

# Urban Archipelago Limits Goldenrod Gall Fly Distribution

Khalil Malcolm and Robert Warren II



---

Volume 10, 2023

Urban Naturalist

No. 61

## Board of Editors

- Hal Brundage, Environmental Research and Consulting, Inc, Lewes, DE, USA  
Sabina Caula, Universidad de Carabobo, Naganagua, Venezuela  
Sylvio Codella, Kean University, Union New Jersey, USA  
Julie Craves, University of Michigan-Dearborn, Dearborn, MI, USA  
Ana Faggi, Universidad de Flores/CONICET, Buenos Aires, Argentina  
Leonie Fischer, University Stuttgart, Stuttgart, Germany  
Chad Johnson, Arizona State University, Glendale, AZ, USA  
Jose Ramirez-Garofalo, Rutgers University, New Brunswick, NJ.  
Sonja Knapp, Helmholtz Centre for Environmental Research-UFZ, Halle (Saale), Germany  
David Krauss, City University of New York, New York, NY, USA  
Joerg-Henner Lotze, Eagle Hill Institute, Steuben, ME.

### Publisher

- Kristi MacDonald, Hudsonia, Bard College, Annandale-on-Hudson, NY, USA  
Tibor Magura, University of Debrecen, Debrecen, Hungary  
Brooke Maslo, Rutgers University, New Brunswick, NJ, USA  
Mike McKinney, University of Tennessee, Knoxville, TN, USA. **Journal Editor**  
Desirée Narango, University of Massachusetts, Amherst, MA, USA  
Zoltán Németh, Department of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary  
Jeremy Pustilnik, Yale University, New Haven, CT, USA  
Joseph Rachlin, Lehman College, City University of New York, New York, NY, USA  
Jose Ramirez-Garofalo, Rutgers University, New Brunswick, NJ, USA  
Travis Ryan, Center for Urban Ecology, Butler University, Indianapolis, IN, USA  
Michael Strohbach, Technische Universität Braunschweig, Institute of Geocology, Braunschweig, Germany  
Katalin Szlavecz, Johns Hopkins University, Baltimore, MD, USA

## Advisory Board

- Myla Aronson, Rutgers University, New Brunswick, NJ, USA  
Mark McDonnell, Royal Botanic Gardens Victoria and University of Melbourne, Melbourne, Australia  
Charles Nilon, University of Missouri, Columbia, MO, USA  
Dagmar Haase, Helmholtz Centre for Environmental Research-UFZ, Leipzig, Germany  
Sarel Cilliers, North-West University, Potchefstroom, South Africa  
Maria Ignatieva, University of Western Australia, Perth, Western Australia, Australia

- ◆ The *Urban Naturalist* is an open-access, peer-reviewed, and edited interdisciplinary natural history journal with a global focus on urban and suburban areas (ISSN 2328-8965 [online]).
- ◆ The journal features research articles, notes, and research summaries on terrestrial, freshwater, and marine organisms and their habitats.
- ◆ It offers article-by-article online publication for prompt distribution to a global audience.
- ◆ It offers authors the option of publishing large files such as data tables, and audio and video clips as online supplemental files.
- ◆ Special issues - The *Urban Naturalist* welcomes proposals for special issues that are based on conference proceedings or on a series of invitational articles. Special issue editors can rely on the publisher's years of experiences in efficiently handling most details relating to the publication of special issues.
- ◆ Indexing - The *Urban Naturalist* is a young journal whose indexing at this time is by way of author entries in Google Scholar and Researchgate. Its indexing coverage is expected to become comparable to that of the Institute's first 3 journals (*Northeastern Naturalist*, *Southeastern Naturalist*, and *Journal of the North Atlantic*). These 3 journals are included in full-text in BioOne.org and JSTOR.org and are indexed in Web of Science (clarivate.com) and EBSCO.com.
- ◆ The journal's editor and staff are pleased to discuss ideas for manuscripts and to assist during all stages of manuscript preparation. The journal has a page charge to help defray a portion of the costs of publishing manuscripts. Instructions for Authors are available online on the journal's website (<http://www.eaglehill.us/urna>).
- ◆ It is co-published with the *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, *Eastern Paleontologist*, *Journal of the North Atlantic*, and other journals.
- ◆ It is available online in full-text version on the journal's website (<http://www.eaglehill.us/urna>). Arrangements for inclusion in other databases are being pursued.

---

**Cover Photograph:** Goldenrod Gall Fly gall on Solidago Goldenrod stem in Western New York, USA. Photograph © R. Warren.

## Urban Archipelago Limits Goldenrod Gall Fly Distribution

Khalil Malcolm<sup>1</sup> and Robert Warren II<sup>1\*</sup>

**Abstract** - Land use and climate shift along urban-rural gradients – generally with temperature and habitat fragmentation increasing with increased urbanization. Many large cities arose adjacent to large water bodies, however, and the water bodies themselves create coastal-to-interior thermal gradients—generally with terrestrial temperature increasing nearer the water. These overlapping gradients, in turn, influence suitable habitat for temperature-dependent plants and animals. *Eurosta solidaginis* (Goldenrod Gall Fly) is a small gall fly with a larval stage occurring entirely inside the tissue of a single plant genus, *Solidago* (Goldenrod; Asteraceae). During diapause at northern latitudes, *E. solidaginis* larvae are exposed to considerable temperature extremes, with higher survival and fecundity in colder temperatures. We surveyed *Solidago* patches of various sizes in Western New York (US) to determine how the distribution of *E. solidaginis* corresponded with an urban-to-rural gradient embedded within a coastal-to-interior gradient. The probability of finding *E. solidaginis* galls increased with proximity to rural areas and in larger patches, with the lowest occupation in small urban patches. Patch size did not matter in rural areas, however, suggesting less dispersal limitation. The presence of *E. solidaginis* also increased with distance to the city center and the lake, both of which are relatively warmer, suggesting that the warmer temperatures negatively impacted the gall fly presence. Overall, these results suggest that gall fly distribution across an urban archipelago of *Solidago* patches is consistent with the predictions of island biogeography theory: *E. solidaginis* presence decreased with distance from the rural landscape and in smaller urban patches.

