Urbanization influences communities of milkweed-specialist herbivorous insects

ON_herb

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Research Question

We tested the hypothesis that urbanization disrupts specialized plant-herbivore species interactions, and these effects vary according to the characteristics of both cities and features of the individual organisms.

Sampling Map

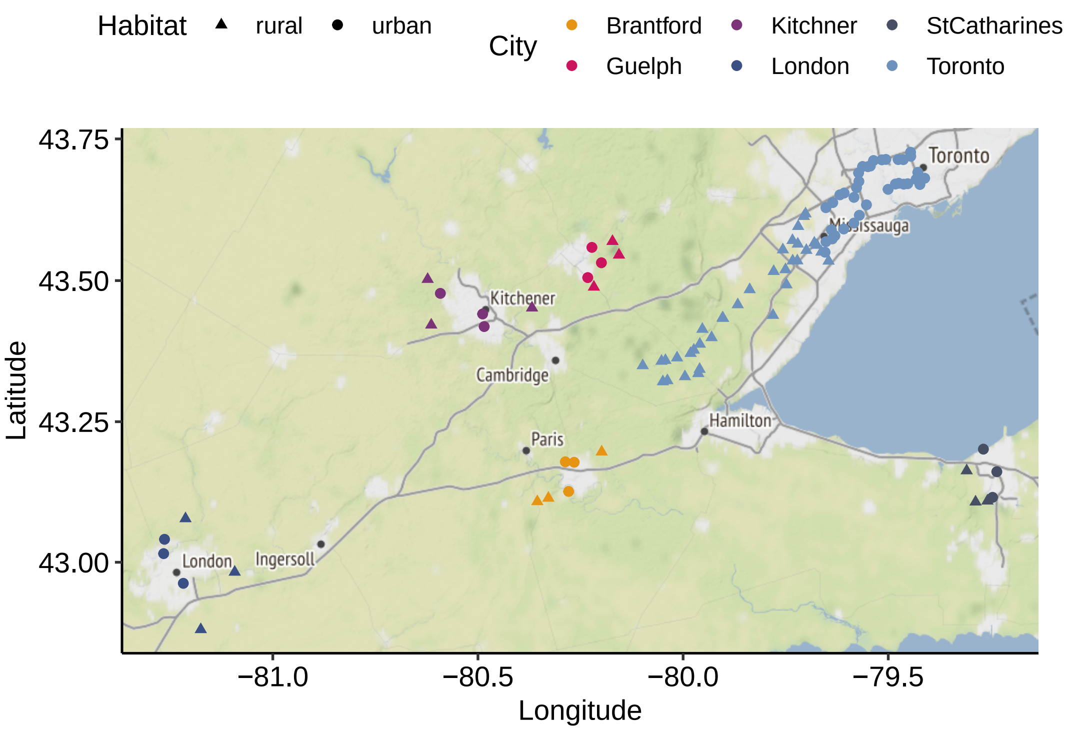

Figure 1: Map of sampling locations, with sites coloured by city. Urban sites are indicated by circles and rural sites by triangles. Toronto was sampled along an urbanization gradient while the 5 Cities were sampled using urban-rural pairs.

Diversity Analyses

We analyzed the effects of urbanization on species diversity (measured as species richness) using generalized linear mixed models. Diversity models for the Toronto dataset were fitted to a Poisson error distribution with a correction for zero inflation using `glmmTMB()` with the following formula:

$$Diversity = Intercept + Distance + (1 \mid Population) + e$$

where diversity was compared against distance from city center, with population fitted as a random effect and e indicating the residual error. Diversity models for the 5 Cities dataset were fitted to a Poisson error distribution using `glmer()` with the following formula:

$$Diversity = Intercept + Habitat + City + Habitat : City + (1 \mid Population) + e$$

where diversity was compared against the main effects of habitat and city and their interaction, with population fitted as a random effect and e indicating the residual error. For all diversity models across the Toronto and 5 Cities datasets, significance of fixed effects was estimated with Type II sums-of-squares implemented using the `Anova()` function in `car`.

Early Season Diversity, Toronto

Table 1: Summary of the early season diversity model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	1.766	1	0.184

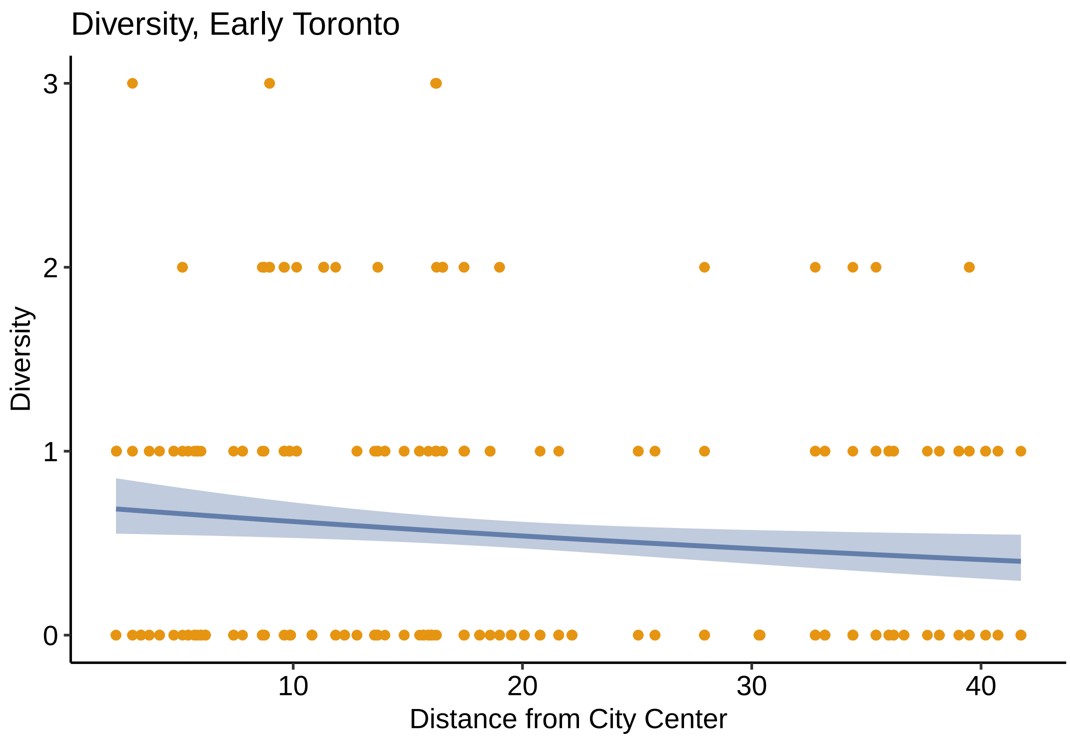

Figure 2: Plot of diversity against distance from city center for the early season in Toronto.

Early Season Diversity, 5 Cities

Table 2: Summary of the early season diversity model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	0.843	1	0.359
City	3.565	4	0.468
Habitat:City	2.611	4	0.625

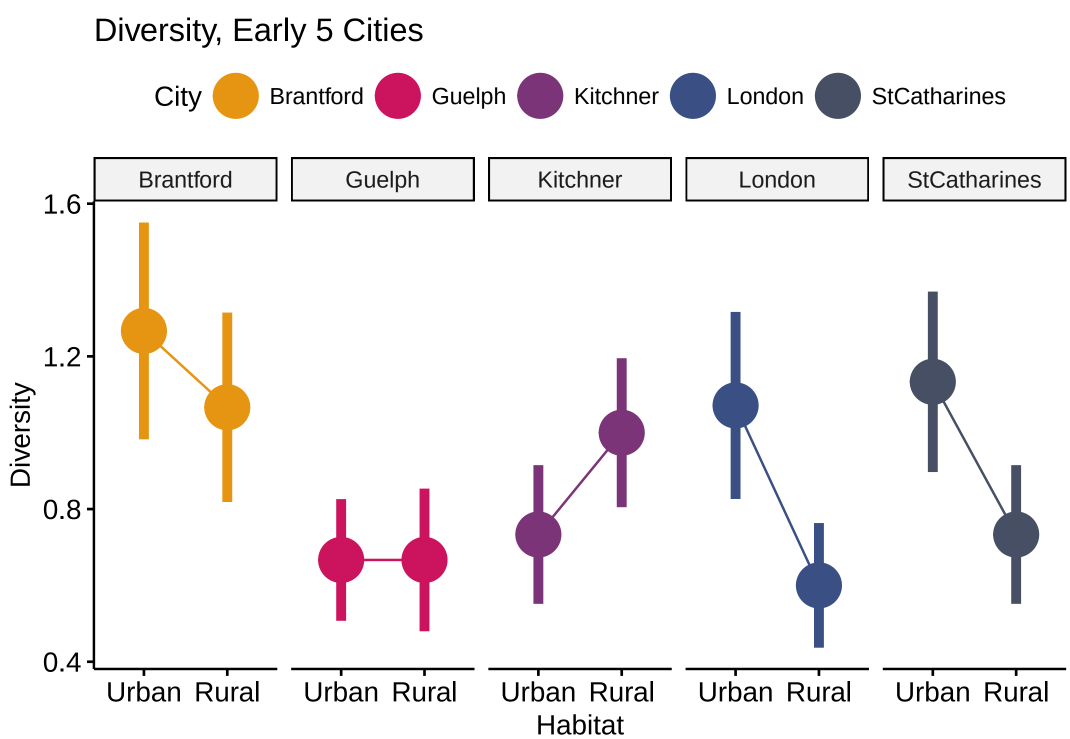

Figure 3: Plot of diversity by habitat and city for the early season across the 5 Cities. Lines connect urban and rural habitats for each city.

Late Season Diversity, Toronto

Table 3: Summary of the late season diversity model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	5.36	1	0.021

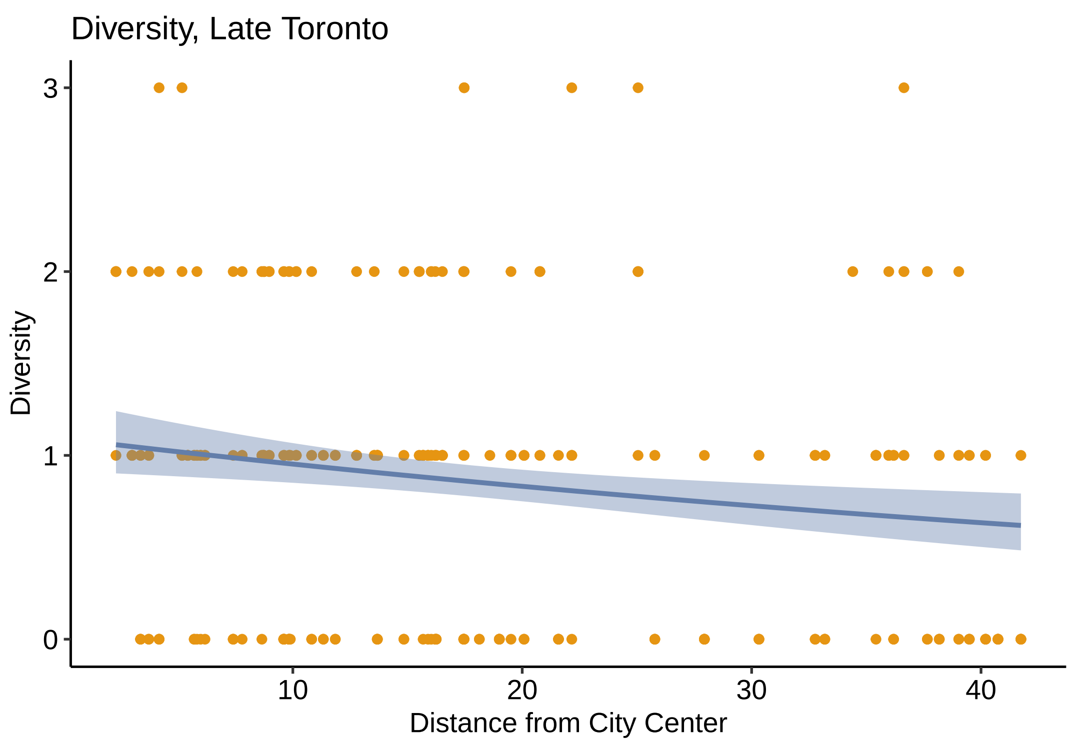

Figure 4: Plot of diversity against distance from city center for the late season in Toronto.

Late Season Diversity, 5 Cities

Table 4: Summary of the late season diversity model for for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	1.410	1	0.235
City	6.945	4	0.139
Habitat:City	9.104	4	0.059

Table 5: Post-hoc comparisons of the interaction between city and habitat for diversity for the late season 5 Cities, where 1 = Rural and 2 = Urban.

