IMPACT OF URBANIZATION ON TRI-TROPHIC INTERACTIONS IN AN ENDEMIC SCRUB COMMUNITY

S. E. SUMOSKI[1], A. J. JOHNCOX[2], D. M. ALTHOFF[3] AND K. A. SEGRAVES[3]
[1]State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210

[2]Department of Biological Sciences, Le Moyne College, 1419 Salt Springs Road, Syracuse, NY 13214

[3]Department of Biology, Syracuse University, 107 College Place, Syracuse, NY 13244

ABSTRACT

Human-mediated disturbances have altered every ecosystem on the planet and these changes may have important consequences for biodiversity and community structure. We tested how the degree of urbanization impacts a tri-trophic interaction among the Florida scrub endemic plant *Palafoxia feayi*, a gallmaking midge, and the associated parasitoid wasps. A combination of field surveys and laboratory rearings were used to determine whether habitat disturbance associated with housing development (e.g., land clearing, fire suppression) was correlated with changes in plant architecture, gallmaker abundance, or parasitoid diversity. We found significant differences in the number of side branches of plants at urban sites, and that the number of galls per plant increased with both the number of side branches and plant height. More parasitoids were found in galls collected from urban sites, but parasitoid diversity was unchanged by urbanization. We conclude that although urbanization influenced plant architecture, there was only a minor impact on gallmaker abundance and parasitoid diversity.

Key Words: *Palafoxia*, *Asphondylia*, parasitoid, tri-trophic interactions, urbanization, conservation

RESUMEN

La urbanización ha alterado cada ecosistema en el planeta y estos cambios pueden tener consecuencias significantes para la biodiversidad y estructura de la comunidad. Nosotros probamos cómo la urbanización afecta una interacción trió-trófica entre el arbusto endémico Floridano de la planta *Palafoxia feayi*, un jején que produce agallas, y las asociadas avispas parasitoides. Una combinación de exámenes y crianzas en el laboratorio fueron utilizadas para determinar si los disturbios con la urbanización (por ejemplo: claro de tierra, supresión de fuego) eran correlacionados con la arquitectura de la planta, la abundancia del jején que crea las agallas, y la diversidad del parasitoide. Encontramos diferencias significativas en el número de ramas laterales de plantas en sitios urbanos, y que el número de irrita en una planta fue correlacionado con el número de ramas laterales y la altura de una planta. Más parasitoides fueron encontrados adentro agallas recogidos en sitios urbanos, pero la diversidad de los parasitoides no fue cambiado por la urbanización. Concluimos que aunque la urbanización influenciara la arquitectura de la planta, tenía un mínimo impacto en la abundancia del jején que produce agallas y la diversidad del parasitoide.

Translation provided by the authors.

Tri-trophic interactions among plants, herbivorous insects, and their natural enemies are a major component of most terrestrial ecosystems. These 3 groups comprise a grand majority of the Earth's described species (Strong et al. 1984). As a consequence, human disturbance of terrestrial ecosystems has a strong potential to produce a cascading impact on biodiversity and community structure across trophic levels. For example, human-mediated disturbance has been shown to have significant consequences for insect communities by influencing species diversity, insect abundance, and community structure (Hamer et al. 1997; Denys & Schmidt 1998; Rambo & Faeth 1999; Botes et al. 2006; Jones & Paine 2006; Comor et al. 2008; Tscharntke et al. 2008). Moreover, disturbance induced changes in plant communities and plant architecture can have cascading effects on plant-feeding insects and their predators (Rambo & Faeth 1999; Scheirs & De Bryun 2002; Thies et al. 2003; Moreau et al. 2006; Tylianakis et al. 2007).

Urbanization is an obvious form of human-mediated disturbance that has been shown to have both rapid and extreme impacts on arthropod abundance, distribution, and community composition (reviewed by McIntyre 2000). For instance, Rango (2005) showed that community composition of arthropods on creosote bush differed substantially between urban and fringe deserts, and that one-third of the species found in fringe deserts were absent from urban sites. Although a number of studies have examined how urbanization affects insect communities, relatively few have addressed how urbanization impacts tritrophic interactions. Examining how urbanization affects interactions among plants, phytophagous insects, and natural enemies is essential for understanding the additive and non-additive effects that these disturbances have on biodiversity.

