Characterizing insect communities within thin-soil environments

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Abstract

Natural thin-soil environments are those which have little to no soil accumulation atop

hard substrates. Many of these natural thin-soil environments, such as alvars, rocky lakeshores or

glades, cliffs and cliff bluffs, and barrens, are found in the Great Lakes Region of North

America. Due to their ubiquity and ecosystem services they provide, characterizing insects in

sensitive environments such as these is important. This study monitored insects in nine thin-soil

sites, within three regions, on a 630 km latitudinal gradient in the Southeastern Great Lakes

Region of North America from June - August 2019. Over 22,000 insect specimens collected

were identified to order or family, and bee specimens were identified to genus or species. Plants

within meter-squared quadrats were identified to genus or species. We found that overall insect

community composition and biodiversity characteristics were similar between the three regions

examined. However, the southern region differed from the northern and central regions for

abundance and evenness, and from the central region for richness. Bee identity was similar

across all regions, finding no differences in biodiversity metrics and similar community

composition, but with certain taxa unique to each region. Although all regions contained unique

plant taxa, insect community characteristics were similar among them. This study provides

taxonomic information about the insect, particularly bees, and plant communities in thin-soil

environments in this region, which could support conservation and management efforts.

Introduction

Ecological communities are shaped by the physical attributes of their environments. In the Great Lakes basin, numerous globally rare habitats occur, including those characterized by their paucity of surface soil. The ecological class "Primary" is characterized by having little to no soil accumulation on top of bedrock, cobble, or exposed mineral soil. There are many natural thin-soil community types, such as alvars, rocky (cobble or bedrock) lakeshores or glades, cliffs and cliff bluffs, and barrens (Cohen et al. 2015). These habitats may experience intense wind and solar radiation, as well as varying precipitation conditions, from heavy rain to drought, due to the bedrock being at or near the surface (Stephenson and Herendeen 1986, Brunton 1988, Albert 2006). Together, these factors limit the primary producers that can survive there (Lundholm 2006), creating naturally open landscapes typically with low growing vegetation (Reschke et al. 1999). These unique and sensitive habitats are often home to rare plant and insect species adapted to these unusual environments, making them areas of research interest and conservation concern (Comer et al. 1997, Reschke et al. 1999, Albert 2006, Neufeld et al. 2018, McMullin 2019).

Insects are ubiquitous organisms that inhabit practically all terrestrial and freshwater ecosystems. In addition to their ubiquity, facilitating large scale data collection, insects play a variety of critical roles in ecosystem function and service, making them ideal sentinel organisms (Rosenberg et al. 1986). One ecosystem service provided by insects is pollination. Plant-pollinator relationships are important for biodiversity in natural and managed ecosystems (Ollerton 2017, Wei et al. 2021). Among insects, certain flies, wasps, beetles, butterflies, and moths perform pollination services, however, bees are considered to be the most efficient insect pollinator (Potts et al. 2016). Both wild and managed bee species are vital to at least 35% of crop

production (Klein et al. 2007), which is crucial for human food security (Ollerton 2017). Bees

are a diverse group of insects, with over 22,000 species worldwide. In North America, north of

Mexico, there are over 4,000 bee species (Wilson and Messinger Carril 2016). However, in

recent years, several high-profile studies have reported mass declines of insect taxa around the

globe (Fox 2013, Hallmann et al. 2017, Lister and Garcia 2018, Loboda et al. 2018, Seibold et al.

2019, Sánchez-Bayo and Wyckhuys 2019, Wepprich et al. 2019, van Klink et al. 2020, Zattara

and Aizen 2020). Bees are not immune to this global loss of biodiversity, with reports of declines

in managed (vanEngelsdorp et al. 2008, Ellis et al. 2010, Steinhauer et al. 2014) and wild bee

species (Colla and Packer 2008, Grixti et al. 2009, Cameron et al. 2011, Scheper et al. 2014, Koh

et al. 2016, Arbetman et al. 2017, Graham et al. 2021). Because of their important roles as

pollinators, characterizing bee communities in different environments, such as thin-soil

environments, is valuable for management and conservation decisions.

