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Note

Lepidoptera species richness and community composition in urban street trees

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Abstract

The triple threats of climate change, habitat loss, and environmental pollution have stimulated discussion on how urban areas can be modified to mitigate heat increases and provide habitat for wildlife such as insects. The strategy of using trees to reduce temperatures has been adopted by numerous cities. However, the majority of street trees planted around the world are non-native. Studies conducted in non-urban areas have demonstrated in comparison to native plants, non-native plants are less likely to support native insect diversity. Here, we use a database approach to quantify the number of native Lepidoptera species associated with 76 of the most common street tree species planted in Vancouver, Canada. We tested the prediction that compared to non-native trees, native street trees will support a higher diversity and unique community of native Lepidoptera. As predicted, native street trees were associated with five times as many native Lepidoptera species, and the Lepidoptera communities supported by native versus non-native street trees were distinct. There was no difference in native Lepidoptera associations between broadleaf versus coniferous street trees. These results are consistent with studies that have used active sampling techniques to investigate insect richness on a smaller subset of native and non-native tree species. Collectively, these data provide good evidence that planting native instead of non-native trees will help stem the loss of insect diversity in urban areas.

Key words: Lepidoptera, native trees, species richness, street trees, urban

Introduction

Urban street trees, broadly defined here as trees planted alongside sidewalks, streets, or next to buildings, provide a myriad of functions such as heat reduction, rainwater absorption, and air filtration (Sjöman et al. 2016; Schlaepfer et al. 2020; McCoy et al. 2022; Anderson et al. 2023). The ability of trees to help offset heat gains caused by climate change has led to the call for a 16%–30% increase in tree coverage across major cities (Marando et al. 2022; Iungman et al. 2023). In addition to providing services to humans, street trees are also important resources for urban biodiversity. Street trees act as nesting habitats for birds (Fernández-Juricic 2000; Jensen et al. 2023), nectar and pollen sources for pollinators (Somme et al. 2016), and shelter for small mammals (Ossola et al. 2019). However, there is considerable variation among street tree species in the biodiversity they support, and the current push to increase the number of street trees in cities begets a more thorough understanding of the ecological roles these trees play in urban environments. In particular, a pressing question in light of widespread insect declines (Wagner 2020) is whether street trees provide suitable habitat for native insects.

Although current data are limited, street trees likely do not provide suitable food sources to a significant fraction of native insects. In many cities worldwide, the majority of planted street trees are non-native (Liu and Slik 2022; McCoy et al. 2022). Studies conducted in urban parks or on non-urban trees have demonstrated that compared to native trees, non-native trees host significantly fewer phytophagous insects (Helden et al. 2012; Grunzweig et al. 2015; Frank et al. 2019; Mata et al. 2021; Tallamy et al. 2021). Most herbivorous insects can only consume a few plant species because they have evolved the ability to overcome the phytochemical and physiological defences found in particular plant lineages (Tallamy et al. 2021). This specialization between phytophagous insects and their plant resources has led to the hypothesis that the replacement of native trees with non-native street trees in urban environments contributes to the overall decline of leaf-eating insects worldwide (Tallamy et al. 2021). To city managers, the inability of local insects to consume street trees may seem like a positive outcome. However, given that insects provide an array of services such as biocontrol of weeds, pollination, and nutrient cycling, and are key food items for birds and small mammals, a substantial loss of native insects would create a noticeable gap in the ecological food web.

Moths and butterflies (Lepidoptera) in particular have experienced significant reductions in abundance and diversity around the world (Panigaj and Panigaj 2008; Bell et al. 2020; Burner et al. 2021; Green et al. 2021; Laussmann et al. 2021; Lewinsohn et al. 2022). In response to these declines, urban green spaces are increasingly being explored as potential sites for Lepidoptera conservation (Majewska and Altizer 2020). However, many species of Lepidoptera are unable to sequester or process novel plant chemicals and can only feed on specific species of plants (Beran and Petschenka 2022). Given the prevalence of non-native trees in cities, a better understanding of whether native or non-native street trees differ in their potential to support Lepidoptera is needed to inform the suitability of urban environments for the conservation of this ecologically important and taxonomically diverse insect group.

