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Source: International Journal of Insect Science, 6(1)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/IJIS.S13896

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International Journal of Insect Science

Herbivore Biodiversity Varies with Patch Size in an Urban Archipelago

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ABSTRACT: The effects of ecosystem fragmentation on biodiversity during urbanization are well established. As a city grows, it replaces much of the native plant life with asphalt, cement, and lawns, yet small patches of native plants remain in greenspaces, which act as refugia for native animals. However, little work has been done on the patterns of re-colonization by native animals as urban decay allows for re-establishment of native plant communities. We found that patterns of biodiversity in the insect herbivore community within an archipelago of abandoned lots follow patterns of island biogeography, with higher biodiversity on large islands. We also found that insect colonization of the abandoned lots was correlated with each species' dispersal ability. The patterns seen here have implications for patterns of species movement into urban systems as new parks are established or as abandoned lots are re-colonized by native plants.

KEYWORDS: urban, biogeography, herbivore, herbivory, Solidago, community ecology, biodiversity, island

CITATION: Bode and Maciejewski. Herbivore Biodiversity Varies with Patch Size in an Urban Archipelago. *International Journal of Insect Science* 2014:6 49–55 doi:10.4137/IJIS.S13896.

RECEIVED: December 12, 2013. **RESUBMITTED:** February 23, 2014. **ACCEPTED FOR PUBLICATION:** February 24, 2014.

ACADEMIC EDITOR: Helen Hull-Sanders, Editor in Chief

TYPE: Original Research

FUNDING: This research was funded by a start-up fund granted by Canisius College.

COMPETING INTERESTS: Authors disclose no potential conflicts of interest.

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Introduction

Urban landscapes are generally regarded as poor environments for natural biodiversity, with many studies done on how a growing urban zone fragments and eliminates patches of the native biome, replacing it with non-native vegetation consisting mostly of weedy annuals.[1,2] With the continued growth of cities, the field of urban ecology has received extensive attention in recent years.[3–7] One focus of urban ecology studies has been on how degradation of the native plant community through habitat fragmentation and replacement has affected arthropod communities. As native plants are likely to support a higher biodiversity of herbivores and thus other trophic levels,[8–10] the process of urbanization is likely to decrease biodiversity through replacement of native plants with invasive plants and overall homogenization of the plant community. This decreased biodiversity can be easily measured by investigating the arthropod community, as arthropods respond quickly to environmental change, reproduce rapidly, and can be affected over even relatively small distances of isolation.[11,12]

Arthropod communities are dynamic and diverse,[13] varying from year to year at a single site as much as from one site to another.[14] These communities can be changed by human alteration of landscapes, especially in urban environments.[6,15,16] Of particular interest to urban ecologists are the effects of habitat fragmentation, specifically how arthropods may be dispersed among remnants with increased edge and a complex matrix between fragments.[3,17] While human interactions degrade natural patches and reduce species diversity, the plants that humans introduce can be followed by new insects.[1] Between remaining patches, distances as small as 500 m may be isolating some arthropods,[11] meaning inner-city arthropod communities are likely to be mainly composed of the best dispersers,[17,18] species that are adapted to novel habitats made by humans,[19] or introduced species. In the case of novel habitats created by urbanization, the arthropod community makeup will be highly dependent on dispersal abilities and isolation.

One type of novel habitat created through urbanization is the abandoned lot. These habitats are formed through a combination of native plant removal and moderate negligence. In the northeastern US, abandoned lots resemble an old-field ecosystem, dominated by perennial herbs and grasses, and largely by the perennial asters *Solidago* spp. and *Artemisia* spp. Annual mowing can act to stabilize the plant community by stopping succession,[2] because trees and shrubs are more negatively affected than perennial herbs and grasses. Within an urban landscape, abandoned lot ecosystems are created after (1) the native ecosystem is cleared, 2) paving/mowing or construction establishes an urban ecosystem for a period, (3) neglect allows succession to begin, and (4) old-field plants dominate the abandoned area. In essence, the rise of an old-field ecosystem from the grass and pavement-dominated urban ecosystem resembles the rise of an island in an ocean.

