



# Monitoring Terrestrial Invertebrate Communities in Restored Wetlands

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## Abstract

Invertebrates are a quintessential and often overlooked aspect of terrestrial communities. Ecosystem restoration work often monitors the success of projects through faunal inventories, but terrestrial invertebrates are not traditionally included. This leaves the effect of restoration on the composition, structure, and function of the most abundant and diverse group of terrestrial animals largely undocumented. In this study, we asked if simple sampling procedures could be used to confidently compare temperate terrestrial invertebrate communities on restoration projects. We used malaise and pitfall traps to document and compare two restored wetland ecosystems in Niagara Region, Ontario: a reference site completed in the 1970's and a test site completed in 2018. We left traps out for an 18-day period in October 2018 and collected 1218 individuals across 18 orders and 87 lower taxonomic assemblages. We found that abundance was higher in the reference restored wetland, but taxonomic richness was not. This result implies that insect biomass is lower in recently restored wetland ecosystems, but is still likely higher than in the degraded condition. We discuss that our results were limited by labour inputs, confidence in identification, and representation of true community diversity. We recommend terrestrial invertebrate monitoring continues as a part of the Global Malaise Trap Program (GMP) because this program provides opportunities for identification to the species level and more comprehensive community comparisons. By joining this international collaborative enterprise, future monitoring could contribute to a growing dataset and work towards effectively elucidating the effects of ecosystem restoration projects on terrestrial invertebrate communities.

**Keywords:** terrestrial invertebrates, animal monitoring, malaise traps, pitfall traps, ecosystem restoration, wetland ecology

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## Introduction

Invertebrates are a critical component of any environment and play a crucial role in the food web, pollination, plant material breakdown, as well as having beneficial interactions with other animals and vegetation (Mortimer *et al.*, 1998). Invertebrate populations have largely been examined through studies targeting specific species and little sampling effort is allocated to large scale biodiversity monitoring. Previously the study of individual species population decline has focused conservation concerns on individual species, while larger scale generalist studies depicted entire communities of arthropods and their biodiversity with respect to biomass (Hallmann *et al.*, 2017). A specific study done by Hallmann *et al.* has highlighted the need for conservation initiatives with respect to declining insect biodiversity and a need for further studies, highlighting a 75% decrease in flying insect biomass throughout Germany alone (Hallmann *et al.*, 2017).

With monitoring in mind, arthropods are also very useful in highlighting the health and dynamics of a particular environment. A similar system to the Ontario Benthos Biomonitoring Network, that uses benthic invertebrates as an indicator of stream health and the success of aquatic restoration initiatives, is needed for the terrestrial biome. Terrestrial invertebrates can be used in the same capacity to analyze the health of vegetation communities and ecological stability of a location. This use of bioindicators can be seen in multiple different capacities throughout literature; for example, syrphid fly populations have been analyzed in order to gain a better understanding of habitat health in rural landscapes (Burgio and Sommaggio, 2007).

Monitoring any location after a restoration initiative will give a representation of the succession of individuals back into the altered environment, as well as serve as an effective gauge of the success of the restoration initiative. This has been seen with the monitoring of vegetation success and animal monitoring protocols, implemented within the monitoring plan of restoration initiatives (Machmer and Steeger, 2002). The importance of evaluating the success of insect communities after a restoration initiative is displayed in the restoration of grasslands for example within Southern Brittan where both were closely monitored to gauge the success of the restoration (Mortimer *et al.*, 1998). Arthropods, being a critical component of any ecosystem and representing 90% of Ontario's species (NHIC, 2018), with various species that are able to be used as bioindicators (Burgio and Sommaggio, 2007), should become a mandatory component of any restoration monitoring plan.

Within this study we examine whether simple sampling procedures can be used to compare terrestrial invertebrate communities within restored wetland systems. The simple sampling procedures used in this study included malaise and pitfall traps. Malaise Traps are a sampling method that has been used extensively around the globe as an effective method for invertebrate monitoring. They have been used at various scales to get an understanding of the presence of one specific species to entire community analyses (Darling and Packer, 1988; Hallmann *et al.*, 2017). These traps function by acting as a tent that funnel individuals into a sampling jar with ethanol for later collection. These traps, unlike others, are not specific to individuals and will target aerial individuals and take advantage of their instincts to flee in an upwardly direction, resulting in these traps being a very effective form of sampling (Malaise, 1937).