In the Great Lakes Region of North America, research in these rare thin-soil

environments, mostly alvars, has generally focused on identifying the taxa that occur in them or

are unique to them. Some of the characteristic rare vascular plants on Great Lakes alvars include:

Carex juniperorum W. J. Crins (Juniper sedge), *Cirsium hillii* (Canby) (Hill's thistle),

Cypripedium arietinum W. T. Aiton (Ram's head lady slipper), and *Solidago houghtonii* A. Gray

(Houghton's goldenrod), as well as *Iris lacustris* Nutt. (Dwarf lake iris) and *Tetraneuris*

herbacea Greene (Lakeside daisy), both of which are endemic to the Great Lakes. Insect taxa

that have been known to show particular affinity for alvars include: carabid beetles, cicadellids,

lepidopterans, orthopteroids, and symphytes (Reschke et al. 1999). In alvar surveys in southern

Ontario, three species of ground beetles were dominant, but rarely collected in other non-alvar

parts of the province: *Agonum nutans* (Say), *Chlaenius p. purpuricolliis* Randall, and

Pterostichus novus Straneo (Bouchard et al. 1998, 2005).

Furthermore, surveys of insects in Great Lakes thin-soil environments have largely

focused on smaller geographical regions, such as the intense sampling of alvars of Ontario,

especially the Saugeen (Bruce) Peninsula, and in Michigan near the northern shorelines of Lakes

Michigan and Huron (Albert et al. 1994, 1995, Reschke et al. 1999, Bouchard et al. 2005, Albert

2006, Cohen et al. 2015). Few surveys have occurred over the entire north-south expanse of this

ecoregion, and none have explicitly examined the communities of insects across these thin-soil

habitats spanning the region. Additionally, to our knowledge bee communities in these thin-soil

environments have not been characterized before. To address these knowledge gaps, we

conducted a study of the community composition of insects in thin-soil environments on a

latitudinal gradient across the Southeastern Great Lakes region of North America. In this study,

we examined biodiversity metrics of insect communities, including bees as our focal taxa,

between northern, central, and southern regions of this area. We predicted that even if habitats

and plant communities differed, insect communities would be similar across these three regions

because the functional traits of the community will be shaped by the abiotic traits of the

landscape.

Methods

Site descriptions

This study was conducted in thin-soil environments along a latitudinal gradient spanning

630 km in eastern North America (Figure 1). Along this gradient, three sites were selected in the

northern Bruce Peninsula in Ontario, Canada, three sites in Cuyahoga County, northeast, Ohio,

USA, and three sites in Hocking County, southeast Ohio, USA (Figure 1). All sites had thin soils

(about 15 cm or less) and typically lacked direct canopy cover, leaving them relatively open and

exposed to solar radiation, winds, and ranging precipitation conditions. Permits to collect insects

and plants were obtained for all sites in accordance with landholder policy.

Northern sites were located in the Northern Bruce Peninsula Ontario, Canada along the

Niagara escarpment and owned by The Nature Conservancy of Canada. All sites were

characterized as alvars, with little to no vegetation on limestone bedrock. The Davis alvar is

further defined as a dry lichen-moss open pavement alvar. It had the most open and flat

landscape, with sparse, low-growing vegetation. The Beaton alvar was a creeping juniper and

shrubby cinquefoil dwarf shrub alvar, with a slightly rocky landscape. The Cape Hurd Alvar was

similar to Beaton in vegetation and landscape, but closer to the lakeshore making it subject to

frequent low floods. All sites occurred in a rural landscape, primarily consisting of undeveloped

land, and protected areas, but the area had previously been subjected to heavy logging pressure.

Central sites were located in the Cleveland area in Northeast Ohio, USA, specifically in

the municipalities of Walton Hills, Parma, and Highland Heights. All sites were embedded in a

greater landscape of mixed use, urban, industrial, and semi-urban land use histories. In Walton

Hills, we sampled a thin-soil mossy barren near a hiking trail, between a meadow and forest,

near a cliff edge over a creek in the Cleveland Metroparks Bedford Reservation. Cleveland

Metroparks also owned the site in Parma, which was a roadside hill with slate shale soil, with

sparse vegetation and trees. The Highland Heights Dusty Goldenrod Preserve is owned by the

West Creek Conservancy, Cuyahoga Soil and Water Conservation District, Friends of Euclid

Creek, and Euclid Creek Watershed Council. The portion of the preserve we sampled was an

open wet meadow in a forest, with tall vegetation, sparse trees, and the only known home in

Ohio to its namesake, the rare and endangered Dusty Goldenrod (*Solidago puberula* Nutt.). This

site has thin soils due to a history of topsoil harvesting.