Thus, the principles of island biogeography have been applied to habitat fragments in a city and can be applied to the scattered abandoned lots found in an urban ecosystem.[1,8,20] In habitat fragmentation studies in urban areas, the assumption can be made that habitat fragments exist at a measurable distance from the mainland, which is often receding as a city grows. In studying abandoned lots, this assumption is not valid, and although a source population can be inferred, the distance from such a source is not as linear as in fragmentation studies. Colonizers come from seeds blown or carried in from the rural landscape around the city, from other abandoned lots (either still extant or since destroyed), or from fragments in the suburban area. As the herbivores on plants in abandoned lots will also come from the outlying areas, the non-urbanized zones outside a city can be considered as a mainland in regard to colonization. Also, because abandoned lots rise and grow in an urban matrix, these habitats function as Darwinian islands in an urbanized area,[21] rising and growing with continued negligence, and maintained through the clearance of superior competitors.

The islands inside urban areas are likely to be dominated by *Solidago* spp. in the northeastern US, especially in the absence of strong herbivore pressure.[22] We investigated the biodiversity of herbivorous arthropods on *Solidago* spp. in an urbanized zone with many abandoned lots (Buffalo, NY). As *Solidago* grows clonally, large patches are likely to be older, and also represent large islands with more food resources for specialized herbivores. We predicted that (1) increased patch size would have a positive effect on herbivore biodiversity at both a per-survey timescale and during the entire season and (2) species with life history traits that enable higher dispersal would be found at more sites.

Methods and Materials

Study system. In the northeastern US, old-field ecosystems, like those found in abandoned city lots, are likely to be dominated by asters, especially *Solidago* spp. These plant species have a diverse herbivore community largely composed of arthropods, with representatives from several orders with different dispersal abilities and reproductive outputs. The arthropod community on *Solidago* consists of a spectrum of different herbivore feeding types, from broadly polyphagous species to monophagous species, making it a good model system for colonization studies.

Sites and surveys. During the fall of 2011, surveys were done in the city of Buffalo to look for patches of goldenrod (*Solidago* spp.) with at least 20 flowering ramets. A patch was defined as a distinct group of ramets at least 250 m from the other closest distinct group of ramets. Many patches were also isolated by wide highways or large structures. Patch size was measured by counting all emergent *Solidago* spp. ramets in May 2012. Many neighborhoods of Buffalo have distinct groups of goldenrod every 50 m in abandoned yards. These neighborhoods were excluded, as were the less-developed suburbs (Tonawanda, Williamsville) that had large old-fields. Both neighborhoods with many close-together groups of goldenrod and less-developed suburbs were considered as part of the source community (functioning like a mainland in island biogeography), as they had high herbivore biodiversity, as confirmed by independent surveys, and could represent a source of colonizers. Our resulting survey area was bounded by Interstate 190 on the west, Interstate 290 on the north, and the Kensington expressway on the south and east (Fig. 1). All three of these highways are lined with *Solidago* species for large stretches.

Most patches were confirmed to be *Solidago altissima* or *Solidago canadensis*, but two patches were *Solidago speciosa*. No effect of species identity was seen on herbivore biodiversity, and the herbivores included in the surveys fed on at least all *Solidago* species included (albeit with genotype preferences),[23] and often other asters.

In May 2012, 97 patches were sorted into 6 transects. Plants in each transect were surveyed four times, every other week from late May to late July. During each survey, 20 plants were chosen at random. Each plant was looked over carefully, including all surfaces of all aboveground parts, and all herbivores present on the plant were recorded. No herbivores were removed, and only spittle bug, *Philaenus spumarius*, larvae were disturbed (spittle was gently wiped away to get an accurate count of nymphs). Moreover, it was assumed that *Eurosta solidaginis* galls contained only one larva of the gall-making species. Independent surveys at other sites confirmed this to be true. After counting herbivores, other plants in the patch were looked at to ensure that no species of insects were missed. During the surveys, several sites were destroyed by human impacts such as weed-whacking and construction. We did not survey these sites after the sites were destroyed, but included pre-destruction data in our analyses.