Although researchers have advocated for more investigations into whether non-native street trees do in fact support fewer native insect species (Helden et al. 2012; Sjöman et al. 2016; Tallamy et al. 2021), sampling insects from urban street trees poses several challenges. These include but are not limited to the infrastructure (and potential street closures) needed to sample the canopy of street trees, the need to sample multiple times over the growing season to capture seasonal variation in insect diversity and abundance, the difficult task of identifying collected insects to species, and the need for an inventory of all of the street trees planted in the urban area. Given these hurdles, here we use a database approach to investigate whether non-native and native street trees potentially support different communities of Lepidoptera. The City of Vancouver, Canada, maintains an updated list of all street trees planted within the city boundaries. We coupled this dataset with published literature and HOSTS (Robinson et al. 2023), which is a global database of known associations between Lepidoptera and their host plants, to test three predictions: (1) that non-native street trees are associated with fewer species of native Lepidoptera; (2) that native and non-native street trees are associated with unique communities of Lepidoptera; and (3) because coniferous and broadleaf trees have been shown to support different communities of Lepidoptera (Hatcher 1990; Ozanne 1999; Brown 2018), we test the prediction that coniferous and broadleaf street trees are associated with unique communities of Lepidoptera.

Materials and methods

Street tree selection

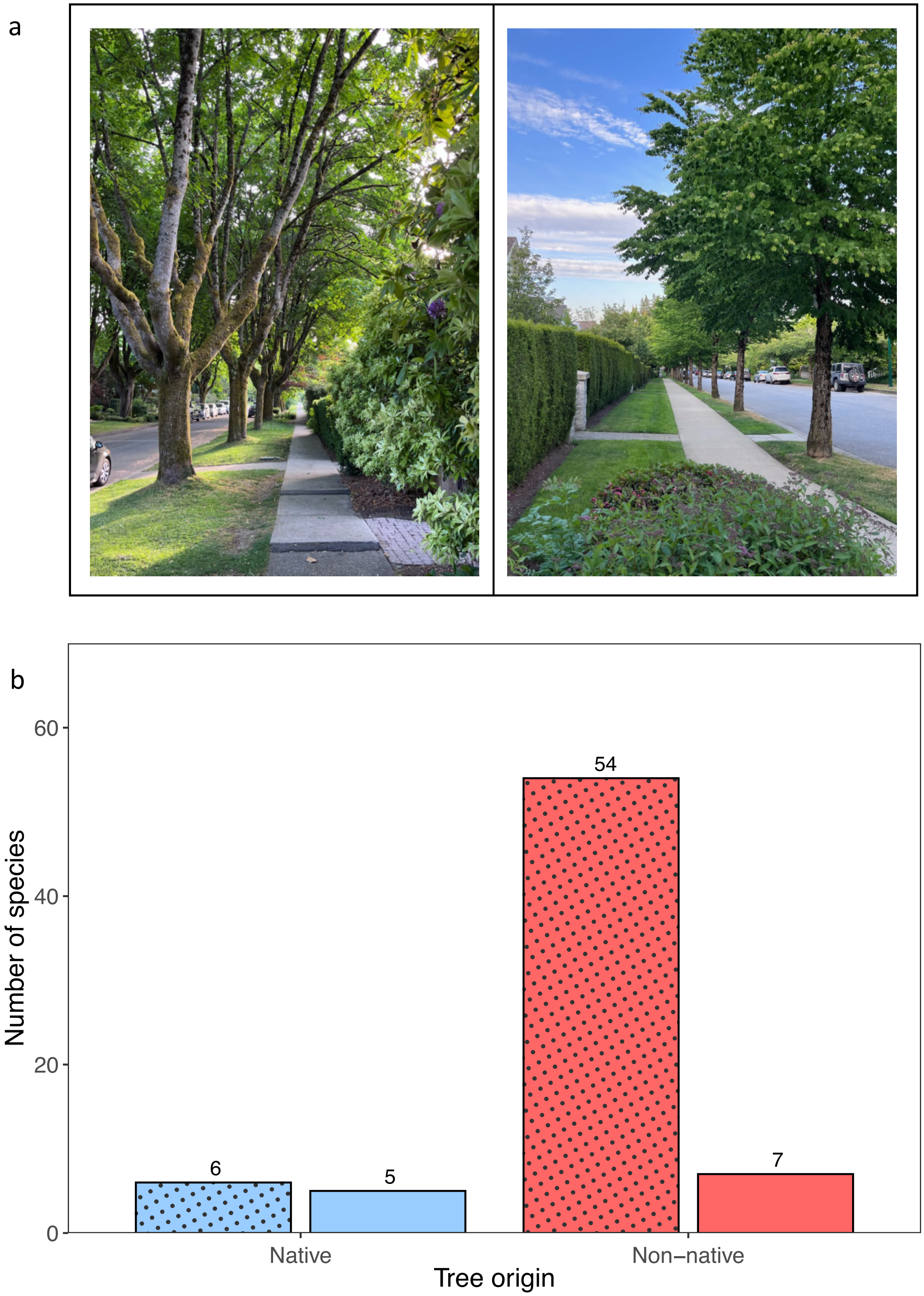
Data on all street trees planted in Vancouver were obtained from the City of Vancouver Open Data Portal (https://opendata.vancouver.ca/). These data include all trees that are planted next to sidewalks and roads (e.g., Fig. 1*a*) but do not include trees planted in boulevards or parks. Data were downloaded by MiT on 27 February 2023. Street trees were first listed in descending order of individuals per species. We chose tree species where 100 or more individuals had been planted in Vancouver. This selection method resulted in 107 unique species (142 094 individuals) and represented approximately 95% of the total individuals in the database. These 107 tree species were haphazardly assigned to all coauthors and each coauthor was tasked with finding all known Lepidoptera associated with those species.