Habitat	term	contrast	null.value	estimate	std.error	df	z.ratio	adj.p.value
1	City	Brantford - Guelph	0	0.865	0.421	Inf	2.052	0.241
1	City	Brantford - Kitchner	0	0.172	0.339	Inf	0.506	0.987
1	City	Brantford - London	0	0.460	0.369	Inf	1.246	0.724
1	City	Brantford - StCatharines	0	0.642	0.391	Inf	1.643	0.470
1	City	Guelph - Kitchner	0	-0.693	0.433	Inf	-1.601	0.497
1	City	Guelph - London	0	-0.405	0.456	Inf	-0.888	0.901
1	City	Guelph - StCatharines	0	-0.223	0.474	Inf	-0.470	0.990
1	City	Kitchner - London	0	0.288	0.382	Inf	0.753	0.944
1	City	Kitchner - StCatharines	0	0.470	0.403	Inf	1.166	0.771
1	City	London - StCatharines	0	0.182	0.428	Inf	0.426	0.993
2	City	Brantford - Guelph	0	-1.299	0.651	Inf	-1.995	0.268
2	City	Brantford - Kitchner	0	-1.735	0.626	Inf	-2.770	0.044
2	City	Brantford - London	0	-1.070	0.690	Inf	-1.551	0.529
2	City	Brantford - StCatharines	0	-0.693	0.764	Inf	-0.908	0.894
2	City	Guelph - Kitchner	0	-0.435	0.387	Inf	-1.125	0.793
2	City	Guelph - London	0	0.229	0.483	Inf	0.473	0.990
2	City	Guelph - StCatharines	0	0.606	0.584	Inf	1.038	0.838
2	City	Kitchner - London	0	0.664	0.449	Inf	1.479	0.576
2	City	Kitchner - StCatharines	0	1.041	0.556	Inf	1.874	0.331
2	City	London - StCatharines	0	0.377	0.627	Inf	0.602	0.975

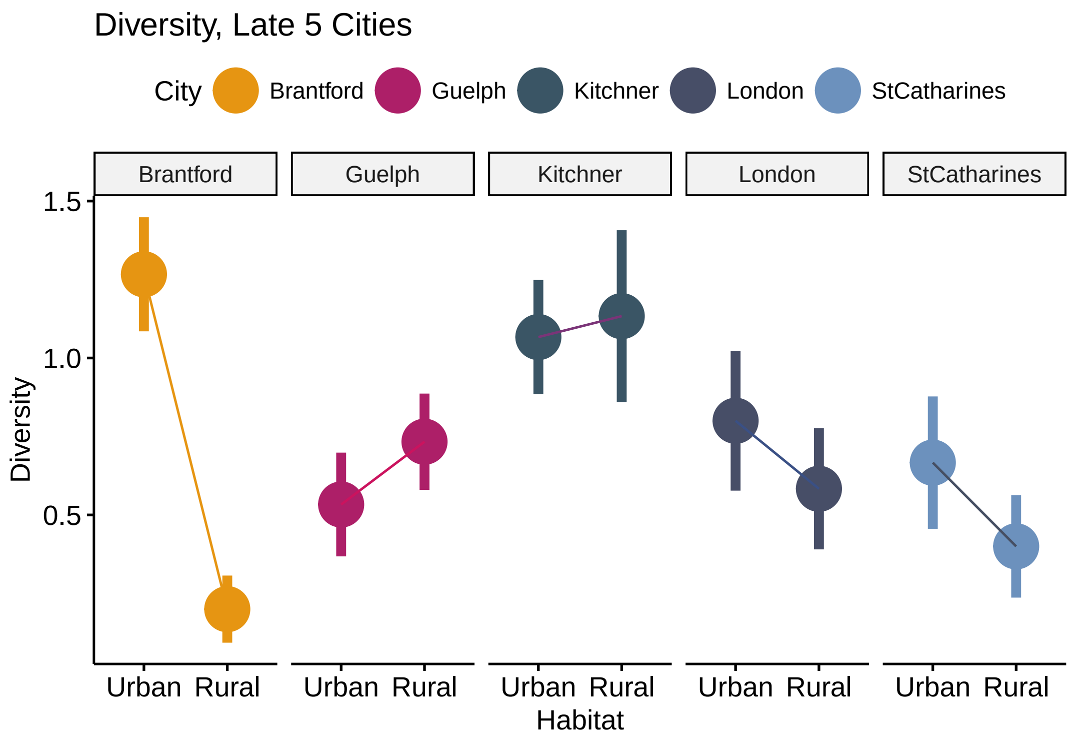

Figure 5: Plot of diversity by habitat and city for the late season across the 5 Cities. Lines connect urban and rural habitats for each city.

Abundance Analyses

We analyzed the effects of urbanization on community abundance using generalized linear mixed models. Models for the both the Toronto and 5 Cities datasets were fitted to a Poisson error distribution with a correction for zero inflation using `glmmTMB()`. Models for the Toronto dataset were fitted to the following formula:

$$Abundance = Intercept + Distance + (1 \mid Population) + e$$

where abundance was compared against distance from city center, with population fitted as a random effect and e indicating the residual error. Diversity models for the 5 Cities dataset were fitted to the following formula:

$$Abundance = Intercept + Habitat + City + Habitat : City + (1 \mid Population) + e$$

where abundance was compared against the main effects of habitat and city and their interaction, with population fitted as a random effect and e indicating the residual error. Aphids were removed from these analyses as they presented major outliers to the data because, when present, their abundance ranged from 10-1000. Aphids were analyzed in herbivore-specific models (see below). For all abundance models across the Toronto and 5 Cities datasets, significance of fixed effects was estimated with Type II sums-of-squares implemented using the `Anova()` function in `car`.

Early Season Abundance, Toronto

Table 6: Summary of the early season abundance model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.005	1	0.945

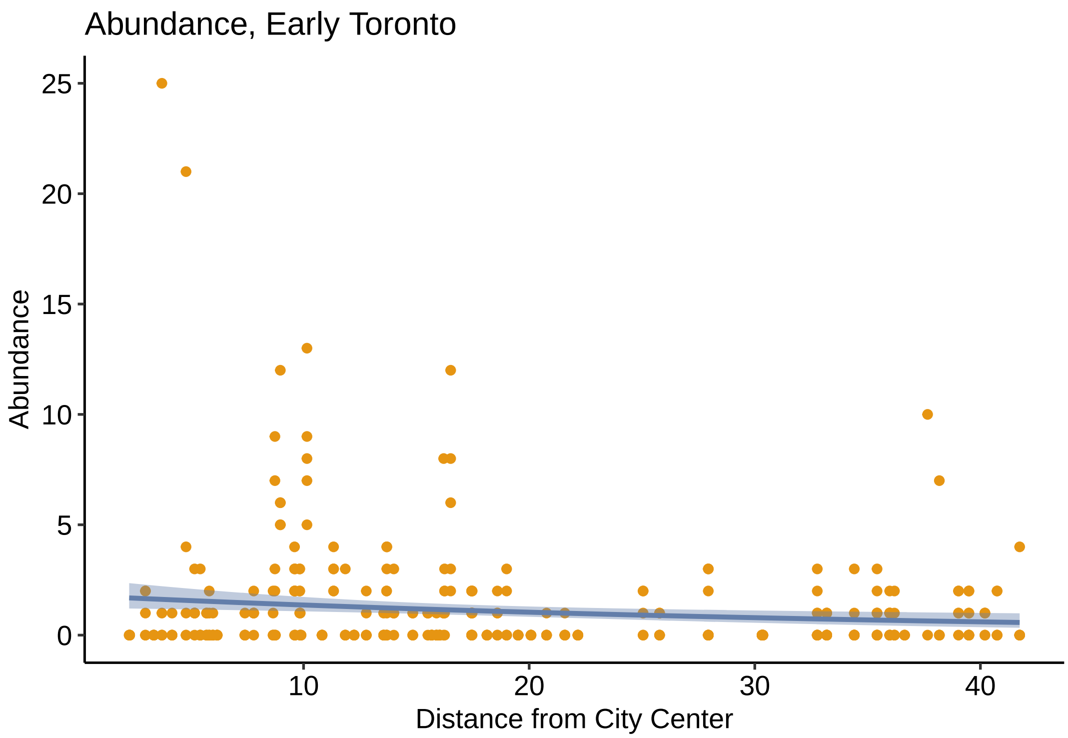

Figure 6: Plot of abundance against distance from city center for the early season in Toronto.

Early Season Abundance, 5 Cities

Table 7: Summary of the early season abundance model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	3.969	1	0.046
City	13.070	4	0.011
Habitat:City	4.784	4	0.310

Table 8: Post-hoc comparisons of the main effect of city for abundance for the early season 5 Cities.

City	estimate	std.error	df	statistic	p.value
Brantford	1.252	0.184	137	6.804	0.000
Guelph	0.380	0.214	137	1.776	0.078
Kitchner	0.634	0.203	137	3.129	0.002
London	0.551	0.203	137	2.712	0.008
StCatharines	0.679	0.214	137	3.164	0.002

Table 9: Post-hoc comparisons of the main effect of habitat for abundance for the early season 5 Cities, where 1 = Rural and 2 = Urban.

Habitat	estimate	std.error	df	statistic	p.value
1	0.869	0.134	137	6.491	0
2	0.530	0.133	137	3.977	0

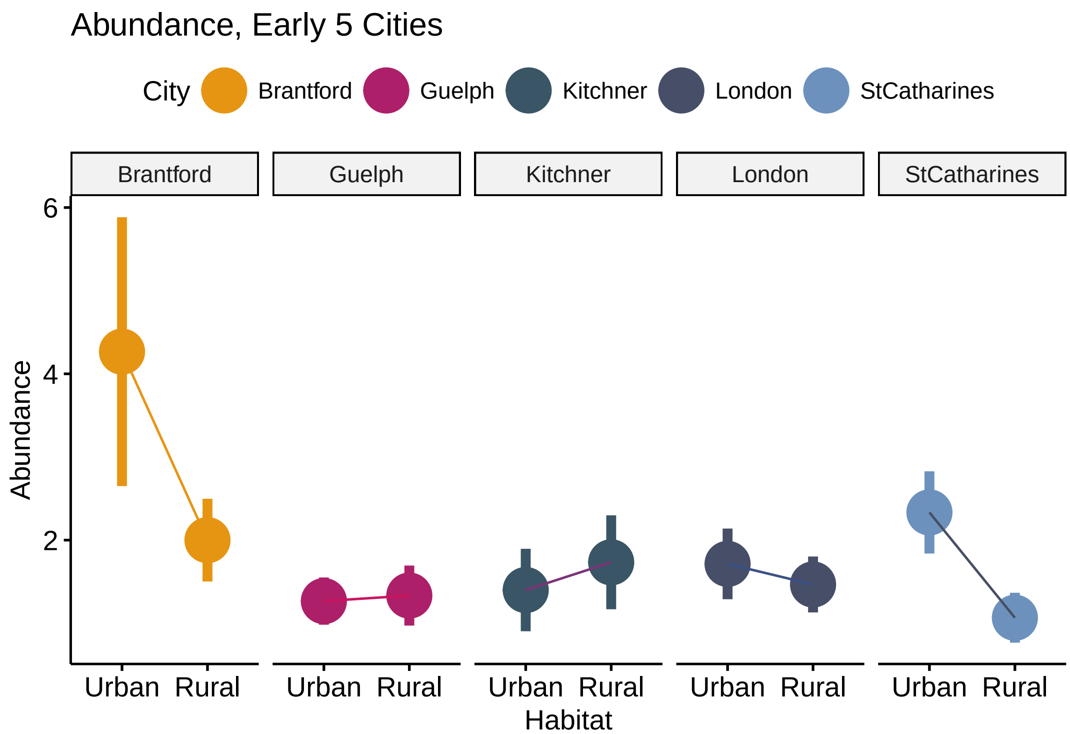

Figure 7: Plot of abundance by habitat and city for the early season across the 5 Cities. Lines connect urban and rural habitats for each city.

Late Season Abundance, Toronto

Table 10: Summary of the late season abundance model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	12.445	1	0

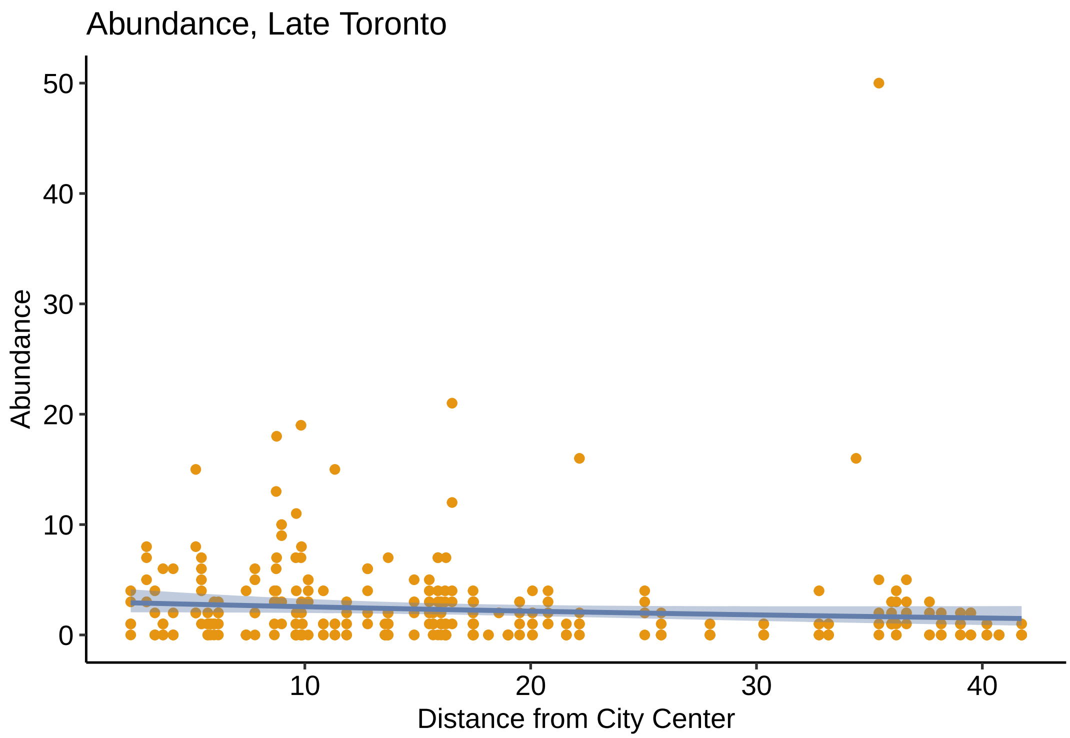

Figure 8: Plot of abundance against distance from city center for the late season in Toronto.

Late Season Abundance, 5 Cities

Table 11: Summary of the late season abundance model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	2.213	1	0.137
City	3.169	4	0.530
Habitat:City	10.490	4	0.033

Table 12: Post-hoc comparisons of the interaction between city and habitat for abundance for the late season 5 Cities, where 1 = Rural and 2 = Urban.