### Introduction

The urban-rural gradient can be a useful simplification of complex landscape patterning whereby the gradient follows a decline in land use intensity from a highly developed urban core toward residential suburbs and ending in less developed rural areas (McDonnell and Pickett 1990, McKinney 2008). Where human population is high, and hence human impacts on native ecosystems also are high, native species generally decline relative to less populated landscapes (Evans 2010, Lososová et al. 2012, Luck and Smallbone 2010). Human population density is often considered the underlying driver in the urban-rural gradient (Gaston 2010, Raciti et al. 2012, Wandl et al. 2014) based on the assumption that associated anthropogenic correlates (e.g., impervious surface, pollution, fragmentation) drive declines in species richness and abundance (Luck and Smallbone 2010, McDonnell and Hahs 2008, McDonnell and Pickett 1990, McKinney 2008). However, local and regional climate also changes along urban-rural gradients. Indeed, urban areas often create ‘heat islands’ that narrow the temperature range due to warmer nights and winters (Hamblin et al. 2017, Imhoff et al. 2010, Ward et al. 2016) resulting in urban temperatures that are 8–10°C greater than proximate rural areas (Angilletta Jr. et al. 2007, Imhoff et al. 2010).

In addition to the urban heat island effects, approximately half of the US population lives on the coasts of the Great Lakes, Atlantic Ocean or Pacific Ocean, and large water bodies create coastal-to-interior climate gradients (Osland et al. 2014, Wong et al. 2015, Tayyebi

---

<sup>1</sup>SUNY Buffalo State University, 1300 Elmwood Avenue, Buffalo, NY 14222 USA. \*Corresponding author: warrenrj@buffalostate.edu.

Associate Editor: Michael McKinney, University of Tennessee.

and Jenerette 2016). Terrestrial regions east of Laurentian Great Lakes water bodies (North America) are generally warmer and wetter than western regions at the same latitudes due to the thermal effects of the lakes (Eichenlaub 1979, Scott and Huff 1996, Vermette 2020). As a result, for example, these regions are climate refuges for plants that otherwise only grow at lower latitudes. Urban-rural and coastal-to-interior gradients are overlapping, and hence, not independent, however. For example, forest patch ant communities in Western New York (US) [east/southeast of Lakes Erie and Ontario] shifted with coastal-to-interior gradients; however, their maximum heat tolerance corresponded with the urban-to-rural gradient (Warren II et al. 2018). Urban development also creates landscape-level fragmentation of natural habitats (McKinney 2008, McDonald et al. 2008, Haddad et al. 2015). As a result, patches of suitable forest and field habitats within urban landscapes become isolated ‘islands’ within unsuitable urbanized habitat (Hobbs 1988, Olejniczak et al. 2018, Tee et al. 2018). Essentially, ecological patterns in urbanized landscapes may follow the theory of island biogeography (MacArthur and Wilson 1967) if the forest or field patches act as isolated island ‘archipelagos’ and rural natural areas as ‘mainland’ sources of colonizers. As a result, only the best dispersing plants and arthropods inhabit natural areas in core urban habitat, and relatively larger patches have relatively larger species richness in all habitats (Bolger et al. 2000, Tschamtkke and Brandl 2004, Olejniczak et al. 2018).

For arthropods, urban warming can be a benefit or curse, depending on the species (Dale and Frank 2018 and references therein). For thermophilic arthropods, urban warming can make cities, particularly relatively colder-climate cities, more hospitable by simulating their warmer native climates (Robinet et al. 2012, Meineke et al. 2013, Youngsteadt et al. 2017). Conversely, for less-thermophilic species, urban warming can decrease habitat suitability (Youngsteadt et al. 2017, McGlynn et al. 2019, Piano et al. 2020). More importantly, for arthropods that depend on specific plant hosts, urban-induced changes in the presence, abundance, phenology and physiology of the urban host plants can disrupt interactions with the species that depend on them (Neil and Wu 2006, Tabea et al. 2016, Dale and Frank 2018). That is, for plant-dependent organisms, habitat suitability is largely based on the abundance of the host plant, making the climate influences on the host species the salient driver.

Herbivores require suitable host plants as much as suitable habitat (Becerra 2003, Zangerl and Berenbaum 2005, Thrall et al. 2012). Plants commonly evolve secondary chemical compounds and other defenses to deter insect attackers and insects, in return, co-evolve better attacks to overcome the defenses (Becerra 1997, Glendinning 2002, Karban and Agrawal 2002). Consequently, herbivores typically specialize on a limited number of plants with defenses that they can overcome (Erhlich and Raven 1965, Bernays and Graham 1988, Novotny et al. 2006). Gall-forming insects, and mites, generally parasitize plants by using chemical or physical attacks to initiate abnormal plant tissue growth (e.g., bulbous or spindle-shaped protrusions) on leaves, stems and other plant parts (Stone and Schönrogge 2003, Tooker et al. 2008, Harris and Pitzschke 2020). The plant tissue typically grows around the insect and mite eggs, which forms a protective layer that often also serves as food for hatched larvae. Most gall-forming species belong to wasp (Hymenoptera), midge (Diptera) and mite (Acarina) taxa, and their interaction with plants typically is very specialized and limited to specific taxa (Harris and Pitzschke 2020).

*Eurosta solidaginis* Fitch (Goldenrod Gall Fly; Diptera: Tephritidae) is a small fly that exclusively attacks and produces galls on a single plant genus, *Solidago* (Goldenrod; Asteraceae), in the Northeastern and Midwestern US – almost exclusively with a single species, *Solidago altissima* L. [Tall Goldenrod/Late Goldenrod; Asterales: Asteraceae] (Uhler 1951, Abrahamson et al. 1989a, Abrahamson and Weis 1997). Adult *E. solidaginis* emerge

from overwintering in *Solidago* galls in spring and mate on the *Solidago* plants. Whereas some researchers have found that *E. solidaginis* readily re-colonize *Solidago* patches where the flies had been eliminated (Abrahamson et al. 1989a, Cappuccino 1992), the flies appear to be quite dispersal limited, male and female adults only travelling approximately 6 m from the galls from which they emerged (Sumerford et al. 2000, Cronin et al. 2001). After verifying the appropriate host plant (Abrahamson et al. 1989a), the females subsequently oviposit fertilized eggs in the terminal buds of newly emerged *Solidago* ramets. Hatched larvae bore down into the meristem tissue and form a chamber, which begins forming a surrounding gall within weeks, and the larvae consume the plant tissue inside. By autumn, the gall grows into a large, spherical swelling in the *Solidago* stem within which the *E. solidaginis* larvae will overwinter in diapause. During diapause in the northern climates, *E. solidaginis* fly larvae are exposed to considerable seasonal and diurnal temperature extremes in the upright plant stem. In response, the larvae undergo dramatic physiological changes that mitigate or prevent freeze damage, allowing them to survive temperatures as low as -20 to -80°C (Irwin and Lee 2000, Yi and Lee 2003, Marshall and Sinclair 2018). The gall flies have higher survival and fecundity in colder temperatures, presumably because the larvae can maintain diapause and conserve energy that would otherwise go toward metabolic processes during warm periods (Abrahamson et al. 1989b, Irwin and Lee 2000).