Lepidoptera associated with Vancouver street trees

We used the HOSTS database of the World's Lepidopteran Hostplants (Robinson et al. 2023) to obtain a list of all Lepidoptera species associated with each street tree species. In the rare situation where the tree species was not included in HOSTS (∼10 species), we also searched the ISI Web of Science Core Collection and Google Scholar using the tree species name and "Lepidoptera∗" as search terms. The vast majority of the Lepidoptera associations were sourced from HOSTS. We were unable to find any Lepidoptera associated with 12 street tree species: *Acer cappadocicum* Gled., *Acer* × *freemanii* A.E.Murray, *Crataegus* × *lavallei* Hérincq ex Lavallée, *Crataegus* × *mordenensis* Boom, *Davidia involucrate* Baill., *Fraxinus ornus* Pall., *Magnolia denudate* Desr., *Magnolia* × *kewensis* Pearce, *Malus* × *zumi* (Matsum.) Rehder, *Quercus frainetto* Ten., *Sequoiadendron giganteum* (Lindl.) J.T.Buchholz, and *Tillia* × *europaea* L. (Table S1). Without these 12 species (10 371 individuals), the dataset represents 131 723 Vancouver street trees (95 species), and 87.7% of the database. We excluded these species from further analyses because it was unknown whether the zero values were true absences or due to a lack of sampling. We next used the British Columbia Conservation Data Centre (BCCDC) database (https://a100.gov.bc.ca/pub/eswp/), the Biota of North America Program (bonap.org), the ISI Web of Science Core Collection, and Google Scholar to determine whether each street tree was broadleaf or coniferous, and whether it was native to British Columbia (BC).

We used the BCCDC to generate a list of all Lepidoptera that have been recorded in BC. The BCCDC database also includes information on whether the insect is "Exotic", which is defined by the website as a species not native to BC. This resource is updated regularly and includes 2930 species of Lepidoptera. The most recently published checklist of BC Lepidopterans (Pohl et al. 2015) includes 2832 species. Thus, the BCCDC list may contain new species to BC, species that are no longer found in BC, or those that were erroneously included in the list prior to 2015. We are unable to verify why the two sources include different numbers of Lepidoptera and be-

Fig. 1. (*a*) Sample street trees from Vancouver, Canada. The left panel shows the common horse chestnut (*Aesculus hippocastanum* L.) and the right panel shows katsura trees (*Cercidiphyllum japonicum* Siebold & Zucc.). Both species are non-native. (*b*) Number of different tree species associated with native (British Columbia) Lepidoptera. Red bars denote non-native trees and blue denote native trees. Bars with dots denote broadleaf trees and those without dots denote coniferous trees. Photo credit: Michelle Tseng.



cause the BCCDC list was available in csv format, we used this list as our source for BC Lepidoptera. We also cross-checked the species categorized as "Exotic" in the BCCDC database with the species categorized as "introduced" in the Pohl et al. (2015) checklist. Insect species labelled as introduced/exotic were consistent between the two sources. For consistency, hereafter we use "non-native" instead of "exotic" to describe this group of Lepidoptera. The final dataset thus included tree species from the Vancouver street tree database, whether the tree was native or non-native to BC, and whether the tree was broadleaf or coniferous. The dataset also included a list of all known Lepidoptera species associated with each tree species (based on the HOSTS database and published literature), whether or not the Lepidoptera has been found in BC, and the native/non-native status of the lepidopteran species. The full compiled dataset used here is publicly available on Dryad (see the "Data availability" section).