Habitat	term	contrast	null.value	estimate	std.error	df	statistic	adj.p.value
1	City	Brantford - Guelph	0	1.457	0.680	130	2.144	0.208
1	City	Brantford - Kitchner	0	0.349	0.593	130	0.588	0.977
1	City	Brantford - London	0	0.485	0.613	130	0.791	0.933
1	City	Brantford - StCatharines	0	1.885	0.712	130	2.649	0.068
1	City	Guelph - Kitchner	0	-1.108	0.687	130	-1.613	0.492
1	City	Guelph - London	0	-0.972	0.700	130	-1.389	0.636
1	City	Guelph - StCatharines	0	0.428	0.781	130	0.548	0.982
1	City	Kitchner - London	0	0.136	0.622	130	0.219	0.999
1	City	Kitchner - StCatharines	0	1.536	0.719	130	2.136	0.211
1	City	London - StCatharines	0	1.400	0.727	130	1.926	0.309
2	City	Brantford - Guelph	0	-0.871	0.742	130	-1.174	0.766
2	City	Brantford - Kitchner	0	-0.466	0.766	130	-0.609	0.974
2	City	Brantford - London	0	0.537	0.850	130	0.631	0.970
2	City	Brantford - StCatharines	0	-0.599	0.835	130	-0.717	0.952
2	City	Guelph - Kitchner	0	0.405	0.678	130	0.596	0.975
2	City	Guelph - London	0	1.408	0.776	130	1.813	0.370
2	City	Guelph - StCatharines	0	0.272	0.770	130	0.354	0.997
2	City	Kitchner - London	0	1.003	0.778	130	1.290	0.698
2	City	Kitchner - StCatharines	0	-0.132	0.786	130	-0.169	1.000
2	City	London - StCatharines	0	-1.135	0.870	130	-1.305	0.689

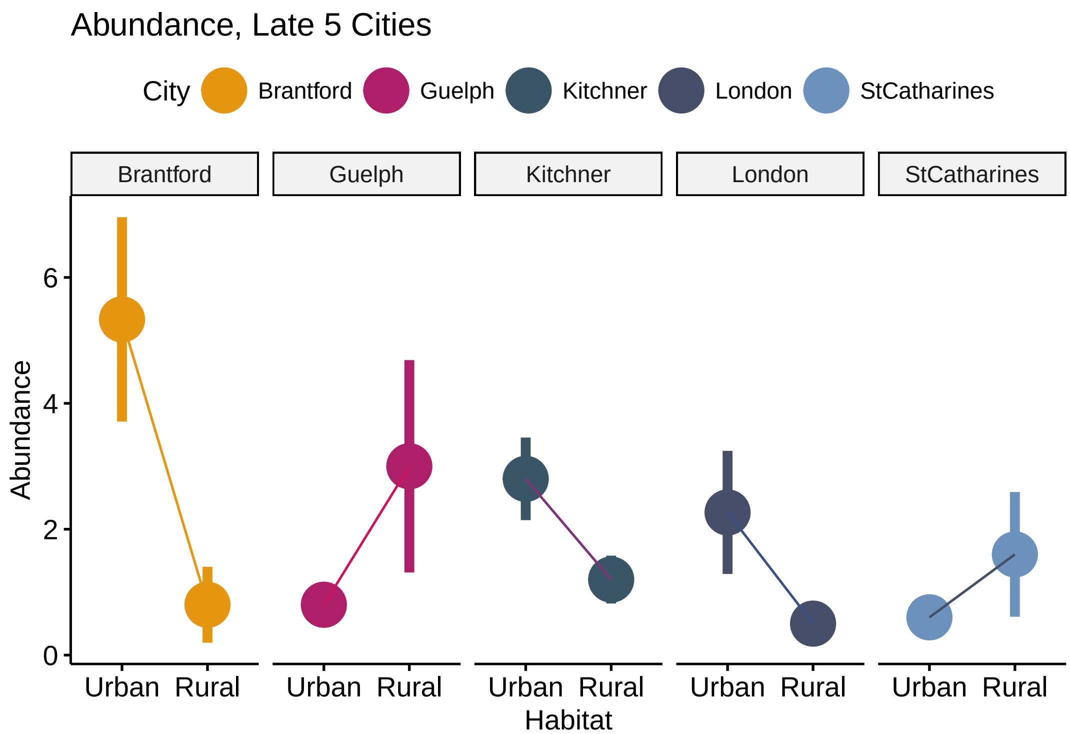

Figure 9: Plot of abundance by habitat and city for the late season across the 5 Cities. Lines connect urban and rural habitats for each city.

Leaf Herbivory

We analyzed the effects of urbanization on average leaf herbivory using linear mixed models.Models for the Toronto and 5 Cities datasets were fitted using `lmer()`. Average leaf herbivory was square-root transformed to better meet model assumptions. Models for the Toronto dataset were fitted to the following formula:

$$Average\ Leaf\ Herbivory\ = Intercept + Distance + (1 \mid Population) + e$$

where average leaf herbivory was compared against distance from city center, with population fitted as a random effect and e indicating the residual error. Diversity models for the 5 Cities dataset were fitted to the following formula:

$$Average\ Leaf\ Herbivory\ = Intercept + Habitat + City + Habitat : City + (1 \mid Population) + e$$

where average leaf herbivory was compared against the main effects of habitat and city and their interaction, with population fitted as a random effect and e indicating the residual error. For all average leaf herbivory models across the Toronto and 5 Cities datasets, significance of fixed effects was estimated with Type II sums-of-squares implemented using the `Anova()` function in `car`.

Early Season Leaf Herbivory, Toronto

Table 13: Summary of the early season leaf herbivory model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	3.186	1	0.074

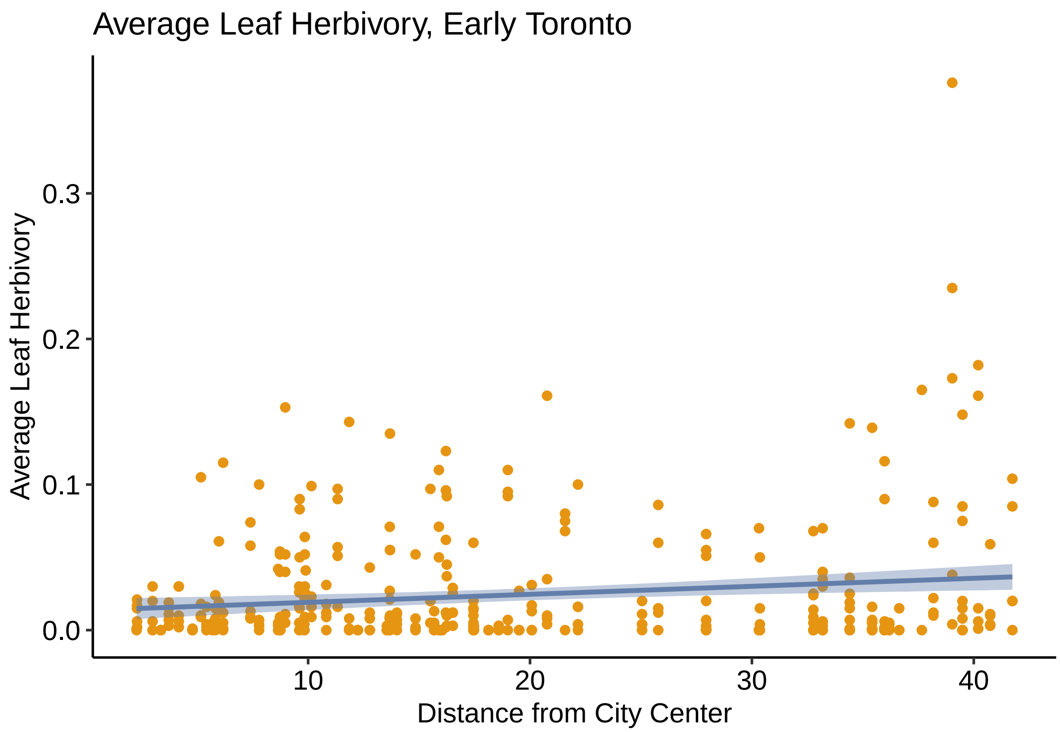

Figure 10: Plot of average leaf herbivory against distance from city center for the early season in Toronto.

Early Season Leaf Herbivory, 5 Cities

Table 14: Summary of the early season leaf herbivory model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	0.002	1	0.961
City	2.166	4	0.705
Habitat:City	11.288	4	0.024

Table 15: Post-hoc comparisons of the interaction between city and habitat for leaf herbivory for the early season 5 Cities, where 1 = Rural and 2 = Urban.

Habitat	term	contrast	null.value	estimate	std.error	df	statistic	adj.p.value
1	City	Brantford - Guelph	0	-0.070	0.04	19.816	-1.748	0.429
1	City	Brantford - Kitchner	0	-0.016	0.04	19.816	-0.394	0.994
1	City	Brantford - London	0	-0.024	0.04	20.689	-0.596	0.974
1	City	Brantford - StCatharines	0	-0.042	0.04	19.816	-1.050	0.829
1	City	Guelph - Kitchner	0	0.054	0.04	19.816	1.354	0.662
1	City	Guelph - London	0	0.046	0.04	20.689	1.132	0.788
1	City	Guelph - StCatharines	0	0.028	0.04	19.816	0.699	0.954
1	City	Kitchner - London	0	-0.008	0.04	20.689	-0.206	1.000
1	City	Kitchner - StCatharines	0	-0.026	0.04	19.816	-0.656	0.964
1	City	London - StCatharines	0	-0.018	0.04	20.689	-0.441	0.992
2	City	Brantford - Guelph	0	0.070	0.04	19.816	1.745	0.431
2	City	Brantford - Kitchner	0	-0.010	0.04	19.816	-0.253	0.999
2	City	Brantford - London	0	-0.041	0.04	19.816	-1.029	0.839
2	City	Brantford - StCatharines	0	0.045	0.04	19.816	1.127	0.791
2	City	Guelph - Kitchner	0	-0.080	0.04	19.816	-1.998	0.303
2	City	Guelph - London	0	-0.111	0.04	19.816	-2.774	0.078
2	City	Guelph - StCatharines	0	-0.025	0.04	19.816	-0.618	0.970
2	City	Kitchner - London	0	-0.031	0.04	19.816	-0.776	0.935
2	City	Kitchner - StCatharines	0	0.055	0.04	19.816	1.379	0.647
2	City	London - StCatharines	0	0.086	0.04	19.816	2.155	0.237

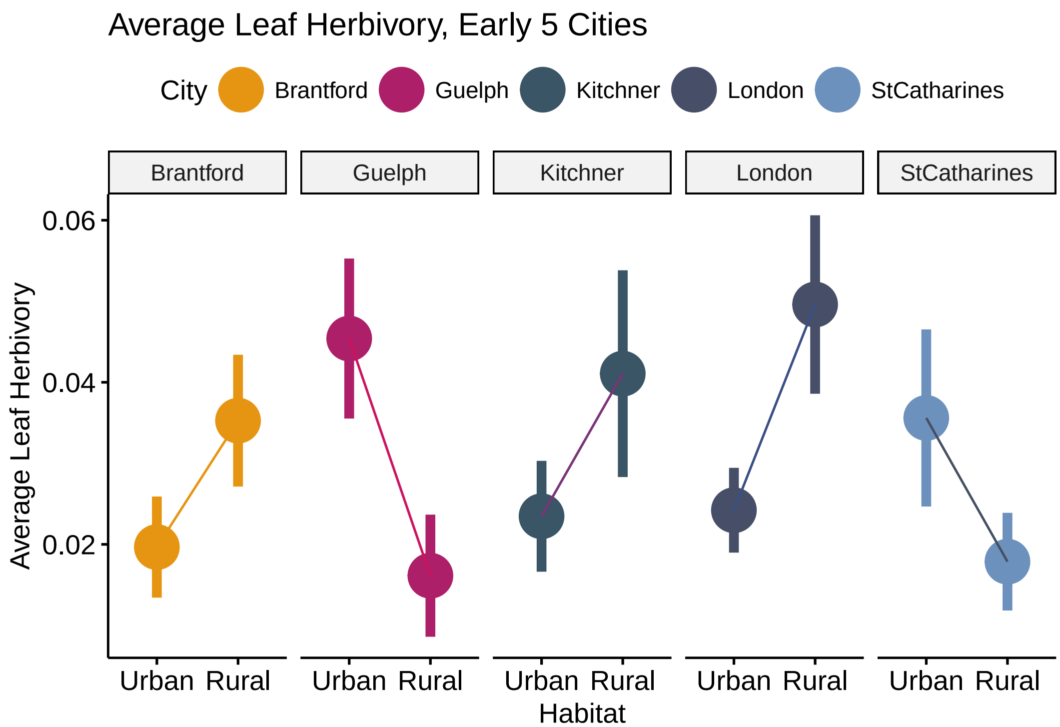

Figure 11: Plot of average leaf herbivory by habitat and city for the early season across the 5 Cities. Lines connect urban and rural habitats for each city.

Late Season Leaf Herbivory, Toronto

Table 16: Summary of the late season leaf herbivory model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	27.573	1	0

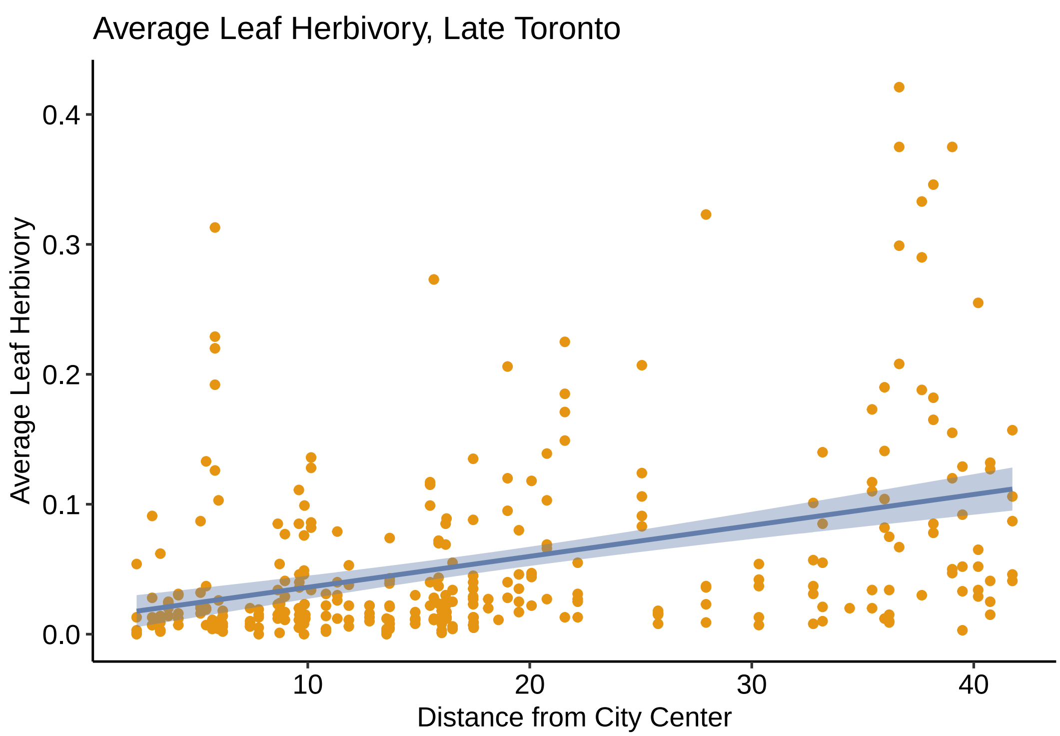

Figure 12: Plot of average leaf herbivory against distance from city center for the late season in Toronto.