The objective of this study was to investigate how the distribution of *E. solidaginis* corresponded with an urban-to-rural gradient embedded within a coastal-to-interior gradient. The project began with observations by the authors that *E. solidaginis* was absent (based on gall presence) from apparently suitable *Solidago* patches on an urban college campus and adjacent city park. We formed multiple competing hypotheses to explain the absence of *E. solidaginis*: (H<sub>1</sub>) given *E. solidaginis* fidelity to *S. altissima* (Uhler 1951, Abrahamson et al. 1989a, Abrahamson and Weis 1997), if urban environments select for non-host species of *Solidago*, then the gall fly would have fewer host plants; (H<sub>2</sub>) if *E. solidaginis* winter diapause is adversely effected by relatively warmer temperatures (Abrahamson et al. 1989b, Irwin and Lee 2000), then gall presence should decrease nearer the city center and the Great Lakes' water bodies; (H<sub>3</sub>) given that *E. solidaginis* appears to be a poor disperser (Sumerford et al. 2000, Cronin et al. 2001), gall presence in the urban landscape should decrease with distance from rural areas and with greater patch fragmentation.

## Methods

### Study Site

The Western New York region (WNY) is bordered by Lake Erie (25,700 km<sup>2</sup> area; 489 km<sup>3</sup> volume) to the West and Lake Ontario (18,960 km<sup>2</sup>; 1,639 km<sup>3</sup>) to the North. Lakes Erie and Ontario are two of the largest freshwater lakes in the world (by area and volume), and they exert considerable effect on WNY temperature and precipitation (Eichenlaub 1979, Scott and Huff 1996, Vermette 2020). Most notably, the prevailing weather systems move west to east, and the lakes moderate temperatures, creating a gradient from warmer annual temperature in the coastal areas that dissipates moving inland (eastward). The Buffalo metropolitan area is located on the shore of Lake Erie, approximately 45 km south of Lake Ontario, and it is the primary urban center of WNY with a population of 257,000 and a city area of 136.0 km<sup>2</sup>. The metropolitan area creates a second temperature gradient with temperatures decreasing with distance from the city. Several studies have confirmed these climate gradients, and biological responses, at the scale used for this study (Olejniczak et al. 2018, Warren II et al. 2018, Vermette 2020, Warren and Vermette 2022).



## Study Species

*Eurosta solidaginis* is a model organism for field biology and the study of insect physiology, ecology and evolution. *Eurosta solidaginis* is widespread in North America, from coast to coast, through the southern US to the middle latitudes of Canada (Abrahamson and Weis 1997). The *Eurosta solidaginis* has been heavily studied in regions near the study area used here, including southern Canada, central Pennsylvania and central New York (Uhler 1951, Abrahamson et al. 1989a, Cappuccino 1992). *Eurosta solidaginis* primarily feeds on *Solidago altissima* L. plants throughout its range, and exclusively feeds on *S. altissima* in the study region (Felt 1940, Uhler 1951, Abrahamson et al. 1989a). The *Solidago* genus includes approximately 77 widely distributed North American species that primarily occur in open habitats (e.g., old fields, roadsides, forest clearings) in the northern regions. *Solidago altissima* is a tall, yellow-flowered perennial that is common in the upper Midwestern and Northeastern US that spreads through rhizomes to form dense patches with dozens to hundreds of ramets. Several similar *Solidago* species, both taxonomically and morphologically, co-occur with *S. altissima* (“Canada Goldenrod complex”: *S. gigantea*, *S. canadensis* and *S. rugosa* – the major differentiating trait being the presence or arrangement of hairs and flowerhead bracts). We used The Plants of Pennsylvania for identification (Rhoads and Block 2007).

## Sampling

We searched roadsides, parks and abandoned lots following approximately 70 km of urban and rural transects parallel and perpendicular with Lake Erie (Supplement A, available online at <http://www.eaglehill.us/URNAonline2/suppl-files/urna-220-Warren-S1.pdf>). As a general categorization, we considered ‘urban’ those areas < 10 km from the city center and ‘rural’ those areas > 10 km from the city center. We also designated patches as occurring at or near “forest edge,” “open field,” “roadside,” “urban edge” and “water’s edge.” We searched mid-September to early October, which is the blooming time for *S. altissima* in the region – making it easier to locate patches. Once located, we searched *S. altissima* patches for the presence of the spherical galls indicative of *E. solidaginis* (we collected a subset of galls to verify identification) and we identified the *Solidago* species. *Solidago altissima* is one of the later blooming goldenrods (aka the “Late Goldenrod”) and, of the 83 patches searched, we only found two patches with a *Solidago* species other than *S. altissima* (specifically, *S. rugosa*). We recorded GPS locations for each patch, and we visually categorized each patch size as small (1–60 m<sup>2</sup>); medium (61–500 m<sup>2</sup>) or large (501–10000 m<sup>2</sup>). We used the GPS locations to calculate each patch distance to the city center (Buffalo NY; 42.886421, -78.878132) and the nearest lakeshore. We also calculated the distance of each patch to its nearest neighbor.

