of Ottawa.

Chapter 2 has been published in the peer-reviewed journal Ecology, with the following citation (thanks to subject editor Dr. Todd Palmer and two anonymous reviewers for their suggestions and comments that substantially improved the final manuscript):

> Gordon, Susan CC, and Jeremy T. Kerr. "Floral diversity increases butterfly diversity in a multitrophic metacommunity." *Ecology* 103.8 (2022): e3735.

Chapter 3 has been published in the peer-reviewed journal Ecology, with the following citation (thanks to subject editor Dr. Julian Resasco and two anonymous reviewers for their suggestions and comments that substantially improved the final manuscript):

Gordon, Susan CC, Julien GA Martin, and Jeremy T. Kerr. "Dispersal mediates trophic interactions and habitat connectivity to alter metacommunity composition." *Ecology* (2023): e4215.

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Indigenous affirmation

Ni manàdjiyànànig Màmìwininì Anishinàbeg, ogog kà nàgadawàbandadjig iyo akì eko weshkad. Ako nongom egawìkàd kì mìgiwewàdj.
Ni manàdjiyànànig kakina Anishinàbeg ondaje kaye ogog kakina eniyagizidjig enigokamigàg Kanadàng eji ondàpinangig endàwàdjin Odàwàng.
Ninisidawinawànànig kenawendamòdjig kije kikenindamàwin; weshkinìgidjig kaye kejeyàdizidjig.
Nigijeweninmànànig ogog kà nìgànì sòngideyedjig; weshkad, nongom; kaye àyànikàdj.

We pay respect to the Algonquin people, who are the traditional guardians of this land. We acknowledge their longstanding relationship with this territory, which remains unceded. We pay respect to all Indigenous people in this region, from all nations across Canada, who call Ottawa home. We acknowledge the traditional knowledge keepers, both young and old. And we honour their courageous leaders: past, present, and future.

This Indigenous Affirmation was written the Office of Indigenous Affairs at the University of Ottawa, in partnership with the Indigenous Education Council, Indigenous student groups, and members of the local Indigenous community (https://www.uottawa.ca/about-us/indigenous/indigenous-affirmation). This statement acknowledges that the University of Ottawa, including the Kerr lab where I completed work for this thesis, was built on the traditional territory of the Algonquin Nation. I collected all the data for this thesis within the boundary of the City of Ottawa, which includes the traditional territory of the Algonquin Nation and the Mohawk Nation (https://native-land.ca/). I acknowledge my own settler history, as well as the colonial history of the University of Ottawa. I will continue to educate myself on Canada’s colonial past and current Indigenous issues, and to leverage any power I have for (re)conciliation.

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Chapter 1: General introduction

A central goal of ecological research is to understand species distribution, abundance, and interactions (Leibold et al. 2004). While there is continuing debate around whether ecology can establish generalizable principles (McGill et al. 2006), with disciplines like community ecology viewed by some as “a mess” (Vellend 2010), important strides continue to be made in the pursuit of answering basic ecological questions. Dispersal and biotic interactions are recognized as fundamental processes shaping ecological patterns (Elton 1927, Vellend 2010, Wisz et al. 2013, Jønsson et al. 2016, Chmielewski and Eppley 2022), with recent emphasis placed on understanding multitrophic interactions (Seibold et al. 2018), and variation in dispersal among species (Grainger et al. 2017). Integrating biotic interactions and dispersal into studies together has offered new insights (Cadotte 2006, Haegeman and Loreau 2014, Zarnetske et al. 2017), but research has been limited by the complexity inherent in studying numerous interacting organisms across spatial scales.

Dispersing individuals leave their natal habitat patch and may rescue populations in other patches (Brown and Kodric-Brown 1977, Thompson et al. 2020), or colonize/recolonize unoccupied patches (Jønsson et al. 2016, Denk and Hallatschek 2022), provided they can disperse far enough to access them (Ponisio et al. 2019). Classic ecological theory predicts that high colonization rates among well connected patches will result in higher species diversity and larger population sizes (MacArthur and Wilson 1967, Hanski 1994), while more recent models suggest that intermediate levels of dispersal will result in higher species diversity (Thompson et al. 2020).

Biotic interactions have long been recognized as influencing the niche a species is able to occupy (Wiens 2011), thereby impacting community assembly and structure (Inouye et al. 1980, Gilinsky 1984, Hartnett and Wilson 1999, De Bello et al. 2012). For example, competitors may exclude other species by filling niches (Romdhane et al. 2022), herbivores may stabilize communities by increasing habitat heterogeneity (Kordas et al. 2017), and mutualists may create new habitats and facilitate new communities (Trivedi et al. 2020). Historically, many studies have focused on interactions among species within a single trophic level (i.e. competition and facilitation), due to a pervasive view of 'communities' as comprising a group of species with similar life history and trophic requirements and also logistical constraints on ecological research (Seibold et al. 2018). However, a species' ecology can only be fully understood when its biotic interactions are considered, both within and among trophic levels (Abdala-Roberts et al. 2019).

Metacommunities, defined as networks of local communities connected by dispersal of multiple interacting species (Leibold et al. 2004), offer an excellent framework to examine the impacts of both dispersal and biotic interactions within and among communities. The theoretical origins of this field lie with island biogeography and metapopulation ecology. The Theory of Island Biogeography considered colonization and extinction of ecologically equivalent species in an island-mainland system, with local diversity varying as a function of island size and distance to the mainland source population (MacArthur and Wilson 1967). Metapopulation ecology focuses on the dynamics of a single species, but also considers processes of extinction and colonization in a fragmented landscape (Levins 1969). Both fields have furthered our theoretical and empirical knowledge of how species dynamics in a local site effect, and are affected by, their congenerics in the broader landscape (Hanski and Gilpin 1991). Advances in metapopulation ecology also include the consideration of how biotic interactions within and among trophic levels affect metapopulation dynamics (Tilman 1994, Opedal et al. 2020). Metacommunity ecology extends island biogeography and metapopulation concepts to consider communities of functionally similar but unique species, and their dynamics across spatial scales. The field of metacommunity ecology is relatively young, and began with the definition of four paradigms driving metacommunity structure: patch dynamics (colonization and extinction in a patchy environment), species-sorting (environmental filtering), mass effects (environmental filtering mediated by dispersal), and the neutral model (stochasticity; Leibold et al. 2004). Early metacommunity work has been criticized for focusing on which of the “Big Four” paradigms dominate individual metacommunities, instead of considering if more than one paradigm is operating, or testing other hypotheses about metacommunity dynamics (Brown et al. 2017). More recently, research has expanded to investigate how metacommunities are structured by trophic and mutualistic interactions (Jones et al. 2015, Grainger et al. 2017), topography (Tonkin et al. 2016), dispersal (Pedersen et al. 2016), evolutionary dynamics (Urban et al. 2008), and meta-ecosystem dynamics (Thompson et al. 2017).

Despite extensive theory, there is conflicting evidence for the importance of dispersal in driving patterns of metacommunity diversity. Experimental studies have demonstrated a variety of positive, negative, and hump-shaped relationships between dispersal rates and various metrics of diversity. However, experimental settings often regulate local and landscape factors that may be important drivers of metacommunity dynamics in natural systems (Grainger and Gilbert 2016). Field studies have examined the importance of dispersal under natural conditions with varying results, including that dispersal does not filter species (Vanschoenwinkel et al. 2008), that its impact on community richness varies across spatial scales (Meynard et al. 2013), and that it strongly impacts species distributions (Downes et al. 2017). This variation may be due in part to the range of methods used to quantify isolation and dispersal, which may bias results (Resasco and Fletcher 2021).

Owing in part to the recent inception of metacommunity ecology, biotic interactions have yet to be fully explored within the context of metacommunity theory (Cottenie 2005, Brown et al. 2017, García-Girón et al. 2020), offering opportunities to improve our understanding of metacommunities and ecological processes more generally. As in community ecology more broadly, most studies considering biotic interactions focus on interactions within trophic levels, and uncertainties remain concerning dynamics of other interactions such as mutualisms (Logue et al. 2011). Studies of multitrophic interactions in metacommunities often focus on predator-prey dynamics (Guzman et al. 2019), demonstrating that predators reduce metacommunity richness and beta-diversity in some systems (Chase et al. 2009), while having no effect on prey diversity in others (Cuellar-Gempeler et al. 2023). More work is needed to understand effects of biotic interactions, particularly interactions across two or more trophic levels, on metacommunity structure (Abdala-Roberts et al. 2019, Guzman et al. 2019).

Butterflies are an ideal study group to examine the effects of dispersal and biotic interactions in metacommunities: they experience mutualistic interactions (with flowering plants), consumptive interactions (with predators and butterfly host plants), and their dispersal abilities are well known (Burke et al. 2011). Butterfly host plants are species-specific plant species or families that are consumed by sedentary butterfly larvae; these plants are essential for the completion of the larval life stage. In contrast, flowering plants act as mutualist partners to mobile adult butterflies, supporting butterflies with nectar resources as they transport pollen between flowers. Because mutualistic interactions between pollinators and flowering plants are relevant to most terrestrial communities (Knight et al. 2018), insights into how such interactions contribute to metacommunity structure may be fundamental to conserving and restoring these systems. This is particularly urgent as, like many pollinators (Soroye et al. 2020, Dicks et al. 2021, Millard et al. 2023), butterflies are in decline globally (Warren et al. 2021, Forister et al. 2021). Yet even in highly modified landscapes, there are opportunities to support butterflies if limits on their diversity can be identified (Lewis et al. 2019, Baldock et al. 2019). The effects of supporting these species may even extend to other groups: in urban systems, where many people experience their only regular contact with nature (Klaus and Kiehl 2021), butterflies can act as a gateway to the natural world, increasing interest in conservation knowledge and action (Lewandowski and Oberhauser 2017).

In this thesis, I investigated the importance of dispersal and biotic interactions within a natural butterfly metacommunity, and among a range of increasingly urbanized butterfly metacommunities. I collected data for all primary research in the city and surrounding landscape of Ottawa, Canada. This region hosts particularly high butterfly diversity (over 90 species), with many widespread species in addition to Southerly and Northerly species whose ranges overlap in Eastern Ontario. Ottawa encompasses Burnt Lands Provincial Park, a globally rare alvar ecosystem that I used as a model of natural butterfly metacommunities. The center of the City of Ottawa is surrounded by a natural and agricultural greenbelt (Gordon and Scott 2008), making it a particularly strong study system for comparing naturalized and urban butterfly metacommunities. First, I examined the direct and indirect effects of multitrophic interactions and habitat connectivity on metacommunity diversity (Chapter 2). I found that interactions with floral mutualist partners directly increase butterfly diversity, while predation and habitat connectivity had no effect. In my second study, I asked how dispersal ability mediates the effects of biotic interactions and the landscape on butterfly species' abundances in a metacommunity

(Chapter 3). I found that the density of strong dispersers was higher in more isolated sites, sites with lower predation pressure, and sites with lower floral density. In contrast, densities of poor dispersers were highest in well connected sites, sites with higher predation pressure, and sites with higher floral density. Next, I investigated how butterfly diversity varied among increasingly urban metacommunities, and what drove community diversity in this system (Chapter 4). I found contrasting drivers of alpha and beta diversity, with only biotic interactions with flowering plants impacting alpha diversity, while beta diversity was driven by biotic interactions, site area, and landscape composition. Finally, I synthesized the results from my three primary research studies and suggested specific implications of this thesis for basic ecology and applied conservation (Chapter 5). While I used butterflies as a study system throughout this thesis, the hypotheses and conclusions from each chapter may apply more broadly furthering our understanding of metacommunity dynamics.

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Chapter 2: Floral diversity increases butterfly diversity in a multitrophic metacommunity

Note: this chapter is a slightly modified version of the following article:

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2.1 Abstract

The impact of multitrophic interactions on metacommunity structure, despite extensive theory and modeling/manipulative studies, has remained largely unexplored within naturally occurring metacommunities. I investigated the impacts of mutualistic partners and predators on a butterfly metacommunity, as well as the impacts that local and landscape characteristics have across three trophic levels: flowering plants, butterflies, and butterfly predators. Using data for butterfly diversity/richness, flowering plant diversity/richness, and butterfly predation (on clay butterfly models) across 15 grassland sites, I posed 3 questions. (1) How do mutualist metacommunity structure, predation pressure, and local and regional habitat characteristics affect butterfly metacommunity structure? (2) How do local and regional habitat characteristics affect flowering plant metacommunity structure? (3) How do local and regional habitat characteristics affect predation pressure? Floral diversity and richness had a positive effect on butterfly diversity and richness (Question 1). Site size positively affected floral diversity and richness (Question 2), and through this relationship site size had an indirect positive effect on butterfly diversity and richness (Question 1). In contrast to previous work, no other variables impacted butterfly diversity/richness. This result was particularly surprising for predation pressure: my results suggest that within my study system, butterfly community diversity and richness are not strongly

impacted by predation. Predator attacks occurred more in larger and more isolated sites (Question 3), suggesting that predators respond more strongly to landscape characteristics than abundance or diversity of butterfly prey species. This decoupling of predation pressure and butterfly communities suggests that conserving and restoring healthy predator populations may not negatively impact butterfly communities. If diverse plant communities are maintained, even small and isolated habitat patches can be valuable for butterfly conservation, which may influence reserve design and habitat restoration strategies.

2.2 Introduction

Studies have shown that biotic interactions have a number of impacts on metacommunity structure and are themselves impacted by landscape characteristics and local factors. Predation has been found to influence colonization and extinction events and reduce beta diversity (Chase et al. 2009). Mutualism and competition have been predicted to impact colonization success in ecological networks (Thompson and Gonzalez 2017), while dispersal and environmental gradients have been predicted to impact the prevalence of these interactions (Filotas et al. 2010), yet field-based tests of mutualism and competition in metacommunities have rarely been attempted (but see Tsang and Bonebrake 2017, Ponisio et al. 2019, Li et al. 2020). Parasitism rates have been shown to decline with increasing patch size and connectivity within a metacommunity (With and Pavuk 2019), while species susceptible to predation have been shown to be less responsive to patch size and connectivity compared to well-defended species (Grainger et al. 2017).

While the number of metacommunity studies incorporating biotic interactions is increasing, multitrophic studies remain rare. In modeled systems, tritrophic interactions have been found to influence the evolution of dispersal (Chaianunporn and Hovestadt 2019), while dispersal, fragmentation, and habitat loss have been shown to stabilize metacommunities (Pedersen et al. 2016), and affect trophic structure (Liao et al. 2020). An experimental study demonstrated that the capacity for dispersal to maintain diversity in disturbed communities varies with trophic level in a multitrophic metacommunity (Limberger et al. 2019), while a field-based study demonstrated that intraspecific phenotypic variation in predators can cause different patterns of diversity in a multitrophic metacommunity (Howeth et al. 2013). These studies all investigated consumptive interactions, such as predation, herbivory, and parasitism. Missing from these studies overall, and specifically the experimental and field-based studies, is the role of facilitative interactions, such as mutualisms.

In this study, I investigated the impacts of multitrophic interactions on the structure (diversity and richness) of a butterfly metacommunity. Because mutualistic interactions between pollinators and flowering plants are relevant to most terrestrial communities (Knight et al. 2018), insights into how such interactions contribute to metacommunity structure may be fundamental to conserving and restoring these systems. Nevertheless, pollinator interactions with predators and nectaring resources have rarely been studied in a metacommunity context.

I explore the impacts of mutualistic partners and predators on the butterfly metacommunity, as well as the effects of local and landscape characteristics across the three trophic levels. I test three hypotheses. The first hypothesis is that increasing mutualist metacommunity diversity/richness, decreasing predation, and increasing site size and connectivity will directly increase butterfly metacommunity diversity and richness. Increasing site size and connectivity will also indirectly increase butterfly metacommunity diversity/richness through the intermediaries of mutualists and predators. Second, increasing site size and connectivity will directly increase flower plant (mutualist) metacommunity diversity/richness. Third, increasing site size and connectivity will increase predation pressure at a site. This study provides the first field-based assessment of how mutualists and predators interact with local- and regional-scale factors to influence metacommunity structure.

2.3 Methods

2.3.1 Study system

The study area was in Burnt Lands Provincial Park and surrounding landscape (Ottawa, Canada) (Figure 2.1). This is a globally rare alvar ecosystem, characterized by shallow soils over limestone bedrock. Alvars exhibit a range of soil depths, from bare rock to deep soil, with the shallower soils experiencing extremes in moisture availability (Belcher et al. 1995). Burnt Lands Provincial Park has several grassland fragments set within a matrix largely consisting of mixed wood or coniferous forest, as well as some small wetland areas. I identified 15 distinct grassland patches within Burnt Lands for this study, ranging in size from 0.027 to 179 ha. The minimum distance between sites was 20 m (Lewis et al. 1997), and the maximum was 330 m. Butterfly species in this metacommunity vary in their mobility, from sedentary to extremely mobile (Burke et al. 2011), so that some species will only rarely disperse between highly connected patches, while others will disperse easily between unconnected sites. This area has a high conservation value, with 50 butterfly species identified in the park, including at-risk monarch butterflies, as well as high flowering plant diversity.

2.3.2 Butterfly and plant surveys

I marked one 50-m transect at each site under 2 ha (except the smallest site, where transect length was limited to 15 m). For larger sites I added 25 m of transect for every additional 2 ha of area. Calculation of the area for the two largest sites (88 and 179 ha) revealed that their area was larger than initially estimated, so the ratio of site area to transect (as well as for quadrats and models described in what follows) is larger for these sites. I surveyed sites in order five times between 6 June and 18 September 2019 on warm days with little cloud cover or wind. Surveys were conducted largely by Susan C. C. Gordon and, occasionally, by other experienced butterfly surveyors. The surveyor walked slowly along the length of each transect at a rate of approximately 10 min per 50-m transect (i.e., a conventional so- called Pollard walk for butterfly sampling). The surveyor identified all butterflies within 5 m from the transect (including 5 m above the transect) (Pollard 1977).

To survey flowering plant communities, I established 1 X 1 m quadrats at the ends of transects in each site, with four quadrats per site for sites under 2 ha. For larger sites I added one quadrat for every additional 2 ha of area. Each time I conducted butterfly surveys, I also surveyed flowering plants within the quadrats. I identified all flowering plants and counted the open flowers: One flower "unit" was counted as an individual flower, each flower on a spike (*Echium vulgare*), one umbellet (*Dacus carotta*), one head (*Trifolium hybridum*), or one branch (*Solidago* sp.; due to dense clustering of inflorescences, I estimated that one branch equaled four umbellets).

2.3.3 Butterfly models

To quantify predation pressure experienced by the butterfly community at each site, I created and deployed butterfly models throughout the summer and scored them for predation (Figure 2.2a). I chose this method instead of predator surveys because of the variety of birds and arthropods that prey on butterflies and the difficulty of detecting all predators in surveys. Predators may also operate at different spatial scales than butterflies (Debinski et al. 2006), raising uncertainties about whether patch boundaries that influence butterfly distribution will affect their predators comparably.

I constructed models using techniques described in Finkbeiner et al. (2012). These models have been found to experience the same attack rate as models made with real butterfly wings (Finkbeiner et al. 2012). Butterfly bodies were crafted from nontoxic modeling clay. High-quality images of pinned butterfly wings were printed onto both sides of cardstock and fastened to clay bodies. Wings were attached in a folded (closed) position. I waterproofed the cardstock and applied a matte finish using Krylon matte sealer. I attached models to trees and shrubs in the field using black thread threaded through the base of the wings (Figure 2.2a).

I made models of four different butterfly species with a range of dispersal abilities and flight periods. Timing for model placement reflects observations of peak activity periods for each species in this geographic location during the study: silvery blue (*Glaucopsyche lygdamus*) between 2 and 10 July, monarch (*Danaus plexippus*) between 23 and 31 July, aphrodite fritillary (*Speyeria aphrodite*) between 5 and 20 August, and clouded sulphur (*Colias philodice*) between 6 and 20 September. We placed four models in each site that had an area under 2 ha. For larger sites I added one model for every additional 2 ha of area. I placed models in trees and shrubs surrounding butterfly survey transects, with each new model placed in a different tree or shrub. After 48 h I returned to collect the models and assess whether a model had been attacked (clearly marked by a predator) or had not been attacked (unmarked by predators).

During the study period, some butterflies were deeply marked (likely by predators), and some had distinctive light markings and “chew marks” around the wings (Figure 2.2b,c). I later observed that this second category of attack was caused by grasshoppers, which sometimes act as scavengers, consuming insect carcasses (Lavigne and Pfadt 1964). I separated the recorded attacks into categories, as attacks by predators or attacks by grasshoppers.

2.3.4 Landscape Metrics

I characterized the landscape by calculating site size, site isolation within the metacommunity, and distance between each site and its nearest habitat patch outside of the metacommunity. I calculated patch size by tracing polygons around the margins of each individual site (Gerner and Sargent 2022) using very high-resolution aerial photography (20 cm) in ArcGIS Pro 2.7 (ESRI, 2020). I calculated site isolation and distance to nearest patches outside the metacommunity based on land-cover data for the area. I characterized matrix areas using field observations and aerial photography.

I distinguished between distinct matrix landcover types (Hall et al. 2014): forest, water and wetland, bare ground paths, cut grass, and roads. I assigned cost values to represent the ease of movement for the butterfly community through those land covers, as well as the grassland sites, based on the number of species I observed that use that habitat type (Hall et al. 2014). I calculated cost by subtracting the number of species that use a landcover type as habitat from the total number of species, for example: 42 (total species) minus 40 (species known to use grassland as habitat) equals 2 (cost for moving through grassland habitat). I calculated the following costs: grassland = 2, wetland = 32, forest = 35. I assigned roads a score of 42. I assigned paths and cut grass a score of 34, reflecting that ease of movement over these land covers would be increased, but few species prefer or use these habitat types. I did not incorporate elevation because there was very little variation within and among sites. I used the least cost path (LCP) function in ArcGIS Pro to calculate the cost, factoring in distance and landcover type, of traveling between each pair of sites. To calculate site isolation, I summed the cost of all paths between each site and all other sites. Distance between each site and the closest habitat patch outside of the metacommunity was measured by identifying the external habitat patch that was closest to each site and computed one LCP between each site and that external patch.

2.3.5 Statistical analysis

To test the direct and indirect effects of environmental and biotic variables within the multitrophic metacommunity, I conducted analyses using directed separation structural equation models (Shipley 2016). This method tests potentially causal links within a hypothesized framework connecting measured variables. The directed separation method is ideal for the study of multitrophic metacommunities because it allows for hierarchical data and nonnormal sampling distributions (Shipley 2009). This approach allowed me to construct testable hypotheses of both direct and indirect determinants of metacommunity structure, which is necessary in understanding how landscape factors and biotic interactions combine to shape metacommunities. Path analysis allows for flexibility in hypothesis-driven and exploratory analyses (Jabot et al. 2020), and, unlike commonly used variance partitioning methods, allows for testing of multiple dependent variables. Taken together, the many benefits of path analysis, and particularly directed separation, make it well suited to a field attempting to untangle the myriad causes of metacommunity structure.

I conducted statistical analyses using R 4.0.5 (R Core Team, 2021). I measured species richness and calculated diversity for butterflies and flowers. I calculated diversity as the Hill number, which is the exponential of Shannon- Weiner diversity (Hill 1973). I centered and scaled all independent variables by their SDs using the “scale” command in base R, creating Z-scores.

I followed these steps to construct and test the directed separation models: (1) identify a causal model, specifying relationships between the variables; (2) obtain the basis set of statements that comprise the independence claims (or null hypotheses) specified by the model; (3) model the independence claims using appropriate tests, identifying the probability (p) that each claim is non- independent; (4) combine these null probabilities using Fisher's combined probability test, rejecting the causal hypothesis if the null probability is significant; and (5) when causal hypotheses are not rejected, fit a series of models following the structure of the hypothesis, in which each dependent variable is predicted by its causal parents, resulting in path coefficients (Shipley 2016). For this technique, failing to reject the independence claims indicates that, based on the data, no dependencies between variables have been incorrectly omitted.

I combined my three hypotheses to propose a causal model for this metacommunity (Step 1). I added a variable for grasshopper attacks to the model to account for the observation that grasshoppers attacked butterfly models, which may have altered the appearance of the models and consequently changed predator attack frequency thereafter (Figure 2.3a).

Next, I used the ggm package to obtain the basis set of independence claims for this causal model (Step 2) (Appendix S2.1: Table S1). The independence claims must be tested in the presence of appropriate random effects, sometimes necessitating mixed effects models. I tested independence claims for these models by constructing linear mixed models (LMMs) and generalized linear mixed models (GLMMs) in the lme4 package (Step 3). For these and all following models, I constructed LMMs when data were normal (dependent variable was diversity) and GLMMs with Poisson distributions for count data (dependent variable was richness). For these and all following LMMs and GLMMs I included site as a random effect and both a linear and quadratic term for sampling day (number of days from first sample, with Day 1 of sampling identified as “1”) to account for temporal autocorrelation. For independence claims, I included all conditional variables (shared causal parents) as fixed effects. I then computed the Fisher’s C statistic for diversity and richness (Step 4) (Shipley 2009). The Fisher’s C statistics calculated for richness (0.28) and diversity (0.61) were both nonsignificant, indicating that I failed to reject my causal model (Appendix S2.1: Table S1).