Late Season Leaf Herbivory, 5 Cities

Table 17: Summary of the late season leaf herbivory model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	4.799	1	0.028
City	5.778	4	0.216
Habitat:City	2.597	4	0.627

Table 18: Post-hoc comparisons of the main effect of habitat for leaf herbivory for the late season 5 Cities, where 1 = Rural and 2 = Urban.

Habitat	estimate	std.error	df	statistic	p.value
1	0.179	0.019	18.596	9.538	0
2	0.235	0.020	19.193	11.848	0

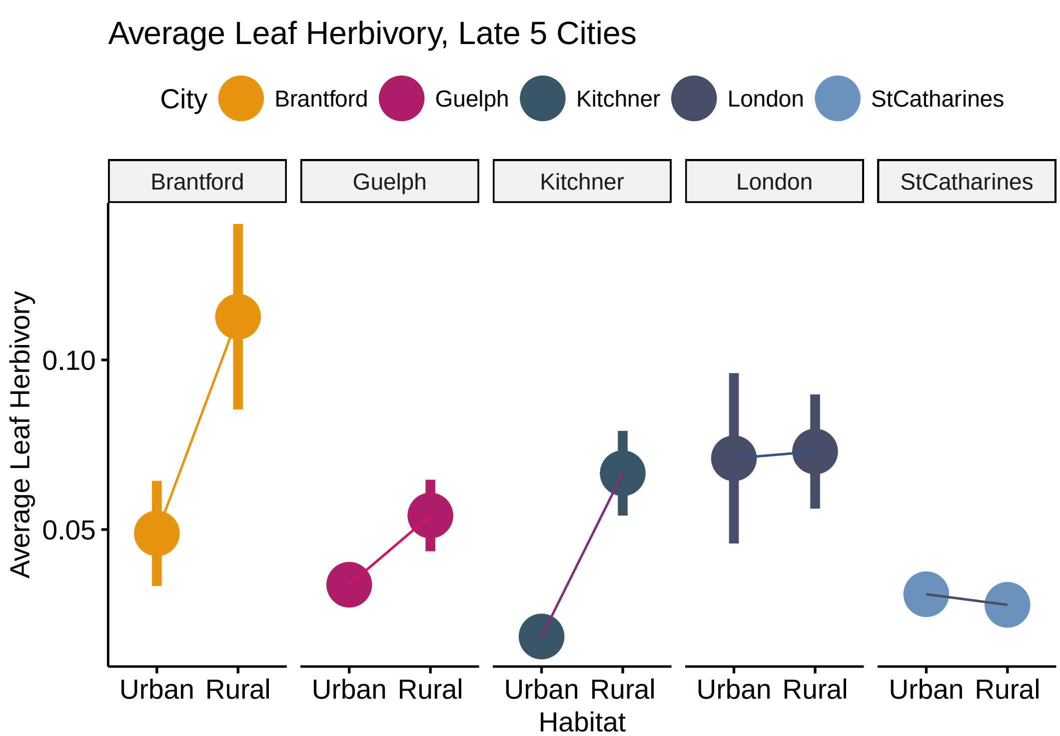

Figure 13: Plot of average leaf herbivory by habitat and city for the late season across the 5 Cities. Lines connect urban and rural habitats for each city.

Herbivore-Specific Models

We analyzed the effects of urbanization on herbivore species abundance using generalized linear mixed models. We focused on the abundances for *Danaus*, *Rhysomatus*, *Aphis*, and *Tetraopes*.

Models for the both the Toronto and 5 Cities datasets were fitted to a Poisson error distribution, but the Toronto models were fitted with a correction for zero inflation using `glmmTMB()` while the 5 Cities models were fitted using `glmer()`. Models for the Toronto dataset were fitted to the following formula:

$$Abundance_i = Intercept + Distance + (1 \mid Population) + e_i$$

where abundance was compared against distance from city center, with population fitted as a random effect and e indicating the residual error. The subscript i indicates the same model structure was fitted for each of the focal herbivore species.

Diversity models for the 5 Cities dataset were fitted to the following formula:

$$Abundance_i = Intercept + Habitat + City + Habitat : City + (1 \mid Population) + e_i$$

where abundance was compared against the main effects of habitat and city and their interaction, with population fitted as a random effect and e indicating the residual error. As with the Toronto dataset, the subscript i indicates the same model structure was fitted for each of the focal herbivore species. For all abundance models across the Toronto and 5 Cities datasets, significance of fixed effects was estimated with Type II sums-of-squares implemented using the `Anova()` function in `car`.

Danaus

Early Season Danaus, Toronto

Table 19: Summary of the early season Danaus model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	1.129	1	0.288

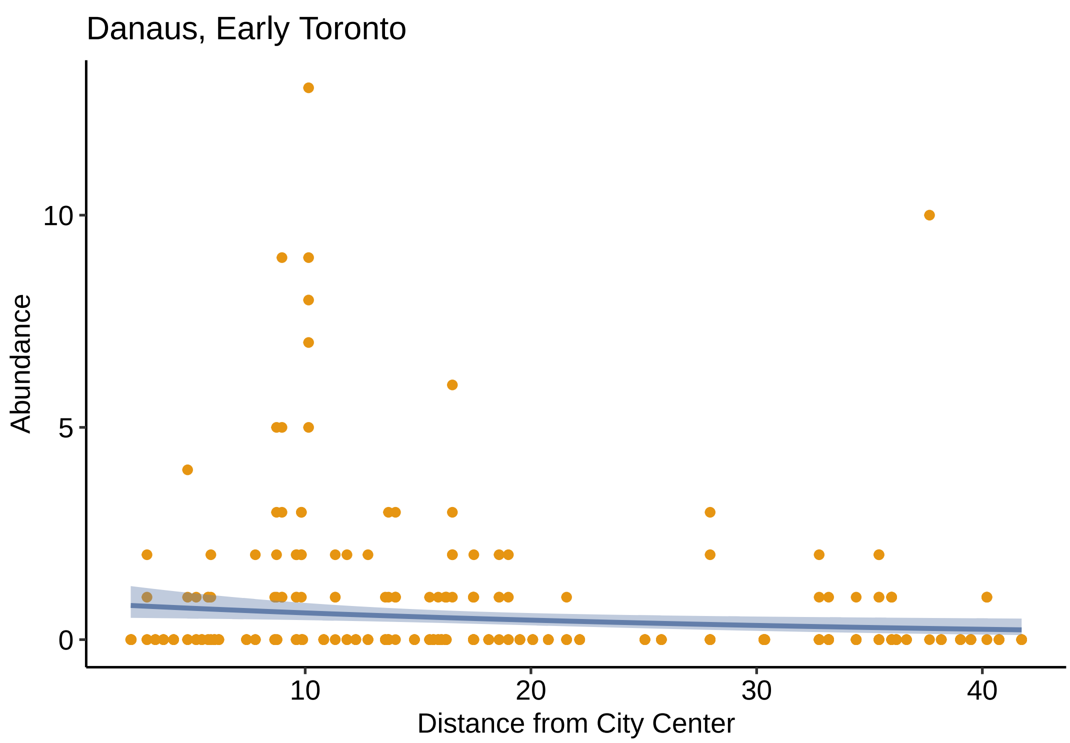

Figure 14: Plot of Danaus abundance against distance from city center for the early season in Toronto.

Early Season Danaus, 5 Cities

Table 20: Summary of the early season Danaus model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	0.902	1	0.342
City	11.019	4	0.026
Habitat:City	2.785	4	0.594

Table 21: Post-hoc comparisons of the main effect of city for Danaus for the late season 5 Cities.

City	estimate	std.error	df	z.ratio	p.value
Brantford	0.018	0.275	Inf	0.066	0.948
Guelph	-1.385	0.421	Inf	-3.289	0.001
Kitchner	-1.314	0.415	Inf	-3.164	0.002
London	-0.764	0.338	Inf	-2.257	0.024
StCatharines	-0.486	0.321	Inf	-1.514	0.130

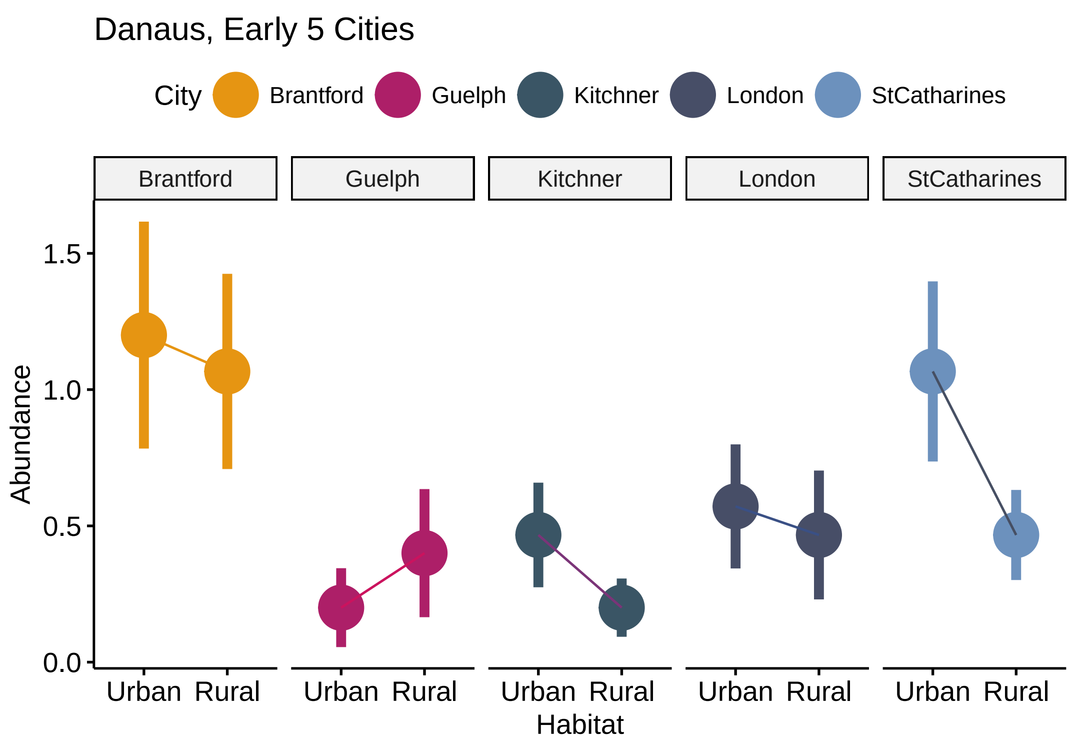

Figure 15: Plot of Danaus abundance by habitat and city for the early season across the 5 Cities. Lines connect urban and rural habitats for each city.

Late Season Danaus, Toronto

Table 22: Summary of the late season Danaus model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.008	1	0.93

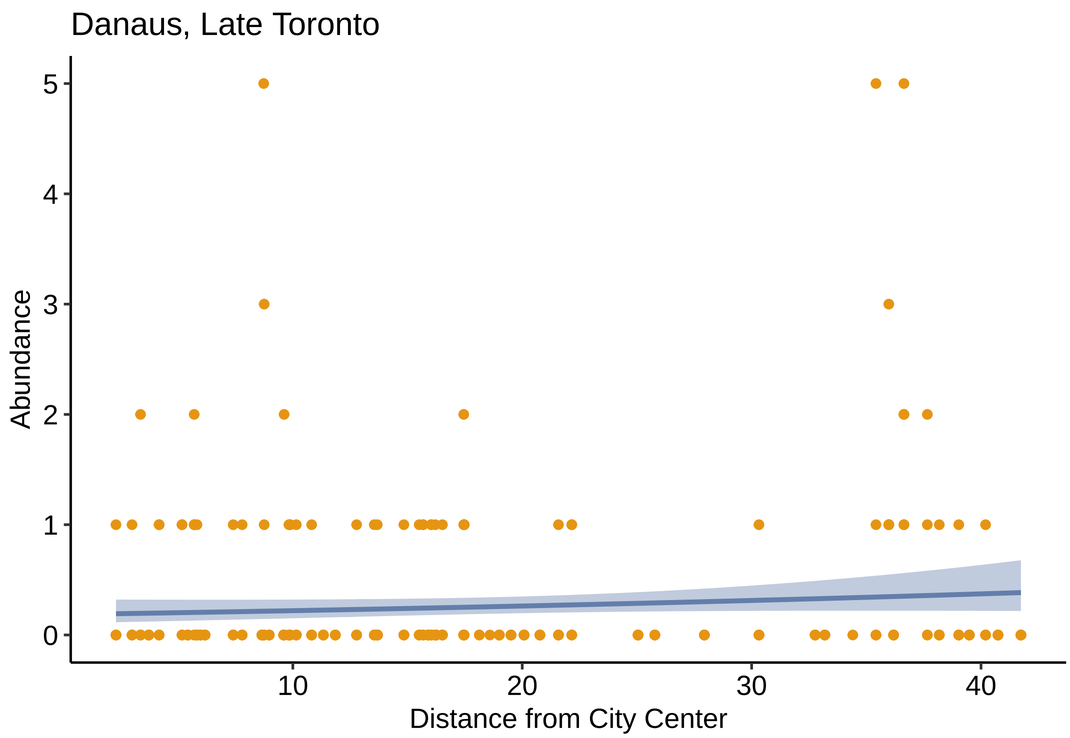

Figure 16: Plot of Danaus abundance against distance from city center for the late season in Toronto.