## Data Analysis

We evaluated gall presence as a function of the patch distance to the city center and the patch distance from the lake using a generalized linear models (GLM) assuming a binomial error distribution. Both distances could not be evaluated in the same model because they were collinear (VIF > 4.0; car package; Fox and Weisberg 2019). We fit the GLMs using an analysis of deviance (ANODEV) approach. ANODEV is a maximum likelihood approach whereby a GLM model is fit using an analysis of variance model with a chi-square test. Neither GLM model was overdispersed ( $\Phi < 1.2$ ). We included patch size (small, medium, large) as a covariable. We also included distance x patch size interaction terms. For *post hoc* comparisons of the ANODEV models, we used the “Tukey” option of the `glht` function in

the *multcomp* package (Hothorn et al. 2008) using the R statistical program (R Development Core Team Version 3.5.1 2020).

## Results

Most of the *S. altissima* patches with *E. solidaginis* present were located at the edges of forests in open fields or along roadsides (Fig. 1a). Fewer Solidago patches were occupied by *E. solidaginis* along urban edges (parking lots and other concrete land use) and along water. In urban areas, *S. altissima* patches were more scattered with the mean ( $\pm$ SE) distance between patches at  $535 \pm 92$  m whereas in rural areas the patches were  $308 \pm 59$  m apart (Fig. 1b).

A distance to city center  $\times$  patch size interaction term indicated that the probability of a patch being occupied by the gall fly increased with distance to the city center faster in large patches than medium and increased more in medium than small (Table 1; Fig. 2). That is, large patches were more likely to be occupied by gall flies in more urban areas than medium patches, which were more likely to be occupied by gall flies in more urban areas than small patches.

Gall flies were more likely to occupy patches with greater distance from the lake (Table 2; Fig. 3). The lack of an interaction effect indicated that the likelihood of occupation did not depend on patch size. That said, the probability that a patch was occupied by gall flies was twice as high in large ( $80 \pm 13\%$ ) than small ( $40 \pm 7\%$ ) patches, with medium-sized patches intermediate between the two (Table 2;  $65 \pm 12\%$ ) [Fig. 4].

## Discussion

*Eurostus solidaginis* (Goldenrod Gall Fly) presence decreased with urbanization, and that pattern appears driven by its poor dispersal abilities across a fragmented landscape and its intolerance of the relatively warmer winters associated with an urban heat island. We found its main host plant, *Solidago altissima* (Tall Goldenrod/Late Goldenrod) blooming

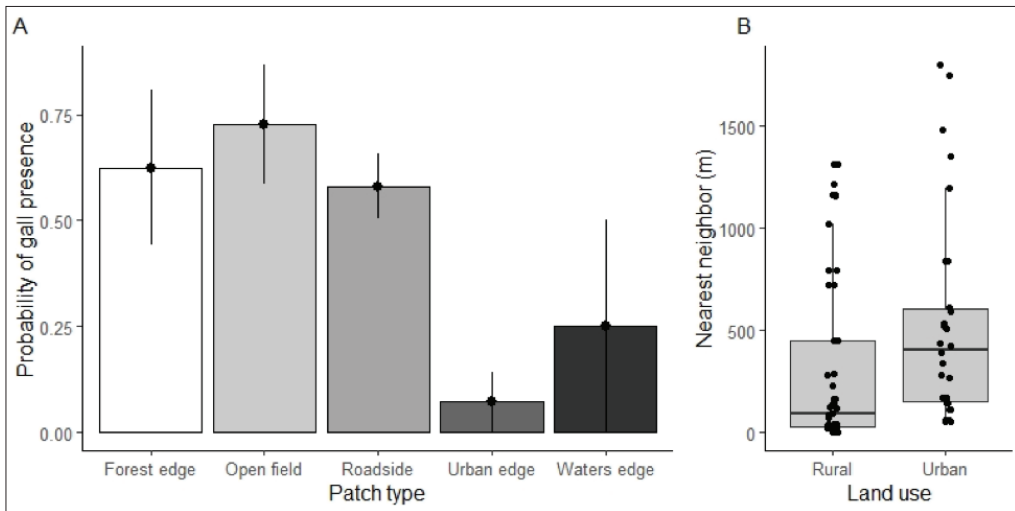


Figure 1. (a) Histogram showing the distribution of the probability ( $\pm$  SE) of finding *Eurosta solidago* (Goldenrod Gall Fly) by *Solidago altissima* (Tall Goldenrod/Late Goldenrod) patch type and (b) boxplots showing the median nearest neighbor distance of each patch (m) by land use type. The boxes include data points that fall within the lower (25<sup>th</sup>) and upper (75<sup>th</sup>) quartiles, and the error lines include the lowest and largest data points, excluding outliers, which fall outside of the boxplots and error lines ( $n = 81$ ).

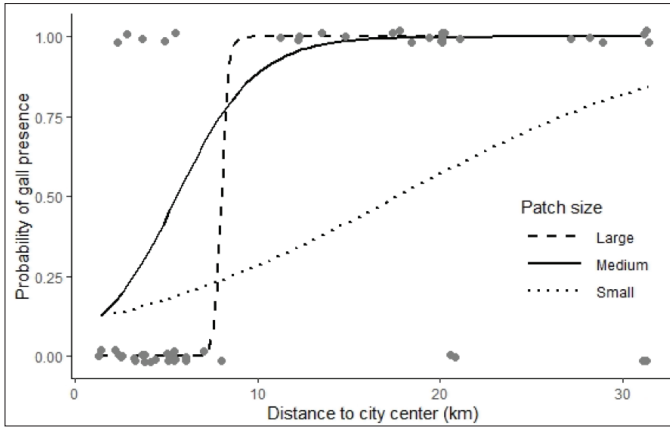


Figure 2. Logistic regression interaction plot showing the probability of *Eurosta solidago* (Goldenrod Gall Fly) presence as a function of *Solidago altissima* (Tall Goldenrod/Late Goldenrod) patch distance to the city center x patch size.

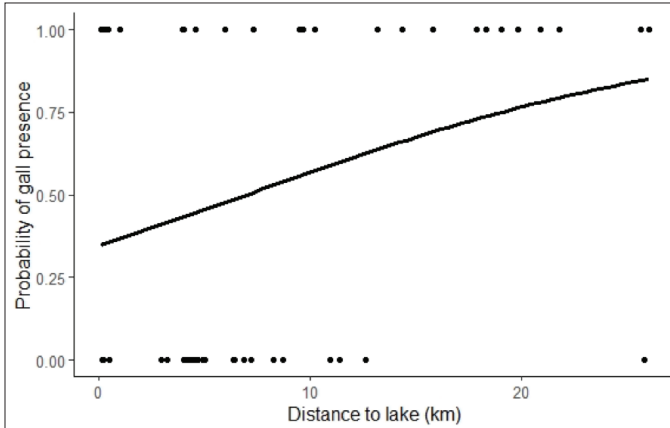


Figure 3. Logistic regression showing the probability of *Eurosta solidago* (Goldenrod Gall Fly) presence as a function of *Solidago altissima* (Tall Goldenrod/Late Goldenrod) patch distance to the lake shore.