Pit fall traps, on the other hand, are an effective method of targeting ground dwelling and foraging species as well as flightless arthropods. These arthropods are targeted by falling into a container that has been placed flush with the ground that includes alcohol to incapacitate the individuals that fall into the trap for later collection (Missa *et al.*, 2009). The combination of simple sampling

procedures has been proven to be an appropriate measure of insect biodiversity to obtain a more representative community composition (Missa *et al*, 2009).

## Methods

### Study Areas

We analyzed and compared terrestrial invertebrate communities between two restored wetland systems. Construction of the test restoration wetland was completed in May of 2018 and was located within the Hansler Heights (HH) subdivision development in Welland, Ontario. This system is composed of a series of 7 wetland ponds extending from a storm water management pond to control water flow leaving the subdivision (L. Price, *pers. comm*). The reference wetland we sampled was located on Niagara College's Niagara on the Lake Campus and is a well-established restored wetland. The Niagara College (NC) wetland is composed of two large lagoons positioned at the base of the Niagara escarpment. We chose these two locations for comparison because they are both restored wetlands in reasonably proximity with similar ruderal plant communities.

### Malaise Traps

We used three malaise traps of the same brand and design (Figure 1). Two malaise traps were implemented at the Hansler Heights wetland and one trap was implemented at the reference wetland at Niagara College (Table 1). We manually cleared selected malaise trap locations of large debris and tall vegetation, only extending the area of the base of the malaise traps to ensure that the surrounding area remained undisturbed. To reduce the potential for damage by wind, we oriented traps so that the smallest face was in the path of the prevailing winds. We positioned the two Hansler Heights malaise traps equidistant throughout the wetland system on an elevated embankment the two rows of wetland ponds in the complex. We positioned the Niagara College

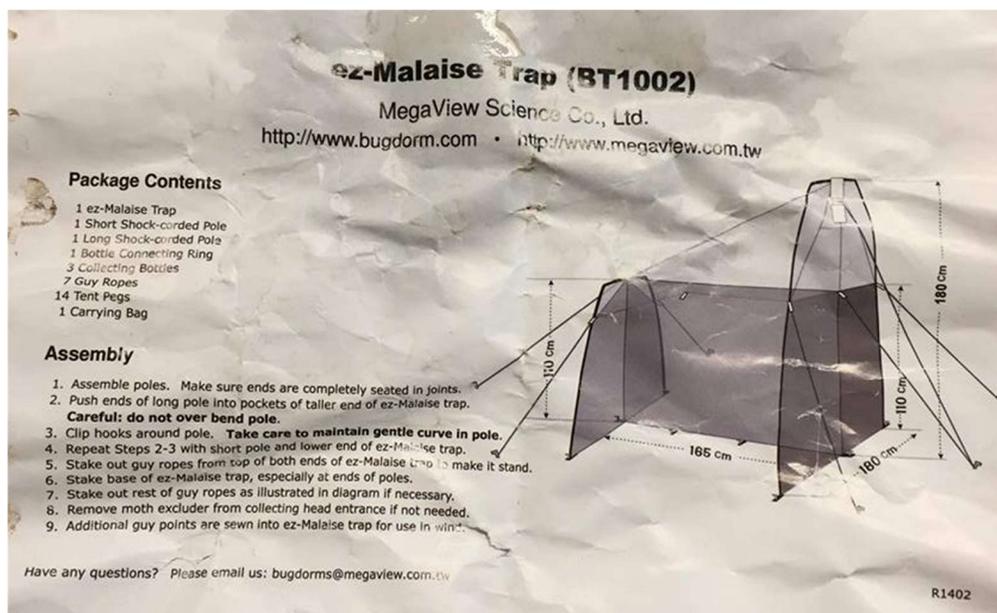


Figure 1: Malaise trap model, specifications, and set-up instructions.

malaise trap approximately 3m from the west side of the Northern most lagoon within a large patch of ruderal vegetation.