Late Season Danaus, 5 Cities

Table 23: Summary of the late season Danaus model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	0.147	1	0.701
City	1.082	4	0.897
Habitat:City	0.000	4	1.000

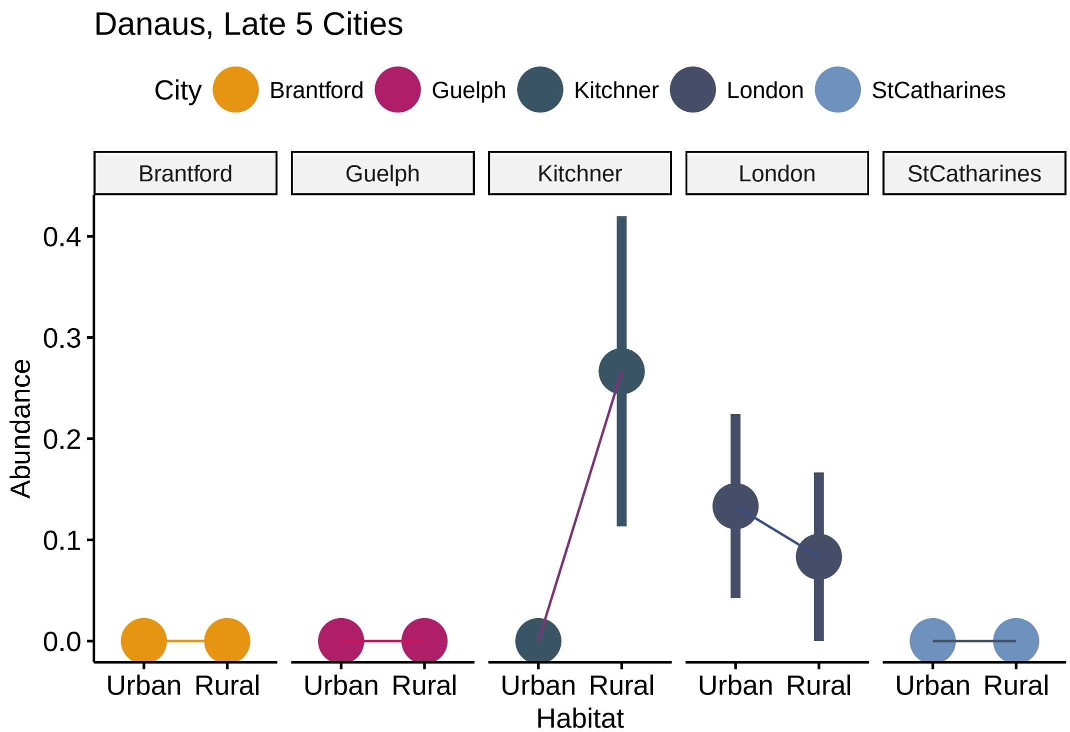

Figure 17: Plot of Danaus abundance by habitat and city for the late season across the 5 Cities. Lines connect urban and rural habitats for each city.

Rhysomatus

Early Season Rhysomatus, Toronto

Table 24: Summary of the early season Rhysomatus model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	5.178	1	0.023

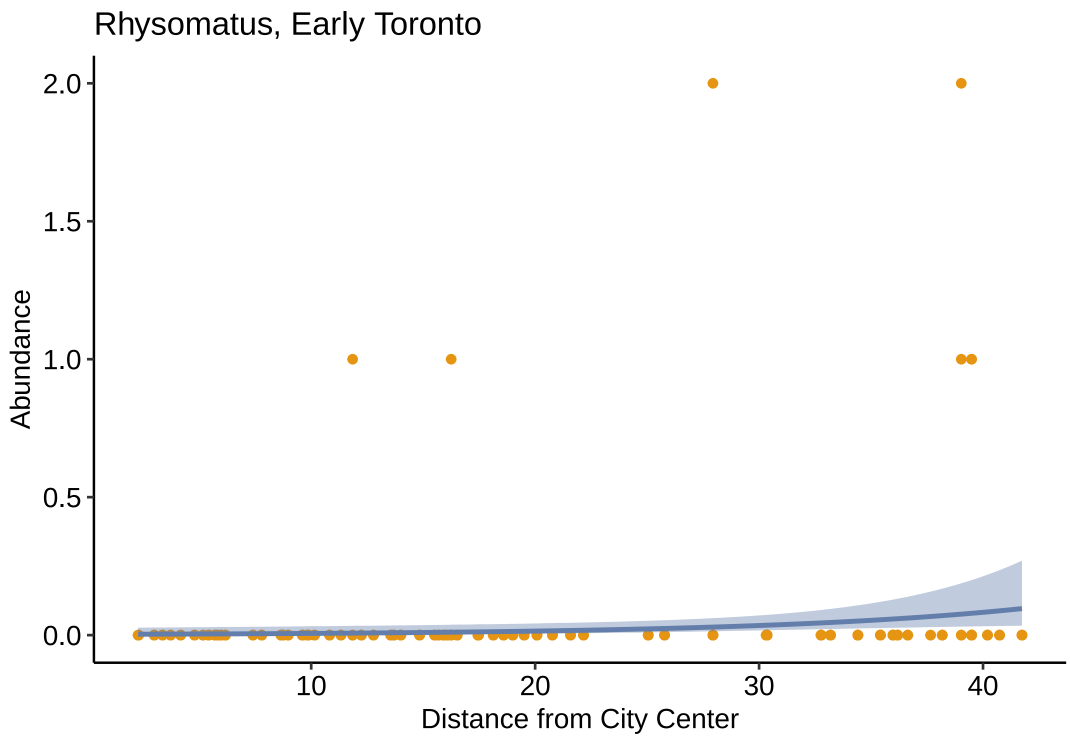

Figure 18: Plot of Rhysomatus abundance against distance from city center for the early season in Toronto.

Early Season Rhysomatus, 5 Cities

Table 25: Summary of the early season Rhysomatus model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	0.259	1	0.611
City	4.951	4	0.292
Habitat:City	0.741	4	0.946

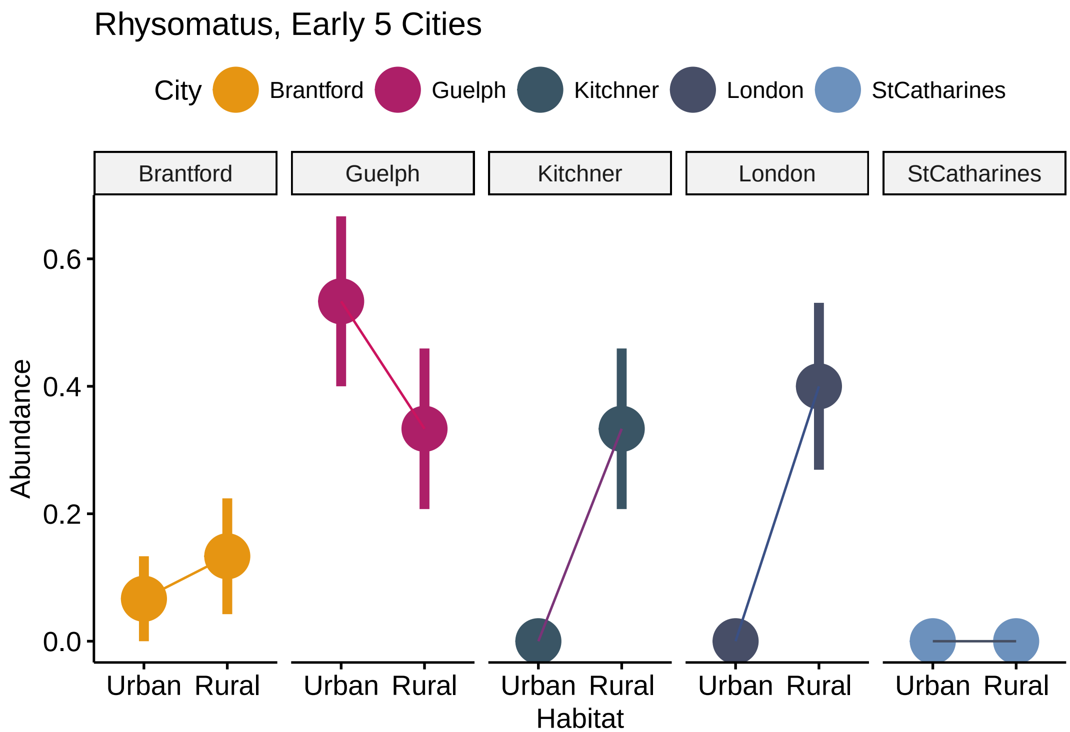

Figure 19: Plot of Rhysomatus abundance by habitat and city for the early season across the 5 Cities. Lines connect urban and rural habitats for each city.

Late Season Rhysomatus, Toronto

Table 26: Summary of the late season Rhysomatus model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.008	1	0.929

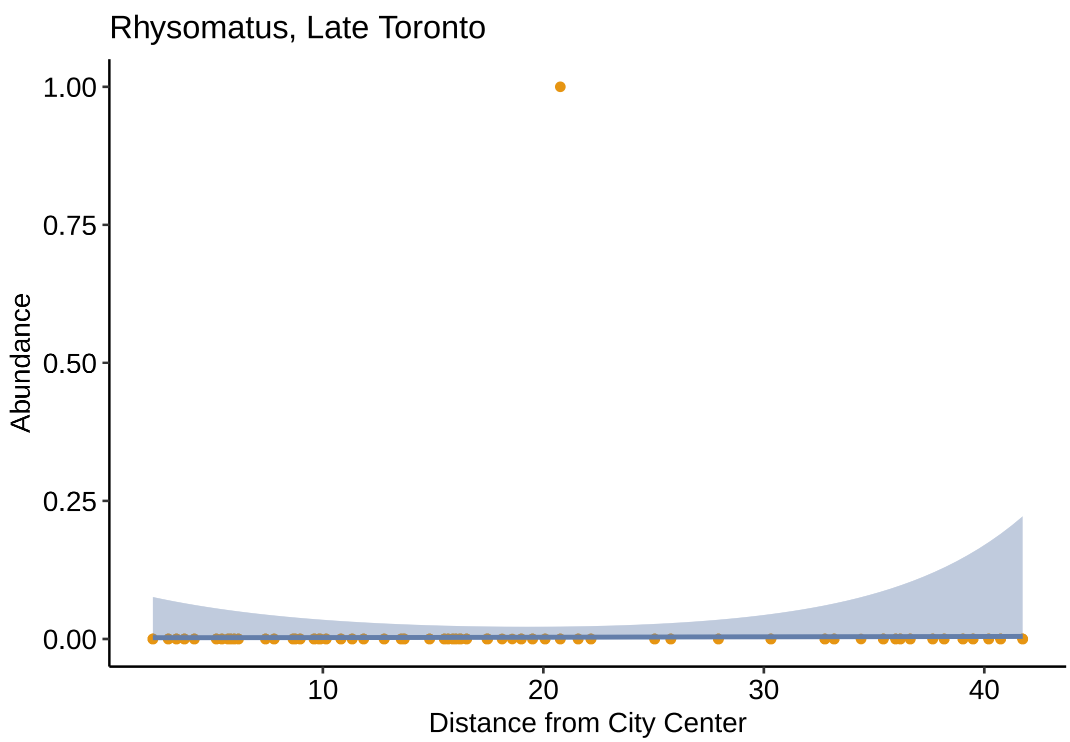

Figure 20: Plot of Rhysomatus abundance against distance from city center for the late season in Toronto.

Late Season Rhysomatus, 5 Cities

Insufficient *Rhysomatus* were collected to fit a model.

Aphis

Early Season Aphis, Toronto

Table 27: Summary of the early season Aphis model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.118	1	0.731

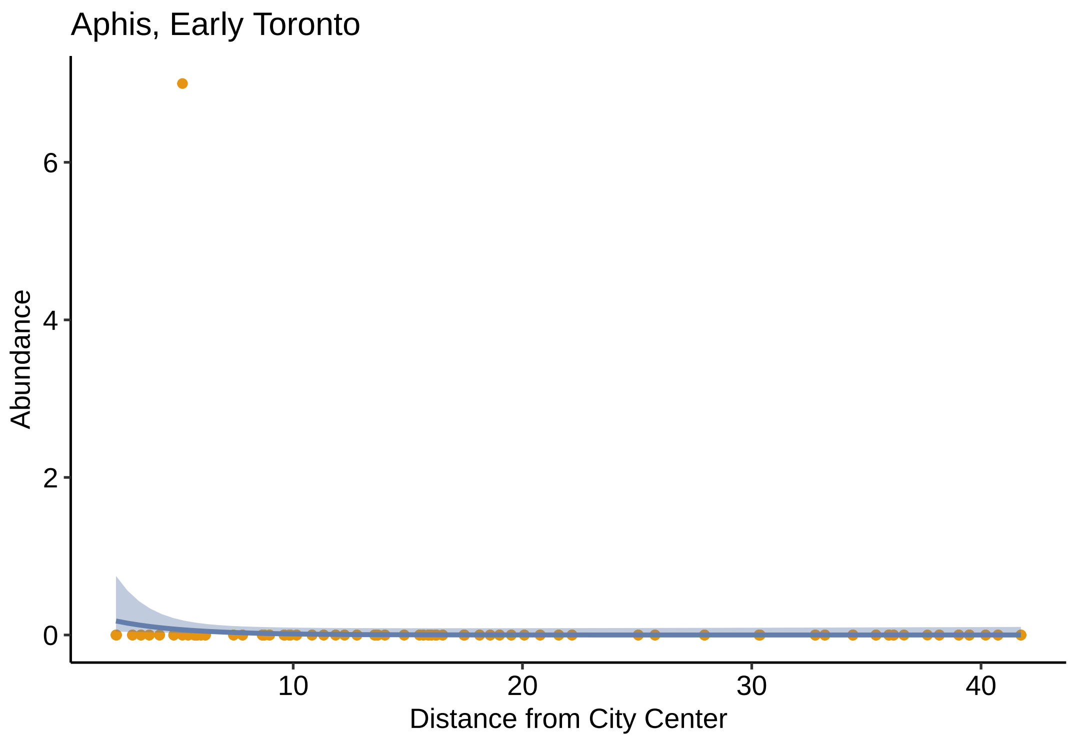

Figure 21: Plot of Aphis abundance against distance from city center for the early season in Toronto.