Finally, I fitted models following the structure of my hypotheses to obtain path coefficients (Step 5). In tests of Hypothesis 3 (Appendix S2.1), grasshopper attacks did not significantly affect numbers of predator attacks (Appendix S2.1: Table S2). Because this variable was added to account for in situ observations and not because of an a priori hypothesis, I returned to Step 1 of the directed separation method, creating a second causal model without the grasshopper attacks variable (Figure 2.3b). I applied the directed separation method to this second model, first testing the independence claims (Steps 2 and 3). Because this model is almost completely saturated, with connections between all variables except predator attacks and floral diversity/richness, there was just a single independence claim, identical to the third claim from my first causal model (Step 4) (Appendix S2.1: Table S3). The Fisher’s C statistics calculated for diversity (0.215) and richness (0.066) were both nonsignificant, indicating that I failed to reject my causal model (Appendix S2.1: Table S3). However, the p value was small for richness, and in both cases I had only one independence claim to test, which reduced statistical power.

I returned to Step 1 of the directed separation method, simplifying my second causal model (Figure 2.3c) to increase power. I removed the distance to nearest site variable and the nonsignificant path between site isolation and floral diversity/richness. The former variable was not significant in any model, and the latter is rarely an important determinant of slow-growing plant community diversity owing to communities' slow responses to landscape change (Helm et al. 2006) (see "Discussion"). I retained nonsignificant paths between predator attacks and butterfly diversity/richness, site area and butterfly diversity/richness, and site isolation and butterfly diversity/richness because they are central to my hypothesis about butterfly metacommunity structure.

I obtained two independence statements for my simplified third causal model (Step 2) (Appendix S2.1: Table S4). As with previous models, I included all conditional variables as fixed effects (Step 3). The Fisher's C statistics calculated for diversity (0.344) and richness (0.200) were both nonsignificant, indicating that I failed to reject my causal model (Step 4) (Appendix S2.1: Table S4). These p values for this reduced model were high enough to give me confidence in this model.

Consequently, I fitted simplified models to test each of my core hypotheses (Step 5). For Hypothesis 1, butterfly diversity and richness were dependent variables, and floral diversity/richness, predator attacks, site area, and site isolation were fixed effects. For Hypothesis 2, floral diversity and richness were dependent variables, and site area was a fixed effect. For the third hypothesis, predator attacks was the dependent variable, and site area and site isolation were fixed effects. I tested model assumptions, including independence and normality of residuals, and the assumptions were not violated.

I repeated my analyses using a rarefaction approach, and my results were qualitatively the same as those obtained with my raw survey data, giving me additional confidence that my sampling reflected the butterfly metacommunity (Appendix S2.2).

2.4 Results

I identified a total of 2148 butterflies from 42 species and counted over 23,000 flowers from approximately 55 species (Appendix S2.3: Tables S1 and S2). Butterfly abundance per site per sampling round ranged from 0 to 353, with a mean of 29.7 and SD of 72.2, while species richness ranged from 0 to 13 with a mean of 3.6 and SD of 3.2, and diversity ranged from 0 to 8.7 with a mean of 2.6 and SD of 1.8. The most commonly observed butterfly species included the common ringlet (*Coenonympha tullia*, 597 observations) and the clouded sulphur (*Colias philodice,* 587 observations). Rarely observed butterfly species included the eastern pine elfin (*Callophrys niphon*, one observation) and the coral hairstreak (*Satyrium titus*, one observation). The flight period of a butterfly species may last only 2 weeks, while some species have multiple generations that span months, resulting in changes in butterfly richness and abundance over the season (Appendix S2.3: Figure S1).

Floral abundance per site per sampling round ranged from 0 to 3255 with a mean of 319.3 and SD of 6694, while species richness ranged from 0 to 19 with a mean of 4.5 and SD of 4.3, and diversity ranged from 0 to 9.9 with a mean of 2.5 and SD of 1.7. The most commonly observed flowers included upland white goldenrod (*Solidago ptarmicoides*, 2549 flowers observed) and black medick (*Medicago lupulina*, 2303 flowers observed). Rarely observed flowers included the Canada thistle (*Cirsium arvense*, one flower observed) and orange hawkweed (*Pilosella aurantiaca*, one flower observed).

I placed 664 butterfly models in the field and recovered 660 of them: 4 models were no longer located in the areas where they had been secured and could not be recovered. The number of models placed at each site ranged from 16 to 256, with a mean of 42.9 and SD of 68.4. The number of models that were attacked by predators at each site ranged from 1 to 38, with a mean of 7.3 and SD of 10.3. The number of models attacked by grasshoppers at each site ranged from 0 to 18, with a mean of 2.1 and SD of 4.8.

My study sites ranged in size from 0.027 to 179 ha, with a mean of 19 ha and SD of 48.3 ha. The results of my LCP analysis showed a range of costs to move through the landscape, with the relative cost of isolation ranging by almost 170%. My analysis also produced a range of costs for movement from each site to the nearest site outside of the metacommunity, with differences of two orders of magnitude.

While my initial causal model included 4 variables and 12 paths, my final, simplified model included 2 independent variables and 7 paths (Figure 2.3). The variables for grasshopper attacks and distance to the nearest patch outside of the metacommunity had no significant effects in my models and were removed, and the nonsignificant path between site isolation and floral diversity/richness was also removed. As discussed previously, I failed to reject the final causal model because the Fisher's C statistics were not significant (0.344 for the diversity model and 0.200 for the diversity model) (Appendix S2.1: Table S4), allowing me to proceed in testing the paths specified by my model.

Floral diversity and richness increased butterfly diversity and richness, respectively (Figure 2.4, Table 2.1 Models 1A and 1B). Site area increased floral diversity and richness (Figure 2.4, Table 2.1 Models 2A and 2B) and increased the number of predator attacks (Figure 2.4, Table 2.1 Model 3). Site area indirectly increased butterfly diversity and richness through its effect on floral diversity and richness (Figure 2.4). Site isolation increased the number of predator attacks (Figure 2.4, Table 2.1 Model 3) but had no other effects. The temporal term Day decreased butterfly richness, while Day2 increased butterfly diversity and richness, indicating a linear decrease in butterfly richness and a nonlinear increase in butterfly diversity and richness through time (Table 2.1 Models 1A and 1B). Day2 decreased floral diversity, indicating a nonlinear reduction in floral diversity through time (Table 2.1 Model 2A). Although I do not have enough data to explore these temporal relationships more deeply, clearly time and seasonality are important components of this system.

2.5 Discussion

This study provides one of the few field-based examinations of multitrophic interactions in a metacommunity and is the first to do so with a mutualistic interaction between trophic levels. By integrating these processes into a metacommunity model, I could assess direct and indirect effects of biotic and landscape factors across three trophic levels in this metacommunity and evaluate how trophic interactions influenced butterfly diversity and richness. While this study focused on alpha diversity and richness within this system, I also explored beta diversity by calculating Bray-Curtis and Sørensen dissimilarity: my results were consistent with the α-diversity findings. Beta diversity is an important component of metacommunity ecology and merits additional research, particularly in natural systems.

Processes important to metacommunity structure may operate at scales larger than the size of a defined metacommunity (Logue et al. 2011). Relatively few studies to date have examined the effect of the broader landscape on metacommunity structure; rather, greater emphasis has been placed on factors operating within the metacommunity (but see Miller et al. 2018). This work was intended to detect potential effects of the landscape beyond the metacommunity, and though the variable measuring this effect was not significant and was removed from the causal model, more work remains to be done on this topic.

Floral diversity and richness had significant, positive, and direct effects on both butterfly diversity and richness. This is consistent with my predictions and previous work in community ecology (Potts et al. 2003, Blaauw and Isaacs 2014), and the few studies in the metacommunity literature that consider mutualistic interactions (Tsang and Bonebrake 2017, Ponisio et al. 2019). Though I predicted that all factors in the path analysis model (except grasshopper attacks) would directly affect butterfly metacommunity structure, floral diversity/richness was its only significant determinant. I tested key biotic interactions that would most likely affect my study taxon, but it will rarely be feasible to capture all biotic interactions important to a metacommunity of interest. Host plant diversity and richness for butterfly larvae may have accounted for additional variation in butterfly diversity and richness (Krämer et al. 2012), so tests of those factors represent an area for further work.

Predators did not affect butterfly metacommunity structure, contrary to previous findings of the effects of predation on metacommunities (Chase et al. 2009, Grainger et al. 2017, García-Girón et al. 2020). This result was unexpected, potentially indicating that predators were not attacking butterflies at a high enough rate to impose detectable structural differences in their communities. Predators may have tracked landscape characteristics to a greater extent than the butterfly communities (as discussed in what follows), seeking out preferred habitat types in the matrix as opposed to rich and diverse butterfly communities and, consequently, decoupling attack rates from butterfly community characteristics. Alternatively, by combining the results of predation on four species of butterfly model throughout the summer, I may have masked temporally variable effects of predation on metacommunity structure (Karakoç et al. 2020). These effects had previously been identified in butterfly communities, with densities of short-lived predators (dragonflies) varying seasonally and, therefore, varying their impact on the butterfly community through time (Tiitsaar et al. 2013). Predation may nevertheless exert effects on butterfly communities if the importance of its effects vary significantly through time (Holyoak et al. 2020).

Clay or plasticine caterpillar models, such as my butterfly models, are commonly used in field ecology (Hernández-Agüero et al. 2020). Predators that rely on olfactory or other chemical cues (Khan and Joseph 2021), and predators that hunt prey in flight, may exert pressures that are not detected using this method. Yet common butterfly predators, such as birds and arthropods, are known to attack caterpillar models (Low et al. 2014). In addition, while I considered attacks as a binary model attacked/not attacked, models may been attacked more than once by different predators, which could not be accounted for using this method. While I chose four butterfly model species with a range of flight periods and dispersal abilities, they could not fully reflect the diverse morphology and phenologies of the entire butterfly metacommunity, and I caution that tests of predation employed here are most powerful for the species for which I constructed models. More work is possible on the role of predation in altering metacommunity structure, but its effects on these butterfly communities were limited.

In contrast to previous work in metacommunity ecology (Tsang and Bonebrake 2017), I found no significant direct effects of either local (site area) or regional (site isolation, distance to closest patch outside metacommunity) factors on the butterfly metacommunity. Site area did have an indirect effect on butterfly metacommunity structure, as floral diversity/richness increased in larger sites, which in turn increased butterfly diversity/richness. In other words, butterfly richness and diversity can both be high even in small, isolated habitats, provided floral resources are sufficient. Butterflies are highly mobile organisms (Burke et al. 2011), and may be less constrained by movement through an inhospitable matrix than expected, allowing small, isolated populations to be maintained by immigration. Because I did not consider traits in the analysis, the results do not indicate how dispersal ability may have varied across the spectrum of site isolation: Dispersal ability of species in isolated versus connected patches could vary, with stronger dispersers able to reach more isolated sites and populations of poorer dispersers benefiting most from higher connectivity (Habel et al. 2021).

In addition, all sampling was conducted within a protected area. Most of the habitat patches identified as the nearest patch outside of the metacommunity were outside the park boundaries. Those privately owned habitats may be degraded relative to the habitat inside the park and may support less rich and diverse communities (Gray et al. 2016). High connectivity with these external patches may therefore do less to maintain or increase butterfly community richness and diversity within the protected area. Though more work is needed, this underscores the benefits of protected areas for maintaining butterfly communities. In addition, when examining connectivity metrics, many studies account only for interpatch distance and do not estimate costs for organismal dispersal through different land covers or across elevation gradients (Logue et al. 2011). Connectivity metrics that exclude cost may misrepresent connectivity in practical terms for the organism, which could obscure the role of connectivity in maintaining diversity in metacommunities (Resasco and Fletcher 2021). Though the cost surface increased the sensitivity of the analysis by incorporating landcover type, the cost surface parameterization was necessarily imperfect, and more research on butterfly movement is needed to fully understand the impact of distance and matrix land-cover types on their movement.

Floral diversity and richness were directly and positively affected by site area. I expected larger sites to increase floral diversity and richness by supporting a greater number of plant species populations (Uroy et al. 2019). In contrast to my predictions, site connectivity within the metacommunity, and connectivity between sites and close patches in the broader landscape, did not relate to floral diversity or richness. Though this result was unexpected, it is not unprecedented (Lindborg and Eriksson 2004, Helm et al. 2006). In slow-growing grassland communities, such as alvars, there may be a time lag of over 50 years for a plant community to reflect a reduction in habitat area and connectivity (Lindborg and Eriksson 2004, Helm et al. 2006). This result suggests that the flowering plant metacommunity may have an extinction debt. Plant diversity would then be expected to decline over time, reflecting reduced habitat area and restricted connectivity in the residential/ agricultural matrix. The flood/drought cycles experienced by plants living in shallow alvar soils could also be a factor important to community diversity and richness, and further study on this topic could inform our understanding of dynamics within this plant metacommunity.

Site size and site isolation had direct positive impacts on observed numbers of predator attacks. Larger sites may support higher predator density (Roberts and King 2020), or cause butterflies to be farther from the protection of shrubs and trees at site edges and, therefore, more exposed to predation. In contrast to my predictions, more isolated sites experienced more predator attacks, and I offer two possible explanations for this result. First, predator density may be higher in the matrix between sites than in sites themselves, causing more isolated sites to experience higher rates of predation. Predators such as birds may search out areas for their specific requirements, such as forested areas for nesting sites, and may prefer to move through forested areas for protection from predators (Silva et al. 2020). Second, predators may linger longer in more isolated areas because there is a greater distance between these and other habitat patches (Shipley and Spalinger 1995, Skórka et al. 2009). This could result in a concentration of attacks in isolated patches after a predator arrives. In future work it would be valuable to identify butterfly predator species (i.e. through video surveillance; Khan and Joseph 2021), allowing me to further probe relationships between predators and the landscape. In addition, I observed no butterfly models attacked by both grasshoppers and other predators. While the effect was not significant, it is possible that grasshopper attacks may have reduced or altered predator attack rates on the models. However, few models bore signs of grasshopper attacks, and such effects are necessarily very small.

I included temporal variables in the models (sampling day and the square of sampling day) to account for variation in diversity and richness with time. Flowering plant and butterfly species exhibit different phenologies, potentially causing temporal clustering of high/low community diversity and richness values across sites. My sampling spanned most of the flight period for the butterfly community, and variable weather from a cooler spring to a hot summer likely impacted temporal trends as well. In addition, due to the shallow soils that characterize the study area, sites inundated with water in spring may have experienced drought conditions later in summer, likely impacting temporal variation in flowering plant diversity and richness.

While this study comprised 1 year of sampling, it is difficult to know how these results may have changed over multiple years of study (Holyoak et al. 2020). In the case of butterfly communities, some have a high degree of similarity between years (Grøtan et al. 2014), whereas others show pronounced variability over the course of years (Grøtan et al. 2012). Interannual variation experienced by one trophic level in a multitrophic system could cascade through the network, impacting other trophic levels (Piovia-Scott et al. 2017). Long-term temporal dynamics of multitrophic metacommunities represent an area worth exploring in future work.

These findings clearly demonstrate the utility of investigating multitrophic interactions, particularly mutualistic interactions, which have rarely been assessed in metacommunity research (Logue et al. 2011, Guzman et al. 2019), and still less commonly in the context of field experimentation. These results have implications for both basic ecological research and conservation. I found that diverse and rich butterfly communities can occur in small and isolated patches, as long as floral resources are available. Development of conservation programs should prioritize floral richness and diversity and consider the importance of conserving smaller and more isolated sites. These findings on the plant metacommunity suggest that work in this field should consider historic connectivity, particularly for communities that likely change slowly. The spatial decoupling of prey diversity and predator attacks indicates that generalist predators may not track specific prey communities but instead choose hunting locations based on landscape features. This decoupling means that predation is unlikely to impair the conservation of diverse and rich butterfly communities. Biotic interactions, and particularly mutualisms, can structure metacommunities, and future work in metacommunity ecology will benefit from the consideration of multitrophic interactions.

2.6 Figures

Figure 2.1

Map of study sites and surrounding area, approximately 40 km from downtown center of the city of Ottawa. The study sites are shown in yellow. Site numbers are shown in white.

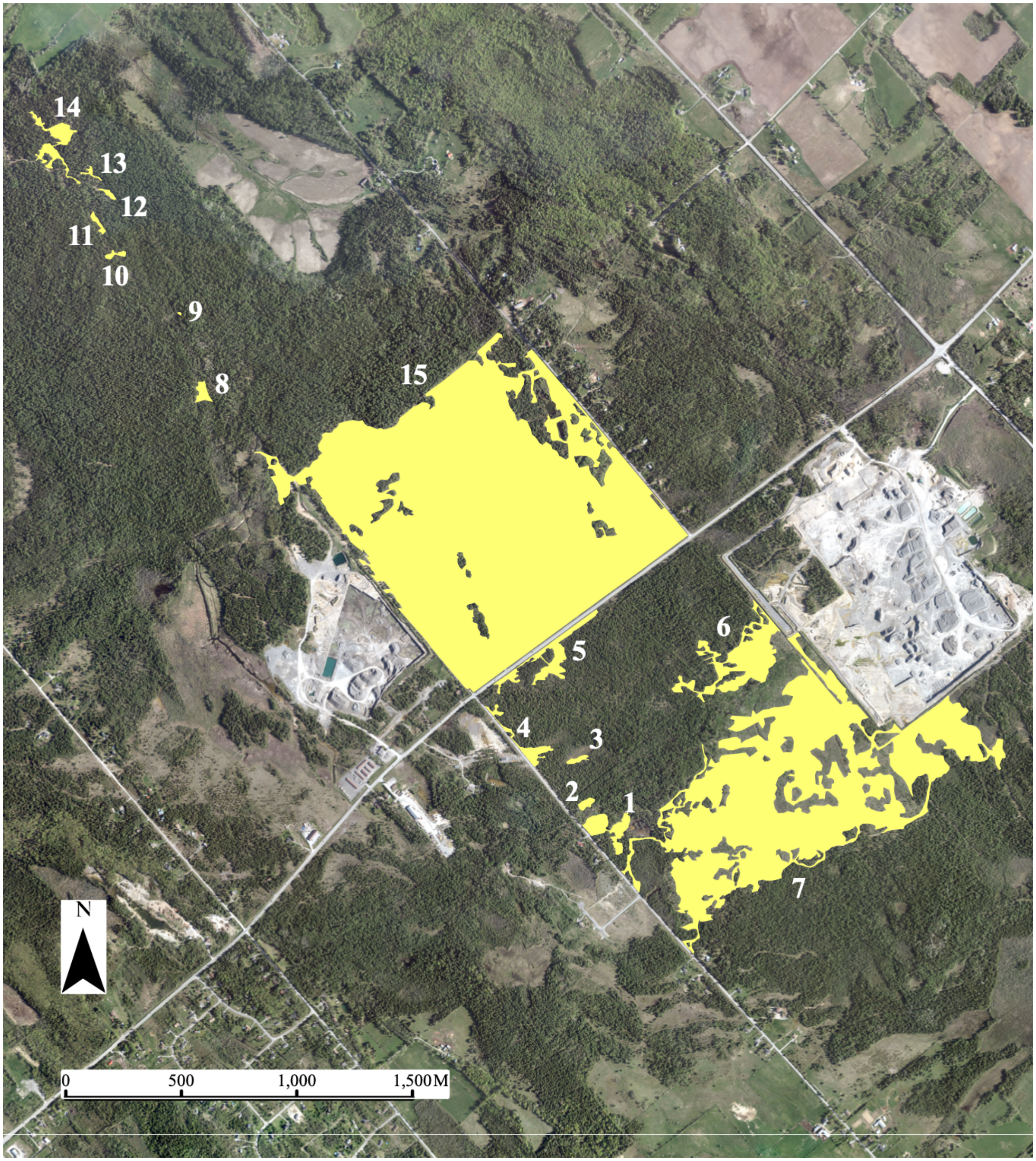


Figure 2.2

Photos of deployed butterfly models, both attacked and untouched. (a) Photo of monarch (*Danaus plexippus*) butterfly model that has not been attacked. (b) Photo of Aphrodite Fritillary (*Speyeria aphrodite*) butterfly model that has been attacked by a predator. (c) Photo of a Clouded sulphur (*Colias philodice*) butterfly model being attacked by a grasshopper. The distinctive chewed edge of the butterfly wing is indicative of a grasshopper attack.

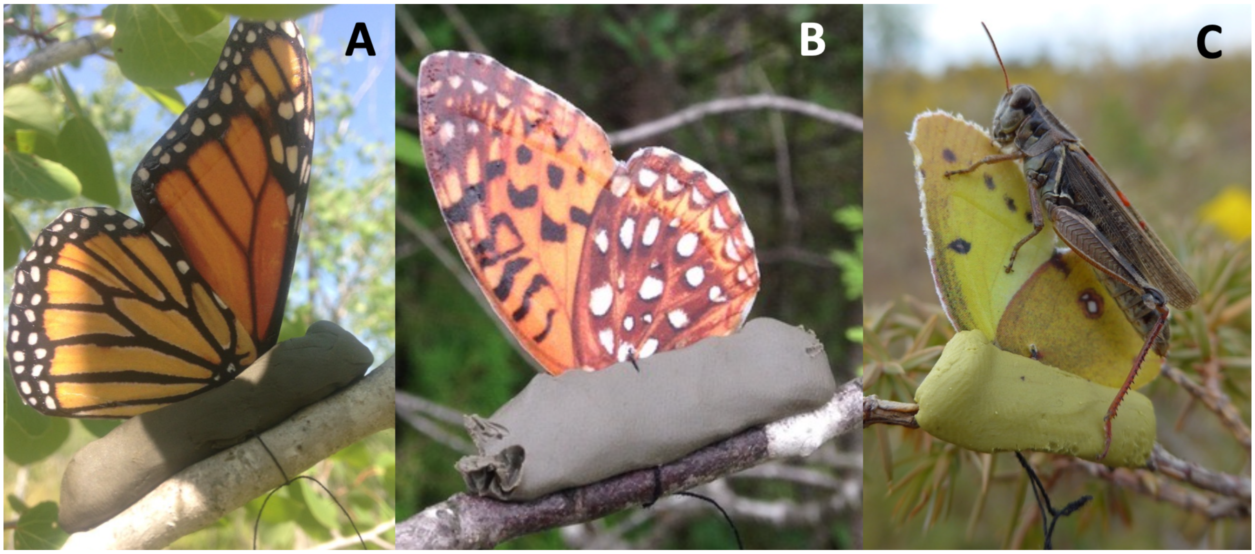


Figure 2.3

Path diagrams, with constituent hypotheses for (a) our original causal model, (b) our causal model without grasshopper attacks, and (c) our simplified causal model. Hypothesis 1: Direct and indirect effects of factors on the butterfly metacommunity; direct effects are in black solid lines, with indirect effects in blue and red dashed lines. Hypothesis 2: Direct effects of factors on floral diversity and richness; all blue short-dashed arrows. Hypothesis 3: Direct effects of factors on predation; all red long-dashed arrows.