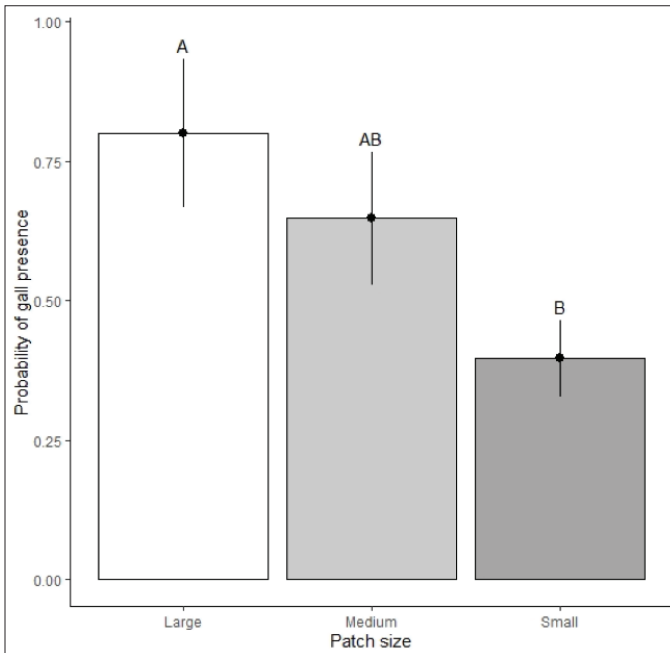


Figure 4. Barplots showing the probability of *Eurosta solidago* (Goldenrod Gall Fly) presence ( $\pm$ SE) as a function of *Solidago altissima* (Tall Goldenrod/Late Goldenrod) patch size. Bars with the same letter are not statistically different.



Table 1 - Analysis of deviance model of gall presence (binomial error distribution) as a function of distance to city center (m), patch size (small, medium, large) and a distance to city center x patch size interaction term.

	DF	Dev.	Res. DF	Res. Dev.	p-value
Distance to city center	1	13.697	78	97.206	<0.001
Patch size	2	11.535	76	85.671	0.003
Distance to city center x patch size	2	6.120	74	79.550	0.046

Table 2 - Analysis of deviance model of gall presence (binomial error distribution) as a function of distance to lake shore (m), patch size (small, medium, large) and a distance to lake shore x patch size interaction term.

	DF	Dev.	Res. DF	Res. Dev.	p-value
Distance to lake shore	1	3.775	78	107.128	0.051
Patch size	2	9.569	76	97.559	0.008
Distance to city center x patch size	2	1.451	74	96.107	0.483

throughout the urban and rural areas used in this study, suggesting that host species limitation did not explain *E. solidaginis*'s decrease in urban areas ( $H_1$ ). We also found that the probability of finding *E. solidaginis* in *S. altissima* patches declined with distance from both the city center and the lake, both of which are relatively warmer than rural and inland areas, suggesting that relatively warmer temperatures negatively impact winter diapause ( $H_2/H_3$ ). Finally, *E. solidaginis* was more likely to be absent from smaller patches in urban areas but did not vary with patch size in rural areas, suggesting that the fly does not disperse well across the patchier urban fragments (relative to the rural areas where *S. altissima* is more widespread and patches nearer each other.)

Plants in the Canada Goldenrod complex, such as *S. altissima* produce 2000–13000 wind-dispersed seeds per ramet (Werner and Platt 1976, Matlack 1987) "plainCitation": "(Werner and Platt 1976; Matlack 1987, making them vigorous colonizers of proximate habitats, particularly as non-native invaders in Europe (Abrahamson et al. 2005). Whereas we found *S. altissima* patches fewer and further apart in the urban relative to rural areas, wind- and bird-dispersed plants do not appear particularly limited across this urban landscape (Olejniczak et al. 2018). For *E. solidaginis*, the primary demarcation of suitable habitat is the presence of *S. altissima*. We found that *E. solidaginis* decreased in urban areas. If one conceptualizes the urban landscape as an 'ocean' of concrete and other inhospitable habitat, the *S. altissima* patches can be considered 'islands' of suitable habitat for *E. solidaginis*. As such, the first prediction from the theory of island biogeography is that, for poor dispersers, islands furthest from the 'mainland' (the rural landscape in this case) are the least likely to be colonized. *Eurostus solidaginis* is reported as quite dispersal limited (Sumerford et al. 2000, Cronin et al. 2001), fitting the results presented here. At about 10 km from the city center, the presence of *E. solidaginis* in *S. altissima* patches flips from absent in most patches to present in most patches (except in small patches where the transition is more gradual). These results suggest that those patches nearest rural areas may readily receive *E. solidaginis* colonizers whereas in the urban center, at a great distance from the rural 'mainland,' colonizers would have to

come from multiple fly generations that have travelled hop-scotch through the urban matrix. Of course, that is assuming all patch sizes equal, which was not the case.

The second prediction of island biogeography theory is that smaller islands undergo higher extinction/extirpation rates than relatively larger islands. Of course, those extirpations can be ameliorated with closer proximity to the mainland where higher colonization rates offset local losses. We found a remarkably similar pattern in *E. solidaginis* presence. In large *S. altissima* patches, *E. solidaginis* only was limited with increased urbanization, and a similar pattern occurred in with medium-sized patches. In small patches, however, *E. solidaginis* presence very gradually increased moving closer to rural areas, suggesting high extirpation across the gradient and low colonization in the core urban areas. In Ontario, Canada, Start and Gilbert (2016) reported island biogeography patterning in interactions between a specialist wasp parasitoid and *E. solidaginis* with fewer wasp attacks in small, isolated *S. altissima* patches. Bode and Maciejewski (2014) and Bode and Gilbert (2016) also conceptualized the Buffalo urban area as an ‘archipelago’ of *S. altissima* patches surrounded by unsuitable habitat, and both reported higher herbivore diversity on larger ‘islands.’ Bode and Maciejewski (2014) noted, however, that because *S. altissima* spreads locally through rhizome growth, patch size and age might be confounded. However, in our surveying of urban *S. altissima* patches, we found them bounded by concrete and landscaping (e.g., mowing) so that further rhizomatous spread would be difficult, if not impossible.