Data analyses

Data were compiled into a master datasheet. We checked for spelling errors in Excel and removed duplicate data in R (R Core Team 2023). We first filtered the full dataset to include only Lepidoptera that have been recorded in BC. This filtering step reduced the total number of Lepidoptera in the dataset from 2449 species to 568, and reduced the total number of street tree species from 95 to 77 (Table S2). This reduction in species number is because 18 tree species (Table S3) were associated with only non-BC Lepidoptera. We used Analysis of variance to investigate whether the number of native BC Lepidoptera species (richness) associated with each tree species differed between native- versus non-native trees or between coniferous versus broadleaf trees. Lepidoptera richness data were log-transformed to remove heteroscedasticity. We next used NMDS plots to visualize whether native versus non-native or broadleaf versus coniferous street trees were associated with distinct communities of Lepidoptera. We used the following parameters: $k = 3$, maxit = 999, trymax = 1000, and distance = bray. The stress value was 0.100 and the stressplot R^2 values were 0.99 and 0.96 for the nonmetric and linear fits, respectively. Finally, we used anosim to examine whether the tree clustering observed in the NMDS plots for native versus non-native trees, or for broadleaf versus coniferous trees, was statistically significant. All statistical analyses were conducted in R Version 4.3.0 (R Core Team 2023). We used the following R packages: tidyverse version 2.0 (Wickham et al. 2019), vegan version 2.6–4 (Oksanen et al. 2022), scales (Wickham et al. 2022), and ggpattern (FC and Davis 2022).

Results

After filtering the street tree database to include only tree species with documented associations with BC Lepidoptera, 77 tree species remained: 11 native and 66 non-native (Fig. 1*b*). These 77 species represent 108 196 (72%) of the 150 182 total planted street trees in Vancouver. Five of the 77 street trees were only associated with non-native Lepidoptera (Table S3). Native trees were comprised of approximately the same number of broadleaf versus coniferous species but non-native street trees were primarily broadleaf (Fig. 1*b*).

Relationship between Lepidoptera richness and street tree type

Of the 568 species of BC Lepidoptera with known associations with Vancouver street trees, 511 species were classified as native and 57 as non-native. On average, each Vancouver street tree species was associated with 21.2 species of native Lepidoptera (range: 1–191, standard deviation: 35). The three species of street trees associated with the most native BC Lepidoptera were *Betula papyrifera* Marshall (paper birch, 191 Lepidoptera species), *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir, 126 species), and *Malus pumila* Mill. (apple, 122 species; Fig. S1).

Native Lepidoptera species richness was approximately five times higher on native than on non-native street trees (Fig. 2*a*; mean ± standard deviation of richness on native and non-native trees, respectively: 67.1 ± 59.2; 13 ± 20.2; $F_{[1,70]} = 21.3$, $p < 0.0001$). Species richness of non-native Lepidoptera did not differ between native and non-native street trees ($F_{[1,56]} = 0.19$, $p = 0.67$). Native Lepidoptera species richness was slightly higher on coniferous versus broadleaf street trees, but this difference was not statistically significant (Fig. 2*b*; coniferous mean ± standard deviation = 36.7 ± 41.4; broadleaf mean ± standard deviation = 18.1 ± 33.1; $F_{[1,70]} = 2.9$, $p = 0.09$). Species richness of non-native Lepidoptera did not differ between broadleaf and coniferous street trees ($F_{[1,56]} = 0.27$, $p = 0.60$). Lastly, when we clustered street trees by their associated Lepidoptera, native street trees clustered separately from non-native trees (Fig. 3*a*; anosim R: 0.16, $p = 0.032$), and broadleaf street trees clustered separately from coniferous street trees (Fig. 3*b*; anosim R: 0.29, $p < 0.0001$).

Discussion

The overall goal of this study was to examine whether native and non-native street trees differed in their potential to support native Lepidoptera. Using the City of Vancouver as a case study, we found that in comparison to non-native street trees, native street trees were associated with almost five times as many species of native Lepidoptera. Native and non-native street trees were also associated with different communities of Lepidoptera, as were broadleaf versus coniferous trees. Together these data support the hypothesis that non-native street trees support fewer native Lepidoptera species because many Lepidoptera are unable to use novel hosts as a food source (Tallamy et al. 2021).