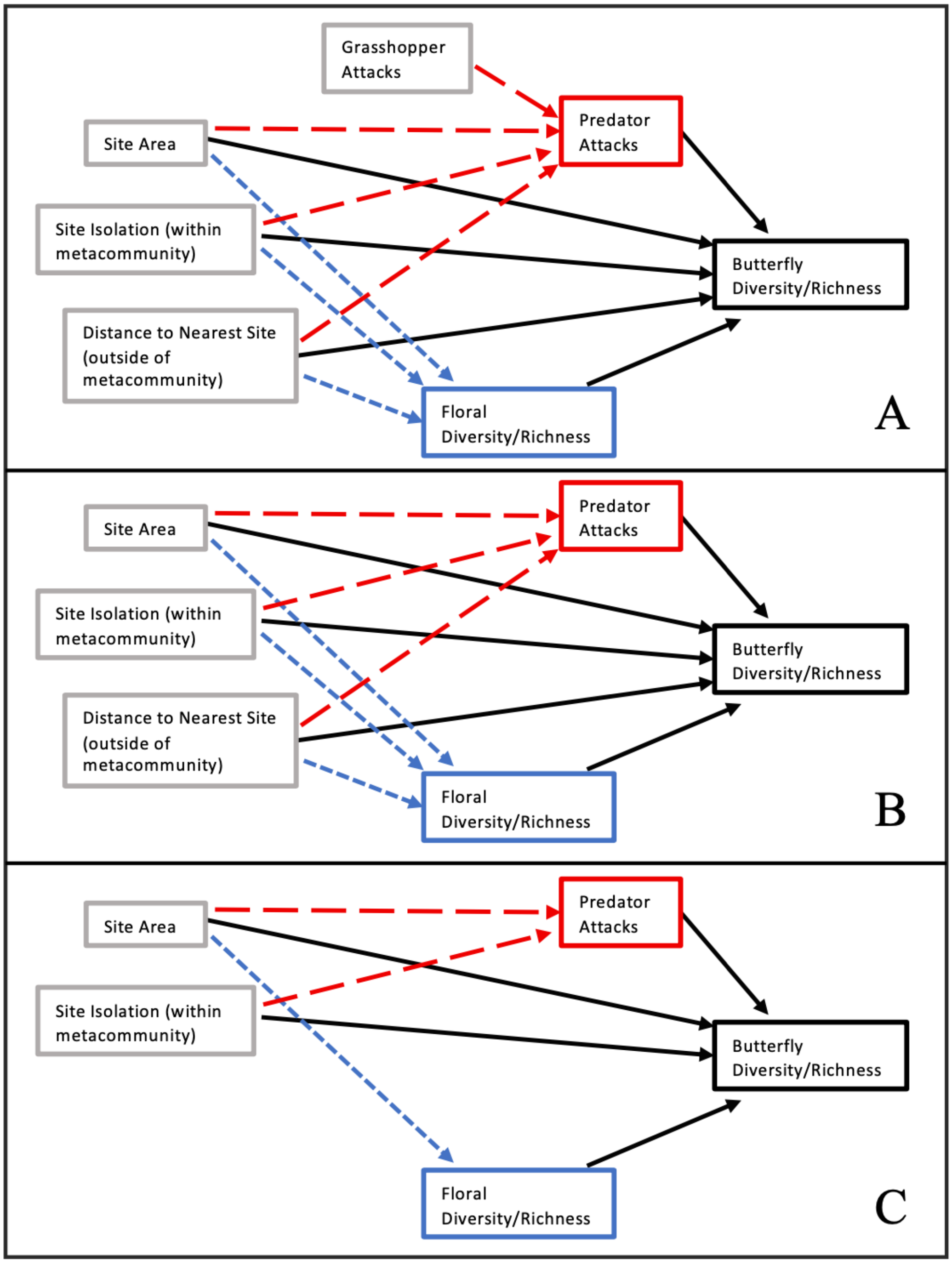
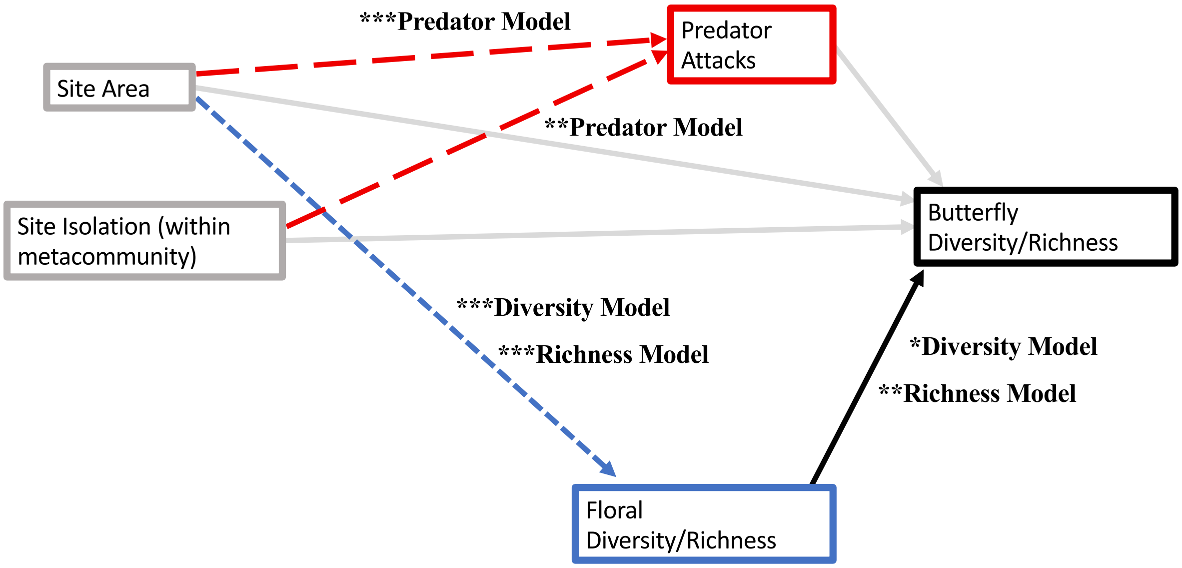


Figure 2.4

Final (simplified) causal model, with constituent hypotheses. Significant path coefficients are shown in dark colors, and nonsignificant paths are shown in light gray. All significant paths are also marked with asterisks, indicating level of significance (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$). Hypothesis 1: Direct and indirect effects of factors on butterfly metacommunity; the significant direct effect is a black solid arrow, while the significant indirect effect is a blue short-dashed arrow. Hypothesis 2: Direct effects of factors on floral diversity and richness; the significant effect is a blue short-dashed arrow. Hypothesis 3: Direct effects of factors on predation; the significant effects are the red long-dashed arrows. Full results can be found in Table 1.



2.7 Tables

Table 2.1

Results of mixed models testing our three hypotheses from our causal model without grasshopper attacks.

Effect	Estimate	SE	*t* or *z* value	*P*
Model 1A: Butterfly Diversity				
Intercept	2.589	0.233	11.105	
Floral Diversity	**0.568**	**0.235**	**2.416**	**0.0157**
Predator Attacks	1.626	1.0714	1.518	0.129
Site Area	-1.195	1.101	-1.086	0.277
Site Isolation	0.133	0.289	0.462	0.644
Day	-1.225	0.650	-1.885	0.0594
Day^2	**1.670**	**0.654**	**2.552**	**0.011**
Model 1B: Butterfly Richness				
Intercept	1.799	0.0664	27.086	
Floral Richness	**0.380**	**0.117**	**3.245**	**0.00118**
Predator Attacks	0.450	0.310	1.453	0.146
Site Area	-0.206	0.307	-0.670	0.503
Site Isolation	0.0581	0.0802	0.725	0.469
Day	**-0.496**	**0.225**	**-2.205**	**0.0274**
Day^2	**0.713**	**0.231**	**3.082**	**0.00206**
Model 2A: Floral Diversity				
Intercept	2.495	0.223	11.180	
Site Area	**0.967**	**0.225**	**4.302**	**<0.000**
Day	0.967	0.527	1.836	0.0664
Day^2	**-1.0970**	**0.527**	**-2.081**	**0.0374**
Model 2B: Floral Richness				
Intercept	1.990	0.107	18.575	
Site Area	**0.622**	**0.108**	**5.756**	**<0.000**
Day	0.256	0.236	1.086	0.277
Day^2	-0.343	0.235	-1.462	0.144
Model 3: Predator Attacks				
Intercept	1.549	0.133	11.633	
Site Area	**0.856**	**0.0946**	**9.050**	**<0.000**
Site Isolation	**0.432**	**0.137**	**3.148**	**0.001**

Note: All estimates and SEs are shown as Z scores for ease of comparison. Model 1A: Hypothesis 1 with butterfly diversity as the dependent variable. Model 1B: Hypothesis 1 with butterfly richness as the dependent variable. Model 2A: Hypothesis 2 with floral diversity as the dependent variable. Model 2B: Hypothesis 2 with floral richness as the dependent variable. Model 3: Hypothesis 3 with predator attacks as the dependent variable. Site was included in Models 1A, 1B, 2A, and 2B. Variables in bold are statistically significant.

2.8 Supplemental materials

2.8.1 Appendix S2.1

D-sep claim of independence	Mixed Model	Variable whose partial regression slope should be zero	Null probability (distribution)
Diversity Model			
$(X_4, X_6) \mid \{X_1, X_2, X_3\}$	$X_6 \sim X_1 + X_2 + X_3 + X_4 + Day + Day^2 + (1 \mid Site)$	X_4	0.988 (Gaussian)
$(X_4, X_8) \mid \{X_1, X_2, X_3, X_6, X_5\}$	$X_8 \sim X_1 + X_2 + X_3 + X_6 + X_5 + X_4 + Day + Day^2 + (1 \mid Site)$	X_4	0.449 (Gaussian)
$(X_5, X_6) \mid \{X_1, X_2, X_4\}$	$X_6 \sim X_1 + X_2 + X_4 + X_5 + Day + Day^2 + (1 \mid Site)$	X_5	0.239 (Gaussian)
Richness Model			
$(X_4, X_7) \mid \{X_1, X_2, X_3\}$	$X_7 \sim X_1 + X_2 + X_3 + X_4 + Day + Day^2 + (1 \mid Site)$	X_4	0.691 (Poisson)
$(X_4, X_8) \mid \{X_1, X_2, X_3, X_7, X_5\}$	$X_8 \sim X_1 + X_2 + X_3 + X_7 + X_5 + X_4 + Day + Day^2 + (1 \mid Site)$	X_4	0.570 (Poisson)
$(X_5, X_7) \mid \{X_1, X_2, X_4\}$	$X_7 \sim X_1 + X_2 + X_4 + X_5 + Day + Day^2 + (1 \mid Site)$	X_5	0.0610 (Poisson)
Fisher's C for Diversity Model	4.486	P	0.61
Fisher's C for Richness Model	7.461	P	0.28

Appendix S2.1: Table 1. The set of independence statements implied by our causal model (Figure 1). Each of our independence claims is conditional on shared causal parents between the variables, shown within the curly brackets. Key to variables: X1=distance to nearest site, X2= site isolation, X3=site area, X4=grasshopper attacks, X5= predator attacks, X6=floral diversity, X7=floral richness, X8=butterfly diversity, X9=butterfly richness. We included Day and Day^2 as fixed effects and Site as a random effect in all models. The AIC scores for the models, starting with the topmost Diversity Model, are as follows: 268, 290, 267, 330, 308, 329.

We explored Hypothesis 1, which predicts that butterfly metacommunity structure will be impacted by mutualist metacommunity structure, predation pressure, and local and regional scale factors (Figure 2.3*A*). We fit two models, with butterfly diversity and richness as dependent variables. For the diversity model, we included floral diversity, predator attacks, site area, site isolation, and distance to the closest external site as fixed effects. For the richness model, we replaced floral diversity with floral richness. We then explored Hypothesis 2, which predicts that flowering plant metacommunity structure depend on measured local and landscape factors. We fit two models, with floral diversity and richness as the dependent variables. For both models, we included site area, site isolation, and distance to the closest external site as fixed effects. Finally, we explored Hypothesis 3, which predicts that predation pressure will be impacted by local and landscape factors, by fitting one model with predator attacks as the dependent variable. We included site area, site isolation, and distance to the closest external site as fixed effects. For this and subsequent models with predator or grasshopper attacks as dependent variables, there was no resampling at the site level so no random effects were included. We constructed generalized linear models with a Poisson distribution in the *glm* package.

Effect	Estimate	SE	*t* or *z* value	*P*
Model 1A: Butterfly Diversity				
Intercept	2.589	0.245	10.577	
Floral Diversity	**0.550**	**0.237**	**2.322**	**0.020**
Predator Attacks	1.606	1.130	1.422	0.155
Site Area	-1.186	1.156	-1.026	0.305
Site Isolation	0.129	0.303	0.427	0.670
Distance to Nearest External Site	-0.073	0.258	-0.283	0.777
Day	-1.206	0.650	-1.855	0.064
Day^2	**1.648**	**0.655**	**2.517**	**0.012**
Model 1B: Butterfly Richness				
Intercept	1.799	0.066	27.064	
Floral Richness	**0.379**	**0.117**	**3.241**	**0.001**
Predator Attacks	0.044	0.031	1.434	0.152
Site Area	-0.205	0.308	-0.666	0.505
Site Isolation	0.057	0.081	0.706	0.480
Distance to Nearest External Site	-0.019	0.071	-0.273	0.785
Day	**-0.496**	**0.225**	**-2.206**	**0.027**
Day^2	**0.711**	**0.232**	**3.073**	**0.002**
Model 2A: Floral Diversity				
Intercept	2.495	0.239	10.445	
Site Area	**1.004**	**0.268**	**3.750**	**0.000**
Site Isolation	0.139	0.259	0.535	0.593
Distance to Nearest External Site	-0.049	0.250	-0.195	0.845
Day	0.970	0.527	1.841	0.066
Day^2	**-1.096**	**0.528**	**-2.077**	**0.038**
Model 2B: Floral Richness				
Intercept	1.990	0.106	18.704	
Site Area	**0.647**	**0.119**	**5.419**	**<0.000**
Site Isolation	0.050	0.116	0.436	0.663
Distance to Nearest External Site	0.027	0.111	0.244	0.807
Day	0.254	0.236	1.075	0.282
Day^2	-0.341	0.235	-1.449	0.147
Model 3: Predator Attacks				
Intercept	1.728	0.255	6.788	
Grasshopper Attacks	-0.087	0.106	-0.823	0.403
Site Area	**1.210**	**0.492**	**2.459**	**0.008**
Site Isolation	**0.356**	**0.146**	**2.437**	**0.011**
Distance to Nearest External Site	-0.104	0.156	-0.666	0.499

Appendix S2.1: Table 2. Results of mixed models testing our three hypotheses. All estimates and standard errors are shown as Z scores for ease of comparison. Model 1A: hypothesis 1 with butterfly diversity as the dependent variable. Model 1B: hypothesis 1 with butterfly richness as the dependent variable. Model 2A: hypothesis 2 with floral diversity as the dependent variable. Model 2B: hypothesis 2 with floral richness as the dependent variable. Model 3: hypothesis 3 with predator attacks as the dependent variable. Site was included in Models 1A, 1B, 2A, and 2B. Variables in bold are statistically significant.

D-sep claim of independence	Mixed Model	Variable whose partial regression slope should be zero	Null probability (distribution)
Diversity Model			
$(X_5, X_6) \mid \{X_1, X_2, X_4\}$	$X_6 \sim X_1 + X_2 + X_5 + \text{Day} + \text{Day}^2 + (1 \mid \text{Site})$	X_5	0.215 (Gaussian)
Richness Model			
$(X_5, X_7) \mid \{X_1, X_2, X_4\}$	$X_7 \sim X_1 + X_2 + X_5 + \text{Day} + \text{Day}^2 + (1 \mid \text{Site})$	X_5	0.066 (Poisson)
Fisher's C for Diversity Model	3.0712	*P*	0.215
Fisher's C for Richness Model	5.451	*P*	0.066

Appendix S2.1: Table 3. The set of independence statements implied by our causal model without grasshopper attacks (Figure 1). Each of our independence claims is conditional on shared causal parents between the variables, shown within the curly brackets. Key to variables: X1=distance to nearest site, X2= site isolation, X5=predator attacks, X6=floral diversity, X7=floral richness, X8=butterfly diversity, X9=butterfly richness. We included Day and Day2 as fixed effects and Site as a random effect in all models. The AIC scores for the models are as follows: Diversity Model 266, Richness Model 327.

D-sep claim of independence	Mixed Model	Variable whose partial regression slope should be zero	Null probability (distribution)
Diversity Model			
$(X_2, X_6) \mid \{X_3\}$	$X_6 \sim X_3 + X_2 + Day + Day^2 + (1 \mid Site)$	X_2	0.561 (Gaussian)
$(X_5, X_6) \mid \{X_2, X_3\}$	$X_6 \sim X_2 + X_3 + X_5 + Day + Day^2 + (1 \mid Site)$	X_5	0.189 (Gaussian)
Richness Model			
$(X_2, X_7) \mid \{X_3\}$	$X_7 \sim X_3 + X_2 + Day + Day^2 + (1 \mid Site)$	X_2	0.680 (Poisson)
$(X_5, X_7) \mid \{X_2, X_3\}$	$X_7 \sim X_2 + X_3 + X_5 + Day + Day^2 + (1 \mid Site)$	X_5	0.0737 (Poisson)
Fisher's C for Diversity Model	4.489	*P*	0.344
Fisher's C for Richness Model	5.988	*P*	0.2000

Appendix S1: Table 4. the set of independence statements implied by our simplified causal model (Figure 2.5). Each of our independence claims is conditional on shared causal parents between the variables, shown within the curly brackets. Key to variables: X2= site isolation, X3=site area, X5= predator attacks, X6=floral diversity, X7=floral richness. We included Day and Day2 as fixed effects and Site as a random effect in all models. The AIC scores for the models, starting with the topmost Diversity Model, are as follows: 265, 264, 326, 325.

2.8.2 Appendix S2.2

Rarefaction Analysis

To determine the butterfly sampling intensity at each site we divided the transect length of each site by the site area. We then calculated the mean sampling intensity across the sites. Using the rarefaction feature in the iNext package for both richness and diversity, we used rarefaction to reduce butterfly sample sizes for sites well above the mean, and used extrapolation to increase butterfly sample sizes for sites well below the mean. We retained the raw samples for sites close to the mean. We used this data for all models that included butterfly richness or diversity. The results of these models were qualitatively the same to those models that used the raw butterfly sample data. The results for the path analysis of the simplified causal model are presented here (Table 1).

Effect	Estimate	SE	*t* or *z* value	*P*
Model 1A: Butterfly Diversity				
Intercept	2.690	0.323	8.317	
Floral Diversity	**0.604**	**0.306**	**1.977**	**0.0480**
Predator Attacks	1.310	1.491	0.878	0.380
Site Area	-0.869	1.527	-0.569	0.569
Site Isolation	0.259	0.401	0.646	0.519
Distance to Nearest External Site	-0.105	0.341	-0.308	0.758
Day	-1.381	0.834	-1.656	0.0978
Day^2	**1.814**	**0.840**	**2.160**	**0.0308**
Model 1B: Butterfly Richness				
Intercept	1.875	0.0964	19.449	
Floral Richness	**0.331**	**0.129**	**2.559**	**0.0105**
Predator Attacks	0.614	0.448	1.370	0.171
Site Area	-0.285	0.453	-0.629	0.529
Site Isolation	0.0351	0.119	0.296	0.767
Distance to Nearest External Site	-0.0941	0.103	-0.917	0.359
Day	**-0.514**	**0.226**	**-2.276**	**0.0228**
Day^2	**0.718**	**0.233**	**3.075**	**0.00210**

Appendix S2.2: Table 1. Results of mixed models testing hypothesis 1. Model 1A: hypothesis 1 with butterfly diversity as the dependent variable. Model 1B: hypothesis 1 with butterfly richness as the dependent variable.

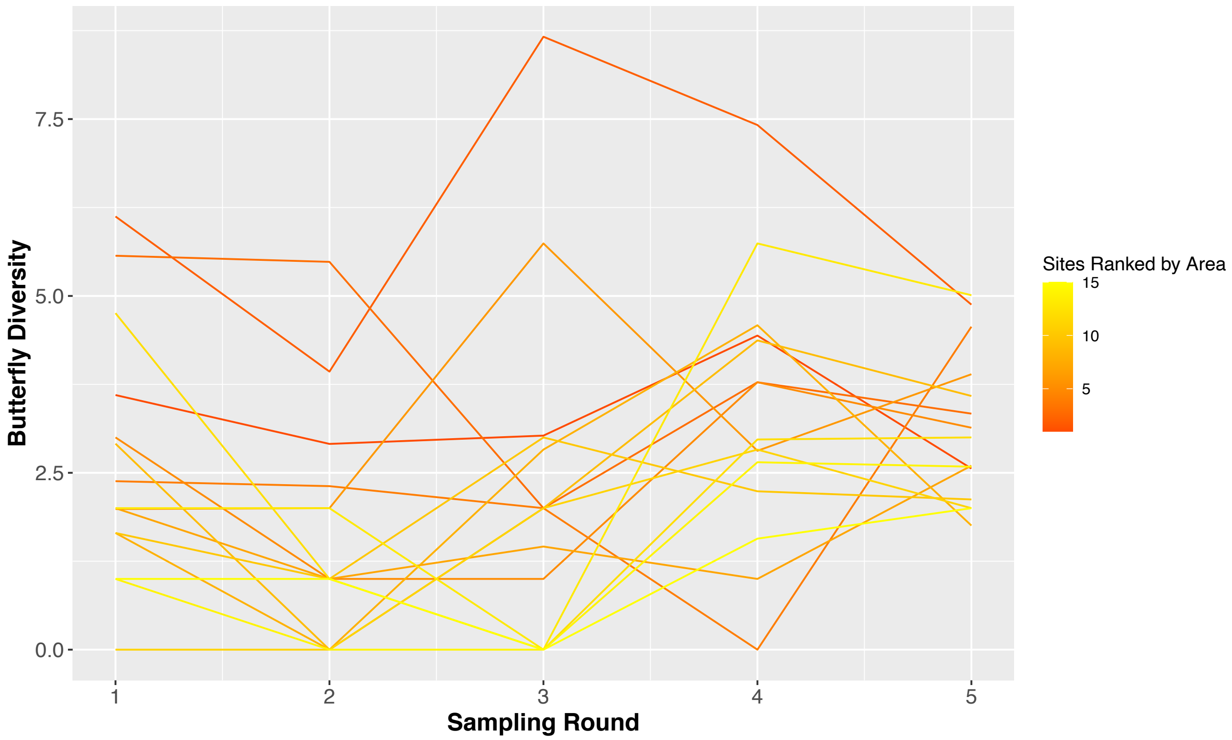
2.8.3 Appendix S2.3

Common Name	Species	Abundance
Common Roadside Skipper	*Amblyscirtes vialis*	1
Meadow Fritillary	*Boloria bellona*	40
Silver Bordered Fritillary	*Boloria selene*	52
Eastern Pine Elfin	*Callophrys niphon*	1
Hoary Elfin	*Callophrys polios*	2
Spring Azure	*Celastrina lucia*	3
Common Wood-Nymph	*Cercyonis pegala*	38
Common Ringlet	*Coenonympha tullia*	598
Clouded Sulpur	*Colias philodice*	587
Eastern Tailed Blue	*Cupido comyntas*	25
Monarch	*Danaus plexippus*	38
Dreamy Duskywing	*Erynnis icelus*	1
Juvenal's Duskywing	*Erynnis juvenalis*	4
Columbine Duskywing	*Erynnis lucilius*	27
Dun Skipper	*Euphyes vestris*	7
Silvery Blue	*Glaucopsyche lygdamus*	150
Leonard's Skipper	*Hesperia leonardus*	1
Northern Pearl-Eye	*Lethe anthedon*	1
Eyed Brown	*Lethe eurydice*	3
Viceroy	*Limenitis archippus*	97
White Admiral	*Limenitis arthemis arthemis*	9
Mourning Cloak	*Nymphalis antiopa*	1
Canadian Tiger Swallowtail	*Papilio canadensis*	6
Giant Swallowtail	*Papilio cresphontes*	2
Black Swallowtail	*Papilio polyxenes*	11
Northern Crescent	*Phyciodes cocyta*	10
Pearl Crescent	*Phyciodes tharos*	440
Mustard White	*Pieris oleracea*	4
Cabbage White	*Pieris rapae*	18
Long Dash Skipper	*Polites mystic*	1
Crossline Skipper	*Polites origenes*	2
Tawny-Edged Skipper	*Polites themistocles*	6
Gray Comma	*Polygonia progne*	2
Coral Hairstreak	*Satyrium titus*	1
Aphrodite Fritillary	*Speyeria aphrodite*	23
Atlantis Fritillary	*Speyeria atlantis*	3
Great Spangled Fritillary	*Speyeria cybele*	11
Northern Cloudywing	*Thorybes pylades*	11
European Skipper	*Thymelicus lineola*	28
Red Admiral	*Vanessa atalanta*	3
Painted lady	*Vanessa cardui*	2
American Lady	*Vanessa virginiensis*	2

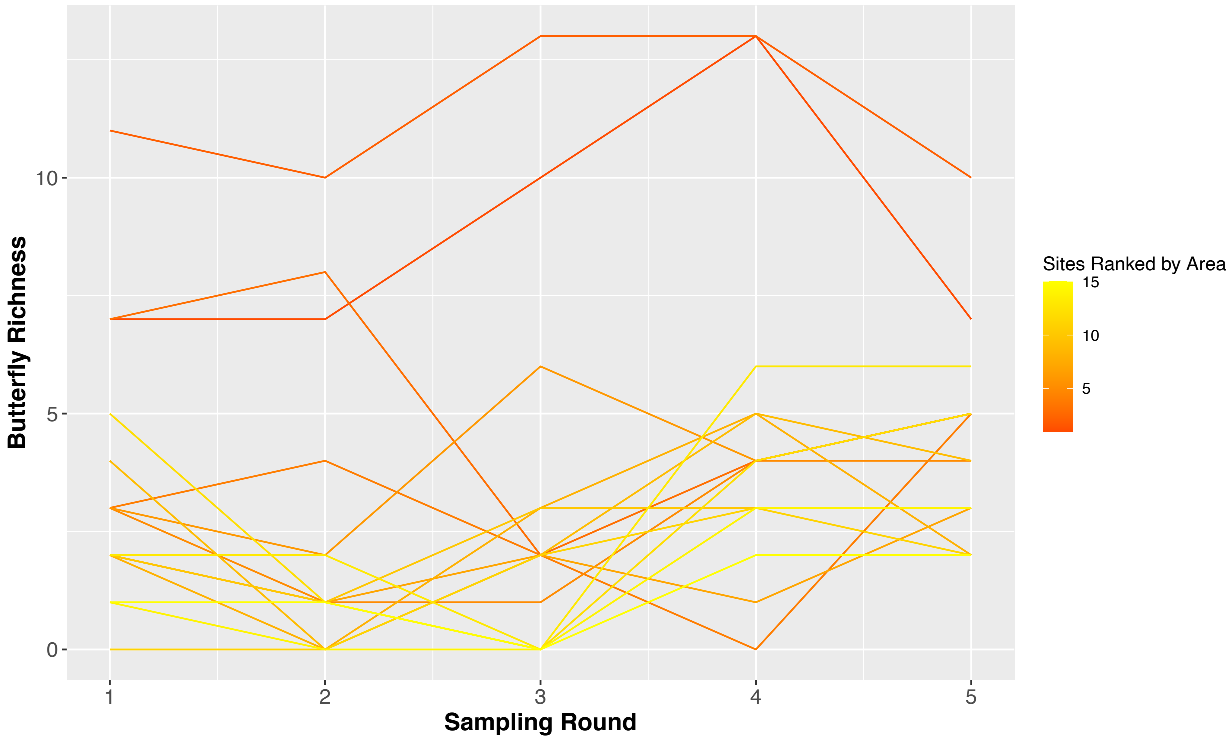
Appendix S2.3: Table S1. The species and abundances of butterflies observed during data collection.