Poor dispersal might not be the only trait limiting *E. solidaginis* in urban areas. During winter diapause, a period in which the larvae can freeze solid, the energetic cost of warming limits fly health and survival (Irwin and Lee 2000, Marshall and Sinclair 2018). Given that urban areas create heat islands (Angilletta Jr. et al. 2007, Imhoff et al. 2010) that can adversely impact arthropods (Youngsteadt et al. 2017, McGlynn et al. 2019, Piano et al. 2020), we expected a decline in *E. solidaginis* with proximity to the city center. Of course, that patterning could be confounded by patch isolation rather than thermal climate, as well as the overlapping coastal-to-interior gradient created by the city center’s proximity to a great lake. Large bodies of water ameliorate temperature extremes, and annual temperatures are warmer with closer proximity to the lake (Eichenlaub 1979, Scott and Huff 1996; Vermette 2020). For this reason, we specifically sampled haphazard transects parallel as well as perpendicular to the lake in both urban and rural areas. Our results showed that the probability of finding *E. solidaginis* in *S. altissima* patches increased with distance from both city center and lake shore; however, the lack of interaction between distance from lake shore and patch size suggested that patch isolation was not a factor in the rural landscape. Certainly, other gradients may be embedded in this pattern, including changes in parasitoids and predators proximate to the lake, but it is suggestive of a thermal gradient pattern. Moreover, the lake climate effects are not simply annual. Conditions nearest the lake are relatively colder than inland during spring and relatively warmer than inland during autumn (but relatively warmer annually overall) so that impacts on *S. solidaginis* may be specific to a certain life history stage (as they are with ants in the same region; Warren II et al. 2018).

We found the distribution of *E. solidaginis* in *S. altissima* patches in an urban landscape consistent with the predictions of island biogeography theory. The probability of finding *E. solidaginis* galls increased with proximity to rural areas and in larger patches. More telling was the interaction between these dynamics resulting in the lowest occupation in small patches at the city core. We incorporated a sampling pattern to account for the heat island effect, which would be expected to be highest at the city core, and our results suggested that urban warming might contribute toward this pattern. In the end, the paucity of *E. solidaginis*

at the urban core was not limited by its host plant but instead by the size and isolation of the host plant patches. A coastal-to-interior thermal gradient embedded in the urban-rural gradient may have added warming as a detriment to the overwintering gall fly.

### Acknowledgments

We thank Derek Beahm and the Buffalo State Department of Biology Honors Program for support of this project. We also thank two anonymous reviewers for helpful comments on the manuscript.

### Data Accessibility

The data generated and analyzed for the current study are available in the SUNY Buffalo State Digital Commons [<http://digitalcommons.buffalostate.edu>].

### Declaration

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Literature Cited

- Abrahamson, W.G., K.B. Doble, H.R. Houseknecht, C.A. Pecone. 2005. Ecological divergence among five co-occurring species of old-field goldenrods. *Plant Ecol* 177:43–56. <https://doi.org/10.1007/s11258-005-2069-2>.
- Abrahamson, W.G., K.D. McCrea, S.S. Anderson. 1989a. Host Preference and Recognition by the Goldenrod Ball Gallmaker *Eurosta solidaginis* (Diptera: Tephritidae). *The American Midland Naturalist* 121:322–330. <https://doi.org/10.2307/2426036>.
- Abrahamson, W.G., J.F. Sattler, K.D. McCrea, A.E. Weis. 1989b. Variation in selection pressures on the Goldenrod Gall Fly and the competitive interactions of its natural enemies. *Oecologia* 79:15–22. <https://doi.org/10.1007/BF00378234>.
- Abrahamson, W.G., and A.E. Weis. 1997. *Evolutionary Ecology across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies (MPB-29)*. Princeton University Press, Princeton, NJ, USA.
- Angilletta Jr., M.J., R.S. Wilson, A.C. Niehaus, M.W. Sears, C.A. Navas, and P.L. Ribeiro. 2007. Urban physiology: City ants possess high heat tolerance. *PLoS ONE*:e258.
- Becerra, J.X. 2003. Synchronous coadaptation in an ancient case of herbivory. *Proceedings of the National Academy of Sciences, USA* 100:12804–12807.
- Becerra, J.X. 1997. Insects on plants: macroevolutionary chemical trends in host use. *Science* 276:253–256.
- Bernays, E.M., and M. Graham. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886–892.
- Bode, R.F., and A.B. Gilbert. 2016. Seed Predators, not Herbivores, Exert Natural Selection on *Solidago* spp. in an Urban Archipelago. *Environ Entomol* 45:150–154. <https://doi.org/10.1093/ee/nvv158>.
- Bode, R.F., and A. Maciejewski. 2014. Herbivore biodiversity varies with patch size in an urban archipelago. *ijis* 6: . <https://doi.org/10.1177/IJIS.S13896>.
- Bolger, D.T., A.V. Suarez, K.R. Crooks, S.A. Morrison, and T.J. Case. 2000. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. *Ecol Appl* 10:1230–1248.
- Cappuccino, N. 1992. The Nature of Population Stability in *Eurosta Solidaginis*, A Nonoutbreking Herbivore of Goldenrod. *Ecology* 73:1792–1801. <https://doi.org/10.2307/1940030>.
- Cronin, J.T., K. Hyland, W.G. Abrahamson. 2001. The pattern, rate, and range of within-patch movement of a stem-galling fly. *Ecological Entomology* 26:16–24. <https://doi.org/10.1046/j.1365-2311.2001.00294.x>.
- Dale, A.G., and S.D. Frank. 2018. Urban plants and climate drive unique arthropod interactions with unpredictable consequences. *Current Opinion in Insect Science* 29:27–33. <https://doi.org/10.1016/j.cois.2018.06.001>.