Table 1: Location, number of surveys, and number of traps of each kind at the two study areas. UTM coordinates are given in metres within zone 17N and represent the centre of the malaise trap. UTM coordinates were only taken for a single trap at the Hansler Heights location.

	Hansler Heights (Restored Site)	Niagara College (Reference Site)
<b>Malaise Traps</b>	2	1
<b>Pitfall Traps</b>	4	2
<b>Surveys (6 days each)</b>	3	2
<b>UTM Coordinates</b>	643748.336 E 4765351.939 N	649408.642 E 47779193.309 N

### **Pitfall Traps**

Pitfall traps have been used repeatedly in literature as a trapping method with little variability and high repeatability, adding a further level of arthropod examination of ground foraging and flightless individuals (Missa *et al*, 2009). Pitfall traps were implemented within this study to get a further representation of the biodiversity within the sample locations. It is understood that this sampling method can introduce error if traps are not set flush with the ground and is selective for those individuals at ground level.

Beneath each malaise trap, we set up two pitfall traps. We made the pitfall traps using a 500ml plastic cup and filled them with 125ml of ethanol to kill and preserve the individuals that fell into the trap. We buried each into the ground such that the trap edge was flush with the ground and covered them with a piece of curved aluminum to prevent debris, precipitation, or vertebrate animals from entering the trap and potentially diluting or altering the traps effectiveness (Missa, et al, 2009) (Figure 2). We placed the traps in the center of the opening on both sides of the malaise traps.



Figure 2: A pitfall trap at the Hansler Heights wetland.

### **Sampling Periods**

We collected samples from October 5-24, 2018. We conducted a pilot trial at Hansler Heights with both malaise and pitfall traps to ensure trapping methods and positioning were effective, as well as to gauge an appropriate time to leave traps before collection. During each of the two subsequent monitoring events, sites were equipped with malaise and pitfall traps on the same day and monitoring at both sites was conducted in tandem. We left traps out for 6 days before collecting specimens and storing them in 80% ethanol solution at 4°C until identification. Detailed listing of the taxonomic groupings used can be found in Appendix A, but identification was to family level using the keys in Marshall (2007) with few exceptions.

### **Data Analysis**

Based on our identification of the captured specimens, we calculated abundance (total specimens captured) and richness (number of taxonomic groups identified) for each trap type by location through time. After excluding our pilot sample with traps set up only at Hansler Heights, we fit linear models using Analysis of Variance (ANOVA) to test for differences in abundance and richness between sites, trap types, and through time. For richness, abundance was included as a covariate for richness due to the high correlation of sampling effort and diversity (Gotelli and Colwell, 2001), and we performed a log-log transformation prior to model fitting to better exemplify the nonlinearity of the relationship.

We then compared community structure through diversity accumulation curves and the Bray-Curtis Similarity Index. Diversity accumulation curves can be used to compare community richness as they rise sharply and then level off when a sample representative of the true taxonomic richness of the system is reached (Gotelli and Colwell, 2001). We qualitatively assessed if diversity accumulation curves leveled off or were still inclining for each site. Additionally, we calculated Bray Curtis Similarity Index values for comparisons within and between sites for each trap type (Bray and Curtis, 1957). We calculated this value by pooling all the specimens caught in a single trap, and determined significant differences based on the overlap of means +/- 1 standard deviation.

Because of the low replication used in this study (see Table 1), statistical analysis violated assumptions of equal sample size with consistent variation and had very low power. To compensate, we used a significance level of  $\alpha = 0.01$  instead of the standard  $\alpha = 0.05$ . However, results should be taken as an indication of potential trends. All analyses were completed using R Statistical Analysis version 3.5.2 (R Core Team, 2019).

## **Results**

In total, 1218 individual specimens were sampled and identified to 87 taxonomic groups across 18 orders of invertebrates (Appendix A). Specimens collected with malaise traps were mostly flies (order Diptera, 53%), true bugs (order Hemiptera, 21%), and wasps (order Hymenoptera, 12%). Specimens collected with pitfall traps were mostly springtails (order Collembola, 27%), wasps (order Hymenoptera, 15%), and flies (order Diptera, 14%). Of the 87 groups collected, we found 23 in both trap types (26%), 49 only in malaise traps (56%), and 15 only in pitfall traps (17%).