The southern sites were all located within the 520 hectare Crane Hollow Preserve in

Rockbridge, Southeast Ohio, USA, part of the unglaciated Allegheny Plateau. These sites

occurred in a highly rural private landscape with sparse human activity and development history.

These sites were located on cliff edges on top of deep ravines with a Black Hand sandstone

bedrock. The "W" ladder and picnic rocks sites were both named for spots along the "W" hollow

and Snyder was along Snyder hollow. All sites were open, xeric, thin-soil areas within forest,

dominated by mosses, lichens, and small shrubs. The two "W" sites were heavily covered in

reindeer lichen (*Cladonia sp.*) and American wintergreen (*Gaultheria procumbens* L.).

Field and laboratory methods

The thin soils in these habitats constrained the methods used to monitor insect

communities, preventing typical pitfall sampling from being deployed. From a conservation

standpoint, disturbing natural thin soil environments is undesirable, and from a practical

standpoint, some of these sites were bedrock with almost no soil. Due to these constraints, all

sampling had to be done above the surface level. Insects were surveyed using three types of

passive sampling traps: yellow sticky cards (Pherocon, Zoecon, Palo Alto, CA, USA), bee bowls

(also known as pan traps, inspired by Leong & Thorp, 1999), and ramp traps (ChemTica

Internacional S.A., Santo Domingo, Costa Rica) (Figure 2), evenly spaced at each site for 48

hours once per month in June, July, and August 2019. The spacing and number of traps was

dependent on the area available for sampling at the site. Number of sticky cards per site ranged

from three to six, bowls ranged from one to three, and ramp traps ranged from two to three. Each

bee bowl was an array of three different colored bowls spray painted fluorescent yellow, blue, or

white (Krylon Industrial, Cleveland, OH, USA). Sticky cards and bee bowls were placed at the

height of the plant community to collect flying insects, and ramp traps were placed on the

surface of the ground to collect ground-dwelling insects. Bowls and ramps were filled with soapy

water (Dawn Original Liquid Dish Soap, Procter & Gamble, Cincinnati, OH, USA) and had

quart zipper-top bags filled with sand placed on top to minimize wind disturbance. Upon

collection, bowls and ramps were strained in the field and samples were placed in a gallon

zipper-top bag with 70% ethanol. Sticky cards were placed directly into gallon zipper-top bags.

Vegetation was sampled at the sites in July-August 2019 by placing a meter-squared

quadrat in a well-vegetated location within the site and identifying the vascular plants to species

or genus (det. John Gerrath, Joe Moosburgger, and Glenn Vande Water) (Table S1). The trees

that directly surrounded the sites, as well as prominent plant species that were not inside the

quadrat were also recorded but not included in the analyses.

In the lab, the liquid samples were strained, and specimens were identified and placed in

vials with 70% ethanol for storage. The sticky cards were frozen and specimens were identified

while remaining in the bag, afterwards they remained stored in the freezer. Specimens were

identified to order (Blattodea, Diptera, Ephemeroptera, Lepidoptera, Mecoptera, Neuroptera,

Orthoptera, Psocodea, Thysanoptera, Trichoptera, Zygoptera), suborder (Symphyta), superfamily

(Apoidea, Chalcidoidea, Ichneumonoidea), group ("wingless parasitoid wasps"), or family. We

identified bees to the highest resolution possible (genus or species) using expert identification

and various interactive Discover Life keys (det. MaLisa Spring, http://www.discoverlife.org).

Statistical methods

All statistical analyses were completed using R 4.1.3 (R Core Team, 2022). Data were

evaluated for statistical assumptions of normality of residuals and homogeneity of variance.