- Eichenlaub, V.L. 1979. Weather and Climate of the Great Lakes Region. University of Notre Dame Press, Notre Dame, IN . USA.
- Erhlich, P.R., and P.H. Raven. 1965. Butterflies and plants: a study in coevolution. *Evolution* 19:586–608.
- Evans K.L. 2010. Individual species and urbanisation. Pp 53–87, *In* K.J. Gaston K.J. (Ed.). *Urban Ecology*. Cambridge University Press, Cambridge, UK.
- Felt, E.P. 1940. *Plant Galls and Gall Makers*. Comstock Publishing Company, Inc., Ithaca, NY . USA.
- Fox, J., and S. Weisberg. 2019. *A companion to Applied Regression*. Sage Publications, Inc., Thousand Oaks, CA, USA. 577 pp.
- Gaston KJ. 2010. Urbanization. Pp 10-34, *In* K.J. Gaston (Ed.). *Urban Ecology*. Cambridge University Press, Cambridge, UK,
- Glendinning, J.I. 2002. How do herbivorous insects cope with noxious secondary plant compounds in their diet? *Entomologia Experimentalis et Applicata* 104:15–25
- Haddad, N.M., Brudvig LA, Clobert J, Kendi F. Davies, Andrew Gonzalez, Robert D. Holt, Thomas E. Lovejoy, Joseph O. Sexton, M.P. Austin, C.D. Collins, W.M. Cook, E.I. Damschen, R.M. Ewers, B.L. Foster, C.N. Jenkins, A.J. King, W.F. Laurance, D.J. Levey, C.R. Margules, B.A. Melbourne, A.O. Nicholls, J.L. Orrock, D.-X. Song, and J.R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. *Science Advances* 1:e1500052. <https://doi.org/10.1126/sciadv.1500052>.
- Hamblin, A.L., E. Youngsteadt, M.M. Lopez-Uribe, and S.D Frank. 2017. Physiological thermal limits predict differential responses of bees to urban heat-island effects. *Biology Letters* 13:20170125.
- Harris, M.O., and A. Pitzschke. 2020. Plants make galls to accommodate foreigners: some are friends, most are foes. *New Phytologist* 225:1852–1872. <https://doi.org/10.1111/nph.16340>.
- Hobbs, E.R. 1988. Species richness of urban forest patches and implications for urban landscape diversity. *Landscape Ecol* 1:141–152. <https://doi.org/10.1007/BF00162740>.
- Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. *Biom J* 50:346–363. <https://doi.org/10.1002/bimj.200810425>.
- Imhoff, M.L., P. Zhang, R.E. Wolfe, and L. Bounoua. 2010. Remote sensing of the urban heat island effect across biomes in the continental USA. *Remote Sensing of Environment* 114:504–513.
- Irwin, J.T., and R.E. Lee Jr. 2000. Mild winter temperatures reduce survival and potential fecundity of the Goldenrod Gall Fly, *Eurosta solidaginis* (Diptera: Tephritidae). *J Insect Physiol* 46:655–661. [https://doi.org/10.1016/S0022-1910\(99\)00153-5](https://doi.org/10.1016/S0022-1910(99)00153-5)
- Karban, R., and A.A. Agrawal. 2002. Herbivore offense. *Annual Review of Ecology and Systematics* 33:641–664.
- Lososová, Z., M. Chytrý, L. Tichý, J. Danihelka, K. Fajmon, O. Hajek, K. Kintrova, D. Lanikova, Z. Otyápkova, and V. Rěhorěk. 2012. Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. *Biological Conservation* 145:179–184.
- Luck, G.W., and L.T. Smallbone. 2010. Species diversity and urbanisation: Patterns, drivers, implications. Pp 88–119, *In* K. Gaston (Ed.). *Urban Ecology*. Cambridge University Press, Cambridge, UK.
- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, USA. 224 pp.
- Marshall, K.E., and B.J. Sinclair. 2018. Repeated freezing induces a trade-off between cryoprotection and egg production in the Goldenrod Gall Fly, *Eurosta solidaginis*. *Journal of Experimental Biology* 221:eb.177956. <https://doi.org/10.1242/jeb.177956>.
- Matlack, G.R. 1987. Diaspore Size, Shape, and Fall Behavior in Wind-Dispersed Plant Species. *American Journal of Botany* 74:1150–1160. <https://doi.org/10.2307/2444151>.
- McDonald, R.I., P. Kareiva, and R.T.T Forman. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation* 141:1695–1703. <https://doi.org/10.1016/j.biocon.2008.04.025>
- McDonnell M.J., and S.T.A. Pickett. 1990. Ecosystem structure and function along urban-rural gradients: An unexploited opportunity for ecology. *Ecology* 71:1232-1237.