Model results are displayed in Appendix B for reference. Abundance was significantly higher in the reference site relative to the restored site ( $p=0.009$ ; Figure 3A). Abundance was also lower in pitfall traps relative to malaise traps ( $p<0.001$ ) and decreased with time ( $p<0.001$ ) but decreased less through time in pitfall traps relative to malaise traps ( $p=0.002$ ). Abundance was the only significant predictor of taxonomic richness ( $p<0.001$ , Figure 3B).

Species accumulation curves did not level off, indicating we did not sample enough individuals to get a representative depiction of the diversity in each site (Figure 4). Bray Curtis Similarity Index values within sites were significantly higher than comparisons between sites (Figure 5).

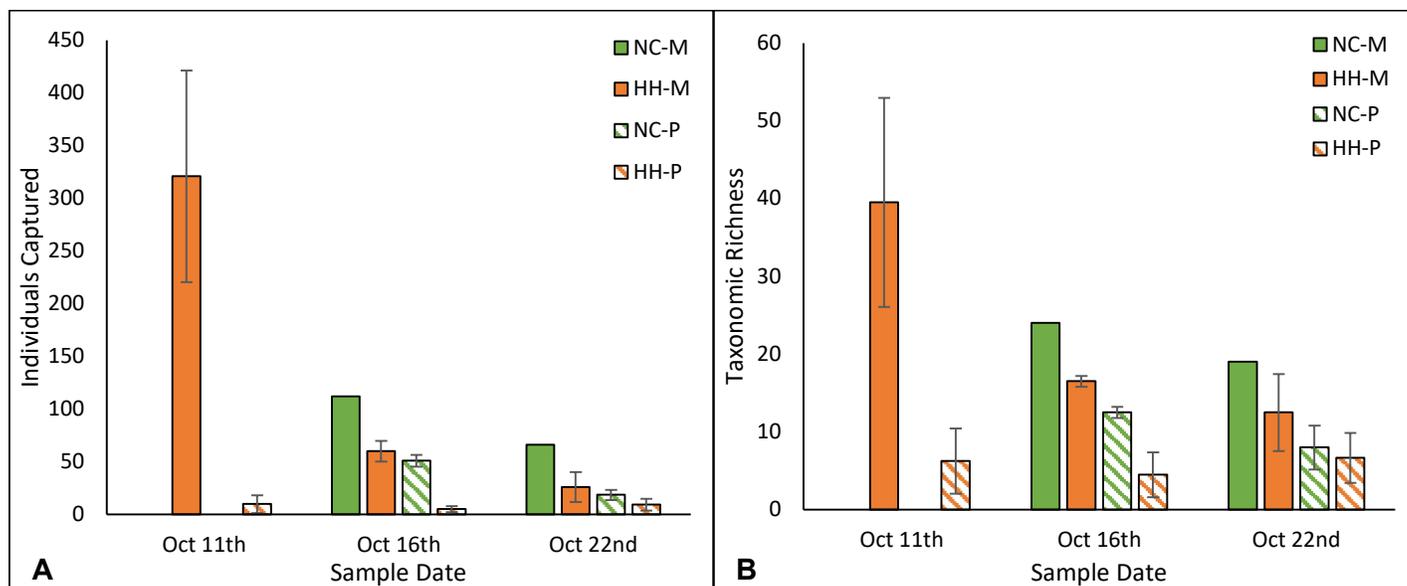


Figure 3: Abundance (A) and richness (B) for each trap type, site, and sampling day. Solid bars show malaise samples (M), striped bars show pitfall samples (P). Green bars show reference site at Niagara College Lagoons (NC), orange bars show restored site at Hansler Heights (HH). Error bars show 1 standard deviation of the mean for the given trap type, location, and sampling day. Abundance was significantly higher in the reference site ( $p=0.009$ ), lower in pitfall traps ( $p<0.001$ ), and decreased through time ( $p<0.001$ ) but decreased more in malaise traps than pitfall traps ( $p=0.002$ ). Abundance was the only significant predictor of richness ( $p=0.01$ ).