Common Name	Species	Floral Abundance
Yarrow	*Achillea millefolium*	96
Purple False Foxglove	*Agalinis purpurea var. parviflora*	42
Field Pussytoes	*Antennaria neglecta*	733
Canada Columbine	*Aquilegia canadensis*	6
Thyme-Leaved Sandwort	*Arenaria serpyllifolia*	12
Giesecke's Bellflower	*Campanula gieseckeana*	82
Centaurea Genus	*Centaurea sp.*	75
Canada Thistle	*Cirsium arvense*	1
Wild Basil	*Clinopodium vulgare*	74
Bastard Toadflax	*Comandra umbellata*	969
Red-Osier Dogwood	*Cornus sericea*	72
Wild Carrot	*Daucus carota*	2509
Flat-Topped White Aster	*Doellingeria umbellata*	22
Common Vipers Bugloss	*Echium vulgare*	1269
Annual Fleabane	*Erigeron annuus*	1182
Erigeron Genus	*Erigeron sp*	3
Grass-Leaved Goldenrod	*Euthamia graminifolia*	660
Wild Strawberry	*Fragaria virginiana*	375
Northern Bedstraw	*Galium boreale*	172
Smooth Bedstraw	*Galium mollugo*	51
Bicknell's Geranium	*Geranium bicknellii*	9
Barren Strawberry	*Geum fragarioides*	5
Rough Hawkweed	*Hieracium scabrum*	36
Common St. John's-Wort	*Hypericum perforatum*	54
Oxeye Daisy	*Leucanthemum vulgare*	136
Virginia Water-Horehound	*Lycopus virginicus*	26
Purple Loostrife	*Lythrum salicaria*	276
Wild Lily-of-the-Valley	*Maianthemum canadense*	15
Star-Flowered False Solomon's Seal	*Maianthemum stellatum*	55
Black Medick	*Medicago lupulina*	2301
White Sweet-Clover	*Melilotus albus*	237
Canada Mint	*Mentha canadensis*	147
Balsam Groundsel	*Packera paupercula*	1471
Hairy Beardtongue	*Penstemon hirsutus*	35
King Devil Hawkweed	*Pilosella ×floribunda*	653
Orange Hawkweed	*Pilosella aurantiaca*	1
Seneca Snakeroot	*Polygala senega*	231
Silvery Cinquefoil	*Potentilla argentea*	14
Sulphur Cinquefoil	*Potentilla recta*	3
Common Self-Heal	*Prunella vulgaris*	1238
Common Buttercup	*Ranunculus acris*	73
Rugosa Rose	*Rosa rugosa*	3
Marsh Skullcap	*Scutellaria galericulata*	4
Strict Blue-Eyed-Grass	*Sisyrinchium montanum*	3
Upland White Goldenrod	*Solidago ptarmicoides*	2546
Goldenrod	*Solidago sp.*	5828
Star Chickweed	*Stellaria pubera*	7
White Panicled Aster	*Symphyotrichum lanceolatum*	7
Calico Aster	*Symphyotrichum lateriflorum*	77
New England Aster	*Symphyotrichum novae-angliae*	112
Arrow-Leaved Aster	*Symphyotrichum urophyllum*	218
Fluxweed	*Trichostema brachiatum*	1154
Alsike Clover	*Trifolium hybridum*	88
Red Clover	*Trifolium pratense*	352
White Clover	*Trifolium repens*	16
Tufted Vetch	*Vicia cracca*	835
Northern Bog Violet	*Viola nephrophylla*	3
Woolly Blue Violet	*Viola sororia*	6
Common Bearberry	*Arctostaphylos uva-ursi*	301

Appendix S2.3: Table S2. The species and abundances of flowers observed during data collection. Plants were identified to species when possible.



Appendix S2.3, Figure S1. Butterfly diversity observed over the five sampling rounds at each site. Larger sites are shown in red, smaller sites in yellow.



Appendix S2.3, Figure S2. Butterfly richness observed over the five sampling rounds at each site. Larger sites are shown in red, smaller sites in yellow.

2.9 References

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Chapter 3: dispersal mediates trophic interactions and habitat connectivity to alter metacommunity composition

Note: this chapter is a slightly modified version of the following article:

> Gordon, Susan C.C., J.G.A. Martin, and J.T. Kerr. "Dispersal mediates trophic interactions and habitat connectivity to alter metacommunity composition." *Ecology* (2023): e4215.

3.1 Abstract

Dispersal contributes vitally to metacommunity structure. However, interactions between dispersal and other key processes have rarely been explored, particularly in the context of multitrophic metacommunities. I investigated such a metacommunity in naturally fragmented habitats populated by butterfly species (whose dispersal capacities were previously assessed), flowering plants, and butterfly predators. Using data on butterfly species abundance, floral abundance, and predation (on experimentally placed clay butterfly models), I asked how dispersal ability mediates interactions with predators, mutualists, and the landscape matrix. In contrast to expectations, high densities of strong dispersers were found in more isolated sites and sites with low floral resource density, while intermediate dispersers maintained similar densities across isolation and floral gradients, and higher densities of poor dispersers were found in more connected sites and sites with higher floral density. These findings raise questions about how strong dispersers experience the landscape matrix and the quality of isolated and low-resource sites. Strong dispersers were able to escape habitat patches with high predation, while intermediate dispersers maintained similar densities along a predation gradient, and poor dispersers occurred at high densities in these patches, exposing them to interactions with predators. This

work demonstrates that species that vary in dispersal capacities interact differently with predators and mutualist partners in a landscape context, shaping metacommunity composition.

3.2 Introduction

Examining differences between dispersal abilities of species within metacommunities, part of the “internal structure” of the metacommunity (Leibold et al. 2022), is a step toward understanding how processes create emergent patterns of species diversity, abundance, and composition. Because strong dispersers should be less constrained by site size and connectivity, theory predicts that they will maintain populations more readily than poor dispersers in small, isolated sites (Bauer et al. 2021). Some tests of this prediction have been attempted, although a consensus has yet to emerge from the results. In a predictive model of a three-species Daphnia metacommunity, the strongest disperser was more likely to colonize a patch far from its natal patch (Luo et al. 2022). In natural aquatic metacommunities, large-bodied species (thought to be poorer dispersers) were more constrained by their capacity to move through the “landscape” matrix, while site characteristics limited populations of small-bodied species (thought to be stronger dispersers; De Bie et al. 2012, Padial et al. 2014). Another study found only marginal support for an interaction between body size (used as an indicator of dispersal ability) and proximity to remnant habitat patches when investigating the persistence of bees in agricultural landscapes (Ponisio et al. 2019). In contrast, the composition of a butterfly metacommunity was influenced by site characteristics and not habitat connectivity, with less mobile species having higher abundances in stable, larger habitat patches and more mobile species favoring disturbed patches (Pavoine et al. 2014). More work is needed to determine whether variable dispersal abilities cause broad patterns in metacommunity composition, yet progress has been constrained by limited capacities to measure most species' dispersal abilities (Jønsson et al. 2016).

Patterns expected when considering dispersal alone may not emerge if other important factors, particularly biotic interactions, are not considered (Grainger et al. 2017). For example, dispersal limitation among seed dispersers can structure plant community diversity in fragmented landscapes (Emer et al. 2018). The presence of predators imposes constraints on prey metacommunity structure by altering how prey interacts with the landscape (Grainger et al. 2017), as the presence of predators can cause prey to disperse (Fronhofer et al. 2018).

In this study, I explored how butterfly dispersal capacity mediated interactions between butterflies and their predators, their mutualist partners/food resources, and the landscape matrix. Butterflies are an excellent model organism for this work as they exhibit a range of dispersal abilities, which have been thoroughly quantified in the study region through expert-based consensus (Burke et al. 2011). There is little evidence for interspecific competition between butterfly species that could govern their abundances in this landscape (Holl 1995, Balfour et al. 2015), so I do not expect competition–colonization tradeoffs to occur as in other taxa. I predicted that strong dispersers would not be constrained by site isolation and would be more abundant in high-quality sites. Furthermore, strong dispersers should be more abundant in sites with high floral abundance and would be less abundant in sites with high predation pressure. Because poor dispersers should be strongly constrained by habitat connectivity, I predicted that they would occur at higher abundances in more connected sites, despite site quality. In addition, poor dispersers should be less able to track sites with high floral abundance and would be unable to escape from sites with high predation pressure.

3.3 Methods

3.3.1 Study system

The study was conducted in Burnt Lands Provincial Park in Ottawa, Canada (Figure 3.1). This area encompasses a globally rare alvar ecosystem, and its utility for research has been demonstrated (Gordon and Kerr 2022). The ecosystem is characterized by pockets of bare rock and shallow soils that host grassland habitat, set within a matrix dominated by forest with patches of wetland. For this study, I identified 15 distinct grassland sites, with areas between 0.027 and 179 ha and distances between sites from 20 to 330 m. Burnt Lands hosts a rich butterfly community of 50 species, as well as a high diversity of flowering plants.

3.3.2 Butterfly and plant surveys

I conducted butterfly and flowering plant surveys by visiting all sites five times over the summer, from 6 June to 18 September 2019. To survey butterflies I walked along marked transects, taking approximately 10 min to survey a 50-m transect, and counted butterflies within 5 m of the transect (Pollard 1977). I marked one 50-m transect at all sites under 2 ha, except at the smallest site, which could only contain a 15-m transect. For sites above 2 ha, I added 25 additional meters to transects for each additional 2 ha of site area. The final area calculated for the two largest sites was larger than my initial estimates, so these sites had a larger ratio of area to transect length (as well as a larger ratio of area to quadrats and models as described below).

Most butterfly species do not have flight seasons throughout the entire summer, having one or more short generations during the season when they can be deemed “active.” Based on the data I collected, I determined whether each species was active during each of the five rounds of transect surveys. If at least one individual of a species was identified during a round, the species was determined to be active, and any negative observations were assigned a value of 0. If no individuals of a species were observed during a round, that species was deemed to be inactive during that period of time and was assigned a value of NA for all sites. This method prevented us from falsely assigning zeros to site visits outside of a butterfly's flight period, at which time it would be impossible to count any individuals of that species, and any assigned zeros would then create errors in model analyses. I extracted mobility scores for all butterfly species from Burke et al. (2011), who surveyed North American butterfly experts to create a consensus around differences in dispersal capacities. Butterflies were scored from 0 (sedentary) to 10 (highly mobile). I marked 1×1-m quadrats at the ends of transects to survey flowering plants, with a minimum of four quadrats per site. For sites over 2 ha, I marked one additional quadrat for each additional 2 ha of site area. I identified and counted all flowers that were open at the time of the surveys and adjusted my counts based on the type of inflorescence (e.g., unbellet vs. spikel Gordon and Kerr 2022).

3.3.3 Butterfly models

While little is known about predation on adult butterflies, a wide variety of generalist birds and arthropods have been observed attacking adults (Wourms and Wasserman 1983, Brown 1984, Tiitsaar et al. 2013), making it difficult to measure all forms of predation in these habitats. Additionally, predators like birds are not constrained by site boundaries, so surveying them at such a small spatial scale may not be appropriate (Debinski et al. 2006). Instead, I quantified predation pressure at the site level by creating and placing butterfly models of four species and measuring rates of predator attack on them (Figure 3.2). Because of the generalist nature of butterfly predators, I expect attack rates on these models to reflect attack rates on the broader butterfly community.

I constructed models using modeling clay and waterproofed paper printed with high-quality images of butterfly wings (Gordon and Kerr 2022). Wings were printed to scale, and butterfly body sizes were made to reflect the length of the photographed specimen. I customized the models to reflect four butterfly species found within the metacommunity. These species exhibit a range of dispersal abilities and are active at different times throughout the season. The models were deployed during the observed peak activity of each species: silvery blue (*Glaucopsyche lygdamus*, mobility 4.37) between 2 and 10 July, monarch (*Danaus plexippus*, mobility 9.5) between 23 and 31 July, aphrodite fritillary (*Speyeria aphrodite*, mobility 6.54) between 5 and 20 August, and clouded sulfur (*Colias philodice,* mobility 7.33) between 6 and 20 September.

For each of the four butterfly species I placed a minimum of four models in each site. I added one additional model for each additional 2 ha of site area to maintain similar likelihoods that models would be detected by predators across sites. I secured the models to the branches of trees and shrubs near the butterfly transects, and each new model was placed in a different location. I collected the models after 48 h and determined whether or not they showed signs of predator attacks. I summed the number of models that were attacked across species for each site as a measurement of predation pressure per site.

Some models had distinctive markings left by grasshoppers, which can scavenge insect carcasses (Gordon and Kerr 2022). These marks included bites around wing edges and shallow markings on the body; no models had both scavenger and predator marks. As these scavenger marks affected the appearance of the models, I tested whether the number of models marked by scavengers affected the number of models attacked by predators. I used a generalized linear model with a Poisson distribution from the MASS package (Venables and Ripley 2002), and modeled the number of models attacked by predators at each site as the dependent variable. I centered and scaled all independent variables by their SDs using the “scale” command in base R, creating Z-scores. I used a Type II ANOVA to determine effect significance. I excluded counts of scavenger marks from further analysis after determining that it was neither informative (including scavenger marks in the model leads to a slightly higher AIC score; see below) nor significant as a predictor of numbers of predator attacks.

3.3.4 Landscape metrics

I calculated site area and site isolation within the metacommunity to characterize the landscape. I traced polygons over high-resolution aerial photographs (20 cm) of each study site in ArcGIS Pro 3.0.1 (ESRI 2022), and used these polygons to calculate site area (Gerner and Sargent 2022).

To calculate how isolated a site was from the rest of the metacommunity, I used the least-cost path function in ArcGIS Pro, which calculates connectivity between sites by combining distance and land cover type. I did not include elevation, a metric often used in least-cost path analysis, because there is little change in elevation across this landscape. I characterized the matrix between sites using aerial photographs and field observations, differentiating between land cover types that are relevant to butterflies in these sites (Hall et al. 2014): forest, wetland and open water, bare ground paths, cut grass, and paved roads. I calculated the cost for the butterfly community to move across all land cover types, including grassland, by subtracting the number of species that use each land cover from the total number of species (Gordon and Kerr 2022). Land cover types used by more species within the metacommunity, such as grassland, had a lower cost, indicating that it was easier for the community to move through that land cover. To determine site isolation, I summed the cost of paths between each site and all other sites.

3.3.5 Statistical analysis

I conducted statistical analyses using R version 4.2.2 (R Core Team 2022). I centered and scaled all independent variables by their standard deviations using the “scale” command in base R, creating Z-scores.

To determine how dispersal ability mediated the interaction between butterflies, their predators, their mutualist partners, and the landscape, I used a generalized linear mixed-effects model with a Poisson distribution from the glmmTMB package (Brooks et al. 2017). I fitted the model with abundances of each butterfly species as the dependent variable. I included the length of transects surveyed at each site as an offset term, which turned the dependent variable into the density of butterflies relative to the transect lengths. I divided floral abundance by the number of survey quadrats at each site and divided predator attacks by the number of models placed at each site, so that these variables were also transformed into rates. I included site isolation, floral abundance, and predator attacks as fixed effects and interaction terms between species mobility and all fixed effects. I included site as a random effect to correct for repeated observations and included a zero-inflation term to correct for the large number of zeros, which can be inflated by detection error for species with low abundance. I calculated Akaike information criterion (AIC) scores using the “AIC” command in base R to compare models with and without site area in the zero-inflation term (AIC score of 5763 with site area and 5825 without site area). Including site area lowered the AIC score, so I retained it in the model. The pseudo-r-squared score for this model was 0.1 and was calculated using the MuMIn package. Note that this measure may be used to compare goodness-of-fit among models using the same data but does not measure explained variance, as does an r-squared value (Nakagawa et al. 2017). I used a Type III ANOVA from the car package to calculate significance for the final model (Fox and Weisberg

2019). This model did not violate any test assumptions, and I did not find evidence of significant spatial autocorrelation.

I also tested a version of the final model with the addition of site area as a main effect and an interaction between site area and mobility. While these effects were significant, the CIs around the interaction were so large as to make the relationships difficult to interpret. When this interaction was removed from the model, the main effect of site area was no longer significant. I removed site area as a fixed effect and proceeded as described previously.

3.4 Results

I identified 42 butterfly species and counted a total of 2148 individuals. Butterfly abundance per species at each site for each sampling round ranged from 0 to 597 (*Coenonympha tullia*), with a mean of 1.5 and SD of 10.6. The mobility of the butterfly species I observed ranged from 3.71 to 9.5, with a mean of 5.87 and a SD of 1.4 (Appendix S3.1: Table S1). Most species had unique mobility scores, although four pairs of species had the same scores: *Amblyscirtes vialis* and *Celastrina lucia* (3.71), *Hesperia leonardus* and *Polites themistocles* (4.73), *Boloria selene* and *Glaucopsyche lygdamus* (5.37), and *Papilio cresphontes and Speyeria atlantis* (7.00). All species in this community are floral generalists, although some show preferences for specific plant families (e.g., Fabaceae; Hall et al. 2014).

I marked between four and 64 floral survey quadrats per site, with a mean of 10.7 and SD of 17.1. I counted over 23,000 flowers, and floral abundance at each site for each sampling round ranged from 0 to 3255, with a mean of 319.3 and SD of 6694.

I deployed 166 butterfly models per species for a total of 664 models and recovered 660 of them (four were lost). I placed totals of between 16 and 256 models per site, with a mean of 42.9 and SD of 68.4. Rates of model attacks at each site ranged from 0.05 to 0.5, with a mean of

0.2 and SD of 0.1. The site isolation results showed a wide range of costs among sites, with the costs of isolation differing by almost 170%.

Butterfly mobility was negatively related to overall butterfly density, as I observed fewer individuals and species at higher levels of mobility (Table 3.1). Sites with high floral density also supported a high density of butterflies. Predation rates were higher in sites with a higher density of butterflies. Butterfly density was lower in sites that were more isolated.

Most butterfly species detected in this system were relatively poor dispersers. While I tested for interactions between species' dispersal abilities, landscape characteristics, and multitrophic interactions (i.e., predation intensity and floral abundance), such interactions can more reliably be interpreted for species with weaker dispersal abilities, as those sample sizes are considerably larger.

Nevertheless, there is clear variation in how butterfly species interact with landscape connectivity, depending on differences in dispersal abilities. The density of weak dispersers was lower in more isolated sites, and this relationship flattened for species with intermediate dispersal abilities (Figure 3.3). Strong dispersers increased in density in more isolated sites. The density of poor dispersers was highest in sites with higher predation rates, with a flattened relationship for intermediate dispersers. The density of strong dispersers was highest in sites with low predation rates (Figure 3.4). Finally, the density of poor dispersers was highest in sites with high rates of floral abundance. The slope of this relationship flattened for intermediate dispersers and then reversed direction as the density of the strongest dispersers decreased with increasing rates of floral abundance (Figure 3.5).

3.5 Discussion

While previous work has examined the effects of dispersal on patterns in metacommunity structure, the processes behind these patterns are poorly understood. By integrating a priori knowledge of the mobility of species present in a large butterfly metacommunity, this study took the first step in showing that dispersal ability governs relationships between butterflies, their predators, their mutualist partners, and habitat connectivity, which in turn may affect community composition.

The density of strong dispersers was higher in isolated sites, while the density of weak dispersers was higher in connected sites. While I predicted that weak dispersers would be limited to highly connected sites and strong dispersers would not be limited by connectivity, the higher density of strong dispersers in isolated sites is unexpected. Previous work suggests a competition–colonization tradeoff (Raffard et al. 2022), which could force poor competitors to disperse farther into more isolated patches that strong competitors cannot reach (A. Driscoll 2008). There is little evidence of competition among butterflies for floral resources (but see Kunte 2008), and I cannot extrapolate resource competition from this data when other pollinators are present in high numbers, as bees were in this system. However, isolation may protect sites from some butterfly parasitoids that are limited by dispersal (Van Nouhuys and Hanski 2002). Populations of parasitoids might be larger in well-connected sites that support large populations of dispersal-limited butterfly species (i.e., apparent competition; Holt and Bonsall 2017), so strong dispersers may move to isolated sites to escape parasitism.

Strong dispersers may respond to predation risk by leaving sites with higher predation pressure, while poor dispersers are dispersal-limited and may be unable to escape high-predation sites. Previous work has found that perceived predation risk is a dispersal driver across species

(Fronhofer et al. 2018). The strongest disperser in the metacommunity was the monarch (*D. plexippus*) with the only mobility score above 9 (9.5), and monarch caterpillars have been shown to exhibit higher occupancy rates in isolated patches when more predators are present across the landscape (Grainger et al. 2017). Many studies have examined the impacts of predation on metacommunity structure (Chase et al. 2010, Pedersen et al. 2016, Karakoç et al. 2020, Pelinson et al. 2022), but investigations of how the impacts of predation vary based on prey species' dispersal abilities within a metacommunity are rare, and the implications of these patterns for metacommunity composition should be further investigated across additional systems.

It is possible that predation rates significantly alter the abundance of poor dispersers in this metacommunity, but I cannot measure such an effect without experimental removal of predators in a before-after-control-impact (BACI) study, which cannot be undertaken in these protected habitats. Predators may exert some control over the abundance of butterfly species in these areas, particularly those with poor dispersal abilities, but variation in abundances nevertheless related to differences in dispersal ability.

In contrast to my prediction, the density of strong dispersers decreased with increasing floral density, while the density of poor dispersers increased. Previous work showed that increasing floral abundance related directly to butterfly abundance (Wix et al. 2019). However, butterfly species in this metacommunity displayed a wide range of dispersal abilities (Burke et al. 2011), and species moved through the landscape differently as a result. Strong dispersers, particularly migratory species like the monarch, are not constrained by the boundaries of a habitat patch. These species may spend more time questing for resources, including larval host plants, across the landscape, making them more likely to be seen in patches with low floral density. Alternatively, strong dispersers may be searching for sites with low floral density, as these sites may have reduced parasitoid attack rates (Choutt et al. 2011, Stenoien et al. 2015). Populations of poor dispersers are more abundant in sites with high floral resource abundance, which supports their populations in the adult stage but may come at a cost to larval survivorship. Host plant abundance may account for additional variation in butterfly abundance (Curtis et al. 2015), and, while difficult to test due to the wide variety of plant species used as hosts, it represents an area for future work.

This research was conducted in a protected area with relatively well-connected sites and minimal disturbance. Species have likely had many generations within a stable landscape to colonize new habitat patches, and despite this, less mobile species were still limited by dispersal.

Species with low dispersal abilities are at a higher risk of extinction, particularly under changing environmental conditions (Backus et al. 2022), and these findings emphasize the need to consider dispersal ability for conservation strategies at a landscape scale. The high density of strong dispersers in isolated sites highlights the disproportionate conservation value of isolated habitats, consistent with previous work (Wintle et al. 2019). In a previous study I found that predators may not need to be considered for conserving diverse butterfly communities (Gordon and Kerr 2022), but here I found that they might alter community composition. Predators may affect the number of strong dispersers who stay at a site, so if maintaining a community of strong dispersers is a goal, these factors should be considered.