Florida scrub is a rare ecosystem that has been heavily impacted by urbanization (Peroni & Abrahamson 1986). Fire suppression, habitat fragmentation, and land clearing are the major threats of concern (Myers 1990). Florida scrub has a high level of endemism, especially of plants, and covers areas along the Lake Wales Ridge of central Florida (Estill & Cruzan 2001). Primarily due to habitat loss, this ecosystem is home to approximately 22 federally listed threatened and endangered plant species. Currently, Florida scrub is highly fragmented and consists of isolated habitat islands encompassing both protected and non-protected areas along the Lake Wales Ridge. In non-protected areas, agriculture and housing developments have created a patchwork mosaic of scrub habitat. Thus, urbanization may have significant effects on species diversity and abundance due to reduction in population sizes through habitat loss and reduction in dispersal among isolated patches.

The purpose of this study was to examine how urbanization influences tri-trophic interactions among the endemic Florida scrub plant *Palafoxia feayi* A. Gray (Asteraceae), a gallmaking midge, *Asphondylia* sp. (Diptera: Cecidomyiidae), and the associated parasitoid guild. We compared plant architecture, number of galls, and parasitoid species diversity between pristine and urban sites situated in and surrounding the Archbold Biological Station in Lake Placid, Florida. In particular, we addressed the following questions: (1) Do plants growing in urban vs. pristine sites differ in architecture? (2) If so, does this difference correspond to a change in the incidence of gall formation? (3) Is parasitoid species diversity and abundance increased or decreased in urban sites?

Study System

The plant *Palafoxia feayi* (Asteraceae) is found in scrub and pinelands of central and southern Florida. The genus *Palafoxia* contains a total of 9 species, and the center of diversity for the genus is in Texas (USDA, NRCS 2009). Members of this genus occur across the southern half of the United States from coast to coast (USDA, NRCS 2009). *Palafoxia feayi* is the only perennial in the genus. These plants are host to an undescribed dipteran gallmaker in the genus *Asphondylia* that produces galls mainly in the floral tissue (Gagné 1989; McIntyre unpublished data). Midge larvae are attacked by 4 undescribed hymenopteran parasitoid species in 3 different families: *Torymus* (Torymidae), *Galeopsomyia* (Eulophidae), *Tenuipetiolus* (Eurytomidae), and *Rileya* (Eurytomidae) (McIntyre unpublished data).

Materials and Methods

Surveys for plants, galls, and insects were conducted during May and Jun 2008 in 2 areas near Lake Placid, Florida—the Archbold Biological Station (ABS), 27°11' 20" N, 81° 20' 26" W, and vacant lots in the Placid Lakes housing subdivision (PL), 27°15' 22" N, 81°22' 57" W. These areas differ in degree of urbanization. The Archbold Biological Station contains some of the last remaining contiguous tracts of Florida scrub. Sites at ABS are pristine and are only disturbed by frequent natural fires and prescribed burns. In contrast, Florida scrub in the Placid Lakes subdivision is subject to land clearing associated with housing development. Many of the urban sites used in this study were vacant lots that had been cleared for prospective development, although some of the sites were relatively undisturbed patches of scrub that were frequently subdivided by paved roads. As a result, urban scrub sites are severely fragmented by roads and development of surrounding lots.

At each of these locations we surveyed 10 m by 10 m plots separated by a minimum of 100 m. Plots were haphazardly selected and only plots containing *P. feayi* were included in the surveys. Initially, plants were surveyed to assess whether the presence of galls was correlated with plant architecture. Ten plots at ABS and 20 plots at PL were surveyed. Each plant with a minimum stem length of 30 cm was measured for a number of architectural features: main stem length to the nearest cm, the number of side branches, and the number of galls. Plants of this size were used because individuals were more easily located in the scrub and were more likely to have flowered (*Asphondylia* primarily forms galls in floral tissue). This survey provided enough plants to test for a correlation between plant architecture and gall presence. Subsequently, 20 plots at ABS and 15 plots at PL were surveyed for the number of plants and the number of galls per plant. This second survey allowed us to test whether there was a difference in the average number of galls per plot in pristine versus urban sites.