Abundance (number of insects per sample), taxonomic richness (number of taxa per sample),

Shannon diversity index (Hill 1973), and Pielou's evenness index (Pielou 1975) were calculated

using the vegan 2.5-7 package (Oksanen et al. 2019).

Generalized linear mixed effects models (GLMM) were developed using the *lme4* (Bates

et al. 2015) and *lmerTest* (Kuznetsova et al. 2017) packages to examine differences in insects

among regions. The response variables examined were abundance, richness, diversity, and

evenness. Each GLMM included region (north, central, south), sampling date (June, July,

August), and trap type (yellow sticky card, bee bowl, ramp trap) as categorical fixed effects and

trap number nested within the site as a random effect. The global model took the form: *Response*

variable ~ region+Date+Trap+(1|Site:Replicate). Poisson family error structure was initially

specified for all models. The model examining insect abundance failed to meet model

assumptions, so the negative binomial error structure was specified instead. The function

'Anova' from the car package (Fox and Weisberg 2019) was used to examine the effect of region

in each model. Tukey pairwise comparisons were performed using the *emmeans 1.7.4-1* package

(Lenth 2021) for all models to compare between regions (north, central, and south).

To visualize the insect communities collected in each region and at the three sites within

each region we used non-metric multidimensional scaling (NMDS, with Bray-Curtis distance),

computed using the *vegan 2.5-7* package. For this analysis we used presence-absence data

pooled by site for each sampling date. Permutational multivariate analysis of variance

(PERMANOVA), analysis of multivariate homogeneity of group dispersions (BETADISPER),

and pairwise multilevel comparison using the adonis function were performed following the

NMDS analysis to assess compositional dissimilarity between regions. NMDS, PERMANOVA,

and BETADISPER were computed using functions in the *vegan 2.5-7* package. Pairwise adonis

(pairwise PERMANOVA) was performed using the *pairwiseAdonis* package (Martinez Arbizu

2020).

Accumulation curves of bees for each region were created using the *BiodiversityR*

package (Kindt and Coe 2005). To estimate sampling efficiency for each trap type, we used

nonparametric Jackknife order 1 estimator to compare observed and estimated richness. Linear

models were used to examine differences in bees among regions, taking the form: *Response*

variable ~ region+Date+Trap+Site. The response variables examined were abundance, richness,

diversity, and evenness. Tukey pairwise comparisons were performed using the *emmeans 1.7.4-1*

package for all models to compare between regions and sites.

Plant data was recorded as presence-absence within the quadrats. The 'multipatt' function

in the *indicspecies* package (De Caceres and Legendre 2009) was used to perform an indicator

species analysis with a point biserial correlation coefficient. The analysis was repeated to

examine groupings by region and site.

Results

Three sampling periods at our nine sites yielded 252 samples: 72 from the north, 107

from the central, and 73 from the south. From these samples, we identified 22,459 specimens:

9,304 from the north sites, 11,107 from central, and 2,048 from the south. In the central and

southern regions, Diptera was the most abundant order. In the northern region, Hymenoptera was

the most abundant order, due to a single emergence event where 6,032 chalcid wasps were

collected, followed by Diptera (Table 1).

Traps at the southern sites produced the fewest unique taxa, followed by northern sites,

although the two regions did not differ statistically from each other in richness. The central sites

captured the most unique taxa, although this did not differ significantly from richness captured at

northern sites. Abundance did not differ between the north and central regions, but fewer insects

were captured at the southern sites. Evenness did not differ between the north and central

regions, but evenness was higher at the southern sites. There were no differences detected for

Shannon diversity between any regions (Figure 3).

Non-metric multidimensional scaling (stress = 0.22) found strong overlap in insect

communities between northern, central, and southern regions at this taxonomic resolution

(Figure 4). When broken down by sites within each region, the communities at all sites

overlapped one another (Figure S1). Homogeneity of multivariate dispersion could be assumed

for site, but not region, indicating that sites in the central region were more similar to one another

than sites from the north and south regions. The PERMANOVA testing for differences between

regions (p = 0.001) and sites (p = 0.01) was statistically significant. Pairwise PERMANOVA

found a statistically significant difference between southern and central regions (p = 0.01), but

between sites no significant differences were found.