Early Season Aphis, 5 Cities

Insufficient *Aphis* were collected to fit a model.

Late Season Aphis, Toronto

Table 28: Summary of the late season Aphis model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.028	1	0.867

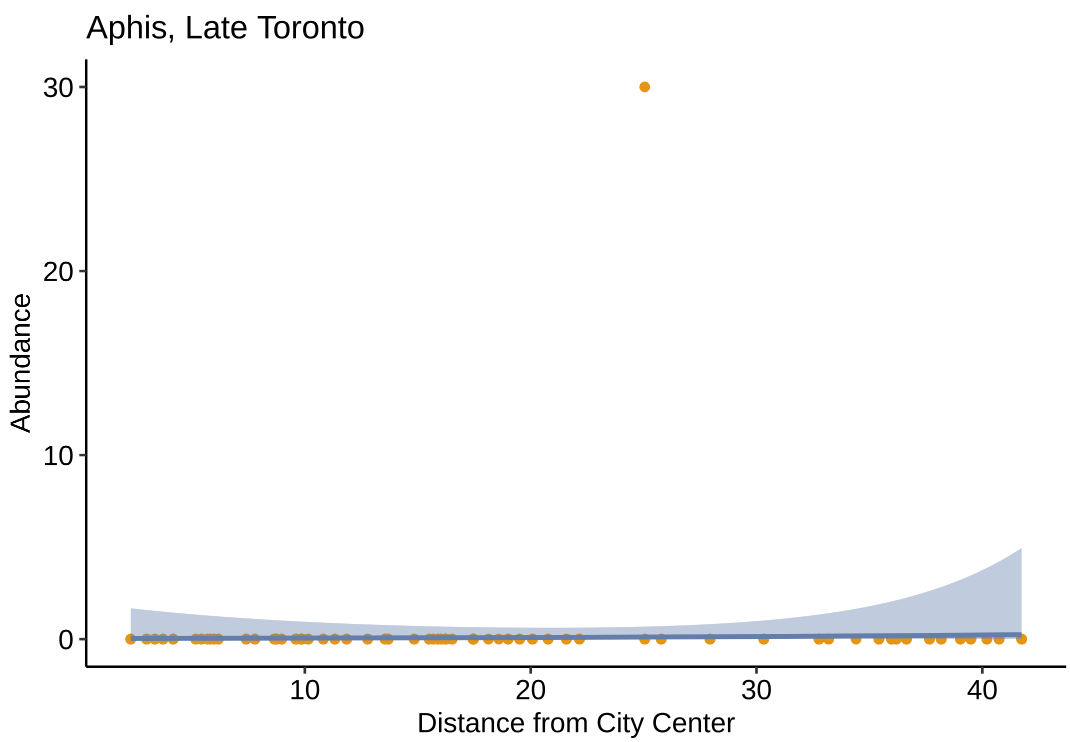

Figure 22: Plot of Aphis abundance against distance from city center for the late season in Toronto.

Late Season Aphis, 5 Cities

Insufficient *Aphis* were collected to fit a model.

Tetraopes

Early Season Tetraopes, Toronto

Table 29: Summary of the early season Tetraopes model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.056	1	0.814

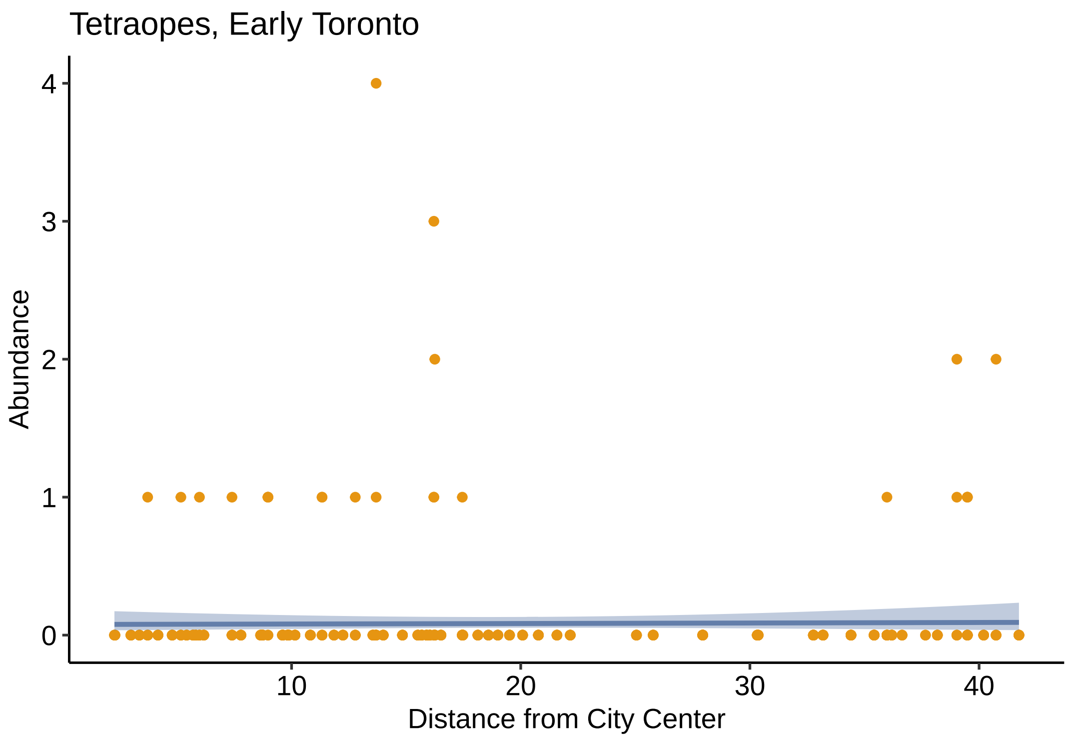

Figure 23: Plot of Tetraopes abundance against distance from city center for the early season in Toronto.

Early Season Tetraopes, 5 Cities

Table 30: Summary of the early season Tetraopes model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	0.933	1	0.334
City	2.397	4	0.663
Habitat:City	0.000	4	1.000

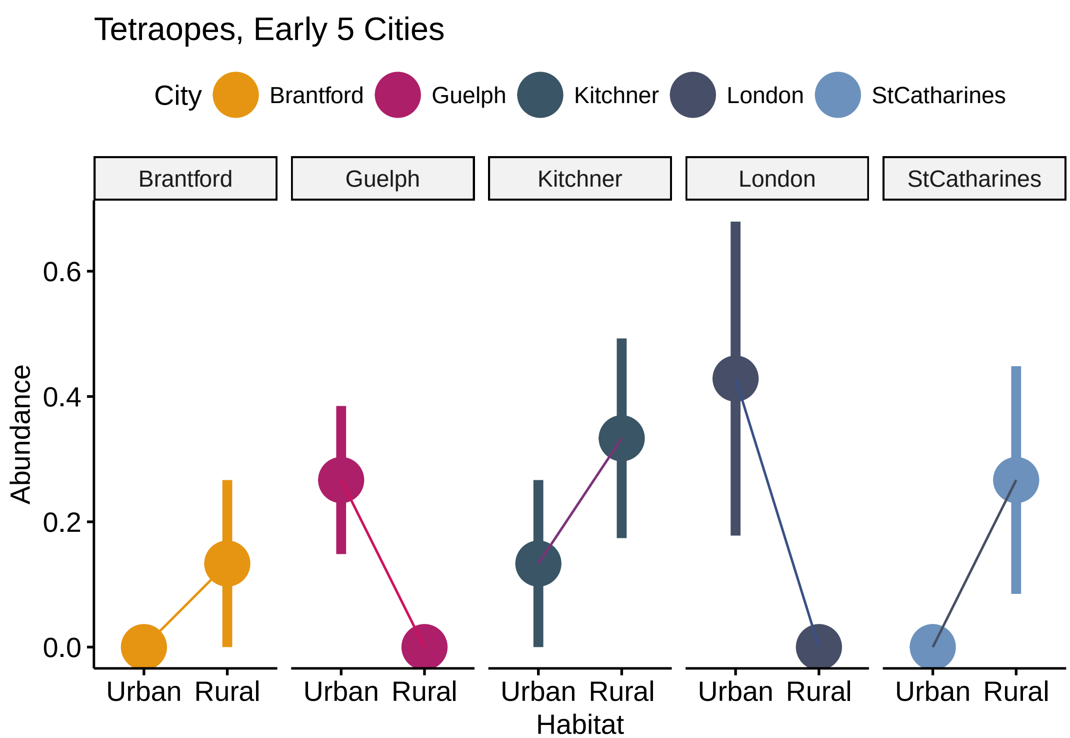

Figure 24: Plot of Tetraopes abundance by habitat and city for the early season across the 5 Cities. Lines connect urban and rural habitats for each city.

Late Season Tetraopes, Toronto

Table 31: Summary of the late season Tetraopes model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.076	1	0.783

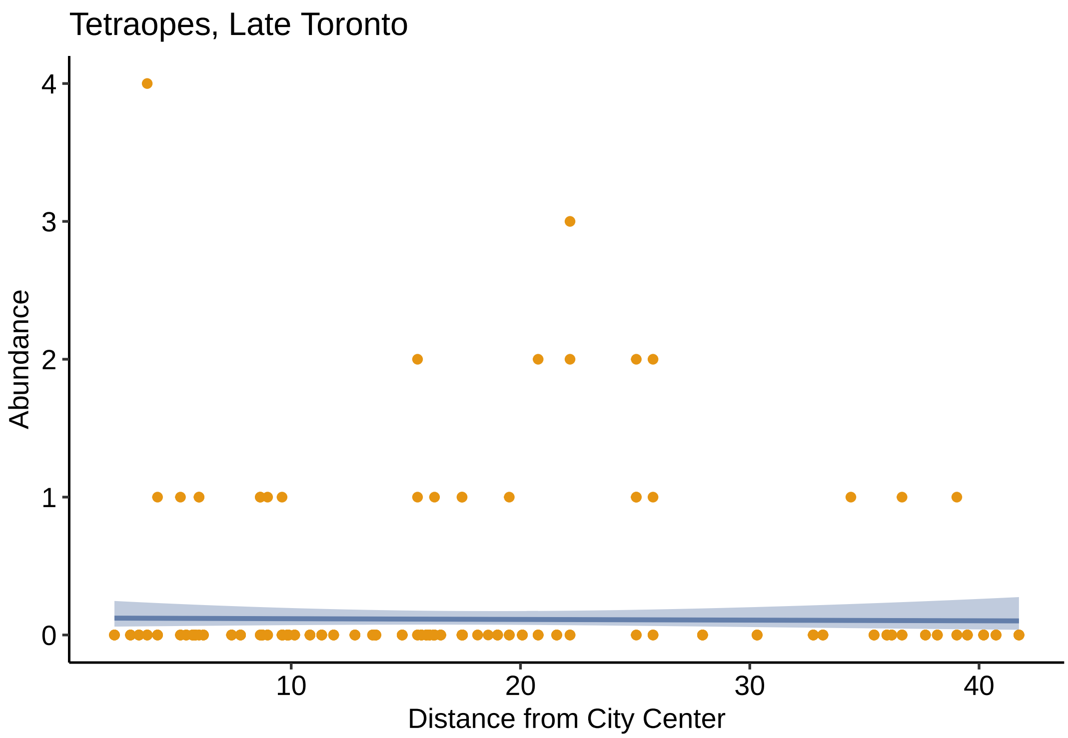

Figure 25: Plot of Tetraopes abundance against distance from city center for the late season in Toronto.

Late Season Tetraopes, 5 Cities

Insufficient *Tetraopes* were collected to fit a model.

Liriomyza

Early Season Liriomyza, Toronto

Table 32: Summary of the early season Liriomyza model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	0.612	1	0.434

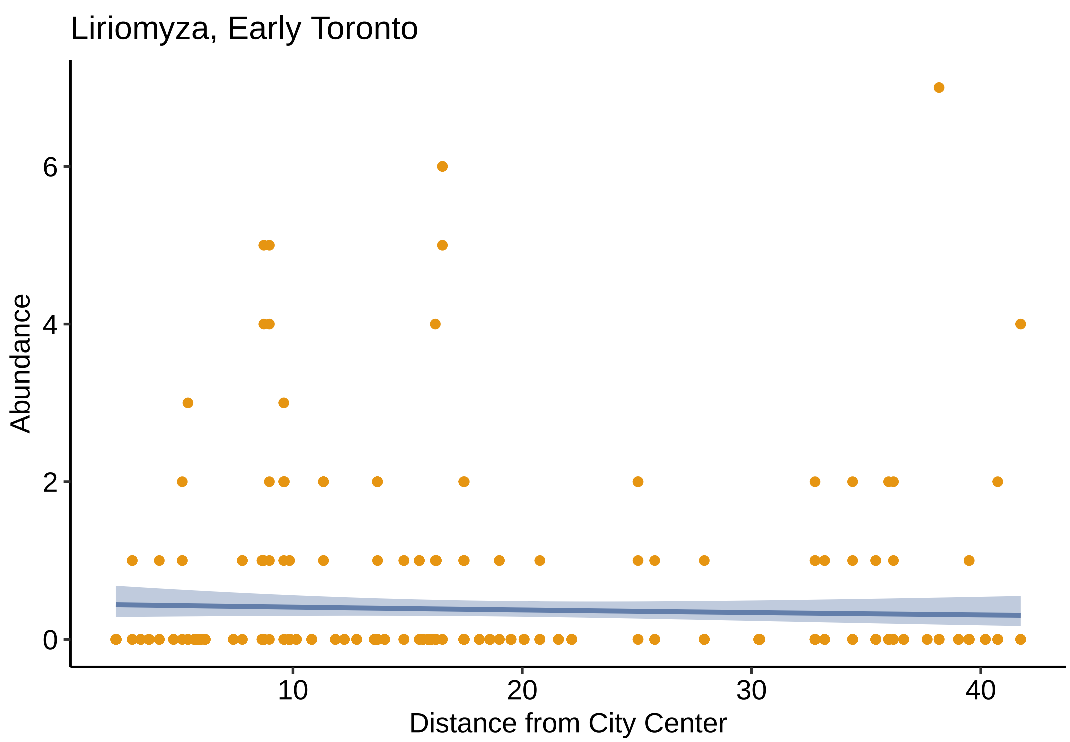

Figure 26: Plot of Liriomyza abundance against distance from city center for the early season in Toronto.