We examined parasitoid diversity by collecting 100 galls from plants at both ABS and PL. The galls were individually placed into 88.7-mL plastic cups and covered with Glad Press'N Seal® wrap. Galls were checked daily and emergence of insects was recorded. Insects were placed in 1.5-mL microcentrifuge tubes containing 70% ethanol and stored in a freezer at -20°C for later identification. If a gall appeared infected with fungus or became severely desiccated, it was dissected immediately to salvage as many collectable, identifiable insects as possible. After a period of 30 d all galls were dissected to determine the abundance of the remaining insects. Parasitoids were identified to genus with keys in Goulet & Huber (1993) and Gibson et al. (1997).

We examined how plant architecture influenced the presence of galls by using linear regression to examine how plant height and the number of side branches related to the number of galls per plant. We also examined whether plant architecture differed between sites by using a *t*-test to compare the length of the main stem of plants at ABS and PL and a Mann-Whitney *U*-test to compare the number of side branches per plant at these sites. For comparisons of urban and pristine plots, we used *t*-tests to determine whether the average number of plants per plot, the average number of galls per plot, and the average gall density per plot differed between sites. Finally, we compared parasitoid species diversity between ABS and PL via the Shannon-Wiener index (a joint measure of species richness and evenness). A chi-square test was used to determine if parasitoid abundance differed with degree of urbanization. All statistical analyses were performed with JMP 5.01 (SAS Institute).

Results

A total of 1473 plants was surveyed— 587 (104 from ABS and 483 from PL) plants were examined for plant morphology and number of galls, and an additional 886 plants for surveys of gall occurrence only (423 from ABS and 463 from PL). Plots from PL had more plants and more galls, but the average gall density per plot did not differ with urbanization (Table 1). Overall, both plant height and the number of side branches were positively correlated with the number of galls per plant; however, neither characteristic explained a large proportion of the variation associated with the presence of galls (Fig. 1). Plants from ABS and PL did not differ in height (ABS = 105.91 cm ± 4.22 (SE), PL = 100.02 cm ± 1.96; $t = 1.267$, $df = 585$, $P = 0.21$), but did differ in the number of side branches per plant (Mann-Whitney *U*-test, $U = 24448$, $P < 0.0001$). PL plants had slightly more and a greater range of side branches (range 1 to 34, median = 3.00) than ABS plants (range 1 to 9, median = 2.00). As a result, the average number of galls per individual plant was slightly greater for PL than ABS (PL = 0.57 ± 0.04 (SE), ABS = 0.42 ± 0.06; $t = 2.105$, $df = 1471$, $P = 0.0354$).

Wasps obtained from *P. feayi* galls were from 4 genera—*Galeopsomyia* (Eulophidae), *Rileya* (Eurytomidae), *Tenuipetiolus* (Eurytomidae), and *Torymus* (Torymidae)—and all genera were represented at both sites (Table 2). Of the 100 galls collected from each site, parasitoids were more frequently found in galls from PL (38 galls from PL and 24 galls from ABS, $\chi^2 = 4.58$, $df = 1$, $P = 0.032$). The rearings and dissections produced 161 hymenopterans, 53 from ABS and 108 from PL. Although more parasitoids were reared from galls at PL, the average rate of successful parasitism per gall was not different between sites ($t = 0.988$, $df = 49$, $P = 0.328$). Similarly, for plots that yielded parasitoids, Shannon-Wiener diversity indices were similar between ABS and PL (ABS = 0.665 ± 0.16 (SE), PL = 0.566 ± 0.232; $t = 0.360$, $df = 9$, $P = 0.72$).

Discussion

The Florida scrub ecosystem is considered to be one of the most endangered ecosystems in Florida and North America (Scott 2003). Urbanization and conversion to agricultural lands have fragmented Florida scrub into a patchwork consisting of a few large, pristine sections and a number of small areas interspersed among urbanized patches. Understanding how the native scrub subsisting in this mosaic has been impacted by urbanization is an important first step to make informed decisions in scrub conservation. Here we compared how urbanization may influence tritrophic interactions among an endemic scrub plant, a gallmaking midge, and the associated parasitoids.