Herbivore identification. A goldenrod arthropod identification guide (See supplementary materials) was developed to facilitate accurate and consistent identification by undergraduate researchers. New herbivore species found were photographed, and the photographs were also used in identifying species. Aphids were divided into four types by color (green, black, red, and yellow). Small leafhoppers (3 mm or less)

Figure 1. Sampled plant community patches in the metropolitan Buffalo area, NY. The black line delineates the surveyed area. Dots indicate survey sites used in at least one survey. Basemap Data Copyright 2014 NYS GIS Program Office.

were classified into two types by color (green and brown). In all, 30 species or morphospecies of insects and 1 species of mollusk (*Cepaea nemoralis*) were found feeding on goldenrod at our study sites.

Dispersal ability. Dispersal ability was calculated using the factors laid out in Figure 2 of Ewers and Didham.[17] We used four of the five factors that were laid out as relevant for species responses to fragmentation events, dividing dispersal abilities between adults and larvae. As trophic level was equal for all, herbivores were ranked by dispersal ability of larvae/juveniles (none = 0, on plant = 1, in patch = 2) and of adults (low = 1, medium = 2, high = 3), body size (large = 1, medium = 2, small = 3), niche breadth (*Solidago* specialist = 1, *Asteraceae* specialist = 2, generalist = 3), and rarity ((average relative frequency at all sites/highest average relative frequency) × 3). Ranks were arbitrarily given based on any data we could find on a per-species basis. The values for these five factors were added, giving dispersal scores from 6 to 12, with 6 having the lowest dispersing ability and 12 having the highest. Relative dispersal scores matched up with relative dispersal as described in publications that covered such.[17,18] The dispersal scores were then compared with the total number of sites at which each species was found.

Data and statistics. The normalized Shannon biodiversity index was calculated as in Ramezani.[24] The relation between patch size and biodiversity for each survey was analyzed using a generalized linear model with all data transformed for normal distributions.[25] The relation between total species found at a patch and patch size was analyzed using a generalized linear model.[25] Patch size varied widely, so we used a $\log_{10}$ transformation on patch size to moderate the effect of large values. The relation between dispersal score and total number of sites was also analyzed using a generalized linear model with R.

Results

Herbivore diversity is correlated with patch size. We saw a total of 33 species, with the largest total number of species (28) seen during the third survey in mid-June 2012. We saw 23 species in our first survey and 26 species in our second survey. The second survey was of special interest to us, because at that point the full complement of species reported in Root and Cappuccino[13] that we found in Buffalo was present. There was a positive correlation between the normalized Shannon Index (e^H) and log patch size ($R = 0.5986$, $P < 0.001$, $N = 66$, Fig. 2B) during the second survey. Positive correlations were also seen during the first ($R = 0.3462$, $P = 0.0033$, $N = 68$) and third ($R = 0.4566$, $P < 0.001$, $N = 61$) surveys (Figs. 2A and C). During the first survey, many herbivores had not emerged, and during the third, some species were pupating underground. By the fourth survey, many of the herbivores commonly seen on *Solidago* were pupating off the plant, had moved to alternate food sources, were encased in galls, or were simply absent. An exceptional dry spell may have contributed to lower species diversity (23) by the fourth survey, as several sites had plants under severe water stress. All three surveys showed the same positive correlation between patch size and herbivore diversity.

Larger patches have more herbivores. Although the diversity of herbivore species varied through the season and between patches, there was a positive correlation between total species found at each patch and patch size ($R = 0.587$, $P < 0.001$, $N = 60$, Fig. 3). Despite some species emerging late, molting and moving or colonizing at a later part of the season, we saw total species number correlates well with patch size.

Individual species are distributed differently based on dispersal ability. On a species-by-species basis, there were no significant correlations between the relative frequency of herbivores and either patch size or distance (Bode, unpublished data, 2012). Larger patches may have supported larger populations, but these populations may have also been dispersed uniformly. Species with high dispersal scores showed no correlation with distance, while poor dispersers were found at too few sites for statistical analysis.[18]

There was a positive correlation between dispersal ability and the number of sites at which each species was seen ($R = 0.4897$, $P = 0.014$, $N = 24$, Fig. 4). Only results for the second survey are shown here. Agromyzid flies were the most common and were seen at most sites (Rarity = 3/3, seen at 65 sites).