Bees

Overall, there were 169 bees collected across all sites during our sampling period. We

identified 151 caught in the bee bowls and ramp traps, and excluded 18 individuals caught by the

sticky cards as the glue damaged the specimens and obscured some identifying features. In the

bee bowls and ramp traps there were 26 taxa. Of the identified specimens, 14 individuals from 5

taxa were collected in the northern region, 88 from 19 taxa in central, and 49 from 16 taxa in the

southern. When compared with first order jackknife richness estimates, capture efficiency in the

northern region was 74%, 71% in the central region, and 63% in the southern region (Figure 5).

The most abundant species in the north was *Augochlorella aurata* (Smith) (4), but the

most abundant genus was *Lasioglossum* (7). In the central region, *A. aurata* (39) was the most

abundant species. In the southern region, *Lasioglossum versatum* (Robertson) (18) was the most

abundant species, and there were 42 specimens in the genus *Lasioglossum* in total. One genus

was unique to the northern region: *Heriades*. Eight taxa were unique to the central region:

Agapostemon virescens Fabricius, *Andrena*, *Halictus*: *Halictus ligatus* (Say) and *Halictus*

confusus Smith, *Holcopasites*, *Lasioglossum coeruleum* (Robertson), *Lasioglossum tegulare*

(Robertson), and *Lasioglossum zonulum* (Smith). Seven taxa were unique to the southern region:

Apis mellifera L., *Ceratina calcarata* Robertson, *Lasioglossum bruneri* (Crawford),

Lasioglossum cressonii (Robertson), *Lasioglossum quebecense* (Crawford), *Megachile*,

Sphecodes.

Region was not found to contribute significantly to bee community variation. There was

no difference in bee richness, abundance, Shannon diversity, or evenness for regions or sites

(Figure 6).

Plants

There were 39 individual taxa identified at the nine sites. Indicator species analysis

revealed that three of the plant taxa were significantly associated with one region. The genus

Aster was significantly associated with the central region (p = 0.01). The designation *Aster* was

given to any plant identified as an aster, but not able to be identified to species. The species

Gaultheria procumbens (American wintergreen, Eastern teaberry) and *Pinus virginiana* Mill

(Virginia pine) were significantly associated with the southern region (p = 0.01). No plant taxa

were significantly associated with the northern region. When indicator species analysis was

grouped by site, no plant taxa were significantly associated with any site.

Discussion

This study suggests that there is strong community similarity among the insect

communities of examined thin-soil environments in the Southeastern Great Lakes region of

North America, at least when using typical sampling and community classification metrics,

suggesting communities using these sites are functionally similar throughout the Great Lakes

basin. We saw no differences in richness, abundance, Shannon diversity, or evenness between

the northern and central regions when compared over a three month span. However, though

richness was also similar between the northern and southern regions, there were differences

detected in richness between the southern and central regions. For abundance and evenness, the

southern region was significantly different from the other two regions, with slightly lower

abundance and higher evenness.

Although some statistical differences were detected between regions, when visualized,

the analysis showed complete overlap of community in all three regions, indicating similar

community composition and suggesting these differences were likely driven by differences in a

few dominant taxa between sites. Similar trends were also observed when data were examined at

the site level.

The Davis alvar performed slightly differently from the other northern sites, as we

observed higher insect abundance, lower Shannon diversity, and lower evenness (Figure 3).

These differences were primarily attributable to large numbers of a parasitoid wasp

(Trichogrammatidae) which emerged during our 12-14 August sampling period.

Trichogrammatidae (superfamily Chalcidoidea) are known to parasitize eggs from several insect

orders. Some genera, especially Trichogramma, are used for biological control of pest insects

(Jalali et al. 2016). We captured over 6,000 individuals of this one Trichogrammatidae species, at

only this site, which can account for the differences between the Davis alvar and the other

northern sites. Presence-absence data was used in the NMDS analysis so this emergence event

would not influence the analysis of insect community composition.