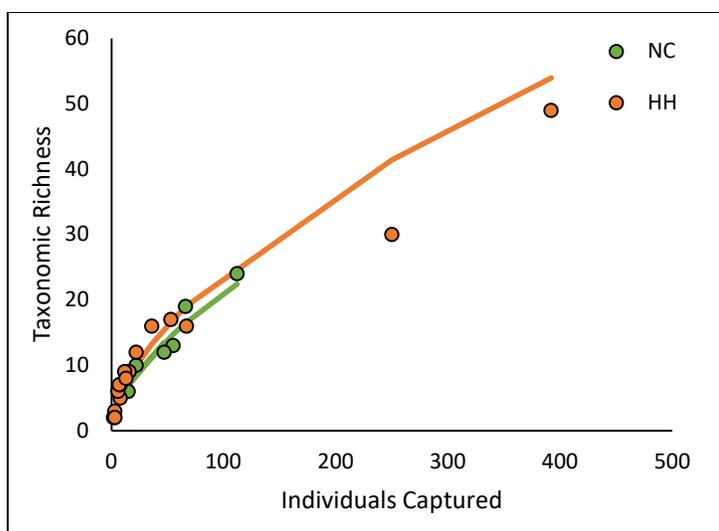


Figure 4: Diversity accumulation curves for study sites. Green dots and line show the reference site at Niagara College, orange dots and line show the restored site at Hansler Heights. Lines show log-log transformed models for each site type. The only significant predictor of richness was abundance ( $p<0.001$ ). The difference in curves between sites is shown here for illustrative purposes only and are predicted by Model B3. Curves do not level off, indicating our samples do represent the true diversity level of the study sites.

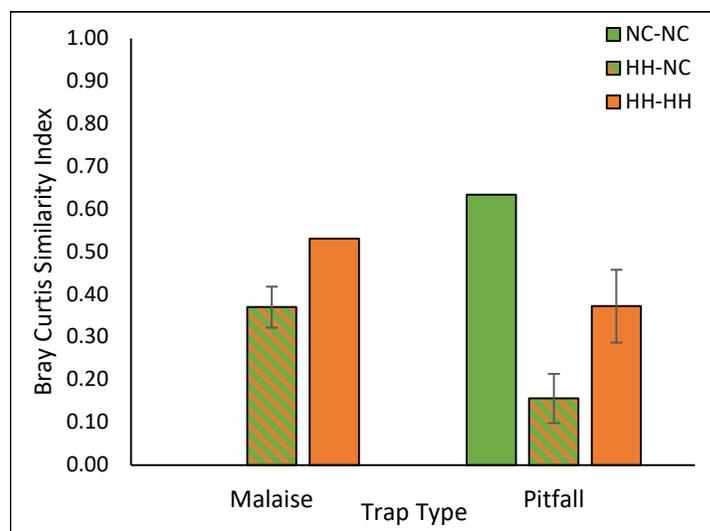


Figure 5: Average Bray-Curtis Similarity Index values for pairwise comparisons within (Solid bars) and between (dashed bars) sites by trap type. Error bars show 1 standard deviation of the mean for the given set of comparisons. Niagara College within site malaise trap comparison is absent as there was only a single trap. Communities are significantly more similar when compared within sites than between sites, indicating moderate robustness in replication of sampling units.

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## Discussion

We designed and implemented sampling procedures to compare the terrestrial invertebrate communities of restored and reference wetland ecosystems. By using two trap types over the course of three 6-day long surveys, we collected 1218 individuals across 87 taxonomic groupings. The ideal comparison to our work is the Global Malaise Trap Program (GMP) run by the Centre for Biodiversity Genomics (GMP, 2017). This program is a partnership of over 33 countries and nearly 160 sites where standardized malaise trap monitoring is paired with DNA barcoding for identification. This comparison allows us to compare the composition and abundance of the samples collected in this study, to over 7 years of extensive data collection.

Despite low trap replication, we found significantly higher abundances of invertebrates in the reference relative to the restored site. If we assume invertebrate abundance as a proxy for biomass, it becomes plausible to extrapolate that the terrestrial invertebrate communities in the Hansler Heights restored wetland will take time to reach reference levels of biomass. However, this level of biomass is likely still higher than in the degraded condition pre-restoration, and the importance of improving insect biomass through restoration is exemplified by significant global declines in insect biomass (Hallman *et al.* 2017).