Here, I showed that variation in dispersal ability might change how species interact with the landscape, predators, and mutualists/food resources, to shape species composition in a metacommunity. Understanding the drivers of species composition is an important goal of ecology and is becoming even more important due to environmental change (Jandt et al. 2022). This examination of the internal structure of the metacommunity gives new insight into the mechanisms behind patterns of species composition and emphasizes the importance of this type of work for understanding metacommunity structure.

3.6 Figures

Figure 3.1

Map of study sites and surrounding landscape matrix approximately 45 km from downtown Ottawa, Canada. The 15 grassland study sites are shown in orange and site numbers in white. The inset of eastern North America identifies the study area with a red circle.

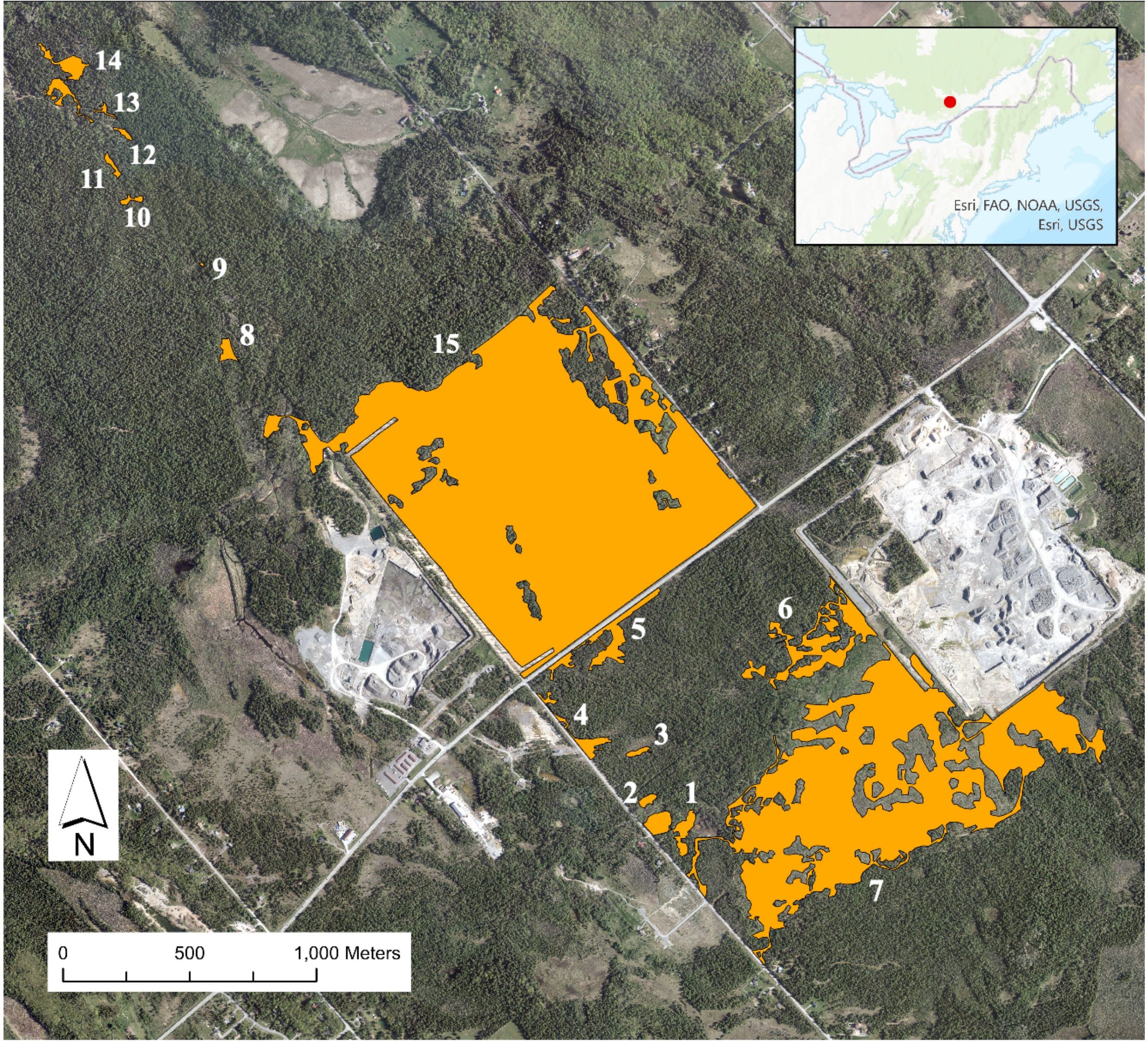


Figure 3.2

Photos of attacked and untouched butterfly models. (a) Photo of untouched monarch (*Danaus plexippus*) butterfly model. (b) Photo of attacked aphrodite fritillary (*Speyeria aphrodite*) butterfly model; note the deep markings in the clay indicating an attempted attack on the model. Photos taken by Susan C. C. Gordon.

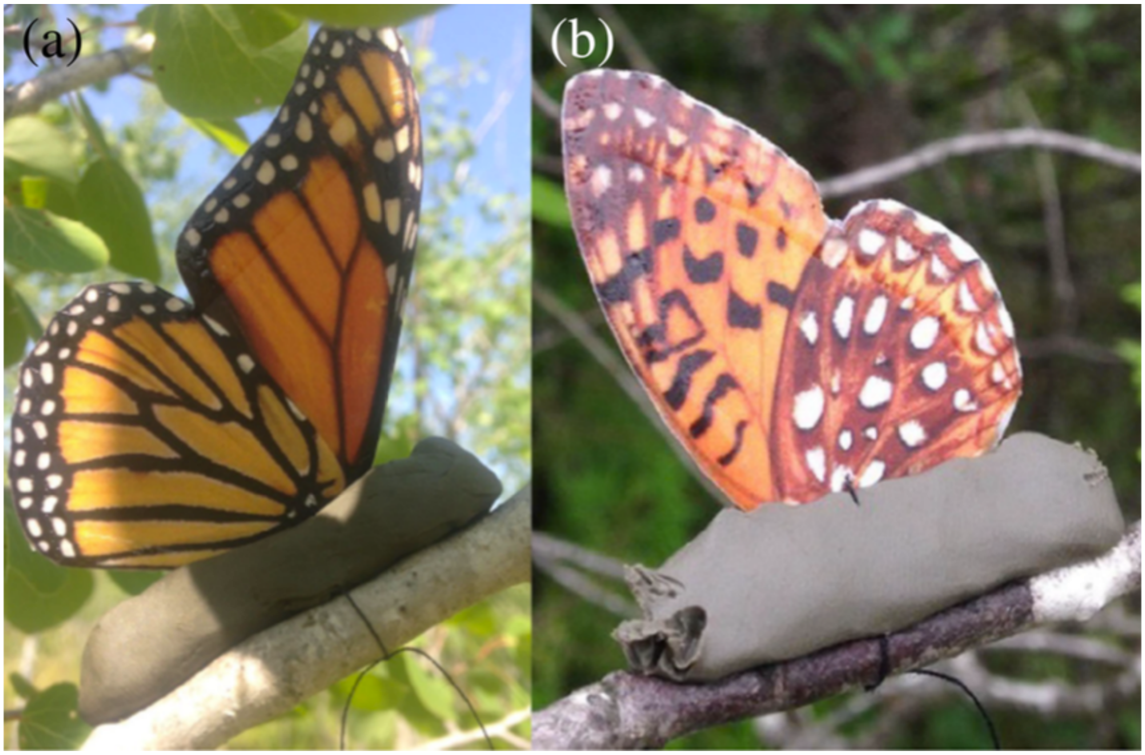


Figure 3.3

Predicted densities of weak (3.5; yellow), intermediate (5.5; orange), and strong (9.5; red) dispersers in sites along an isolation gradient. Light yellow, orange, and red bands are 95% CIs around fitted lines. Appendix S3.2: Figure S1 shows this figure overlaid with raw data.

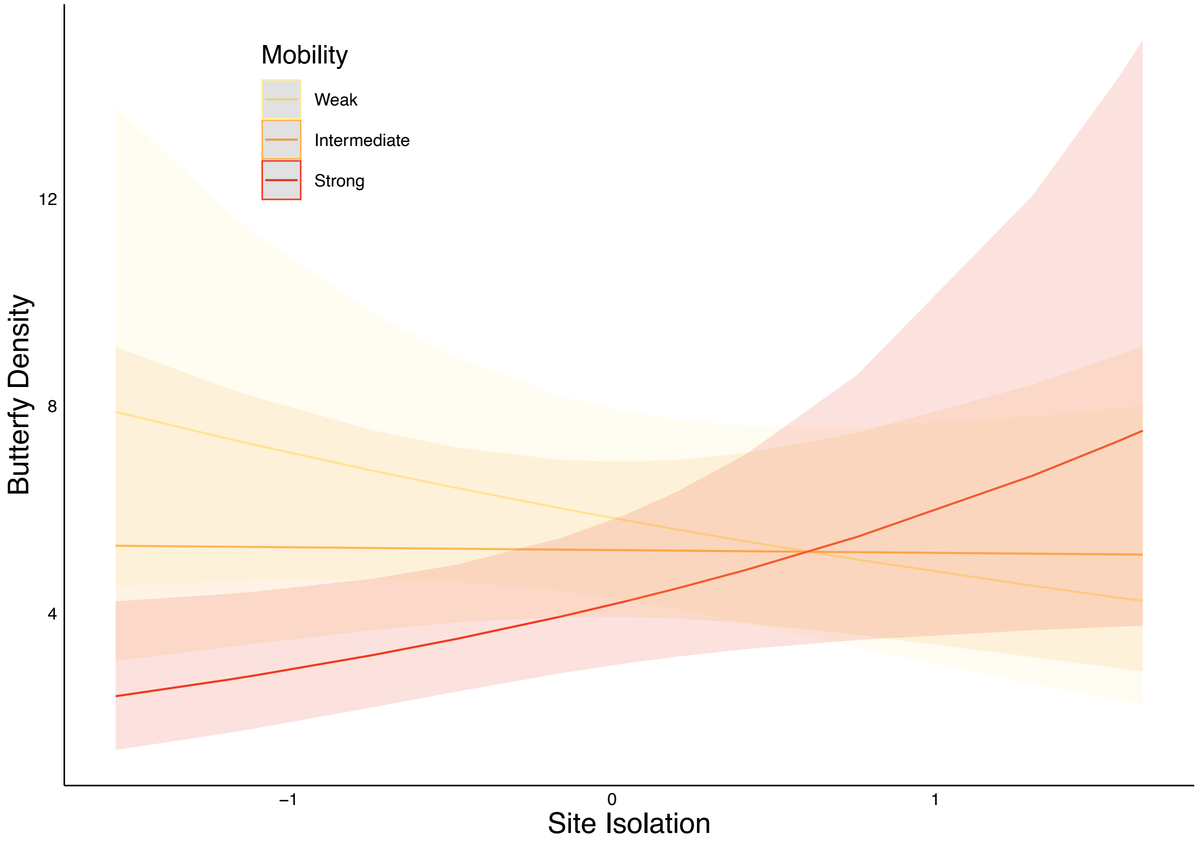


Figure 3.4

Predicted densities of weak (3.5; yellow), intermediate (5.5; orange), and strong (9.5; red) dispersers in sites along a gradient of predator attack rates. Light yellow, orange, and red bands are 95% CIs around fitted lines. Appendix S3.2: Figure S2 shows this figure overlaid with raw data.

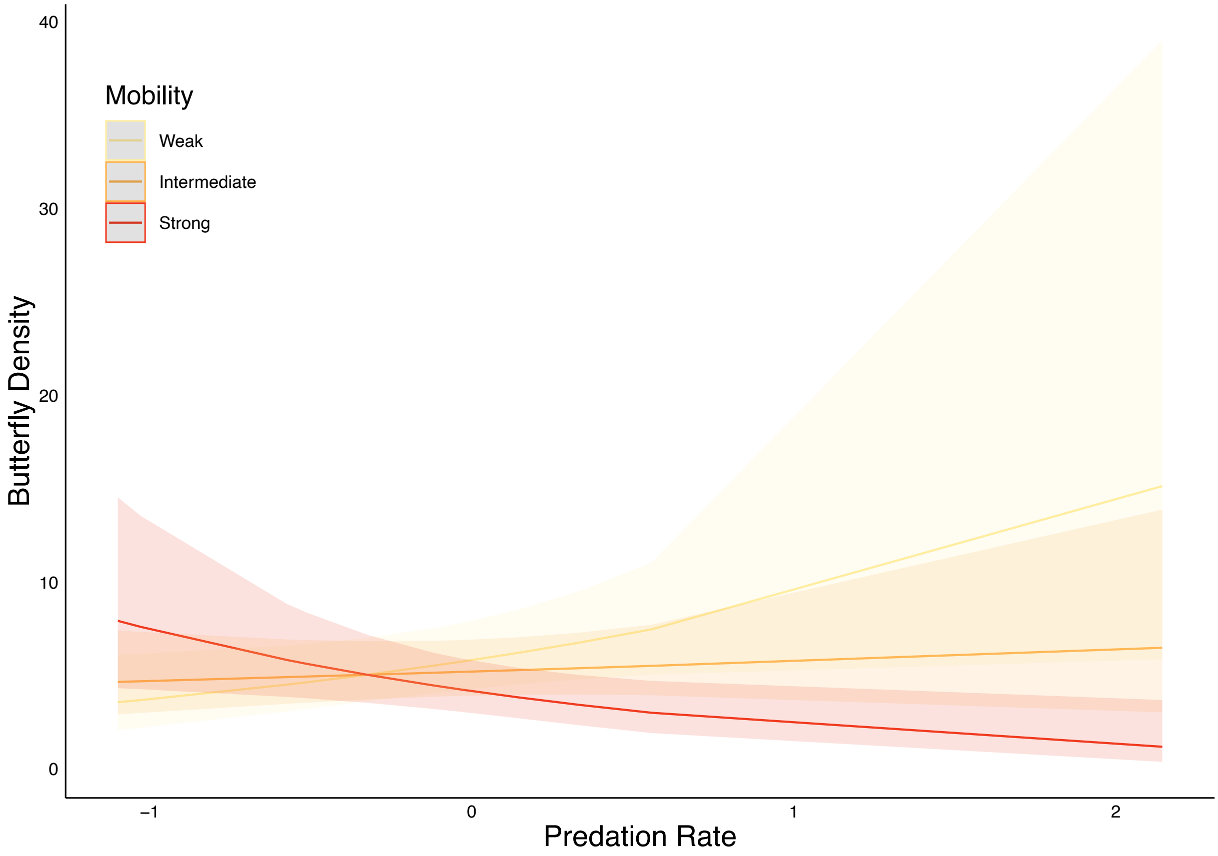
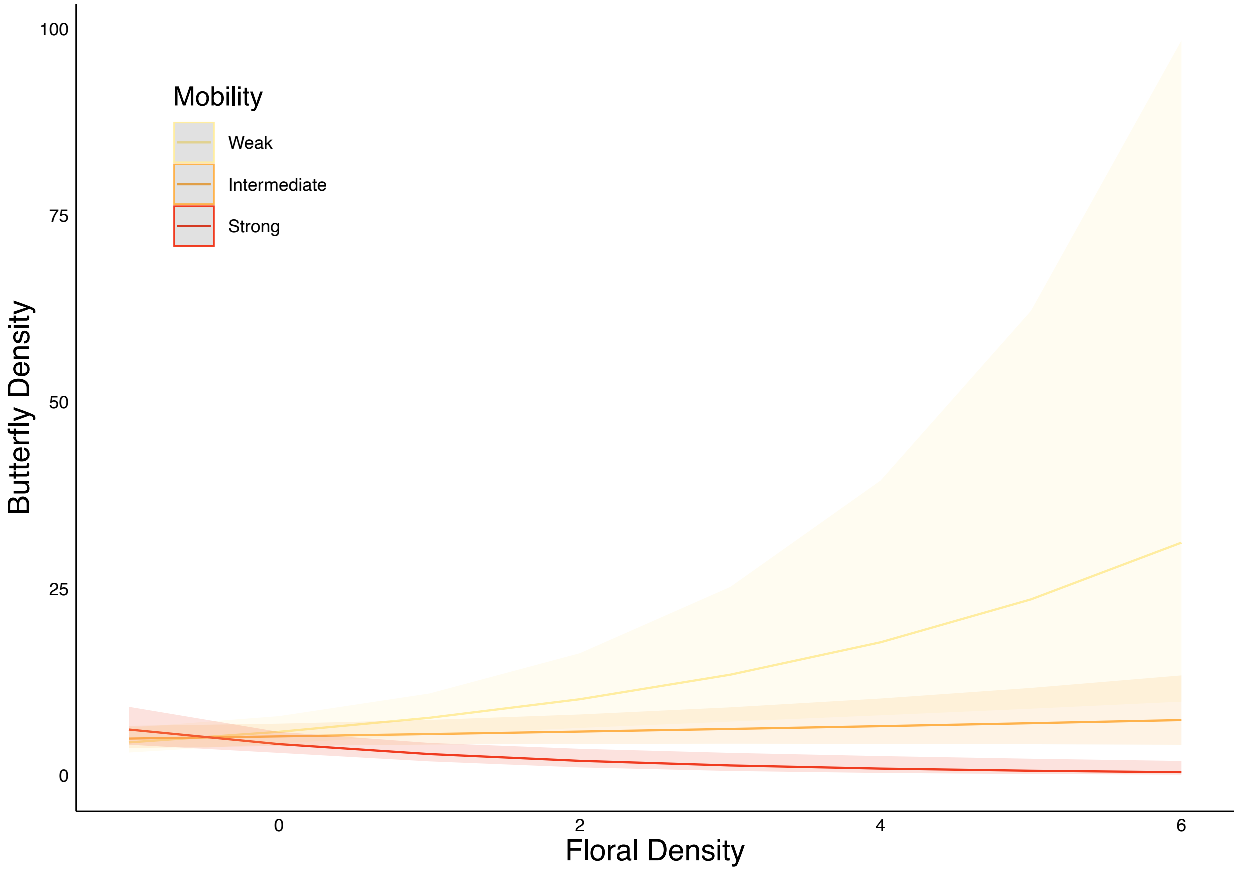


Figure 3.5

Predicted densities of weak (3.5; yellow), intermediate (5.5; orange), and strong (9.5; red) dispersers in patches along a gradient of site-level floral density. Light yellow, orange, and red bands are 95% CIs around fitted lines. Appendix S3.2: Figure S3 shows this figure overlaid with raw data.



3.7 Tables

Table 3.1

Fixed-effect estimates and associated statistics from the generalized linear mixed-effects models of butterfly density.

Effect	Estimate	SE	*z* value	*P*
Intercept	-3.415	0.209	-16.336	<0.000
Site Isolation	-0.520	0.201	-2.582	0.00981
Predation Rate	1.045	0.351	2.975	0.00293
Floral Density	0.666	0.210	3.176	0.00149
Mobility	-0.0554	0.0253	-2.193	0.0283
Isolation : Mobility	0.0927	0.0213	4.315	<0.000
Predation Rate : Mobility	-0.172	0.0521	-3.294	0.001
Floral Density : Mobility	-0.111	0.0342	-3.237	0.00121

Note: All estimates and SEs are shown as Z-scores for ease of comparison.

3.8 Supplementary materials

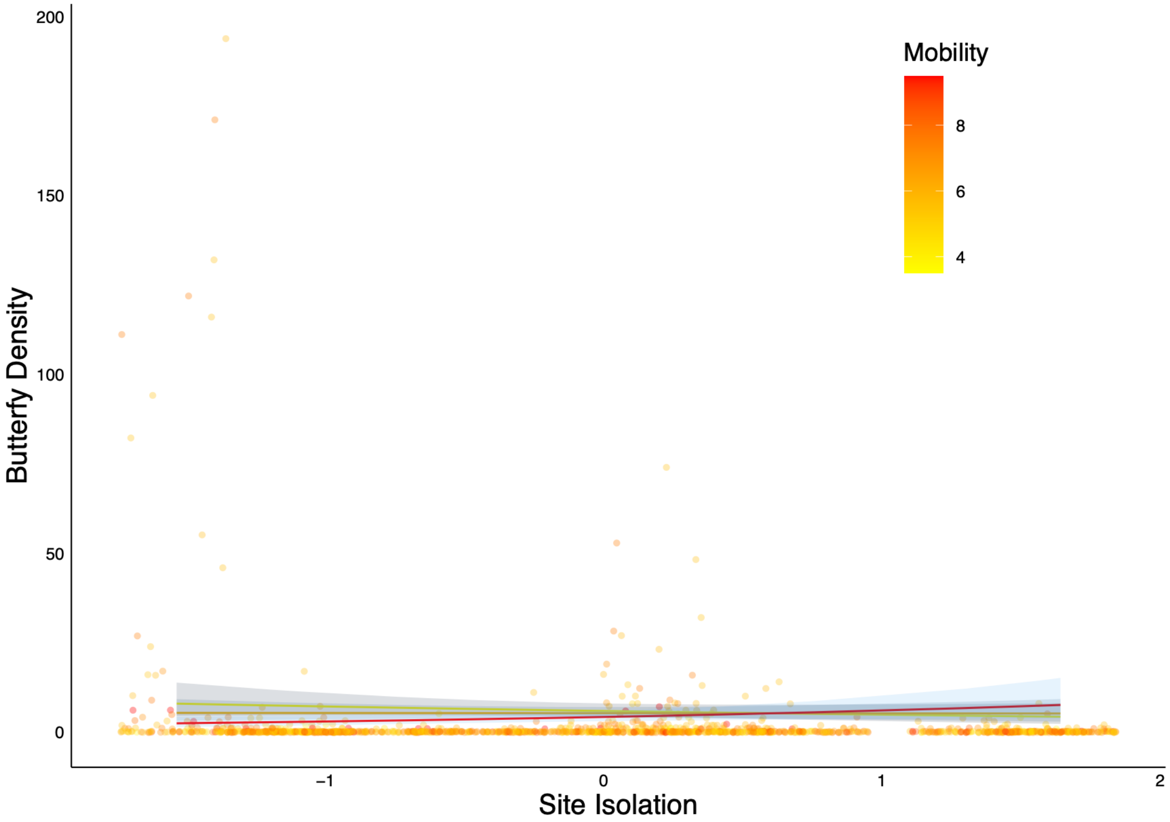
3.8.1 Appendix 3.1

Species Name	**Mobility Score**
Amblyscirtes vialis	3.71
Callophrys polios	3.81
Erynnis lucilius	4
Callophrys niphon	4.2
Erynnis icelus	4.27
Lethe eurydice	4.29
Polites origenes	4.5
Satyrium titus	4.54
Hesperia leonardus	4.73
Polites themistocles	4.73
Thorybes pylades	4.79
Euphyes vestris	4.97
Erynnis juvenalis	5
Polites mystic	5.1
Lethe anthedon	5.12
Cercyonis pegala	5.24
Cupido comyntas	5.34
Pieris oleracea	5.36
Boloria selene	5.37
Glaucopsyche lygdamus	5.37
Boloria bellona	5.42
Phyciodes cocyta	5.43
Coenonympha tullia	5.47
Celastrina lucia	5.5
Thymelicus lineola	5.5
Phyciodes tharos	5.61
Polygonia progne	5.96

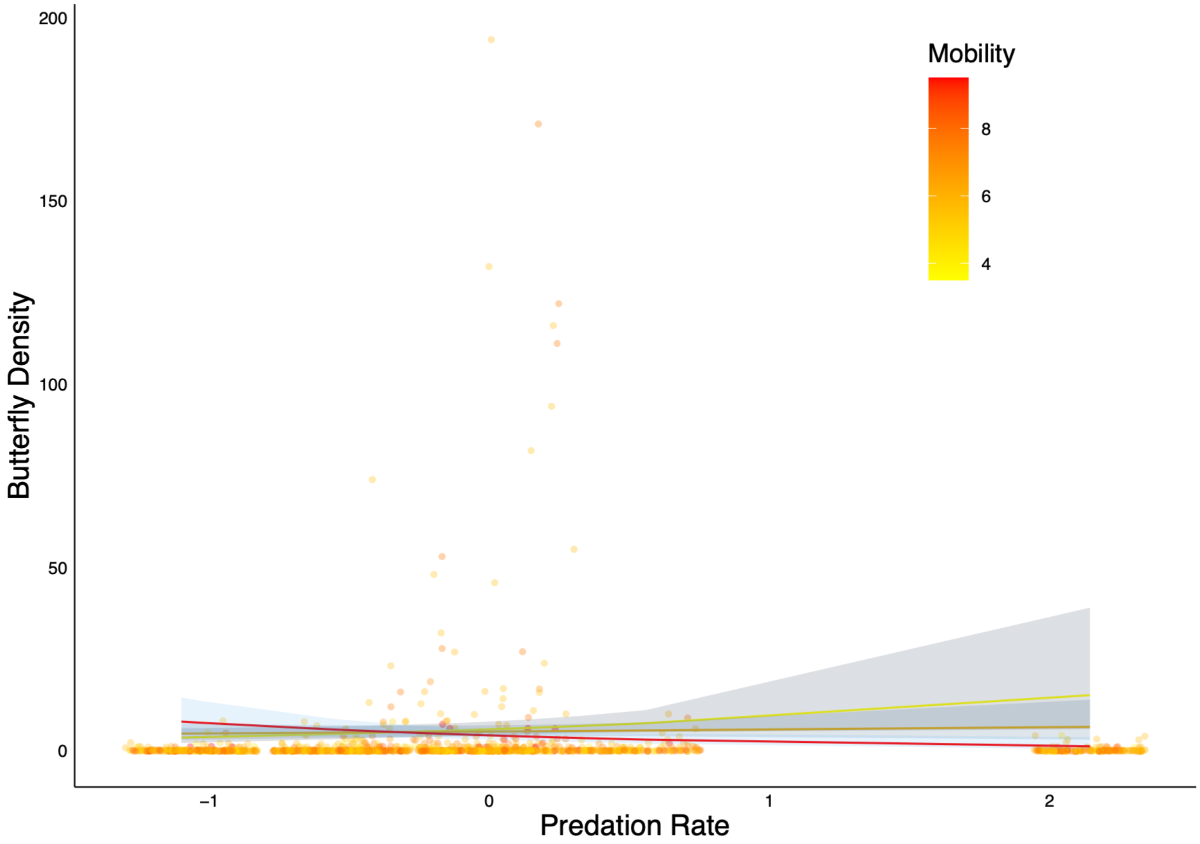
Speyeria aphrodite	6.54
Limenitis archippus	6.81
Limenitis arthemis arthemis	6.97
Papilio cresphontes	7
Speyeria atlantis	7
Speyeria cybele	7.1
Nymphalis antiopa	7.19
Colias philodice	7.33
Pieris rapae	7.56
Papilio polyxenes	7.67
Papilio canadensis	7.79
Vanessa virginiensis	8.09
Vanessa atalanta	8.31
Vanessa cardui	8.63
Danaus plexippus	9.5

Appendix S3.1: Table 1. List of all observed butterfly species and their associated mobility scores (Burke et at. 2011).