- McDonnell, M.J., and A.K. Hahs. 2008. The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. *Landscape Ecology* 23:1143–1155.
- McGlynn, T.P., E.K. Meineke., C.A. Bahlai, E. Li, E.A. Hartop, B.J. Adams and B.V. Brown. 2019. Temperature accounts for the biodiversity of a hyperdiverse group of insects in urban Los Angeles. *Proceedings of the Royal Society B: Biological Sciences* 286:20191818. <https://doi.org/10.1098/rspb.2019.1818>.
- McKinney, M. 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems* 11:161–176.
- Meineke, E.K., R.R. Dunn, J.O. Sexton, and S.D. Frank. 2013. Urban Warming Drives Insect Pest Abundance on Street Trees. *PLOS ONE* 8:e59687. <https://doi.org/10.1371/journal.pone.0059687>.
- Neil, K., and J. Wu. 2006. Effects of urbanization on plant flowering phenology: A review. *Urban Ecosyst* 9:243–257. <https://doi.org/10.1007/s11252-006-9354-2>
- Novotny, V., P. Drozd, S.E. Miller, M. Kulfan, M. Janda, Y. Basset, and G.D. Weiblen. 2006. Why are there so many species of herbivorous insects in the tropical rainforests? *Science* 313:1115–1118.
- Olejniczak, M., D.J. Spiering, D.L. Potts, and R.J. Warren II. 2018. Urban forests form isolated archipelagos. *Journal of Urban Ecology* 4:1–8
- Osland, M.J., N. Enwright, and C.L. Stagg. 2014. Freshwater availability and coastal wetland foundation species: Ecological transitions along a rainfall gradient. *Ecology*, 95, 2789–2802.
- Piano, E., F. Bona, and M. Isaia. 2020. Urbanization drivers differentially affect ground arthropod assemblages in the city of Turin (NW-Italy). *Urban Ecosystem* 23:617–629. <https://doi.org/10.1007/s11252-020-00937-z>.
- R Development Core Team Version 3.5.1 . 2020. R: A Language and Environment for Statistical Computing.
- Raciti, S.M., L.R. Hutyra, A.C. Finzi. 2012. Inconsistent definitions of 'urban' result in different conclusions about the size of urban carbon and nitrogen stocks. *Ecological Applications* 22:1015–1035.
- Rhoads, A.F., and T.A. Block. 2007. *The Plants of Pennsylvania*, 2nd edn. University of Pennsylvania Press, Philadelphia, USA. 1042.
- Robinet, C., C.-E. Imbert, J. Rousselet J, D. Sauvard, J. Garcia, F. Goussard, and A. Roques. 2012. Human-mediated long-distance jumps of the pine processionary moth in Europe. *Biol Invasions* 14:1557–1569. <https://doi.org/10.1007/s10530-011-9979-9>.
- Scott, R.W., and F.A. Huff. 1996. Impacts of the Great Lakes on regional climate conditions. *Journal of Great Lakes Research* 22:845–863.
- Start, D., and B. Gilbert. 2016. Host–parasitoid evolution in a metacommunity. *Proceedings of the Royal Society B: Biological Sciences* 283:20160477. <https://doi.org/10.1098/rspb.2016.0477>.
- Stone, G.N., and K. Schönrogge. 2003. The adaptive significance of insect gall morphology. *Trends in Ecology and Evolution* 18:512–522. [https://doi.org/10.1016/S0169-5347\(03\)00247-7](https://doi.org/10.1016/S0169-5347(03)00247-7).
- Sumerford, D.V., W.G. Abrahamson, and A.E. Weis. 2000. The effects of drought on the *Solidago altissima*-*Eurosta solidaginis*-natural enemy complex: population dynamics, local extirpations, and measures of selection intensity on gall size. *Oecologia* 122:240–248. <https://doi.org/10.1007/PL00008852>.
- Tabea, T., S. Dirk, and K. Eva. 2016. Effects of urbanization on direct and indirect interactions in a tri-trophic system. *Ecol Appl* 26:664–675. <https://doi.org/10.1890/14-1787>
- Tayyebi, A., and G.D. Jenerette. 2016. Increases in the climate change adaptation effectiveness and availability of vegetation across a coastal to desert climate gradient in metropolitan Los Angeles, CA, USA. *Science of the Total Environment*:548–549, 60–71.
- Tee, S.L., L.D. Samantha, N. Kamarudin, Z. Akbar, A.M. Lechner, A. Ashton-Butt, and B. Azhar. 2018. Urban forest fragmentation impoverishes native mammalian biodiversity in the tropics. *Ecol Evol* 8:12506–12521. <https://doi.org/10.1002/ece3.4632>.
- Thrall, P.H., A.L. Laine, M. Ravensdale, A. Nemri, P.N. Dodds, L.G. Barrett, and J.J. Burdon. 2012. Rapid genetic change underpins antagonistic coevolution in a natural host-pathogen metapopulation. *Ecology Letters* 15:425–435.



- Tooker, J.F., J.R. Rohr, W.G. Abrahamson, and C.M.D. Moraes. 2008. Gall insects can avoid and alter indirect plant defenses. *New Phytologist* 178:657–671. <https://doi.org/10.1111/j.1469-8137.2008.02392.x>.
- Tscharntke, T., R. Brandl. 2004. Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology* 49:405–430.
- Uhler, L.D. 1951. *Biology and Ecology of the Goldenrod Gall Fly: Eurosta Solidaginis* (Fitch). Cornell University Agricultural Experiment Station, Ithaca, NY, USA. 51 pp.
- Vermette, S.J. 2020. Western New York's (WNY's) five climate zones. *Proceedings of the Rochester Academy of Science* 21:23–37.
- Wandl, D.I.A., V. Nadin, W. Zonneveld, and R. Rooi. (2014) Beyond urban -rural classifications: Characterising and mapping territories-in-between across Europe. *Landscape and Urban Planning* 130:50-63.
- Ward, K., S. Lauf, B. Kleinschmit, and W. Endlicher. 2016. Heat waves and urban heat islands in Europe: A review of relevant drivers. *Science of the Total Environment*:569–570, 527–539.
- Warren II, R.J., S. Bayba, and K. Krupp. 2018. Interacting effects of urbanization and coastal gradients on ant thermal responses. *Journal of Urban Ecology* 4:1.
- Warren, R.J., and S. Vermette. 2022. Laurentian Great Lakes warming threatens northern fruit belt refugia. *Int J Biometeorol* 66:669–677. <https://doi.org/10.1007/s00484-021-02226-6>
- Werner, P.A., and W.J. Platt. 1976. *Ecological Relationships of Co-Occurring Goldenrods (Solidago: Compositae)*. *The American Naturalist* 110:959–971.
- Wong, G.J., E.C. Osterberg, R.L. Hawley, Z.R. Courville, D.G. Ferris, and J.A. Howley. 2015. Coast-to-interior gradient in recent northwest Greenland precipitation trends (1952 -2012). *Environmental Research Letters* 10:114008.
- Yi, S.-X., R.E. Lee. 2003. Detecting freeze injury and seasonal cold-hardening of cells and tissues in the gall fly larvae, *Eurosta solidaginis* (Diptera: Tephritidae) using fluorescent vital dyes. *Journal of Insect Physiology* 49:999–1004. [https://doi.org/10.1016/S0022-1910\(03.00168-9](https://doi.org/10.1016/S0022-1910(03.00168-9).
- Youngsteadt, E., A.F. Ernst, R.R. Dunn, and S.D. Frank. 2017. Responses of arthropod populations to warming depend on latitude: evidence from urban heat islands. *Global Change Biology* 23:1436–1447. <https://doi.org/10.1111/gcb.13550>.
- Zangerl, A.R., and M. Berenbaum. 2005. Increase in toxicity of an invasive weed after reassociation with its coevolved herbivore. *Proceedings of the National Academy of Sciences, USA* 102:15529–15532.