The increase in abundance observed was accompanied by a higher taxonomic richness in the reference site, but this was explained by the higher number of individuals captured as opposed to an actual difference in diversity. This was apparent upon viewing the diversity accumulation curves, which neither leveled off nor differed between sites. Visual extrapolation of species accumulation curves on the GMP website revealed that flattening of species accumulation curves can take anywhere from 125,000 to over 1,000,000 individual specimens (GMP, 2017). Thus, the lack of quantifiable differences in richness between our sites is likely due to a non-representative number of individuals sampled.

Our most collected individuals were flies (order Diptera), true bugs (order Hemiptera), and wasps (order Hymenoptera), forming 86% of our malaise trap samples. This is comparable to the GMP (2017), where Dipterans, Hemipterans, and Hymenopterans comprised approximately 75% of their total sample base. An important difference in composition is the lack of moths and butterflies (order Lepidoptera) in our samples. Lepidopterans are the fourth most common specimens collected by the GMP but comprised only a small proportion of our samples. This may be attributed to our sampling late in the season and highlights the importance of additionally examining seasonal variation in community composition.

In terms of comparing community composition, both our trap types served reasonably well for replication. Bray Curtis Similarity was higher when comparing traps from the same site than when comparing traps from different sites, meaning that communities sampled were quantifiably more similar when looking within replicates from a site. This may immediately seem likely but is an important metric to consider when attempting to replicate sampling units across space and time. In order to develop more robust depictions of terrestrial invertebrate communities, higher replication of sampling units within sites is necessary.

Having multiple trap types as part of our design increased our ability to examine the terrestrial invertebrate community more holistically. Because trap types are inherently biased to collecting some taxa over others, the importance of varying sampling apparatus has been well documented in the literature (Su and Woods, 2001; Missa *et al.*, 2009). However, like invertebrate monitoring

itself, methodology diversification is frequently overlooked. Inclusion of pitfall traps allowed us to collect 15 invertebrate families that would have been otherwise undocumented. The GMP (2017) does not sample invertebrates by any other method than malaise sampling, but by invoking such methods as we have used in this study could more accurately depict terrestrial invertebrate communities.

Based on the results of our study, using simple sampling procedures to monitor terrestrial invertebrate communities in restoration projects is promising, but unlikely to be widely successful. The effort that was required to collect, process, and identify the ~1000 specimens in this study was substantial, nearing 80 manhours. Accordingly, the labour required to sample the thousands of individuals necessary to gain a representative depiction of community composition would be unrealistic. Additionally, the subjectivity associated with the dichotomous keys we used for family level identification required extensive training to circumvent, and even then, could be unreliable at times. Identification to species level was impractical, and identification to family level limits examination of the functional diversity present within the sampled community. In considering these aspects of our study, our work highlights the necessity of joining a larger collaborative monitoring program, whereby expert information, resources, and data can be shared on a scale truly elucidating the effect of ecosystem restoration on terrestrial invertebrate communities.

## Conclusions & Recommendations

Our study showed that invertebrate abundance was higher in reference restoration areas than in recent restoration areas, but our analysis was limited by unrepresentative sampling amounts, high labour required for sample processing, and a lack of directly comparable data. In order to address these and other issues outlined in our discussion, we have several recommendations for future terrestrial invertebrate monitoring endeavors by Niagara College students.

1. **Join the Global Malaise Trap Program (GMP):** this program presents funding and opportunities for more robust and consistent monitoring. Standardized traps are provided, specimens are identified to species level using DNA barcoding methods, and databases are available for comparison. This will increase the ability to compare between sites and analyze the composition, structure, and function of invertebrate communities.
2. **Increase Replication Within Sites:** In order to gain a representative depiction of community richness and composition, more replicate traps should be used. Higher replication will increase the ability to compare sites and facilitate statistical analysis.
3. **Continue to Use Variable Trap Types:** Although not an aspect of the GMP, multiple trap types are essential for viewing differences in community structure and function. If more types of sampling methods (i.e. light traps, Berlese Funnels, sticky paper, etc.) are used, it will only serve to further elucidate invertebrate diversity on sites.
4. **Sample Earlier to Avoid Massive Reductions in Biomass:** Our data clearly depicts the temporal reductions in the invertebrate community moving into autumn. Future groups should begin sampling earlier in the semester to gain a more robust depiction of community composition – ideally throughout the entirety of the spring and summer months.
5. **Collect Data on Ecosystem Parameters:** This study focused mostly on the feasibility of monitoring using simple equipment, but to truly compare invertebrate communities between areas, it becomes more important to document ecosystems properties such as weather/climate, vegetation types, hydrological characteristics, and substrate conditions.