Comparisons of plants in urban versus pristine scrub indicated substantial differences in plant

TABLE 1. SURVEY RESULTS FOR *ASPHONDYLIA* GALLS ON *PALAFOXIA FEAYI* IN PRISTINE AND URBAN PLOTS (MEAN ± SE). STATISTICAL SIGNIFICANCE BASED ON *T*-TESTS.

Site	Pristine (ABS)	Urban (PL)	Significance
No. Plots	30	35	
Average no. plants/plot	17.57 ± 2.62	27.03 ± 2.42	*P* < 0.007
Average no. galls/plot	7.33 ± 1.65	15.37 ± 3.39	*P* < 0.038
Average gall density/plot	0.41 ± 0.11	0.54 ± 0.09	*P* < 0.349

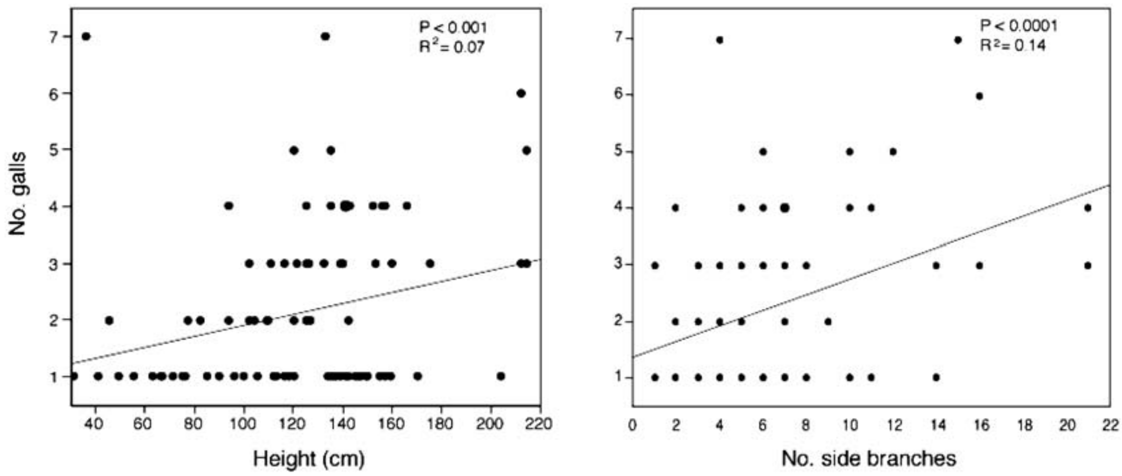

Fig. 1. Linear regression of the number of galls produced by the gall midge *Asphondylia* in comparison to plant height and the number of side branches for *Palafoxia feayi*. Only plants taller than 30 cm that had galls were included (n = 145 plants).

architecture. Plants growing in urban sites did not differ in overall height from plants growing in pristine scrub, but urban plants did have significantly more and a greater range of side branches. Unlike other *Palafoxia* species, *P. feayi* is a perennial and continues growing by initiating side branches on already existing stems that have finished flowering (McIntyre unpublished data). One potential reason for the difference in the number of side branches is that plants growing in housing subdivisions are less likely to experience fire. Although *P. feayi* can resprout after fire, all aboveground stems of the plant are destroyed. Plots located at the Archbold Biological Station are regularly subjected to natural and prescribed burns to maintain the Florida scrub ecosystem (Ostertag & Menges 1994). Hence, plants have to re-initiate above ground growth more often at ABS. The higher density of *P. feayi* at urban sites suggests that the plants may potentially avoid mortality associated with fire.

Although there were clear differences in the architecture of plants with the degree of urbanization, this did not transcend into differences at higher trophic levels. At the individual plant level, we detected a significant correlation between gall density and plant height and gall density and number of side branches; however, this pattern only explained a small proportion of the variation. Plants at urban sites had more side branches and a higher density of galls per plant than plants in pristine scrub. At the plot level, however, gall density did not differ with degree of urbanization. Urban plots had more plants with a greater number of side branches, but the average density of galls per plot was not significantly different from pristine sites. This was surprising given that differences in the number of plants and the number of side branches has direct implications for the number of galls that are possible at a plot. Because each side branch terminates in a flower head that is the primary site of *Asphondylia* gall formation, this result suggests that *Asphondylia* has not responded to the increase in availability of potential oviposition sites or that other factors may limit midge populations at these sites.