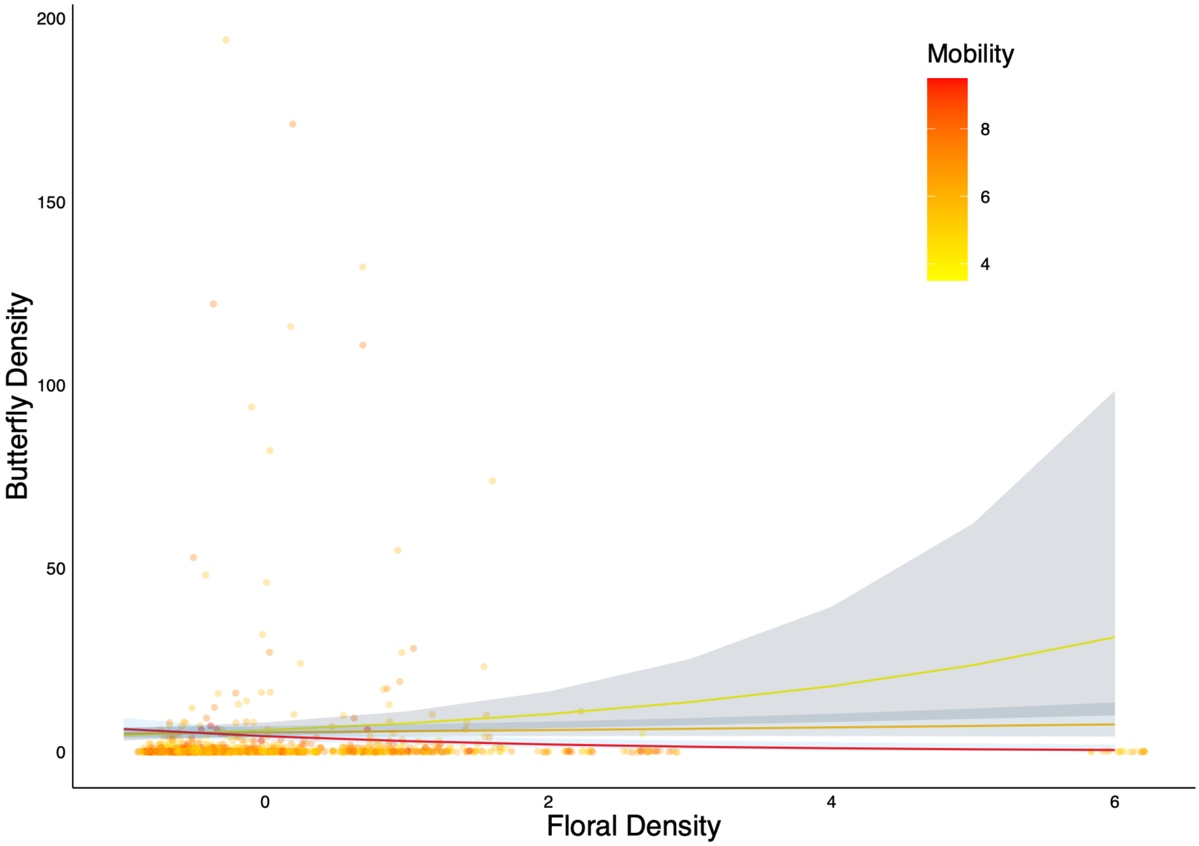
3.8.2 Appendix 3.2



Appendix S3.2: Figure S1. Predicted densities of weak (3.5; yellow), intermediate (5.5; orange), and strong (9.5; red) dispersers in sites along an isolation gradient. Grey are 95% confidence intervals around fitted lines. Figure is overlayed with raw data.



Appendix S3.2: Figure S2. Predicted densities of weak (3.5; yellow), intermediate (5.5; orange), and strong (9.5; red) dispersers in sites along a gradient of predator attack rates. Grey bands are 95% confidence intervals around fitted lines. Figure is overlayed with raw data.



Appendix S3.2: Figure S3. Predicted densities of weak (3.5; yellow), intermediate (5.5; orange), and strong (9.5; red) dispersers in patches along a gradient of site-level floral density. Grey bands are 95% confidence intervals around fitted lines. Figure is overlayed with raw data.

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Chapter 4: Identifying factors driving the "urban biodiversity gap" in butterfly metacommunities

4.1 Abstract

Urbanization reduces biodiversity and accelerates biotic homogenization, including among pollinators that provide vital ecological services in natural and human-dominated systems. However, questions remain concerning urban pollinator ecology and conservation, particularly: to what extent does pollinator diversity decline across urban landscapes, and what drives these patterns? I investigated the impacts of local and landscape characteristics on community diversity in four increasingly urban butterfly metacommunities. I collected data on butterfly diversity, butterfly host plant richness, flowering plant richness, and impervious surface area in the landscape. I asked how alpha and beta diversity change among increasingly urban metacommunities, and what drives these changes. Alpha and beta diversity decreased in urban metacommunities compared to a natural peri-urban metacommunity, and there was little variation in both alpha and beta diversity among urban metacommunities. Host plant richness increased butterfly diversity, but floral richness was correlated with reduced diversity, suggesting that many people are planting gardens that are rich in diversity but low in diversity of plants that support butterflies. In contrast, butterfly community dissimilarity was driven by both local and landscape scale factors. Dissimilarities in site area and landscape impervious surface area drove overall dissimilarity, while these factors in addition to host and floral communities drove butterfly turnover (loss of species/abundance with replacement) and nestedness (loss of species/abundance without replacement). In contrast to previous work showing higher levels of diversity in landscapes at intermediate and low levels of urbanization, suburban and urban metacommunities supported similarly low levels of butterfly diversity. However, my findings

demonstrate that even small sites can support diverse butterfly communities if they contain rich assemblages of butterfly host and nectar plants. Species are being filtered out of landscapes with large amounts of impervious surface area, suggesting that both local and landscape scale conservation measures are needed to support urban butterflies.

4.2 Introduction

As the proportion of Earth's surface covered by urban landscapes continues to grow (Liu et al. 2020), it is becoming increasingly urgent to identify factors that limit urban biodiversity and how to mitigate them (Ramalho and Hobbs 2012, Brum et al. 2023). Urbanization creates novel conditions by introducing impervious surface area that raises temperatures (Ziter et al. 2019, Corsini et al. 2021), creating light, noise, air, and water population (Grimm et al. 2008, Lokatis et al. 2023), and increasing interactions between native species and humans/human-associated species (Fardell et al. 2023, Li et al. 2023), among others (Johnson and Munshi-South 2017, Des Roches et al. 2021). Many species respond negatively to urbanization, causing widespread losses of native biodiversity (Aronson et al. 2014, Fenoglio et al. 2020, Liang et al. 2023). While some species are relatively successful in urban systems (Kark et al. 2007, Banaszak-Cibicka and Żmihorski 2012, Martin and Bonier 2018), shifts in conditions, such as growing populations of invasive competitors, can cause population declines among other species (Colléony and Shwartz 2020). Patterns of expansion among species more suited to urban landscapes and declines among other, often rarer, species, contribute to biotic homogenization within and among cities (McKinney 2006, Groffman et al. 2014), although some studies have suggested such changes are limited at low or moderate levels of urbanization (Wenzel et al. 2020, Fidino et al. 2021).

Many factors limit biodiversity in cities, and these factors can differ across spatial scales (Egerer et al. 2020, Piano et al. 2020) and among taxa (Faeth et al. 2011, Piano et al. 2017). In urban landscapes, semi-natural areas are rare and often small (Beninde et al. 2015, Schütz and Schulze 2015); highly managed patches with low structural diversity and limited resources are more common (i.e. lawns and parks dominated by turfgrass; Aronson et al. 2017, Aznarez et al. 2022). Plant communities are directly modified by humans (Faeth et al. 2011), while other communities are dominated by invasive species (Shochat et al. 2010, Gaertner et al. 2017). At larger spatial scales, many aspects of the urban landscape filter sensitive species (Laforge et al. 2019, Callaghan et al. 2021), such as increased impervious surface area that reduces habitat and creates barriers to movement (Jha and Kremen 2013, Braaker et al. 2014, Martin et al. 2023). In spite of these constraints, urban gardens and other city greenspaces have the potential to act as refuges for biodiversity (Lewis et al. 2019), with cities sometimes providing essential habitat for conservation (Soanes and Lentini 2019). However, the extent to which cities can support biodiversity is still unclear for many regions and taxa (Shwartz et al. 2014, Collins et al. 2021).

When examined together, alpha and beta diversity can offer complementary perspectives on the drivers of urban diversity, species loss, and community homogenization across scales (La Sorte et al. 2014, Beninde et al. 2015, Medeiros et al. 2018, Silva et al. 2023). It is particularly valuable to study these facets of diversity concurrently as they have often been shown to have contrasting drivers (Kessler et al. 2009, Fournier et al. 2017, Neilan et al. 2019), and the analysis of both alpha and beta may be necessary to develop conservation solutions to diversity loss (Jones et al. 2022, Boinot and Alignier 2023). Metacommunity ecology, the study of networks of habitat patches connected by dispersal, offers an excellent framework for examining both alpha and beta diversity, and disentangling effects of urbanization across spatial scales (Wang and Loreau 2016, Thompson et al. 2020, Swan et al. 2021).

In this study, I tested whether butterfly diversity varied among increasingly urban metacommunities, and what factors drove reductions in diversity between urban butterfly metacommunities and a nearby natural butterfly metacommunity. I surveyed four metacommunities, ranging from a peri-urban greenbelt to a densely urban area, composed of sites ranging from highly managed parks, to gardens, to semi-natural areas. I expected that alpha and beta diversity would be highest in the greenbelt metacommunity, decreasing in metacommunities closer to the urban center. I predicted that alpha diversity would increase with increases in patch quality (site area, host plant richness, and floral richness), but decrease as the landscape becomes increasingly resistant to movement due to increasing impervious surface. I predicted that beta diversity would increase with increasingly dissimilar site characteristics (area and host plant communities), as different species are able to exploit resources in small vs large sites, and use different host plants. I did not expect the floral generalist butterfly community to change with increasing floral community dissimilarity. I predicted that increasing dissimilarity in impervious surface area would increase butterfly community dissimilarity, as the landscape filters out poorer dispersers.

4.3 Methods

4.3.1 Study system

This study was conducted in the city of Ottawa, Canada (Figure 4.1), a large metropolitan area with over 1 million residents. A large protected greenbelt surrounds the suburban and urban core (Gordon and Scott, Richard 2008), containing forests, wetlands, grasslands, and agriculture areas. I identified a metacommunity of 10 grassland sites in the peri-urban greenbelt (hereafter referred to as Greenbelt), as well as three 10-site metacommunities along a suburban to urban gradient within the core of Ottawa (Figure 4.1). The location of these ‘city’ metacommunities was determined in part by the location of volunteers who allowed us to survey the front and/or backyards of their homes (Gerner and Sargent 2022). I identified six private properties for survey in each of the suburban Centrepointe neighborhood (Suburban), the urban Westboro neighborhood (Urban), and the central urban Sandy Hill/Overbrook neighborhood (Central; Figure 4.1). I also surveyed one community garden and three urban parks in each city metacommunity. At least one park in each of the city metacommunities was semi-natural, but others were intensively managed, with short grass and little plant diversity.

4.3.2 Butterfly and plant surveys

I identified a path for a 200m butterfly and plant survey transect at each site large enough to accommodate it. This included all Greenbelt sites, as well as some of the park and community garden sites in the Suburban/Urban/Central metacommunities. I conducted all butterfly sampling by walking steadily along the transect for 20 minutes, and identifying butterflies within 5m of the transect in every direction (Pollard 1977). Some sites, particularly those on private property, were too small for a transect. For these small sites, I walked continuously around the site at a steady pace for 20 minutes, identifying all butterflies within the site boundaries. I conducted three rounds of surveys across all sites from mid June to mid September 2022, beginning later than anticipated due to a destructive extreme weather event (derecho) in late May 2022 (Green-Mignacca et al. 2023).

To survey flowering plant communities in larger sites, I identified all flowering plants within 5m to either side of the butterfly survey transect. For small sites without a transect, all flowering plants in the site were identified. Plants were identified to species when possible.

Flowering plants were separated into two categories: butterfly host plants (Hall, Peter W. et al. 2014), and other flowering plants.

4.3.3 Landscape metrics

I characterized the landscape by calculating site area and the amount of impervious surface area around each site. I determined site area by drawing polygons around the margins of each site in ArcGIS Pro (ESRI 2023). For some urban sites both front and backyards were surveyed but were disconnected by impervious landcover (houses and driveways); in these cases I drew separate polygons and summed the area. I calculated the amount of impervious landcover within 250 meter buffer zones around each site in ArcGIS Pro using a high resolution (20cm) map of impervious surface obtained from the City of Ottawa. For single sites with two polygons (some urban/suburban houses with front and backyards) I created the buffer around the backyard polygon.

4.3.4 Statistical analysis

I conducted statistical analyses using R (R Core Team 2023). All dependent variables were scaled and centered using the scale() function in base R.

To determine whether butterfly metacommunities became increasingly homogenized with urbanization, I compared Bray-Curtis (abundance-based) and Jaccard (binary) dissimilarity among metacommunities. Both indices range from 0 to 1, with 0 indicating that communities are identical, and 1 indicating that there are no shared group members between communities. I used the vegan package to calculate a pairwise distance matrix for both Bray-Curtis and Jaccard dissimilarities, for all pairs of unique sites/sampling round combinations within each metacommunity (Oksanen et al. 2022). Any site/round combinations with no observations was excluded from this analysis. I fit a PERMANOVA with the beta-diversity distance matrices as the dependent variable, and with metacommunity, survey round, and their interaction as predictor variables. I included site as a strata variable so that any permutations would be restricted to occur within the level of site. Next, I used the pairwise distance matrices to compare beta diversity between pairs of metacommunities with a PERMANOVA from the pairwiseAdonis package (Arbizu 2020). I modeled pairwise beta-diversity as the dependent variable, included metacommunity, survey round, and their interaction as predictor variables, and specified site as a strata variable. While I found some evidence of heterogeneity among group variances, PERMANOVA is robust to heterogeneity of variances in cases of balanced design.

To investigate whether butterflies observed in suburban metacommunities were a subset of the Greenbelt species (nested), or were unique species assemblages (turnover), I used the betapart package (Baselga et al. 2023). I calculated nestedness and turnover using both Bray-Curtis and Jaccard dissimilarities among the four metacommunities.

I examined the drivers of alpha diversity by calculating Hill numbers for each site (observations pooled across sampling rounds; Li 2023). I modeled hill numbers as the dependent variable in a linear model (Bates et al. 2023), with host richness, floral richness, included site area, impervious surface area, and metacommunity identity as independent variables. Non-significant effects were removed from the model based on their importance to our biological hypothesis, and their impact on model fit as assessed by AIC scores ("AIC" command in Base R). We tested the assumptions of this model, including independence and normality of residuals, and no assumptions were violated.

I calculated pairwise Bray-Curtis and Jaccard dissimilarity metrics for all pairwise sites, and partitioned the turnover and nestedness components using the betapart package. I calculated Jaccard dissimilarity, turnover, and nestedness for host plant and floral communities at each pair of sites. I calculated pairwise euclidean distances for site area and impervious surface area, and created a variable that identified the combination of metacommunities in each pairing (Greenbelt-Greenbelt, Greenbelt-Suburban, etc.). I constructed six linear models with each of Bray-Curtis and Jaccard dissimilarity, turnover, and nestedness as a dependent variable, and included host dissimilarity, floral dissimilarity, site area, impervious surface area, and metacommunity pairing as independent. Non-significant effects were removed from the model based on their importance to our biological hypothesis, and their impact on model fit as assessed by AIC scores.

4.4 Results

I identified 25 butterfly species and counted 1047 individuals, with over half of the individuals counted in the Greenbelt metacommunity (595), 118 in the Suburban metacommunity, 193 in the Urban metacommunity, and 141 in the Central metacommunity. Butterfly species richness per site ranged from 5 to 10 with a mean of 7.3 in the Greenbelt, 1 to 5 with a mean of 2.2 in Suburban, 1 to 4 with a mean of 2.6 in Urban, and 1 to 4 with a mean of 1.8 in Central. Butterfly abundance per site ranged from 18 to 153 with a mean of 59.5 in the Greenbelt, 4 to 23 with a mean of 11.8 in Suburban, 2 to 75 with a mean of 19.3 in Urban, and 3 to 71 with a mean of 14.1 in Central. The most abundant butterfly species in the Greenbelt was the invasive European skipper (*Thymelicus lineola*) with 298 observations, while the invasive cabbage white (*Pieries rapae*) was most abundant in Suburban, Urban, and Central, with 95, 130, and 102 observations, respectively. The second most abundant species in all metacommunities was native: the common ringlet (*Coenonympha tullia*) in the Greenbelt, Suburban, and Urban, with 152, 12, and 34 observations respectively; and the clouded sulphur (*Colias philodice)* in Central with 20 observations.

Host plant richness per site ranged from 5 to 10 with a mean of 8.2 in the Greenbelt metacommunity, from 2 to 9 with a mean of 4.8 in the Suburban metacommunity, from 0 to 15 with a mean of 4.8 in the Urban metacommunity, and from 0 to 10 with a mean of 5 in the Central metacommunity. Flowering plant richness per site ranged from 17 to 26 with a mean of 20.8 in the Greenbelt metacommunity, from 2 to 42 with a mean of 24.8 in the Suburban metacommunity, from 6 to 45 with a mean of 21.5 in the Urban metacommunity, and from 8 to 53 with a mean of 26.4 in the Central metacommunity. Plant communities differed between the Greenbelt and urban metacommunities, with more native or invasive species present in the Greenbelt (i.e. fleabane, *Erigeron hyssopifolius*), and more ornamental and food plants present in the urban metacommunities (i.e. *Geranium sp.*). Site area and impervious surface area in the landscape ranged widely within and among metacommunities (Appendix S4.1: Figure S1 and Figure S2).

Butterfly community composition varied among metacommunities (Figure 4.2). Butterfly community dissimilarity changed with sampling round, and with metacommunity among sampling rounds, but these factors explained a much smaller proportion of the variance than metacommunity alone (Table 4.1). When pairs of metacommunities were compared, dissimilarity differed significantly by metacommunity and round, with the interaction between metacommunity and round significant in some pairings (Appendix S4.2: Table S1 and Table S2). Pairings including the Greenbelt metacommunity explained 34% or more of the variance, with most variance explained by the metacommunity term, while other pairings explained 11% or less of the variance. There was more turnover than nestedness among the metacommunities for both Bray-Curtis and Jaccard indices (Bray-Curtis dissimilarity = 0.763, turnover = 0.491, nestedness = 0.273; Jaccard dissimilarity = 0.802, turnover = 0.619, nestedness = 0.183).

Alpha diversity was significantly higher in the Greenbelt compared to the three city metacommunities (Table 4.2; adjusted $R^2 = 0.65$). Host plant richness increased butterfly community diversity, while increased floral richness was associated with lower butterfly community diversity. To better understand the relationship between the host plant and floral plant community I used a simple linear regression of host plant richness on floral richness; there was no significant relationship.

Bray-Curtis and Jaccard dissimilarity increased with increasing dissimilarity in impervious surface area, while dissimilar site area increased only Bray-Curtis dissimilarity (Table 4.3). There was significantly more Jaccard dissimilarity among Greenbelt sites compared to other metacommunities, although Bray-Curtis dissimilarity was not significantly different.

Bray-Curtis and Jaccard turnover increased with turnover in flowering plants (Table 4.4). Host turnover increased Bray-Curtis turnover, and was retained in the Jaccard model although it was not significant as it improved model fit (AIC score of 455 versus 484). Dissimilarity in impervious surface area also increased Bray-Curtis turnover. Butterfly community turnover was higher in the Greenbelt than other metacommunities.

Host nestedness and site area dissimilarity increased Bray-Curtis nestedness, which was highest in two of the city metacommunities (Table 4.5). Jaccard nestedness increased with dissimilarity in impervious surface area between sites, and host nestedness was retained in the model due to improved model fit (AIC score of 343 vs 346). The Greenbelt metacommunity was significantly less nested than other metacommunities. The Jaccard nestedness model should be interpreted with caution due to the small R^2 value (adjusted $R^2 = 0.06$).

4.5 Discussion

While previous work has examined butterfly communities in urban environments, how butterfly diversity varies across spatial scales and degrees of urbanization, and what drives this variation, is poorly understood. By using a unique system of one natural and three increasingly urban metacommunities, I was able to demonstrate an 'urban biodiversity gap' for butterfly communities that persists across an urban landscape. I identified multiple drivers of biodiversity loss across scales, and suggest actions that can help close the diversity gap for urban butterflies.

Diversity was consistently higher in the Greenbelt compared to the city metacommunities, but there was little variation in alpha and beta diversity among city metacommunities. While pairwise community dissimilarities were significantly different between all metacommunities, R^2 values for comparisons between city metacommunities were small, with particularly small values for the metacommunity term in those models. City sites had lower alpha diversity, and city metacommunities had lower beta diversity and turnover, consistent with other studies reporting biotic homogenization in urban systems (Knop 2016, Deguines et al. 2016, Colléony and Shwartz 2020). These results indicate that, contrary to previous work showing higher biodiversity in low/intermediate vs highly urban landscapes (i.e. Wenzel et al. 2020), all regions of the city supported similarly low butterfly diversity. As all sites were sampled for butterflies for 20 minutes, small city yards were more thoroughly surveyed, in a relative sense, than city parks and Greenbelt sites, which were sometimes too expansive to survey comprehensively. Greenbelt and semi-natural city sites had higher butterfly diversity than city yards, and highly managed city park sites had uniform habitat structure (e.g. extensive areas of mowed lawns) that reduced the likelihood of missing difficult-to-detect species. While I acknowledge differences in sampling intensity, this has led to a more conservative estimation of diversity differences between small managed and large semi-natural sites.

Surprisingly, a high proportion of dissimilarity Bray-Curtis and Jaccard similarity among the metacommunities was due to species turnover, indicating that, while more homogenized than the Greenbelt, urban metacommunities hosted species that were distinct from those I detected in the Greenbelt. While some butterflies may be better suited to urban environments than others due to generalist life history strategies, thermophilic traits, and stronger mobility (Franzén et al. 2020, Callaghan et al. 2021, Piano et al. 2023), I don't expect any native species to be better suited to an urban environment than a natural environment. In contrast, I expected the invasive *Pieris rapae* to thrive in the city metacommunities as it uses introduced food plants as hosts. High abundances of *P. rapae* in the city metacommunities, compared to its relative rarity in the Greenbelt, likely drove the trend in Bray-Curtis (abundance) turnover. Five species were unique to the city metacommunities: two large and highly mobile species (the black swallowtail *Papilio polyxenes* and the morning cloak *Nymphalis antiopa*), and three small, less mobile species (the least skipper *Ancyloxypha numitor*, the silver-bordered fritillary *Boloria selene*, and the banded hairstreak *Satyrium calanus*). While individuals from the highly mobile species may have dispersed into the city from peri-urban greenbelt sites outside of our Greenbelt metacommunity, this is unlikely for less mobile species, suggesting that populations of these species can persist in city sites. This also indicates that there is room for restoration in the Greenbelt, which hosts lower butterfly and plant richness than a nearby protected area (Gordon and Kerr 2022), but as a relatively protected natural system, has the potential to host a more diverse butterfly metacommunity.