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### Photograph Credits

Cover photograph, Figure 2: Zachary Moore, 2019

Figure 1: Taken from Baron and Cole, 2018

## Appendix A – Specimens Collected

Table A1: Number of individuals sampled at each study area by order and trap type. Blank cells indicate no specimens were found.

Order	Hansler Heights		Niagara College		Total	% Total Malaise	% Total Pitfall
	Malaise	Pitfall	Malaise	Pitfall			
acari	5	9	8	1	23	1%	4%
araneae	5	12	7	7	31	1%	8%
coleoptera	43	14	2	7	66	5%	9%
collembola	18	9	21	52	100	4%	27%
diplopoda				5	5	0%	2%
diptera	417	7	104	25	553	53%	14%
endomychidae		1			1	0%	0%
gastropoda				2	2	0%	1%
hemiptera	203	15	10	4	232	21%	8%
hymenoptera	101	13	21	22	157	12%	15%
isopoda		5		8	13	0%	6%
lepidoptera	13	1		2	16	1%	1%
lithobiomorpha				4	4	0%	2%
neuroptera			2		2	0%	0%
orthoptera		1			1	0%	0%
phthiraptera	1				1	0%	0%
psocoptera	5				5	1%	0%
thysanoptera	2				2	0%	0%
trichoptera	1		3		4	0%	0%
<b>Total</b>	<b>814</b>	<b>87</b>	<b>178</b>	<b>139</b>	<b>1218</b>		

Table A2: Number of individuals sampled at each study area by taxonomic grouping. Numbers shown combined malaise and pitfall trap results. Blank cells indicate no specimens were found.

Taxonomic Group	Hansler Heights	Niagara College	Total	Taxonomic Group	Hansler Heights	Niagara College	Total
"caterpillar"	1	1	2	drosophilidae		24	24
"centipede"		4	4	elateridae	1		1
"grub"	1		1	empididae	1		1
"maggot"	2		2	endomychidae	1		1
"millipede"		5	5	entombobryidae	12	72	84
"mite"	14	9	23	fanniidae	1		1
"moth"	13	1	14	formicidae	6	22	28
"pill beetle"	11	1	12	gryllidae	1		1
"snail"		2	2	heleomyzidae	4		4
"unknown coleoptera"	7		7	helicopsychidae		1	1
"unknown diptera"	15	1	16	hemerobiidae		2	2
"unknown trichoptera"	1	1	2	histeridae	3		3
acalyptratae		2	2	ichneumonidae	32	5	37
agelenidae	1	3	4	isotomidae	6		6
agromyzidae		1	1	latridae	6		6
amaurobiidae	11	1	12	linyphiidae		3	3
anobiidae	1		1	lycosidae		1	1
anthocoridae	3		3	miltogramminae		1	1
anthomyiidae	1		1	miridae	4		4
aphidae	17	11	28	muscidae	4		4
araneidae	1	1	2	mycetophilidae	9	9	18
bethylidae	2		2	nabidae	1		1
bostrichidae	1		1	nitidulidae	5		5
braconidae	2	8	10	oniscidae	5	8	13
bruchidae	2		2	pcp (misc.)	33	3	36
calliphoridae	3		3	parasitoid wasps)			
carabidae	3		3	phryganeidae		1	1
cecidomyiidae	10		10	phthiraptera	1		1
ceratopogonidae	81	5	86	psocidae	5		5
cercopidae	2		2	psychodidae	9	11	20
chalcidoidea	30	4	34	psyllidae	1		1
chaoboridae	3		3	ptychopteridae	2		2
chironomidae	95	26	121	salticidae	4	5	9
chloropidae	2		2	sarcophagidae	1		1
chrysomelidae	8	2	10	scathophagidae	6	1	7
cicadellidae	186	3	189	sciaridae	113	42	155
ciidae	1		1	simulidae	9	4	13
clusiidae	1		1	sminthuridae	3	1	4
coccinelidae	6	1	7	staphylinidae	7	4	11
cryptophagidae		1	1	syrphidae	7		7
cynipoidea	8	1	9	thripidae	2		2
dixidae	9	1	10	tingidae	4		4
dolichopodidae	2		2	tipulidae	33	1	34
				trichoceridae	1		1
				vespidae	1		1
				<b>Total</b>	<b>901</b>	<b>317</b>	<b>1218</b>