TABLE 2. DISTRIBUTION OF HYMENOPTERANS REARED OR DISSECTED FROM EQUAL NUMBERS (100) OF GALLS ON *PALAFOXIA FEAYI* FROM PRISTINE AND URBAN FLORIDA SCRUB. (MEAN ± S.E.; N.S. = NOT SIGNIFICANT).

Parasitoids	Pristine (ABS)	Urban (PL)	Significance
Number of *Galeopsomyia*	28	54	—
Number of *Rileya*	1	8	—
Number of *Tenuipetiolus*	16	2	—
Number of *Torymus*	8	44	—
Percent galls parasitized	24%	38%	$P < 0.05$
Average parasitism per gall	2.51 ± 0.84	3.6 ± 0.70	n.s.
Average Shannon-Wiener index/plot	0.665 ± 0.16	0.566 ± 0.232	n.s.

One possible factor that may limit midge populations in urban areas is suppression by parasitoids. Indeed, more parasitoids were reared from galls collected in disturbed sites and these sites also exhibited a higher proportion of parasitized galls (38% parasitized versus 24% in pristine sites). These results, however, should be interpreted with caution as studies have shown year to year variation and among site variation in parasitoid attack rate (e.g., Heard et al. 2006). The question remains whether these modest differences in parasitism translate into consistently higher mortality rates of the gallmakers across years.

Differences in the degree of urbanization did not appear to influence species richness of parasitoids attacking *Asphondylia*. The parasitoid communities in urban and pristine sites were similar. All 4 species were found at both sites and Shannon-Wiener indices of diversity were similar. Whether these parasitoid species are specialists on *Asphondylia* utilizing *P. feayi* is unclear. Species from the same 4 genera are found on *Asphondylia borrichiae* that uses sea oxeye daisy *Borrichia fructescens* along Florida's Gulf Coast (Stiling et al. 1992; Rossi et al. 2006). If parasitoids that attack *Asphondylia* are recruited from other gallmakers in the local community, then there may be a stable species pool of parasitoids in scrub habitats that can use galling larvae on *P. feayi*. If this were the case, changes caused by urbanization would need to influence the entire host-parasitoid insect community in order to potentially change parasitoid species diversity on urban *P. feayi*.

Urbanization has direct impacts on plant community structure and plant architecture of the Florida endemic *P. feayi*. These impacts, however, do not appear to significantly influence utilization patterns by the galling midge *Asphondylia* and its associated parasitoid community.

ACKNOWLEDGMENTS

We thank H. Swain and M. Deyrup for valuable advice on the study system, and P. McIntyre for sharing his unpublished study. Mylenne Salinas graciously translated the abstract. The Archbold Biological Station kindly provided facilities and access to field sites. This project was supported by a grant to K. A. S. and D. M. A. from the National Science Foundation (DEB 0743101).

REFERENCES CITED

BOTES, A., MCGEOCH, M. A., AND VAN RENSBURG, B. J. 2006. Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. Biol. Cons. 130: 573-583.

COMOR, V., ORGEAS, J., PONEL, P., ROLANDO, C., AND DELETTRE, Y. R. 2008. Impact of anthropogenic disturbances on beetle communities of French Mediterranean coastal dunes. Biodiversity Cons. 17: 1837-1852.

DENYS, C., AND SCHMIDT, H. 1998. Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. Oecologia 113: 269-277.

ESTILL, J. C., AND CRUZAN, M. B. 2001. Phytogeography of rare plant species endemic to the Southeastern United States. Castanea 66: 3-23.

GAGNÉ, R. J. 1989. The Plant-feeding Gall Midges of North America. Cornell University Press, Ithaca, New York.