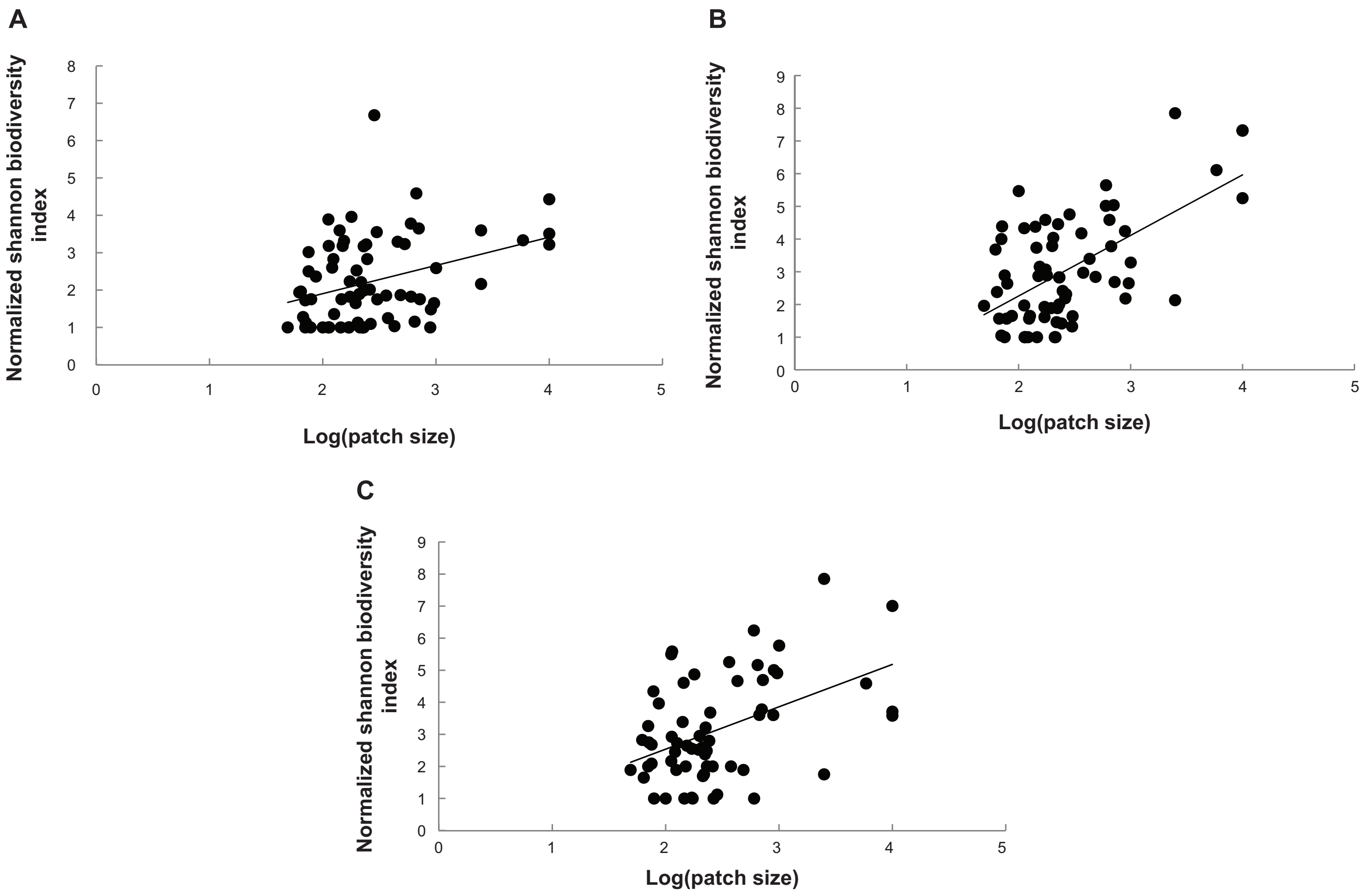

Figure 2. Relationship between log(patch size) and normalized herbivore biodiversity in surveys 1 (**A**), 2 (**B**), and 3 (**C**).