Bee analyses followed similar trends to the overall insect community analysis. However,

it is important to note that the traps in the northern region captured a very low number of bees

(14), compared to the central (87) and southern (49) region. *Augochlorella aurata*, a species in

the family Halictidae, amounted to about 45% of specimens collected in the central region. All

but two of these individuals were captured at one site, a sparsely vegetated hill with coarse slate

and shale soil. *A. aurata* is a primitively eusocial, common, generalist, ground-nesting species

(Wilson and Messinger Carril 2016). The genus *Lasioglossum*, in the family Halictidae, is the

largest genera of bees and notoriously difficult to identify (Gibbs 2018), however, 80% of

Lasioglossum specimens were identified to species in our study. Half of the bees captured in the

northern region were *Lasioglossum*, with three of the seven species collected belonging to the

subgenera *Dialictus. Lasioglossum* dominated the southern region, amounting to over 85% of

bees captured, most of these (43%) were *Lasioglossum (Dialictus) versatum. L. versatum* is a

primitively eusocial, generalist, ground-nesting species (Michener 1966). This species was

captured at all three southern sites, on sandstone cliff bluffs. Overall, we captured relatively few

large-bodied bees, and notably no bumble bees, during the study, but that is most likely a result

of the bias of bee bowls to collect smaller bodied genera (Wilson et al. 2008, Berglund and

Milberg 2019, Portman et al. 2020).

Plant communities differed between regions, both within our analyses and from our

qualitative observations of the broader landscape. Asters were significantly associated with the

central region as these plants were present at all three central sites, and absent at all other sites.

Gaultheria procumbens (American wintergreen) and *Pinus virginiana* (Virginia pine), both

associated with the southern region, were present at all three southern sites, and absent at all

other sites. American wintergreen prefers sandy, acidic soils (Homoya and Namestnik 2022),

which the sandstone soils of the southern region provide. Virginia pines are often found in soil

derived from sandstone and its range overlaps with only the southern region (Snow 1965). In

addition to these indicator taxa, there were many taxa that were unique to each region. Only one

taxa, *Acer rubrum* (red maple) was sampled in more than one region: Central and South (Table

S1).

These results mostly aligned with our expectations. Although the plant communities

differed, these regions had similar structural characteristics and environmental conditions,

creating a similar set of functional niches, and favoring overall similar insect communities. In

general, insect communities were more similar in the north and central regions and both differed

from the southern region sites. This is an interesting result, given that the northern and central

sites represent very different recent land-use histories, but having the common history of both

being within the extent of glaciation. Given that the former two sites are situated well within the

Great Lakes basin and the latter site is situated at the edge of this region, as it transitions into the

Allegheny plateau, the structural considerations may not alone explain the contemporary insect

community. It is interesting to note that we observed the highest variability in insect

communities among the southern sites. Yet, the sites of the southern region have the least

distance between them and perhaps the most similar plant community among sites of any of the

regions. However, the landscape at the southern sites is made up of deep hollows that could

make movement between sites difficult, especially for those with lower dispersal ability, such as

ground-crawling insects (Frampton et al. 1995, Doak 2000).

Other factors with the potential to drive insect community measurements is the history

and severity of human disturbance at the sites. One difference between the regions is their

vehicular and pedestrian access and proximity to urban areas. The sites of the central region are

proximate to urban areas while northern or southern region sites are rural, and furthermore the

northern and southern sites are on privately held nature preserve property. The central sites are

open to the public, however not in areas typically directly accessed by humans. Human

disturbance has been well-established to affect insect abundance and diversity (Winfree et al.

2009, Quintero et al. 2010, Owens et al. 2020, Fenoglio et al. 2021, Raven and Wagner 2021,

Wagner et al. 2021) but from our analyses, we do not detect a signal of these impacts using our

methodology at these sites.