GIBSON, G. A. P., HUBER, J. T., AND WOOLLEY, J. B. 1997. Annotated Keys to the Genera of the Nearctic Chalcidoidea (Hymenoptera). NRC Research Press, Ottawa, Canada.

GOULET, H., AND HUBER, J. T. 1993. Hymenoptera of the world: an identification guide to families. Agriculture Canada Research Branch Monograph No. 1894E, Ottawa, Canada.

HAMER, K. C., HILL, J. K., LACE, L. A., AND LANGAN, A. M. 1997. Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. J. Biogeogr. 24: 67-75.

HEARD, S. B., STIREMAN, J. O. III, NASON, J. D., COX, G. H., KOLACZ, C. R., AND BROWN, J. M. 2006. On the elusiveness of enemy-free space: spatial, temporal, and host-plant-related variation in parasitoid attack rates on three gallmakers of goldenrods. Oecologia 150: 421-434.

JONES, M. E., AND PAINE, T. D. 2006. Detecting changes in insect herbivore communities along a pollution gradient. Environ. Pollut. 143: 377-387.

MCINTYRE, N. E. 2000. Ecology of urban arthropods: a review and a call to action. Ann. Entomol. Soc. America 93: 825-835.

MCINTYRE, P. J. unpublished. Interactions between *Palafoxia feayi* (Asteraceae), a gallmaker (Diptera: Cecidomyiidae), and natural enemies in central Florida. Archbold Biological Station Intern Report 1998. pjmcintyre@ucdavis.edu.

MOREAU, G., EVELEIGH, E. S., LUCAROTTI, C. J., AND QUIRING, D. T. 2006. Ecosystem alteration modifies the relative strengths of bottom-up and top-down forces in a herbivore population. J Anim. Ecol. 75: 853-861.

MYERS, R. L. 1990. Scrub and high pine, pp. 150-193 *In* R. L. Myers and J. J. Ewel [eds.], Ecosystems of Florida. University of Central Florida Press, FL. 765 pp.

OSTERTAG, R., AND MENGES, E. S. 1994. Patterns of reproductive effort with time since last fire in Florida scrub plants. J Veget. Sci. 5: 303-310.

PERONI, P. A., AND ABRAHAMSON, W. G. 1986. Succession in Florida sandridge vegetation: a retrospective study. Florida Sci. 49: 176-191.

RAMBO, J. L., AND FAETH, S. H. 1999. Effect of vertebrate grazing on plant and insect community structure. Cons. Biol. 13: 1047-1054.

RANGO, J. J. 2005. Arthropod communities on creosote bush (*Larrea tridentata*) in desert patches of varying degrees of urbanization. Biodivers. Conserv. 14: 2185-2206.

ROSSI, A. M., MURRAY, M., HUGHES, K., KOTOWSKI, M., MOON, D. C., AND STILING, P. 2006. Non-random distribution among a guild of parasitoids: implications for community structure and host survival. Ecol. Entomol. 31: 557-563.

SCHEIRS, J., AND DE BRUYN, L. 2002. Temporal variability of top-down forces and their role in host choice evolution of phytophagous arthropods. Oikos 97: 139-144.

SCOTT, C. 2003. Endangered and Threatened Animals of Florida and their Habitats. University of Texas Press, Austin, TX.

STILING, P., ROSSI, A. M., STRONG, D. R., AND JOHNSON, D. M. 1992. Life history and parasites of *Asphondylia borrichiae* (Diptera: Cecidomyiidae), a gall maker on *Borrichia frutescens*. Florida Entomol. 75: 130-137.

STRONG, D. R., LAWTON, J. H., AND SOUTHWOOD, R. 1984. Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific Publications, Oxford, U.K.

THIES, C., STEFFAN-DEWENTER, I., AND TSCHARNTKE, T. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101: 18-25.

TSCHARNTKE, T., SEKERCIOGLU, C. H., DIETSCH, T. V., SODHI, N. S., HOEHN, P., AND TYLIANAKIS, J. M. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89: 944-951.

TYLIANAKIS, J. M., TSCHARNTKE, T., AND LEWIS, O. T. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. Nature 445: 202-205.

USDA, NRCS. 2009. The PLANTS Database (http://plants.usda.gov, 23 March 2009). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.