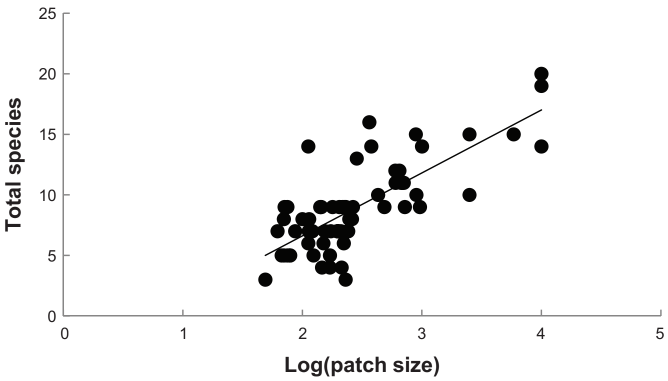

Figure 3. Relationship between log(patch size) and the total number of species found in all surveys.

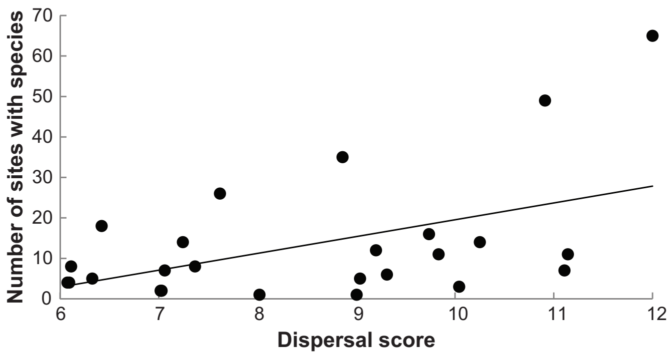

Figure 4. Relationship between dispersal score and the number of sites with each species. Each data point represents one herbivore species.

Discussion

The city of Buffalo represents a highly variable matrix of diverse habitats, with diverse plant life and therefore diverse herbivore communities. However, herbivore community composition is limited by dispersal and patch size in urban environments.[3,16,17] In our study, we found that patch size was positively correlated with herbivore biodiversity on Darwinian island habitats formed by monospecific stands of *Solidago* spp. We saw that herbivores varied in their distributions, as would be predicted according to their size, how specialized they were, and their dispersal abilities,[17] and we saw that the total number of herbivores found at a site correlated positively with the size of that site. These findings are in accordance with island biogeography theory, which is often applied to the fragmented communities found in urban areas. By analyzing biodiversity within a single trophic level and on a single genus of plant, we eliminated complications because of multitrophic interactions and variation of the plant community between patches. However, it is important to note that our study utilized patches of multiple sizes, which are probably also of different ages, thus adding a potential complicating factor.[26] As goldenrod plants age, they reproduce clonally. Thus, a patch of goldenrod will increase in size as the plants within increase in age. Assuming this link, we propose that as a goldenrod genet ages, in the absence of other genetically independent conspecifics, it will be exposed to a higher diversity of herbivores. As goldenrod can be destroyed by disturbances (especially the human-related disturbances in urban environments), size is also related to time of last disturbance, which could further influence herbivore diversity. As a further confounding factor, ramets affected by an attacking herbivore may prime the defenses of adjacent ramets.[26] This could lead to changed interactions not only in the affected ramet but also in the adjacent ramets. We propose that this would have larger effects in small patches, where a higher proportion of ramets would share headspace. However, it is also possible that defense induction or priming could make a plant more attractive and enhance biodiversity.[27]

We found that the herbivore communities we saw were variable in composition, and that the most common herbivores were those with high dispersal scores (Fig. 4).[17] Many of the herbivores on goldenrod are specialists, and the complex matrix in between sites may severely limit colonization. We neither did find correlations between the presence/number of specialists and the number of generalist herbivores, nor did we see any correlation between distances from nearby Lake Erie (from which prevailing summer winds come) and herbivore diversity. We also saw relatively low damage relative to the amount of available leaf tissue, suggesting that herbivores were not limited by resources. Agromyzid flies were seen at 53 out of 60 sites at some point during the season, and were the most common herbivores in our study. Previous literature has confirmed that agromyzid flies are good dispersers in urban ecosystems.[18]

We saw large population booms of aphids in several sites during the first surveys, which declined precipitously in the third survey. By this time, several new sites now had many aphids, and *Corythucha marmorata* was found in high numbers at any sites where it was present. Although there were not enough sites with species of aphids or *Corythucha marmorata* for a statistical analysis of patterns, the population booms of these herbivores coupled with the low damage found (Bode, unpublished data, 2012) strongly suggest that reproductive output and colonization have stronger impacts on herbivore density than interspecific competition. An added point of interest is that *Corythucha* is also a pest on other asters, including chrysanthemums. It is possible that local populations may be reservoirs of future infestations. In as much as other goldenrod herbivores are also pests, management of vacant lots could yield benefits in terms of pest management.