Thin-soil environments, while considered important rare habitats, may also serve a more

utilitarian role as model systems. These habitats have been studied as biotic and abiotic templates

for urban green, or vegetated, roof design because of their structural similarities (Lundholm

2006, Lundholm and Walker 2018). Extensive green roofs are a type of living architecture in

which plants are intentionally grown on top of a human-built structure in shallow (typically 15

cm or less) growing medium (Getter and Rowe 2006). Like the natural thin-soil environments

they may face similar weather patterns as they are in an exposed area: varying precipitation

conditions, intense solar radiation, and wind, thus our expectations for biotic function in these

environments should too be modeled after natural systems with similar traits. Green roofs have

the potential to provide urban areas with many services, including stormwater retention, reduced

building energy consumption, accessible green space, and habitat for organisms, among others

(Dunnett and Kingsbury 2004). Plants and other physical structures from natural thin-soil

environments may be used to design green roofs that feature native plants and landscapes similar

to those found outside of the urban area (Lundholm 2006, Lundholm and Walker 2018). These

habitat patches may aid in conservation of plants and insects found in those natural ground-level

environments and increase certain ecosystem services, such as pollination and pest control, for

the city (Kadas 2006, Colla et al. 2009, MacIvor and Lundholm 2011).

Conclusions

Thin-soil environments, characterized by thin or absent soils atop hard substrates, are

unique and globally rare environments. Due to the nature of their soils, these open habitats can

be quite harsh from an abiotic standpoint and thus home to unique communities of plants and

animals. While previous work has examined the composition of these habitats, in this study, we

examined how these environments shape similarities in insect communities. This study leverages

a unique design that encompasses a large area of the Southeastern Great Lakes region, spanning

over 600 km north to south.

By examining the plant and insect communities in three separate regions of this area of

North America, we found that overall insect community composition and biodiversity

characteristics are similar. Though some variation in richness, abundance, and evenness was

detected, Shannon diversity was similar across all three regions. Bee identity was similar across

all regions, finding no differences in biodiversity metrics and similar community composition.

Though all regions contained unique plant taxa, insect community metrics were similar across

sites and regions.

This study provides taxonomic information about the insect, particularly bees, and plant

communities in thin-soil environments in this region. This knowledge supports conservation and

management efforts of rare thin-soil habitats such as alvars. Furthermore, this study provides

insights into how communities of insects assemble in habitats with these structural

characteristics. If these habitats are modeled by architects or urban planners for green roofs or

other urban infrastructure, insights can be used to create realistic expectations for biodiversity

outcomes in the built environment.

Data and code: https://github.com/katiemmanning/Thin-soil

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Figures

Figure 1: General location of sampling sites in each region. Figure adapted from Google Maps.

Figure 2: Sticky cards, bee bowls, and ramp traps (left to right) deployed at various field sites in the
Southeastern Great Lakes Region in 2019.

Table 1: Insect abundances by region

Order		North	Central	South
Blattodea		0	1	0
Diptera		2510	5334	1142
	Syrphidae	163	316	21
Ephemeroptera		5	0	0
Hymenoptera		6280	687	591
	Apoidea	15	99	54
	Chalcidoidea	6189	433	179
	Chrysididae	0	0	1
	Ichneumonoidea	41	104	76
	Dryinidae	0	1	0

	Formicidae	28	35	272
	Pompilidae	2	0	0
	Unknown wasp	2	15	9
	Wingless parasitoid	3	0	0
Hemiptera		274	4681	127
	Aleyrodidae	2	133	11
	Aphididae	148	4317	13
	Cercopidae	0	7	1
	Cicadellidae	110	163	70
	Fulgoroidae	0	3	0
	Membracidae	0	3	11
	Miridae	1	1	0
	Orius	0	1	0
	Psyllidae	7	24	2
	Tingidae	0	1	0
	Unknown Hemipteran	6	28	19
Coleoptera		235	404	188
	Buprestidae	0	0	2

	Cantharidae	5	18	1
	Carabidae	1	1	0
	Chrysomelidae	6	48	2
	Coccinellidae	0	1	1
	Curculionidae	2	17	4
	Elateridae	2	1	0
	Lampyridae	25	1	1
	Meloidae	1	0	1
	Mordellidae	8	25	14
	Scarabaeidae	1	3	5
	Staphylinidae	20	4	32
	Unknown Coleoptera	21	36	18
Lepidoptera		38	17	1
Lepismatidae		0	0	1
Mecoptera		2	0	0
Neuroptera		0	5	0
Orthoptera		13	18	12
Psocodea		0	2	12

Symphyta		2	0	0
Thysanoptera		79	207	80
Trichoptera		9	0	1

Figure 3: Box plots displaying richness, abundance, Shannon diversity, and evenness of insects, comparing sites by region. Letters shared indicate no statistical difference in estimated marginal means by Tukey method, P <0.05. Note that abundance is transformed by log10.