Host plant richness increased alpha diversity among butterfly communities, while butterfly abundance and richness declined when host plants were lost from communities without replacement (nestedness). This is consistent with findings from other urban and natural systems (Menéndez et al. 2007, Pendl et al. 2022), and suggests that an overall increase in host plant richness in urban sites will significantly increase urban butterfly diversity. Host plant turnover increased butterfly community turnover, reflecting that specific host plants are necessary for the survival of the larval stage of each butterfly species.

Without host plants that enable butterfly species to overwinter, butterflies cannot maintain populations in a site and must recolonize the site each year. Butterfly species present in few sites in a metacommunity, such as semi-natural parks, could maintain populations in private yards and community gardens, as well as other metacommunities, if their host plants are introduced. Although most butterflies use a broad range of host plants, many of these may be species that are not traditionally planted in public urban spaces or gardens (i.e. native asters, *Symphyotrichum sp.*), or are considered weeds and removed (i.e. white clover; *Trifolium repens*). The two butterfly species more commonly observed in the city sites included cabbage whites (*Pieris rapae*) and common ringlets (*Coenonympha tullia*), both of which feed on host plants that are common in the city (*Brassica* and grass species, respectively). Other species found in city sites also feed on common urban plants, including: the least skipper (*Ancyloxypha numitor*) and European skipper (*Thymelicus lineola*) which feed on grasses, the silver-bordered fritillary (*Boloria selene*) which feeds on *Viola* species, the clouded sulphur (*Colias philodice*) which feeds on *Fabaceae* species, and the monarch (*Danaus plexippus*) which feeds on milkweed species. While butterfly diversity may not always be constrained by host plant diversity (Hawkins and Porter 2003, Tsang and Bonebrake 2017), in this system depauperate host plant communities limited butterfly diversity. There is an opportunity to increase pollinator diversity through the active management of host plant communities, and to the extent that society values urban pollinators, host plants should be further integrated into urban plant communities.

In contrast to predictions and previous work in natural butterfly communities (Blaauw and Isaacs 2014, Gordon and Kerr 2022), floral richness was negatively associated with butterfly alpha diversity. Positive relationships between flowering plant and butterfly diversity have also been shown in urban systems, but these studies often exclude plants that are not identified as nectar sources (Lange-Kabitz et al. 2021, Pendl et al. 2022), which was not done in this study. Urban greenspaces support novel plant species assemblages, with many species selected by humans based on socioeconomic factors, as opposed to through natural ecological processes (Knapp et al. 2012, Cavender-Bares et al. 2020, Chang et al. 2021). Some sites in our system with particularly high richness, such as community gardens and yards, were largely composed of crop or ornamental plants. These results suggest that those urban sites with high overall flowering plant richness may not include enough beneficial plants to support diverse butterfly communities. My results do not necessarily imply that crop and ornamental plants should be removed from gardens and other semi-natural urban areas, but that active planting of hostplants and nectar-producing plants could exert a strongly positive effect on pollinator diversity. Educating individuals and organizations that determine plant assemblages, including gardeners and park managers, and encouraging them to plant more nectar-producing plants, should help reduce the urban biodiversity gap for butterflies (Majewska and Altizer 2020, Tew et al. 2022). Future urban butterfly studies should include all flowering plants in their analyses, as these results can inform conservation actions. While nectar production in urban plant assemblages has been previously considered (Tew et al. 2021, 2022), I could not test for effects of floral and host plant abundance on urban butterfly diversity, and such effects require further investigation.

Floral turnover was the only significant predictor of the Jaccard butterfly turnover model. This finding is surprising as many butterfly species are floral generalists; however, this pattern may be driven by a tendency for rich urban floral communities to support a single, diverse and commonly-planted butterfly host plant genus (*Brassica*). There was no correlation between flowering plant richness and host plant richness, suggesting that gardeners planting rich plant assemblages may not be including butterfly host plants. The exception in some cases was the *Brassica* genus, containing many cultivated food plants that host the invasive cabbage white butterfly *Pieris rapae*. *Brassica* crop species were present in rich plant communities in seven community gardens and private yards, while we found *Brassica* plants in only one Greenbelt site (*B. rapae*). The association between *Brassica* and *P. rapae*, a rare butterfly in the Greenbelt but the most abundant species in the city, may have driven this pattern of community turnover. Alternatively, while many butterfly species are floral generalists, some have been shown to exhibit preferences for specific taxa (Hardy et al. 2007, Stefanescu and Traveset 2009), with pollinators shown to preferentially visit a limited number of species in an urban system (Lowenstein et al. 2019). These results underline the importance of planting flowering plants that produce nectar and are preferred by butterflies (i.e. Hall, Peter W. et al. 2014).

In contrast to previous studies, site area did not impact alpha diversity (Majewska and Altizer 2020), although dissimilarity in site area did increase Bray-Curtis dissimilarity and nestedness. In natural systems I would expect larger sites to support larger populations and more diverse ecological niches (Kohn and Walsh 1994, Griffen and Drake 2008), but large urban sites were often highly managed parks with low host plant richness and floral resource availability.

Urban sites are also unusual as property lines may not fragment habitats for species (Belaire et al. 2014), so that the site area measured as within the boundaries of a distinct green space may be a poor estimator of useable habitat area. Still, it seems that only a subset of the butterfly community, likely those with weedy host plants that grow in highly managed parks, can exploit resources in these sites. Cities should take advantage of parks and greenspaces to support butterflies by planting nectar and host plants. By managing their properties together, private landowners can also create larger patches of connected habitat across multiple yards (Goddard et al. 2010, Belaire et al. 2014).

The amount of impervious surface area in the landscape did not impact butterfly alpha diversity, in contrast to expectations and previous studies (Kurylo et al. 2020). However, similar to previous work (Merckx and Van Dyck 2019), dissimilarity in impervious surface area between sites increased butterfly community dissimilarity, affecting both turnover (Bray-Curtis) and nestedness (Jaccard). This suggests that while some species may be more abundant in highly urbanized sites, species richness overall declines. These findings are consistent with a natural butterfly metacommunity, where alpha diversity did not vary with site connectivity due to an increased abundance of strong dispersers in isolated sites where poor dispersers were often absent (Gordon and Kerr 2022, Gordon et al. 2024). This suggests that, while some species are able to exploit resources in an intensely urban matrix, urban affinity likely varies with species traits like dispersal ability, so that trait diversity is homogenized with increasing urbanization (Marcacci et al. 2021, Pla-Narbona et al. 2022, Piano et al. 2023). Indeed, many butterfly species we observed in city sites, including monarchs (*Danaus plexippus*), clouded sulphurs (*Colias philodice*), and cabbage whites (*Pieris rapae*) are strong dispersers, although others (i.e. least skipper *Ancyloxypha numitor*; common ringlet *Coenonympha tullia*; eastern-tailed blue *Cupido* *comyntas*) are notably poor dispersers (Burke et al. 2011). Butterflies, and pollinators more generally, may also avoid crossing areas of impervious surfaces like roads (Andersson et al. 2017, Dániel-Ferreira et al. 2022), and a species' willingness to move through impervious areas would strongly affect their distribution in cities. More work is needed to understand how butterflies with different dispersal abilities, willingness to cross impervious surfaces, as well as other traits like thermal position (Ednie and Kerr 2024), interact with the urban matrix, and how this may determine diversity and species composition in urban habitat fragments.

By identifying characteristics of urban environments that limit biodiversity, and using them to inform urban conservation, there is strong potential to transform cities into more effective refuges for diversity (Soanes and Lentini 2019, Villaseñor et al. 2020, Deschamps-Cottin et al. 2023), particularly for pollinators (Lewis et al. 2019, Baldock et al. 2019). Here, I used analyses of both alpha and beta diversity to identify contrasting drivers of the 'urban biodiversity gap' for butterflies. I find that, while impervious surface area filters species out of highly urbanized landscapes, planting rich communities of host and nectar-producing plants in small gardens can increase butterfly diversity, pointing to the potential conservation value of private and community gardens in this system. Conserving butterflies, a group of ecologically important species that can help connect people to nature, is increasingly important and feasible in urban systems.

4.6 Figures

Figure 4.1

Map of study site locations in Ottawa, Canada, with impervious surface area shown in grey. Greenbelt metacommunity sites are shown in green, Suburban metacommunity sites are shown in yellow, Urban metacommunity sites are shown in light orange, and Central metacommunity sites are shown in dark orange.

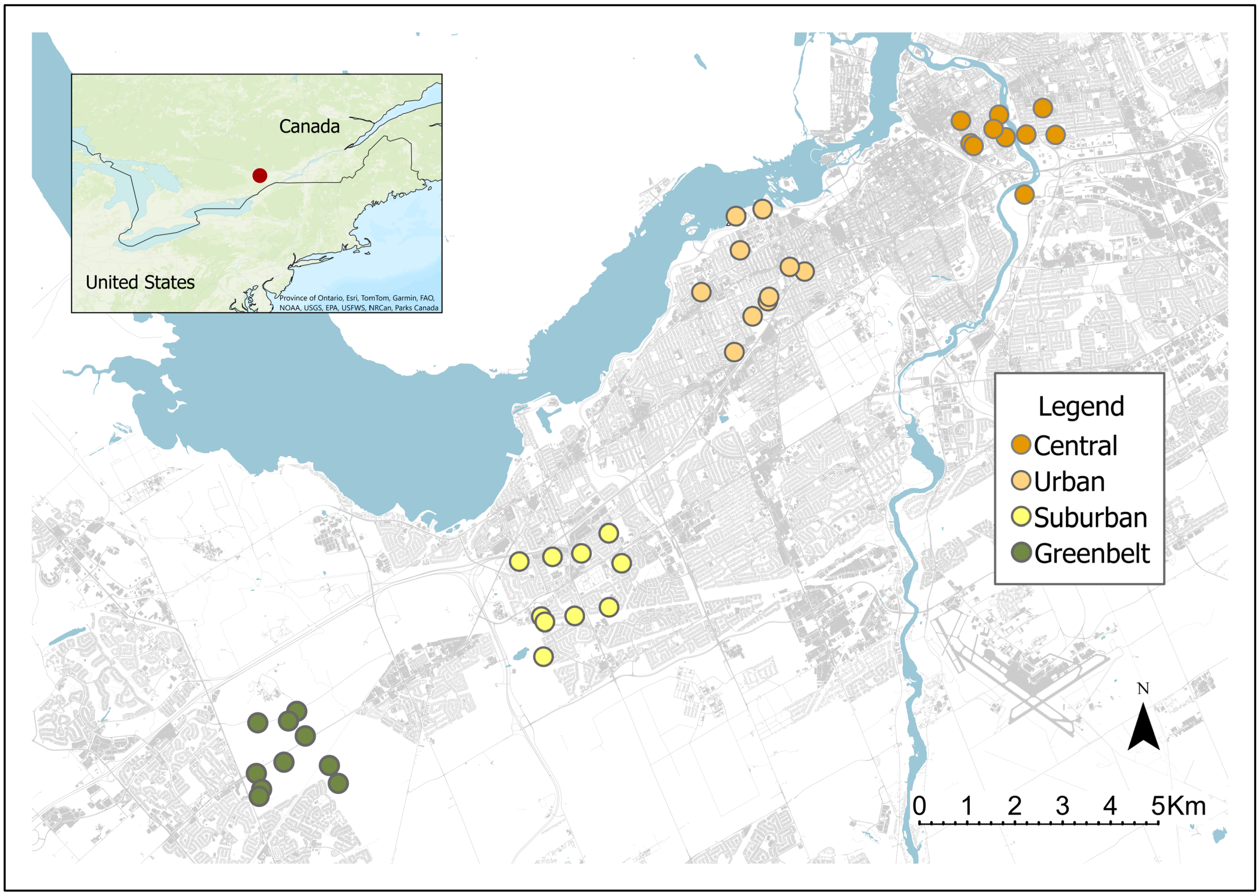
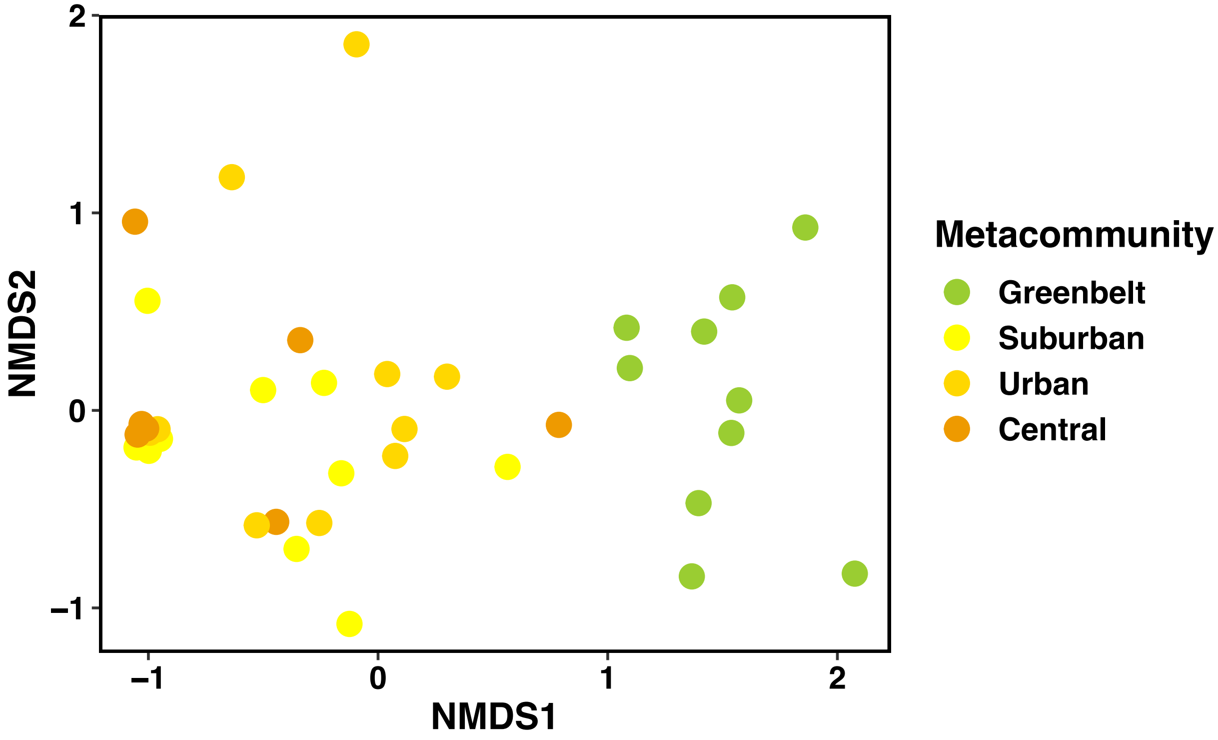


Figure 4.2

Ordination of butterfly diversity at 40 sites within the four metacommunities: Greenbelt (green), Suburban (yellow), Urban (light orange), and Central (dark orange). Each point represents one site. Non-metric multidimensional scaling (NMDS) values were calculated with Bray-Curtis dissimilarity coefficients (Vegan). NMDS1 corresponds to the dimension explaining the greatest variance, while NMDS2 corresponds to the dimension explaining the second greatest variance. The closer that sites are plotted to each other, the more similar their community compositions. To better visualize data, the jitter() function in ggplot2 was used to separate overlapping points (Wickham et al. 2023).



4.7 Tables

Table 4.1

R^2 values and associated statistics from the Bray-Curtis (a) and Jaccard (b) PERMANOVA models of dissimilarity among pairs of sites within metacommunities.

a) Bray-Curtis dissimilarity

Effect	DF	SumofSqs	R^2	F.Model	*p*
Metacommunity	3	8.155	0.263	13.860	0.001
Round	1	1.182	0.038	6.029	0.001
Metacommunity:Round	3	1.514	0.049	2.574	0.001
Residual	103	20.202	0.651		
Total	110	31.054	1		

b) Jaccard dissimilarity

Effect	DF	SumofSqs	R^2	F.Model	*p*
Metacommunity	3	7.696	0.280	15.144	0.001
Round	1	1.361	0.050	8.033	0.001
Metacommunity:Round	3	0.976	0.036	1.921	0.005
Residual	103	17.447	0.635		
Total	110	27.479	1		

Table 4.2

Estimates and associated statistics from the linear model of butterfly alpha diversity. The adjusted R^2 of the model is 0.65.

Effect	**Estimate**	**SE**	***t* Value**	***p***
Intercept	1.713	0.234	7.320	<0.000
Host richness	0.373	0.134	2.776	0.009
Floral richness	-0.336	0.123	-2.741	0.010
Greenbelt	1.680	0.362	4.645	<0.000
Urban	0.290	0.327	0.888	0.381
Central	-0.147	0.326	-0.452	0.654

Note: All estimates and SEs are shown as Z-scores for ease of comparison.

Table 4.3

Estimates and associated statistics from the linear models of Bray-Curtis (a) and Jaccard (b) dissimilarity among pairs of sites. Impervious SA indicates impervious surface area within a 250 meter buffer around each site. The adjusted R^2 is 0.59 for the Bray-Curtis model, and 0.36 for the Jaccard model.

a) Bray-Curtis Dissimilarity

Effect	Estimate	SE	t Value	*p*
Intercept	0.420	0.031	13.443	0.000
Site Area	0.039	0.007	5.558	0.000
Impervious SA	0.052	0.009	5.784	0.000
Greenbelt/Greenbelt	0.198	0.043	4.659	0.000
Greenbelt/Suburban	0.482	0.037	13.028	0.000
Greenbelt/Urban	0.426	0.038	11.238	0.000
Greenbelt/Central	0.450	0.039	11.477	0.000
Suburban/Urban	0.120	0.036	3.298	0.001
Suburban/Central	-0.010	0.036	-0.282	0.778
Urban/Urban	0.194	0.043	4.475	0.000
Urban/Central	0.089	0.036	2.447	0.015
Central/Central	-0.032	0.042	-0.763	0.446

b) Jaccard Dissimilarity

Effect	Estimate	SE	t Value	*p*
Intercept	0.575	0.033	17.317	0.000
Impervious SA	0.036	0.010	3.740	0.000
Greenbelt/Greenbelt	0.127	0.045	2.808	0.005
Greenbelt/Suburban	0.243	0.039	6.174	0.000
Greenbelt/Urban	0.186	0.040	4.617	0.000
Greenbelt/Central	0.261	0.042	6.253	0.000
Suburban/Urban	0.009	0.039	0.240	0.810
Suburban/Central	-0.079	0.038	-2.050	0.041
Urban/Urban	0.072	0.046	1.583	0.114
Urban/Central	-0.016	0.039	-0.404	0.686
Central/Central	-0.166	0.045	-3.706	0.000

Note: All estimates and SEs are shown as Z-scores for ease of comparison.

Table 4.4

Estimates and associated statistics from the linear models of Bray-Curtis (a) and Jaccard (b) turnover among pairs of sites. Impervious SA indicates impervious surface area within a 250 meter buffer around each site. The adjusted R^2 is 0.71 for the Bray-Curtis model, and 0.21 for the Jaccard model.

a) Bray-Curtis Turnover

Effect	Estimate	SE	t Value	*p*
Intercept	0.208	0.032	6.462	0.048
Host turnover	0.020	0.008	2.468	0.014
Floral turnover	0.047	0.009	5.191	0.000
Impervious SA	0.031	0.009	3.285	0.001
Greenbelt/Greenbelt	0.299	0.048	6.275	0.048
Greenbelt/Suburban	0.519	0.039	13.435	0.000
Greenbelt/Urban	0.449	0.040	11.301	0.000
Greenbelt/Central	0.110	0.038	-2.895	0.004
Suburban/Urban	-0.078	0.038	-2.035	0.042
Suburban/Central	0.094	0.037	-2.511	0.012
Urban/Urban	-0.089	0.047	-1.896	0.058
Urban/Central	-0.110	0.038	-2.895	0.004
Central/Central	-0.159	0.044	-3.634	0.000

b) Jaccard Turnover

Effect	Estimate	SE	t Value	*p*
Intercept	0.191	0.053	3.598	0.000
Host turnover	-0.017	0.013	-1.266	0.206
Floral turnover	0.046	0.015	3.035	0.002
Greenbelt/Greenbelt	0.485	0.078	6.202	0.000
Greenbelt/Suburban	0.261	0.063	4.141	0.000
Greenbelt/Urban	0.233	0.063	3.686	0.000
Greenbelt/Central	0.266	0.063	4.214	0.000
Suburban/Urban	-0.067	0.062	-1.093	0.275
Suburban/Central	0.003	0.063	0.055	0.956
Urban/Urban	0.049	0.078	0.628	0.530
Urban/Central	-0.062	0.063	-0.979	0.328

Central/Central	-0.124	0.072	-1.707	0.088

Note: All estimates and SEs are shown as Z-scores for ease of comparison.