The makeup of the herbivore community on goldenrod species represents a selective pressure affecting the evolution of herbivore resistance.[28] Species that exert strong selective pressures on goldenrod can change the makeup of the goldenrod population to favor more resistant individuals. However, these same species can do sufficient foliar damage to allow woody plants to overgrow goldenrod; thus, herbivores are a mechanism by which succession can occur.[29] Goldenrod genotypes have been shown to differ in their resistance to different herbivores,[30] and these different levels of resistance may represent a population response to variable selective pressures resulting from a variable and biologically diverse herbivore community. Strong selective pressure by only a few herbivore species may influence genotype diversity in favor of a relatively few genotypes. In a patch of goldenrod with only a few herbivore species, it is entirely possible that no herbivore or combination of herbivores will do sufficient damage to limit the growth of *Solidago* spp.[31] Plants in these patches may suffer no fitness or growth reduction from the herbivores that have found and lived in that community. If the plants are not suffering fitness reductions through herbivory, they may have effectively escaped natural selection by herbivores until the herbivore population increases or new herbivores colonize.

Not all members of the herbivore community represent an equal threat to goldenrod growth and reproduction, as very few species have been shown to have fitness-reducing effects on *Solidago* spp.[32] Of the herbivores known to have fitness-reducing effects, only *P. spumarius* was commonly found in our study sites. *Trirhabda virgata* and *Microrhopala vittata*, two chrysomelid beetles, have both been shown to expedite succession away from goldenrod-dominated old-fields by allowing sunlight to filter through a highly damaged canopy.[22,29] The absence of these herbivores from many of our sites could represent a longer period of goldenrod dominating the old-field communities in Buffalo. A direct consequence of the longer period of a goldenrod-dominated flora would be a longer period for insects found primarily on goldenrod to find, colonize, and inhabit these patches. As rural fields progress in succession, urban lots could act as reservoirs for some species and would enhance the gamma diversity of the region.[19] Indeed, some patches could support herbivores and not be found by the predators, which would allow these patches to act as refugia in a metacommunity. These dynamics may function in tandem with urban management practices to ensure that urban habitats are repositories for biodiversity rather than the poor environments they are often seen as.[33] However, it should be noted that biodiverse environments will include some pests as well as the predators that may control pest populations.

Acknowledgements

We would like to thank Jordan Tripi for her work on the guidebook used to identify herbivores, the people at www.bugguide.net, and the many property owners who allowed us to view goldenrod on their property. Thanks also to Bob Johnson for helpful comments on an early draft of this manuscript and four reviewers who gave us comments critical to improving this manuscript.

Author Contributions

RFB and AM conceived and designed the experiments. AM analyzed the data. RFB wrote the first draft of the manuscript. RFB and AM contributed to the writing of the manuscript. RFB and AM agreed with manuscript results and conclusions. RFB and AM jointly developed the structure and arguments for the paper. RFB and AM made critical revisions and approved the final version. Both authors reviewed and approved the final manuscript.

DISCLOSURES AND ETHICS

As a requirement of publication the authors have provided signed confirmation of their compliance with ethical and legal obligations including but not limited to compliance with ICMJE authorship and competing interests guidelines, that the article is neither under consideration for publication nor published elsewhere, of their compliance with legal and ethical guidelines concerning human and animal research participants (if applicable), and that permission has been obtained for reproduction of any copyrighted material. This article was subject to blind, independent, expert peer review. The reviewers reported no competing interests.

Supplementary Data

Supplementary file 1. Goldenrod Guidebook: A primer on herbivorous species commonly found on *Solidago* spp.

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