Figure 4: Non-metric multidimensional scaling figure (stress = 0.22) representing insect communities by region: North, Central, and South.

Figure 5: Accumulation curves for bee richness in each region.

Figure S1: Non-metric multidimensional scaling figure (stress = 0.22) representing insect communities by site within the regions.

Figure S2: Box plots displaying richness, abundance, Shannon diversity, and evenness of bees, comparing sites by region. Letters shared indicate no statistical difference in estimated marginal means by Tukey method, P <0.05.

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 Table S1: Plant taxa

Region	Site	Plant identification
South	"The W" - Ladder	*Gaultheria procumbens*
South	"The W" - Ladder	*Vaccinium pallidum*
South	"The W" - Ladder	*Pinus virginiana*
South	"The W" - Ladder	*Cladonia sp.*
South	"The W" - Ladder	*Gaylussacia baccata*
South	"The W" - Ladder	*Acer rubrum*
South	"The W" - Picnic Rock	*Gaultheria procumbens*
South	"The W" - Picnic Rock	*Pinus virginiana*
South	"The W" - Picnic Rock	*Cladonia sp.*
South	"The W" - Picnic Rock	*Carex sp.*
South	"The W" - Picnic Rock	*Acer rubrum*
South	Snyder	*Gaylussacia baccata*
South	Snyder	*Pinus virginiana*
South	Snyder	*Photinia melanocarpa*
South	Snyder	*Gaultheria procumbens*

South	Snyder	*Amelanchier aborea*
Central	Dusty goldenrod meadow	*Schizachyrium scoparium*
Central	Dusty goldenrod meadow	*Rhynchospora*
Central	Dusty goldenrod meadow	*Apocynum sp.*
Central	Dusty goldenrod meadow	*Polygala nuttallii*
Central	Dusty goldenrod meadow	*Potentilla sp.*
Central	Dusty goldenrod meadow	*Viola sp.*
Central	Dusty goldenrod meadow	*Aster sp.*
Central	Dusty goldenrod meadow	*Solidago sp.*
Central	Dusty goldenrod meadow	*Sphagnum sp.*
Central	Bedford barren	*Danthonia spicata*
Central	Bedford barren	*Aster sp.*
Central	Bedford barren	*Elymus sp.*
Central	Bedford barren	*Acer rubrum*
Central	Slate shale hill	*Danthonia spicata*
Central	Slate shale hill	*Schizachyrium scoparium*

Central	Slate shale hill	*Viola sp.*
Central	Slate shale hill	*Amelanchier sp.*
Central	Slate shale hill	*Hieracium sp.*
Central	Slate shale hill	*Aster spp.*
Central	Slate shale hill	*Prunus sp.*
Central	Slate shale hill	*Acer rubrum*
North	Davis alvar	*Clinopodium arkansanum*
North	Davis alvar	*Dichanthelium implicatum*
North	Davis alvar	*Solidago ptarmicoides*
North	Davis alvar	*Coreopsis lanceolata*
North	Davis alvar	*Minuartia michauxii*
North	Beaton alvar	*Dasiphora fruticosa*
North	Beaton alvar	*Juniperus horizontalis*
North	Beaton alvar	*Arctostaphylos uva-ursi*
North	Beaton alvar	*Solidago hirsuta*
North	Beaton alvar	*Clinopodium arkansanum*

North	Beaton alvar	*Hypericum prolificum*
North	Beaton alvar	*Carex richardsonii*
North	Beaton alvar	*Dichanthelium implicatum*
North	Cape Hurd alvar	*Juniperus horizontalis*
North	Cape Hurd alvar	*Carex eburnea*
North	Cape Hurd alvar	*Carex richardsonii*
North	Cape Hurd alvar	*Anticlea elegans*
North	Cape Hurd alvar	*Packera paupercula*
North	Cape Hurd alvar	*Solidago ptarmicoides*
North	Cape Hurd alvar	*Houstonia sp.*

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