## Appendix B – Models

*Model B1 – Abundance (n) predicted by site, trap type and time over comparable (“comp”) surveys.*

Call:

```
lm(formula = n ~ site * trap.type * survey, data = comp)
```

Residuals:

Min	1Q	Median	3Q	Max
-10.0	-3.5	0.0	3.5	10.0

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	94.000	11.070	8.491	1.37e-05	***
siteNC	64.000	19.174	3.338	0.008690	**
trap.typeP	-93.333	13.708	-6.809	7.83e-05	***
survey	-34.000	7.001	-4.856	0.000901	***
siteNC:trap.typeP	18.833	23.570	0.799	0.444842	
siteNC:survey	-12.000	12.127	-0.990	0.348247	
trap.typeP:survey	38.333	8.810	4.351	0.001847	**
siteNC:trap.typeP:survey	-24.833	14.989	-1.657	0.131945	

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Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 7.001 on 9 degrees of freedom  
 Multiple R-squared: 0.9709, Adjusted R-squared: 0.9483  
 F-statistic: 42.95 on 7 and 9 DF, p-value: 3.32e-06

*Model B2 – Log-log Transformed Richness (S) predicted by site, trap type and time over comparable (“comp”) surveys. Because of the low sample sizes used in this study, we used the significance level of  $\alpha = 0.01$  instead of the standard  $\alpha = 0.05$ .*

Call:

```
lm(formula = log(S) ~ log(n) + site * trap.type * survey, data = comp)
```

Residuals:

Min	1Q	Median	3Q	Max
-0.31902	-0.06271	0.02790	0.08613	0.20153

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	-1.19732	0.57528	-2.081	0.0710	.
log(n)	0.86417	0.10042	8.606	2.57e-05	***
siteNC	0.07437	0.48795	0.152	0.8826	
trap.typeP	1.30224	0.54224	2.402	0.0431	*
survey	0.46792	0.20001	2.340	0.0475	*
siteNC:trap.typeP	-1.46112	0.71287	-2.050	0.0746	.
siteNC:survey	-0.24452	0.31056	-0.787	0.4538	
trap.typeP:survey	-0.51005	0.27011	-1.888	0.0957	.
siteNC:trap.typeP:survey	0.69830	0.43088	1.621	0.1438	

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.1779 on 8 degrees of freedom  
 Multiple R-squared: 0.9712, Adjusted R-squared: 0.9425  
 F-statistic: 33.78 on 8 and 8 DF, p-value: 2.232e-05

*Model B3 – Log-log Transformed Richness (S) predicted only by abundance and site using all the data collected (“data”). We used predictions from this model used to exemplify the lack of difference in diversity accumulation curves between the two study sites in Figure 4.*

Call:

```
lm(formula = log(S) ~ log(n) + site, data = data)
```

Residuals:

Min	1Q	Median	3Q	Max
-0.4221	-0.1284	0.0246	0.1726	0.3310

Coefficients:

	Estimate	Std. Error	t value	Pr(> t )	
(Intercept)	0.46748	0.11236	4.160	0.000484	***
log(n)	0.58966	0.03608	16.344	4.9e-13	***
siteNC	-0.14063	0.11500	-1.223	0.235606	

---

Signif. codes: 0 ‘\*\*\*’ 0.001 ‘\*\*’ 0.01 ‘\*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.2286 on 20 degrees of freedom

Multiple R-squared: 0.9348, Adjusted R-squared: 0.9283

F-statistic: 143.3 on 2 and 20 DF, p-value: 1.393e-12