Table 4.5

Estimates and associated statistics from the linear models of Bray-Curtis (a) and Jaccard (b) nestedness among pairs of sites. Impervious SA indicates impervious surface area within a 250 meter buffer around each site. The adjusted R^2 is 0.20 for the Bray-Curtis model, and 0.64 for the Jaccard model.

a) Bray-Curtis Nestedness

Effect	Estimate	SE	t Value	*p*
Intercept	0.219	0.036	6.021	0.000
Host nestedness	0.037	0.009	4.218	0.000
Site area	0.053	0.008	6.356	0.000
Greenbelt/Greenbelt	0.006	0.049	0.117	0.907
Greenbelt/Suburban	-0.045	0.043	-1.058	0.290
Greenbelt/Urban	-0.046	0.043	-1.066	0.287
Greenbelt/Central	-0.046	0.043	-1.065	0.287
Suburban/Urban	0.126	0.043	2.915	0.004
Suburban/Central	0.079	0.042	1.870	0.062
Urban/Urban	0.182	0.054	3.396	0.001
Urban/Central	0.142	0.043	3.278	0.001
Central/Central	0.121	0.050	2.434	0.015

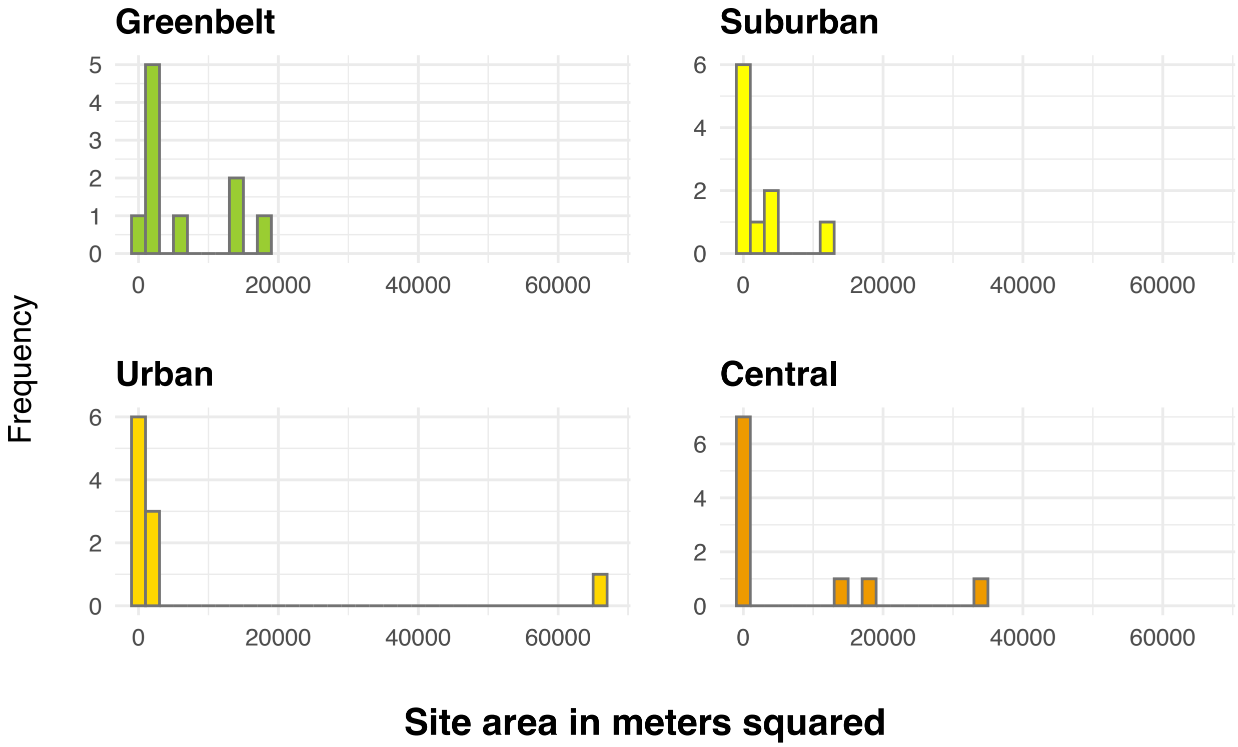
b) Jaccard Nestedness

Effect	Estimate	SE	t Value	*p*
Intercept	0.401	0.049	8.105	0.000
Host nestedness	-0.015	0.012	-1.257	0.209
Impervious SA	0.054	0.015	3.707	0.000
Greenbelt/Greenbelt	-0.266	0.068	-3.943	0.000
Greenbelt/Suburban	0.052	0.059	-0.890	0.374
Greenbelt/Urban	-0.098	0.061	-1.619	0.106
Greenbelt/Central	-0.054	0.063	-0.868	0.386
Suburban/Urban	-0.020	0.058	-0.337	0.736
Suburban/Central	-0.022	0.057	-0.376	0.707
Urban/Urban	0.005	0.072	0.076	0.940
Urban/Central	0.030	0.058	0.517	0.605
Central/Central	0.005	0.072	0.076	0.940

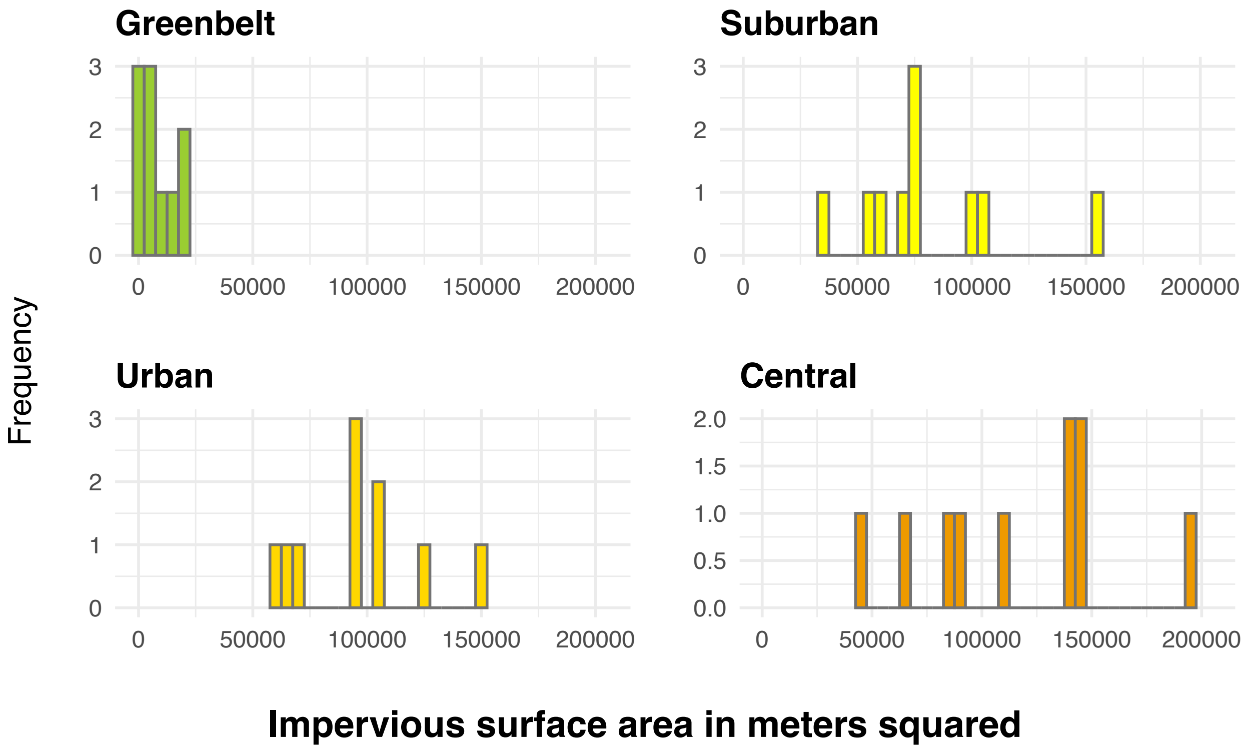
Note: All estimates and SEs are shown as Z-scores for ease of comparison.

4.8 Supplementary materials

4.8.1 Appendix 4.1



Appendix S4.1: Figure S1. Histogram of site area in meters squared for the Greenbelt metacommunity (green), the Suburban metacommunity (yellow), the Urban metacommunity (light orange), and the Central metacommunity (dark orange).



Appendix S4.1: Figure S2. Histogram of impervious surface are within a 250 meter buffer around each site, measured in meters squared, for the Greenbelt metacommunity (green), the Suburban metacommunity (yellow), the Urban metacommunity (light orange), and the Central metacommunity (dark orange).

4.8.2 Appendix 4.2

Appendix S4.2: Table S1. R^2 values and associated statistics from the Bray-Curtis PERMANOVA model comparing dissimilarity among pairs of sites within metacommunities.

Greenbelt vs. Suburban

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	5.353	0.272	24.057	0.001
Round	1	1.366	0.069	6.140	0.001
Metacommunity:Round	1	0.950	0.048	4.267	0.001
Residual	54	12.015	0.610		
Total	57	19.684	1		

Greenbelt vs. Central

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	5.738	0.295	25.710	0.001
Round	1	1.071	0.055	4.799	0.001
Metacommunity:Round	1	0.828	0.043	3.712	0.002
Residual	53	11.828	0.608		
Total	56	19.465	1		

Greenbelt vs. Urban

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	4.436	0.234	18.213	0.001
Round	1	1.289	0.068	5.291	0.001
Metacommunity:Round	1	0.593	0.031	2.434	0.006
Residual	52	12.665	0.667		
Total	55	18.982	1		

Suburban vs. Central

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	0.072	0.009	0.485	0.005
Round	1	0.622	0.074	4.206	0.003
Metacommunity:Round	1	0.194	0.023	1.311	0.165
Residual	51	7.537	0.895		
Total	54	8.424	1		

Suburban vs. Urban

Effect	**DF**	**SumofSqs**	**R2**	**F.Model**	***p***
Metacommunity	1	0.114	0.012	0.683	0.005
Round	1	0.584	0.063	3.487	0.001
Metacommunity:Round	1	0.214	0.023	1.276	0.099
Residual	50	8.374	0.902		
Total	53	9.286	1		

Urban vs. Central

Effect	**DF**	**SumofSqs**	**R2**	**F.Model**	***p***
Metacommunity	1	0.174	0.020	1.044	0.037
Round	1	0.203	0.023	1.215	0.035
Metacommunity:Round	1	0.178	0.020	1.066	0.102
Residual	49	8.186	0.936		
Total	52	8.742	1		

Appendix S4.2: Table S2. R^2 values and associated statistics from the Jaccard PERMANOVA model comparing dissimilarity among pairs of sites within metacommunities.

Greenbelt vs. Suburban

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	4.787	0.260	21.989	0.001
Round	1	1.365	0.074	6.269	0.001
Metacommunity:Round	1	0.514	0.028	2.360	0.018
Residual	54	11.755	0.638		
Total	57	18.421	1		

Greenbelt vs. Central

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	5.763	0.318	28.738	0.001
Round	1	0.999	0.055	4.981	0.001
Metacommunity:Round	1	0.722	0.040	3.601	0.002
Residual	53	10.629	0.587		
Total	56	18.113	1		

Greenbelt vs. Urban

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	4.062	0.234	18.513	0.001
Round	1	1.444	0.083	6.581	0.001
Metacommunity:Round	1	0.447	0.026	2.036	0.032
Residual	52	11.410	0.657		
Total	55	17.363	1		

Suburban vs. Central

Effect	DF	SumofSqs	R2	F.Model	*p*
Metacommunity	1	0.106	0.016	0.892	0.001
Round	1	0.364	0.055	3.076	0.001
Metacommunity:Round	1	0.082	0.012	0.694	0.525
Residual	51	6.036	0.916		
Total	54	6.588	1		

Suburban vs. Urban

Effect	**DF**	**SumofSqs**	**R2**	**F.Model**	***p***
Metacommunity	1	0.057	0.008	0.419	0.002
Round	1	0.597	0.080	4.379	0.001
Metacommunity:Round	1	0.019	0.003	0.138	0.956
Residual	50	6.818	0.910		
Total	53	7.491	1		

Urban vs. Central

Effect	**DF**	**SumofSqs**	**R2**	**F.Model**	***p***
Metacommunity	1	0.221	0.035	1.899	0.012
Round	1	0.343	0.054	2.956	0.004
Metacommunity:Round	1	0.115	0.018	0.993	0.273
Residual	49	5.691	0.893		
Total	52	6.370	1		

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Chapter 5: Synthesis and conclusions

Butterflies are recognized as important pollinators in ecological and agricultural systems, but many species are in decline globally (Warren et al. 2021, Forister et al. 2021). As pollinators, butterflies are engaged in a mutualistic interaction with flowering plants, but are also herbivores as larvae, and are targets of predation, making them an excellent focal taxon for multitrophic interactions. This group also exhibits a range of dispersal abilities (Burke et al. 2011), allowing for comparisons of how species of along a dispersal gradient interact with local and landscape factors. In this thesis, I used a metacommunity ecology framework to increase our understanding of basic ecological processes involving biotic interactions and dispersal, as well as to further our knowledge of how to conserve butterfly communities.

5.1 Metacommunity Ecology

A relatively young field (Jacobson and Peres-Neto 2010), metacommunity ecology has grown rapidly as scientists take advantage of its evolving framework to address fundamental research questions in ecology and conservation. Metacommunity ecology specifically integrates landscape scale processes into community ecology, acknowledging the importance of dispersal to local scale processes (Leibold et al. 2004). This framework allowed me to investigate effects of habitat connectivity in Chapter 2, effects of dispersal ability in Chapter 3, and effects of landcover in Chapter 4. While increasing study complexity by integrating landscape factors, metacommunity ecology still falls behind in other areas long studied by community ecology, including biotic interactions (Logue et al. 2011). As shown throughout this thesis, and discussed in more detail below, these factors need to be considered concurrently to fully understand the drivers of metacommunity structure.

Metacommunity ecology's consideration of dispersal and community structure make it particularly suited to applied conservation, although relatively few studies have considered its potential (Chase et al. 2020). Metapopulation ecology is more often associated with conservation, and has similar advantages to metacommunity ecology, such as the ability to identify source and sink habitats, and evaluate the effectiveness of habitat corridors (Akçakaya et al. 2007). A metacommunity framework has additional benefits inherent in considering whole communities, including understanding effects of biotic interactions and coexistence across species assemblages (Chase et al. 2020). Managing species at the level of networks of communities facilitates the prioritization of habitat patches for protection in light of both local and landscape characteristics (Albert et al. 2017), highlighting the importance of connectivity in improving the capacity of species to reach suitable habitats (Patrick et al. 2021).

Functioning metacommunities may also require less management intervention for conservation purposes, as dispersal between communities facilitates genetic rescue, population rescue, and recolonization in the event of local extinction (Low-Décarie et al. 2015). There is a significant advantage, therefore, to conserving systems at a metacommunity level (Chase et al. 2020), but to function as a metacommunity, some landscapes will require significant restoration. In Chapters 2 and 3, I studied a protected natural metacommunity within a provincial park: although the landscape is divided by a busy road, and surrounded by agriculture, resource extraction, and housing, little conservation action is needed. This is a fairly robust system with high levels of diversity across sites ranging in size and connectivity, although it is highly dependent on the continued health of a diverse floral metacommunity. In contrast, the urban metacommunities examined in Chapter 4 support much lower butterfly richness and abundance. Reduced connectivity and habitat suitability appear to limit the potential for rescue effects for a number of species. As cities and agricultural landscapes continue to expand (Liu et al. 2020), reducing habitat area and creating increasingly hostile matrices (Jha and Kremen 2013, Schütz and Schulze 2015), these depauperate urban systems are becoming increasingly common (Aronson et al. 2014, Fenoglio et al. 2020, Liang et al. 2023). These systems could benefit from habitat restoration measures, as many potential source habitats likely act as sinks due to low resource availability and connectivity. Metacommunities might also benefit from species reintroductions to overcome obstacles to dispersal from habitats outside cities. Despite intensive upfront management, restoring healthy metacommunities that provide rescue effects among habitat patches is a worthwhile goal, and should reduce the necessity for future conservation intervention. This thesis represents the first steps towards understanding the ecology of these systems, and future work should prioritize their conservation and management within the metacommunity framework.

5.2 Dispersal and the landscape

Dispersal is a key process driving ecological patterns and has been increasingly considered with the development of metapopulation and metacommunity ecology (Jacobson and Peres-Neto 2010). However, dispersal and habitat connectivity are sometimes measured only as Euclidean distances between sites, ignoring effects of topography and landcover, and potentially masking the importance of landscape-scale processes (Logue et al. 2011, Germain et al. 2019). While the techniques used in this thesis to describe landscape connectivity and dispersal are indirect, such measures are often the only feasible options in metacommunity ecology, and still represent an improvement over simple Euclidean distances (Jacobson and Peres-Neto 2010).

The importance of considering dispersal and the landscape is demonstrated empirically throughout this thesis. Chapters 2, 3, and 4 show that alpha diversity is not affected by connectivity and landcover type, but beta diversity and community composition are. I did not expect metacommunity diversity to be independent of habitat connectivity in Chapter 2, but this could arise due to a low disturbance regime in this system, which provides opportunities for colonization over many generations. I expected the harsh urban matrix to limit immigration and therefore community diversity in Chapter 4, but I found no effect of impervious surface area on alpha diversity. However, increasingly dissimilar amounts of impervious surface area in the landscape did increase urban community dissimilarity, consistent with expectations that a harsh urban matrix would filter species (Pla-Narbona et al. 2022). The results from Chapter 3 suggest that dispersal ability may drive community composition across landscapes, with higher densities of strong dispersers in isolated versus connected sites, and higher densities of weak dispersers in connected versus isolated sites.

Butterflies vary widely in their mobility, with some species unlikely to leave their natal habitat patch, and other migratory species inhabiting large ranges and flying hundreds of kilometers (Burke et al. 2011). Due to this huge span, different species are able to exploit more or less connected habitats, so that even isolated sites can host rich butterfly communities. This illustrates the effects of trait diversity on community composition, as densities of strong and poor dispersers varied strongly across both a high-disturbance gradient in Chapter 4, and a low-disturbance landscape in Chapter 3. These patterns should be tested in other systems, as they have serious implications for basic ecology and conservation. Although highly mobile species are still vulnerable to extinction (Pelton et al. 2019), it seems likely that poor dispersers, unable to colonize small and isolated sites in a stable, protected area, will need particular consideration for conservation in fragmented landscapes.

5.3 Biotic interactions

Despite their demonstrated importance to community structure, biotic interactions are still understudied in metacommunity ecology (Leibold et al. 2022), with a particular need for more work on mutualisms and multitrophic interactions (Logue et al. 2011). In this thesis, I investigated two biotic interactions in each chapter: mutlitrophic interactions with plants and predators in Chapters 2 and 3, and interactions with plants as hosts and nectar sources in Chapter 4. In Chapter 2, I found that only one biotic interaction, between flowering plants and butterflies, drove butterfly community diversity. However, interactions with both predators and flowering plants were important for species composition (Chapter 3). Strong dispersers seemed to escape sites with high predation, a process documented across taxa (Fronhofer et al. 2018), but also appeared at lower densities in sites with high floral density. Weak dispersers exhibited the opposite pattern, seemingly unable to escape high predation sites. These species occurred at high densities in sites with high floral diversity, likely relying on local floral resources to support their populations.

In Chapter 4, host plant richness was associated with high butterfly diversity, while flowering plant richness was associated with low butterfly diversity. The positive effect of host plant richness is consistent with previous work in butterfly communities (Menéndez et al. 2007, Pendl et al. 2022). I was not able to consider host plant availability in Chapters 1 and 2 due to the richness of our butterfly community and the wide range of host plants they use, but results from Chapter 3 emphasize that host plants should be considered whenever possible, with less rich urban butterfly communities offering an opportunity to do so. The negative association between butterfly diversity and flowering plant richness contrasts with the findings of Chapter 2 and previous work (Blaauw and Isaacs 2014, Lange-Kabitz et al. 2021), but is likely driven by the highly managed urban plant community, which has a different composition than the natural plant community in Chapters 2 and 3. This demonstrates the importance of plant identity in influencing butterfly diversity, as nectar producing species may compose only a small subset of some urban floral communities (Tew et al. 2022).

The results from this thesis demonstrate the importance of biotic interactions in investigations of community diversity and composition. In addition, biotic interactions can mediate the impacts of other factors, and by considering biotic interactions concurrently with other processes we can evaluate their relative contributions. In Chapter 2, site area had an indirect effect on butterfly diversity: increasing site area increased floral diversity, which then directly increased butterfly diversity. If this mutualistic interaction with flowering plants had not been included, site area may have appeared to directly impact the butterfly metacommunity, changing the interpretation of this system's basic ecology and recommendations for conservation.

5.4 Multifaceted analyses reveal contrasting drivers of diversity

Analyses that consider multiple measures of diversity and composition are particularly powerful, offering different perspectives on community dynamics (Medeiros et al. 2018, Silva et al. 2023). In Chapters 2 and 3, I analyzed data from the same butterfly metacommunity in different ways to reach contrasting, but complementary, conclusions. In Chapter 2, I found that only flowering plant diversity directly impacted butterfly diversity, with site area indirectly increasing butterfly diversity through a positive effect on flowering plant diversity. However, when I analyzed species' abundances within the metacommunity as a function of dispersal ability in Chapter 3, densities of strong vs weak dispersers varied with site connectivity, predation pressure, and floral diversity. I reached similarly contrasting conclusions in Chapter 4, showing that different factors drive alpha and beta diversity in urban butterfly metacommunities. Alpha diversity related to biotic factors (host plant richness and floral richness), while beta diversity also changed with site area and impervious surface area in the landscape. These contrasting results are consistent with other work that examined alpha and beta diversity concurrently (Kessler et al. 2009, Fournier et al. 2017, Neilan et al. 2019), as well as with expectations for comparisons of metacommunity level analyses to analyses of species' contributions to metacommunity dynamics (Leibold et al. 2022). These results demonstrate the importance of understanding multiple facets of community and metacommunity diversity, as well as the local and landscape factors that structure them. There are drawbacks, however, in using the same dataset for both Chapters 2 and 3, and in examining one study landscape in Chapter 4. As these studies were not replicated in space or time, the stochasticity inherent in ecological systems means that future work should attempt to replicate these findings in different, as well as similar, systems, to increase confidence in the generalizability of the findings.

5.5 Implications for conservation

Butterflies are an important group to consider for conservation: they provide pollination services to natural and agricultural plants (Holland et al. 2015), are used as indicator species for environmental change and degradation (Dennis et al. 2003), and are charismatic species that connect people to nature (Lewandowski and Oberhauser 2017). The results from this thesis have important implications for butterfly conservation, in both natural and urban landscapes. In Chapter 2, I found that butterfly diversity increased with floral diversity, and while site area had an indirect effect on butterflies by increasing floral diversity, it did not directly affect butterfly diversity. Similarly, Chapter 4 demonstrated that host richness increased alpha diversity in urban habitats, with no effect of site area or impervious surface area in the landscape. In these two different systems, even small, isolated sites can host diverse butterfly communities if high floral and host diversity are maintained. However, floral richness had a negative effect on the diversity of urban butterflies in Chapter 4. This suggests that there are important differences in plant community composition between the natural metacommunity studied in Chapters 2 and 3, and the urban metacommunities studied in Chapter 4. Urban floral communities are increasingly composed of ornamental flowers and human food plants that may produce little or no nectar (Tew et al. 2022), compared to natural communities composed largely of nectar producing native and invasive plants (Chapter 2 and 3). This suggests that urban plant communities need to better reflect natural communities to further conservation goals. These findings point towards the potential conservation value of butterfly gardens if butterfly host and nectar plants are grown: more work should be done highlighting these findings to property owners.

Additional findings from Chapters 3 and 4 showed that, while diverse communities can be maintained in small and isolated sites, community composition changes with site area and isolation. In Chapter 4, turnover and nestedness were both impacted by site area and impervious surface area surrounding sites, demonstrating that only some species can access resources in these sites. Results from Chapter 3 showed that community composition varies significantly between connected and isolated sites, with stronger dispersers appearing at much higher densities than poor dispersers in isolated sites, and poor dispersers appearing at higher densities than strong dispersers in connected sites. While isolated sites may be important contributors to populations of migratory and highly mobile butterflies like monarchs and swallowtails, poor dispersers may be lost in highly fragmented systems (Pla-Narbona et al. 2022). Different strategies are needed for these species: a mix of large and connected sites, and small and isolated sites, are needed to conserve functionally diverse butterfly metacommunities.

While floral communities and landscapes can be managed for butterfly conservation, it may not be possible to control all factors influencing butterfly communities. Predation did not impact diversity (Chapter 2), but strong dispersers occurred at lower densities in sites with high predation pressure (Chapter 3), suggesting that those species left high predation patches. Attracting strong dispersers like monarchs is often a goal of butterfly conservation (Stenoien et al. 2015, Pelton et al. 2019), but it may be logistically difficult and ecologically harmful to remove butterfly predators to increase the abundance and diversity of strong dispersers. Still, interactions like predation are important to understand, as they may contribute to community composition and therefore also alter conservation outcomes.

5.6 Future directions

Butterflies are an excellent study taxon for metacommunity ecology, as dispersal ability, as well as other traits like host specificity, phenology, and voltinism (number of generations per year) are known for many species (Shirey et al. 2022). Due to their mutualistic interactions with flowering plants, as well as other interactions with predators and host plants, they are an excellent taxon with which to ask ecologically important questions about dispersal and biotic interactions. Despite being a widely studied group, there are many opportunities for further research (Warren et al. 2021). I identified parasitoids as a possible explanation for high densities of strong dispersers in isolated sites (Chapter 3), as butterfly parasitoid abundances have been shown to be reduced in small and isolated habitats (Van Nouhuys and Hanski 2002, Choutt et al. 2011). This provides a testable hypothesis for this system: low parasitoid density in small and isolated habitat patches increases the relative quality of these patches, increasing abundances of strong dispersers that can seek out higher quality sites. More work is needed on butterfly-parasitoid interactions: so far studies have largely considered only one or two butterfly species at once (i.e. van Nouhuys and Kraft 2012, Opedal et al. 2020), but the interaction may have important implications for butterfly metacommunity dynamics. This thesis provides insight into metacommunity interactions with food resources (host plants), mutualist partners (flowering plants), and predators, and future work should test whether the patterns demonstrated here are applicable to other taxa.

Dispersal ability has long been theorized to be important for ecological processes (Macarthur and Wilson 1967, Levins 1969), and its importance has been repeatedly demonstrated (e.g. Chapter 3). While dispersal abilities are known for a number of butterfly species, data type varies widely, from expert-based consensus, to mark-release-recapture studies, to genetic analyses (Stevens et al. 2010). This variety of methods and data quality makes it difficult to draw comparisons across systems; this is considered in light of the fact that butterflies are a well studied group (Shirey et al. 2022), and much less is known about dispersal among other taxa (Driscoll et al. 2014). This lack of knowledge prevents us from testing ecological hypotheses, and can also impair conservation decision making (Kerr 2020). The investigation of dispersal and other key functional traits should be prioritized more highly as the field of ecology continues to advance.

5.7 Conclusion

In this thesis, I investigated the importance of dispersal and biotic interactions in driving butterfly metacommunity diversity and composition. I found that butterfly diversity increases with mutualist diversity in a natural metacommunity (Chapter 2), but that this pattern is reversed in urban metacommunities (Chapter 4), likely due to changes in urban plant communities that limit the availability of mutualist partners. I found that interactions between butterflies, other trophic levels, and the landscape are mediated by butterfly species' dispersal abilities (5).

Finally, I found that while biotic interactions with flowering plants and hosts drive alpha diversity in urban butterfly metacommunities, abiotic site and landscape characteristics are also important drivers of community dissimilarity (Chapter 2).

In addition to furthering our basic knowledge of ecological communities, I identified important considerations for butterfly conservation. Small and isolated sites can host diverse butterfly communities if they contain rich nectar and host plants assemblages (Chapters 2 and 4). Small yards and community gardens have the potential to be particularly impactful for butterfly conservation if they include plants that support urban butterflies (Chapter 4). Strong dispersers are best able to access resources in isolated sites (Chapter 2), and a range of isolated to connected habitat patches must be maintained in order to conserve taxonomically and functionally diverse metacommunities.

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