Early Season Liriomyza, 5 Cities

Table 33: Summary of the early season Liriomyza model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	1.353	1	0.245
City	3.193	4	0.526
Habitat:City	3.565	4	0.468

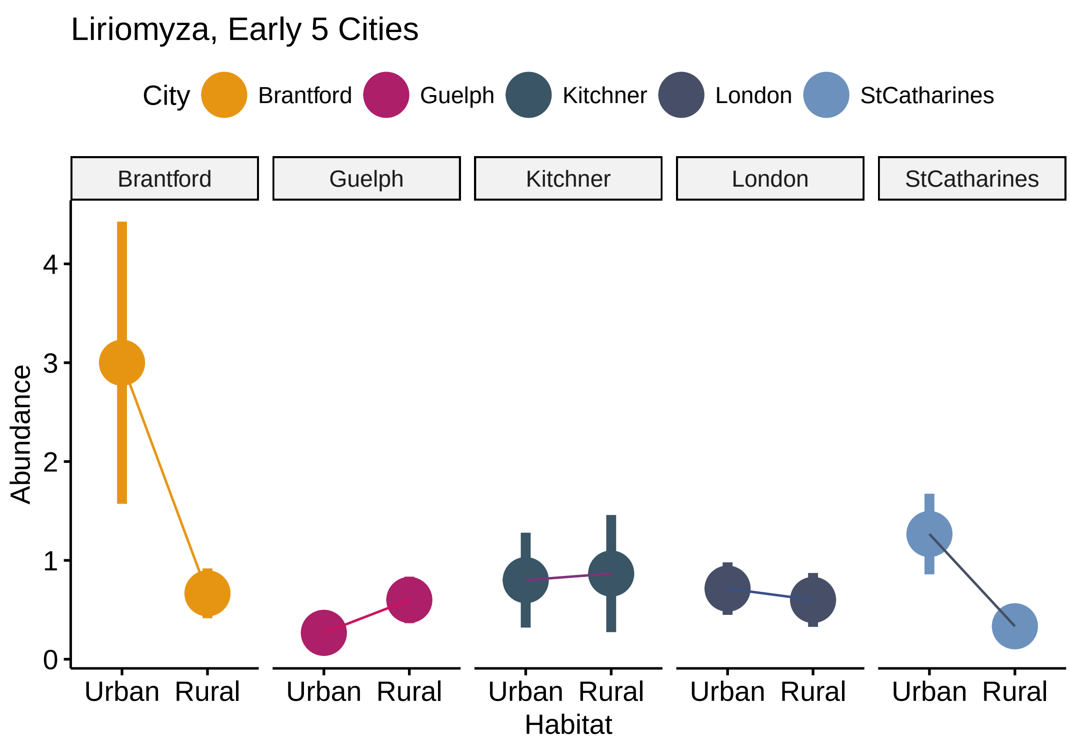

Figure 27: Plot of Liriomyza abundance by habitat and city for the early season across the 5 Cities. Lines connect urban and rural habitats for each city.

Late Season Liriomyza, Toronto

Table 34: Summary of the late season Liriomyza model for Toronto with Type II sums-of-squares.

Term	chi-squared	df	P-value
Distance	19.921	1	0

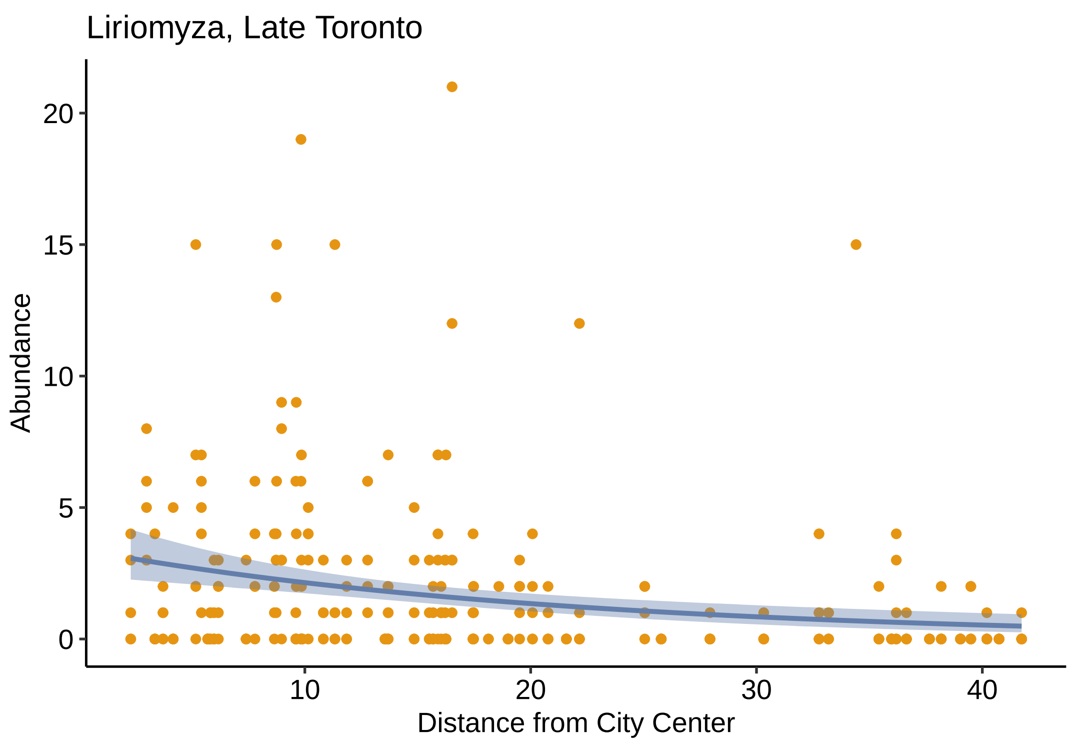

Figure 28: Plot of Liriomyza abundance against distance from city center for the late season in Toronto.

Late Season Liriomyza, 5 Cities

Table 35: Summary of the late season Liriomyza model for the 5 Cities with Type II sums-of-squares.

Term	chi-squared	df	P-value
Habitat	6.370	1	0.012
City	7.024	4	0.135
Habitat:City	17.088	4	0.002

Table 36: Post-hoc comparisons of the main effect of habitat for Liriomyza for the early season 5 Cities, where 1 = Rural and 2 = Urban.

Habitat	estimate	std.error	df	z.ratio	p.value
1	0.327	0.204	Inf	1.605	0.108
2	-0.501	0.264	Inf	-1.896	0.058

Table 37: Post-hoc comparisons of the interaction between city and habitat for Liriomyzay for the late season 5 Cities, where 1 = Rural and 2 = Urban.

Habitat	term	contrast	null.value	estimate	std.error	df	z.ratio	adj.p.value
1	City	Brantford - Guelph	0	1.931	0.618	Inf	3.124	0.015
1	City	Brantford - Kitchner	0	0.529	0.556	Inf	0.951	0.877
1	City	Brantford - London	0	1.127	0.579	Inf	1.946	0.293
1	City	Brantford - StCatharines	0	2.361	0.659	Inf	3.581	0.003
1	City	Guelph - Kitchner	0	-1.402	0.625	Inf	-2.241	0.165
1	City	Guelph - London	0	-0.803	0.645	Inf	-1.246	0.724
1	City	Guelph - StCatharines	0	0.431	0.717	Inf	0.600	0.975
1	City	Kitchner - London	0	0.598	0.588	Inf	1.018	0.847
1	City	Kitchner - StCatharines	0	1.832	0.667	Inf	2.747	0.047
1	City	London - StCatharines	0	1.234	0.681	Inf	1.813	0.366
2	City	Brantford - Guelph	0	-0.705	0.675	Inf	-1.044	0.835
2	City	Brantford - Kitchner	0	-0.344	0.695	Inf	-0.495	0.988
2	City	Brantford - London	0	1.307	0.957	Inf	1.365	0.650
2	City	Brantford - StCatharines	0	-0.750	0.741	Inf	-1.011	0.850
2	City	Guelph - Kitchner	0	0.361	0.644	Inf	0.561	0.981
2	City	Guelph - London	0	2.012	0.923	Inf	2.180	0.187
2	City	Guelph - StCatharines	0	-0.045	0.701	Inf	-0.064	1.000
2	City	Kitchner - London	0	1.651	0.935	Inf	1.765	0.394
2	City	Kitchner - StCatharines	0	-0.406	0.719	Inf	-0.565	0.980
2	City	London - StCatharines	0	-2.057	0.976	Inf	-2.108	0.217

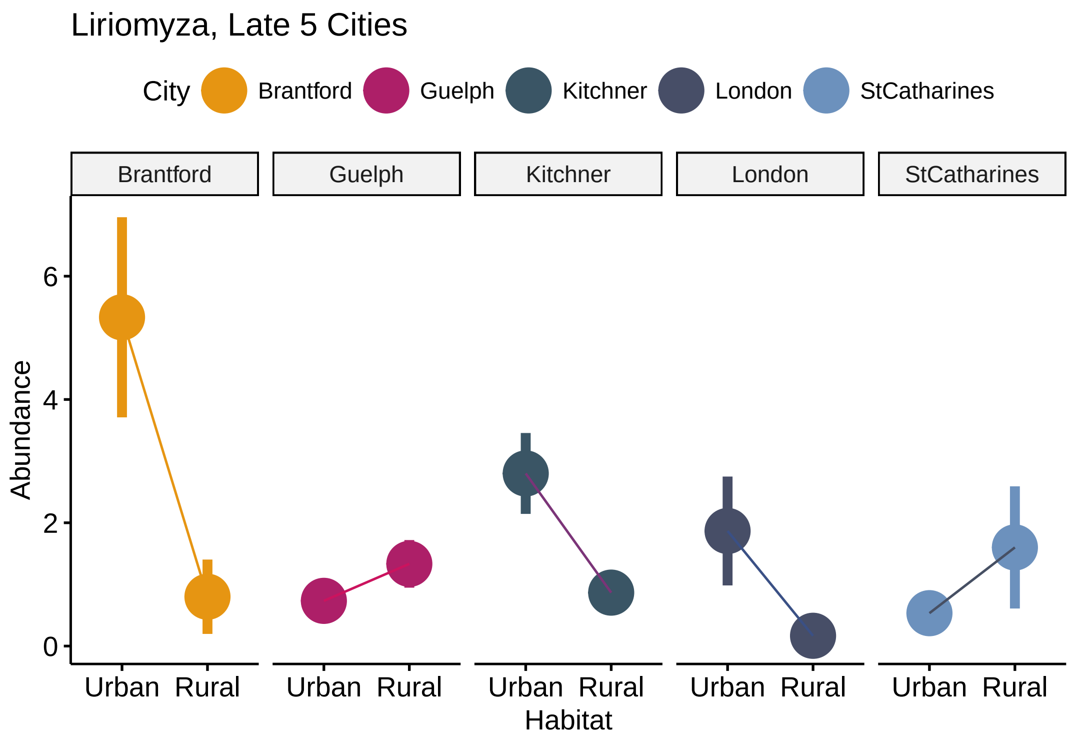

Figure 29: Plot of Liriomyza abundance by habitat and city for the late season across the 5 Cities. Lines connect urban and rural habitats for each city.

Piecewise Structural Equation Modelling

Piecewise SEM is a flexible form of confirmatory path analysis that allows for non-normal distributions, hierarchical data structures, and correlated data (Lefcheck, 2015). In contrast to traditional SEM that assesses the variance-covariance of the entire model structure (i.e., global estimation; Grace, 2006), pSEM separately evaluates each model in the structural equation set (i.e., local estimation; Lefcheck, 2015). We fitted pSEMs to test for (1) effects of urbanization, (2) effects of herbivore species interactions, and (3) the combined effects of urbanization and species interactions within and between seasons during the sampling periods. Species were pruned from the focal list if that species did not (1) comprise at least 5% relative abundance of the total insect abundance and (2) occur in at least 5% of the populations.

For more information on pSEM and SEM:

Lefcheck, J. S. 2015, piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology & Evolution* 7: 573-579.

Grace, J. B. 2006. Structural Equation Modeling and Natural Systems. *Cambridge University Press.*

Grace, J. B., et al. 2010. On the specification of structural equation models for ecological systems. *Ecological Monographs* 80: 67-87.

Pathway Matrix

Table 38: Matrix of causal pathways from early (columns) to late (rows) taxa, with 1 indicating a causal pathway between the two taxa from early to late period. Correlations within trial periods will be fitted for herbivores as a measure of potential competition or antagonism.

	Danaus	Rhysomatus	Aphis	Tetraopes	Liriomyza
Danaus	1	0	1	1	1
Rhysomatus	1	1	1	1	1
Aphis	1	0	1	1	1
Tetraopes	1	0	1	1	1
Liriomyza	1	0	1	1	1

Urbanization pSEM

Table 39: Path coefficients for each causal and correlational pathway in the herbivore pSEM for the Toronto dataset. Global model fit: Fisher's $C = 79.403, df = 90, P = 0.780$; AIC = 119.403. R^2 values for endogenous variables: $Danaus_{early} = 0.01, Danaus_{late} = 0.04, Rhysomatus_{early} = 0.10, Rhysomatus_{late} = 0.01, Aphis_{early} = 0.21, Aphis_{late} = 0.08, Tetraopes_{early} < 0.01, Tetraopes_{late} < 0.01, Liriomyza_{early} = 0.04, Liriomyza_{late} = 0.09$.

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate
Danaus.early	Distance	-0.012	0.021	64	-0.560	0.576	-0.077
Danaus.late	Distance	-0.029	0.022	64	-1.335	0.182	-0.184
Rhysomatus.early	Distance	0.065	0.039	64	1.654	0.098	0.384
Rhysomatus.late	Distance	0.019	0.082	64	0.229	0.819	0.121
Aphis.early	Distance	-0.162	0.086	64	-1.882	0.060	-0.722
Aphis.late	Distance	-0.060	0.036	64	-1.662	0.097	-0.358
Tetraopes.early	Distance	0.002	0.025	64	0.063	0.950	0.010
Tetraopes.late	Distance	-0.007	0.024	64	-0.284	0.777	-0.044
Liriomyza.early	Distance	0.032	0.022	64	1.441	0.150	0.203
Liriomyza.late	Distance	-0.052	0.028	64	-1.863	0.062	-0.315

Herbivore pSEM

Table 40: Path coefficients for each causal and correlational pathway in the herbivore pSEM for the Toronto dataset. Global model fit: Fisher's $C = 1.404, df = 10, P = 0.999$; AIC = 51.404. R^2 values for endogenous variables: $Danaus_{late} = 0.22, Rhysomatus_{late} = 0.02, Aphis_{late} = 0.17, Tetraopes_{late} = 0.17, Liriomyza_{late} = 0.12$.

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate	
Danaus.late	Danaus.early	0.222	0.5544	60	0.400	0.689	0.020	
Danaus.late	Rhysomatus.early	-1.565	1.1915	60	-1.313	0.189	-0.077	
Danaus.late	Aphis.early	17.144	1585.7562	60	0.011	0.991	0.916	
Danaus.late	Tetraopes.early	-0.127	0.6619	60	-0.191	0.848	-0.010	
Danaus.late	Liriomyza.early	-0.755	0.5659	60	-1.333	0.182	-0.070	
~~Danaus.early	~~Rhysomatus.early	0.031	-	64	0.251	0.803	0.031	
~~Danaus.early	~~Aphis.early	0.183	-	64	1.488	0.142	0.183	
~~Danaus.early	~~Tetraopes.early	0.059	-	64	0.476	0.636	0.059	
~~Danaus.early	~~Liriomyza.early	0.206	-	64	1.680	0.098	0.206	
~~Danaus.late	~~Rhysomatus.late	-0.130	-	66	-1.040	0.151	-0.130	
~~Danaus.late	~~Aphis.late	0.209	-	66	1.696	0.048	0.209	*
~~Danaus.late	~~Tetraopes.late	-0.214	-	66	-1.736	0.044	-0.214	*
~~Danaus.late	~~Liriomyza.late	-0.081	-	66	-0.646	0.260	-0.081	
Rhysomatus.late	Rhysomatus.early	-15.472	4809.3409	64	-0.003	0.997	-0.915	
~~Rhysomatus.early	~~Liriomyza.early	0.031	-	64	0.251	0.803	0.031	
~~Rhysomatus.late	~~Liriomyza.late	0.040	-	66	0.314	0.377	0.040	
Aphis.late	Danaus.early	-0.152	0.7484	60	-0.204	0.839	-0.016	
Aphis.late	Rhysomatus.early	-16.381	1716.5214	60	-0.010	0.992	-0.926	
Aphis.late	Aphis.early	1.768	0.9826	60	1.800	0.072	0.109	
Aphis.late	Tetraopes.early	1.092	0.7697	60	1.419	0.156	0.098	
Aphis.late	Liriomyza.early	-0.097	0.7305	60	-0.133	0.894	-0.010	
~~Aphis.early	~~Rhysomatus.early	-0.090	-	64	-0.727	0.470	-0.090	
~~Aphis.early	~~Tetraopes.early	-0.046	-	64	-0.366	0.715	-0.046	
~~Aphis.early	~~Liriomyza.early	-0.135	-	64	-1.088	0.281	-0.135	
~~Aphis.late	~~Rhysomatus.late	-0.046	-	66	-0.362	0.359	-0.046	
~~Aphis.late	~~Tetraopes.late	0.287	-	66	2.377	0.010	0.287	*
~~Aphis.late	~~Liriomyza.late	0.062	-	66	0.494	0.311	0.062	
Tetraopes.late	Danaus.early	-0.311	0.6109	60	-0.509	0.611	-0.030	
Tetraopes.late	Rhysomatus.early	0.050	1.0518	60	0.047	0.962	0.003	
Tetraopes.late	Aphis.early	-16.388	1578.7479	60	-0.010	0.992	-0.914	
Tetraopes.late	Tetraopes.early	1.090	0.6712	60	1.624	0.104	0.089	
Tetraopes.late	Liriomyza.early	0.542	0.633	60	0.856	0.392	0.052	
~~Tetraopes.early	~~Rhysomatus.early	0.255	-	64	2.106	0.039	0.255	*
~~Tetraopes.early	~~Liriomyza.early	0.132	-	64	1.065	0.291	0.132	
~~Tetraopes.late	~~Rhysomatus.late	0.199	-	66	1.611	0.056	0.199	
~~Tetraopes.late	~~Liriomyza.late	0.111	-	66	0.890	0.188	0.111	
Liriomyza.late	Danaus.early	-0.409	0.709	61	-0.577	0.564	-0.041	
Liriomyza.late	Rhysomatus.early	-0.124	1.2033	61	-0.103	0.918	-0.007	
Liriomyza.late	Aphis.early	16.426	1579.2807	61	0.010	0.992	0.948	
Liriomyza.late	Liriomyza.early	1.119	0.7182	61	1.558	0.119	0.112	

Urbanization + Herbivore pSEM

Table 41: Path coefficients for each causal and correlational pathway in the herbivore pSEM for the Toronto dataset. Global model fit: Fisher's $C = 2.218, df = 10, P = 0.994$; AIC = 82.218. R^2 values for endogenous variables: $Danaus_{early} = 0.01, Danaus_{late} = 0.22, Rhysomatus_{early} = 0.10, Rhysomatus_{late} = 0.03, Aphis_{early} = 0.21, Aphis_{late} = 0.19, Tetraopes_{early} < 0.01, Tetraopes_{late} = 0.19, Liriomyza_{early} = 0.04, Liriomyza_{late} = 0.21$.

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate	
Danaus.early	Distance	-0.012	0.0213	64	-0.560	0.576	-0.077	
Danaus.late	Distance	-0.007	0.024	59	-0.296	0.767	-0.015	
Danaus.late	Danaus.early	0.211	0.556	59	0.380	0.704	0.020	
Danaus.late	Rhysomatus.early	-1.502	1.211	59	-1.240	0.215	-0.074	
Danaus.late	Aphis.early	17.082	1586.8512	59	0.011	0.991	0.912	
Danaus.late	Tetraopes.early	-0.150	0.6688	59	-0.224	0.823	-0.012	
Danaus.late	Liriomyza.early	-0.724	0.5747	59	-1.260	0.208	-0.067	
~~Danaus.early	~~Rhysomatus.early	0.066	-	66	0.529	0.299	0.066	
~~Danaus.early	~~Aphis.early	0.206	-	66	1.673	0.050	0.206	*
~~Danaus.early	~~Tetraopes.early	0.060	-	66	0.479	0.317	0.060	
~~Danaus.early	~~Liriomyza.early	0.220	-	66	1.788	0.039	0.220	*
~~Danaus.late	~~Rhysomatus.late	-0.127	-	66	-1.014	0.157	-0.127	
~~Danaus.late	~~Aphis.late	0.201	-	66	1.630	0.054	0.201	
~~Danaus.late	~~Tetraopes.late	-0.219	-	66	-1.782	0.040	-0.219	*
~~Danaus.late	~~Liriomyza.late	-0.079	-	66	-0.630	0.266	-0.079	
Rhysomatus.early	Distance	0.065	0.0391	64	1.654	0.098	0.384	
Rhysomatus.late	Distance	0.025	0.0826	63	0.298	0.766	0.064	
Rhysomatus.late	Rhysomatus.early	-15.695	4786.7317	63	-0.003	0.997	-0.927	
~~Rhysomatus.early	~~Liriomyza.early	-0.007	-	66	-0.055	0.478	-0.007	
~~Rhysomatus.late	~~Liriomyza.late	0.037	-	66	0.296	0.384	0.037	
Aphis.early	Distance	-0.162	0.086	64	-1.882	0.060	-0.722	
Aphis.late	Distance	-0.036	0.0369	59	-0.968	0.333	-0.089	
Aphis.late	Danaus.early	-0.134	0.7696	59	-0.174	0.862	-0.014	
Aphis.late	Rhysomatus.early	-15.950	1731.749	59	-0.009	0.993	-0.903	
Aphis.late	Aphis.early	1.484	1.0175	59	1.458	0.145	0.091	
Aphis.late	Tetraopes.early	0.979	0.7775	59	1.259	0.208	0.088	
Aphis.late	Liriomyza.early	0.045	0.7557	59	0.060	0.952	0.005	
~~Aphis.early	~~Rhysomatus.early	-0.041	-	66	-0.324	0.373	-0.041	
~~Aphis.early	~~Tetraopes.early	-0.055	-	66	-0.437	0.332	-0.055	
~~Aphis.early	~~Liriomyza.early	-0.082	-	66	-0.653	0.258	-0.082	
~~Aphis.late	~~Rhysomatus.late	-0.043	-	66	-0.344	0.366	-0.043	
~~Aphis.late	~~Tetraopes.late	0.280	-	66	2.316	0.012	0.280	*
~~Aphis.late	~~Liriomyza.late	0.043	-	66	0.338	0.368	0.043	
Tetraopes.early	Distance	0.002	0.0252	64	0.063	0.950	0.010	
Tetraopes.late	Distance	-0.025	0.0274	59	-0.929	0.353	-0.057	
Tetraopes.late	Danaus.early	-0.392	0.6254	59	-0.627	0.530	-0.038	
Tetraopes.late	Rhysomatus.early	0.343	1.0867	59	0.316	0.752	0.018	
Tetraopes.late	Aphis.early	-16.554	1584.0398	59	-0.011	0.992	-0.923	
Tetraopes.late	Tetraopes.early	1.032	0.6728	59	1.534	0.125	0.084	
Tetraopes.late	Liriomyza.early	0.678	0.6591	59	1.029	0.304	0.066	
~~Tetraopes.early	~~Rhysomatus.early	0.243	-	66	1.990	0.025	0.243	*
~~Tetraopes.early	~~Liriomyza.early	0.133	-	66	1.064	0.146	0.133	
~~Tetraopes.late	~~Rhysomatus.late	0.200	-	66	1.623	0.055	0.200	
~~Tetraopes.late	~~Liriomyza.late	0.088	-	66	0.705	0.242	0.088	
Liriomyza.early	Distance	0.032	0.0224	64	1.441	0.150	0.203	
Liriomyza.late	Distance	-0.060	0.0316	60	-1.905	0.057	-0.133	
Liriomyza.late	Danaus.early	-0.494	0.7274	60	-0.679	0.497	-0.047	
Liriomyza.late	Rhysomatus.early	0.319	1.2553	60	0.254	0.799	0.016	
Liriomyza.late	Aphis.early	16.848	2558.7154	60	0.007	0.995	0.918	
Liriomyza.late	Liriomyza.early	1.415	0.7639	60	1.852	0.064	0.134	

Toronto Urban pSEM Takeaways

Table 42: Below are the ecologically relevant causal pathways from the urbanization pSEM. Note: the herbivore pSEM had better model fit.

Pathway	Standardized Estimate	P-value
$Rhysomatus_{early} \sim Distance$	0.38	0.098
$Aphis_{early} \sim Distance$	-0.72	0.060
$Aphis_{late} \sim Distance$	-0.36	0.097
$Liriomyza_{late} \sim Distance$	-0.32	0.062

Toronto Herbivore pSEM Takeaways

Table 43: Below are the ecologically relevant causal and correlational pathways from the herbivore pSEM.

Pathway	Standardized Estimate	P-value
$Danaus_{early} \sim\sim Liriomyza_{early}$	0.21	0.098
$Danaus_{late} \sim\sim Aphis_{late}$	0.21	0.048
$Danaus_{late} \sim\sim Tetraopes_{late}$	-0.21	0.044
$Aphis_{late} \sim Aphis_{early}$	0.11	0.072
$Aphis_{late} \sim\sim Tetraopes_{late}$	0.29	0.010
$Tetraopes_{early} \sim\sim Rhysomatus_{early}$	0.26	0.039
$Tetraopes_{late} \sim\sim Rhysomatus_{late}$	0.20	0.056

Toronto Urban + Herbivore pSEM Takeaways

Table 44: Below are the ecologically relevant causal and correlational pathways from the urbanization + herbivore pSEM. Note: the herbivore pSEM had better model fit.

Pathway	Standardized Estimate	P-value
$Danaus_{early} \sim\sim Aphis_{early}$	0.21	0.050
$Danaus_{early} \sim\sim Liriomyza_{early}$	0.22	0.039
$Danaus_{late} \sim\sim Aphis_{late}$	0.20	0.054
$Danaus_{late} \sim\sim Tetraopes_{late}$	-0.22	0.040
$Rhysomatus_{early} \sim Distance$	0.38	0.098
$Aphis_{early} \sim Distance$	-0.72	0.060
$Aphis_{late} \sim\sim Tetraopes_{late}$	0.28	0.012
$Tetraopes_{early} \sim\sim Rhysomatus_{early}$	0.24	0.025
$Tetraopes_{late} \sim\sim Rhysomatus_{late}$	0.20	0.055
$Liriomyza_{late} \sim Distance$	-0.13	0.057
$Liriomyza_{late} \sim Liriomyza_{early}$	0.13	0.064