The results reported here are consistent with studies that have found higher herbivorous insect diversity on native versus introduced plants. These previous studies have used both database-based (Tallamy and Shropshire 2009; Padovani et al. 2020) and experiment-based approaches (Hartley et al. 2010; Helden et al. 2012; Clem and Held 2018; Mata et al. 2021; Jensen et al. 2022) but none have examined an almost complete inventory of street trees in an urban area. Jensen et al. (2022) used active sampling to compare inver-

Fig. 2. The number of native Lepidoptera species associated with (*a*) native versus non-native street tree species ($p < 0.0001$) and (*b*) broadleaf versus coniferous street tree species ($p = 0.67$). Open circles represent individual broadleaf trees and triangles represent individual coniferous trees. Blue circles represent unique native tree species and red circles represent unique non-native tree species.

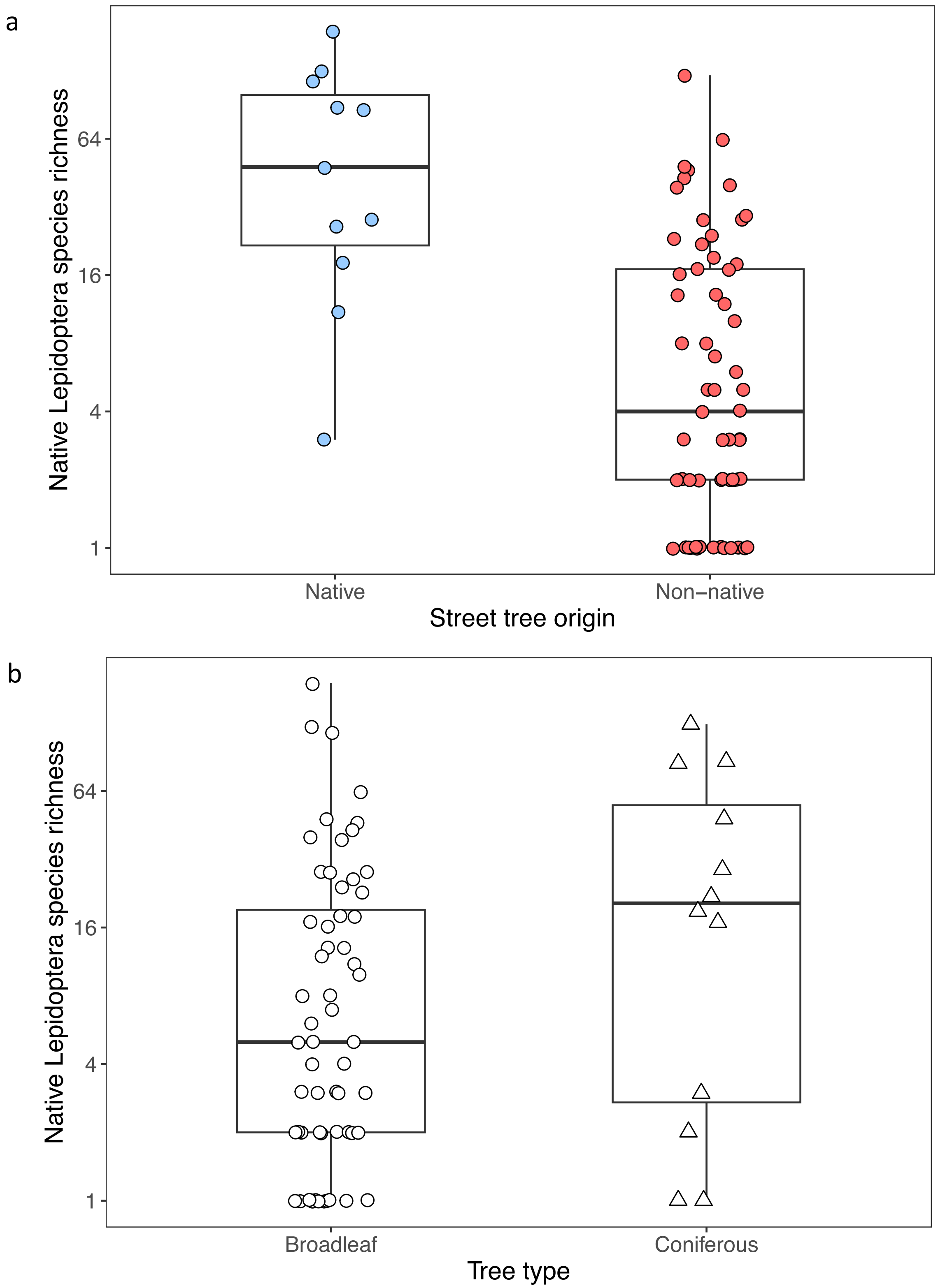
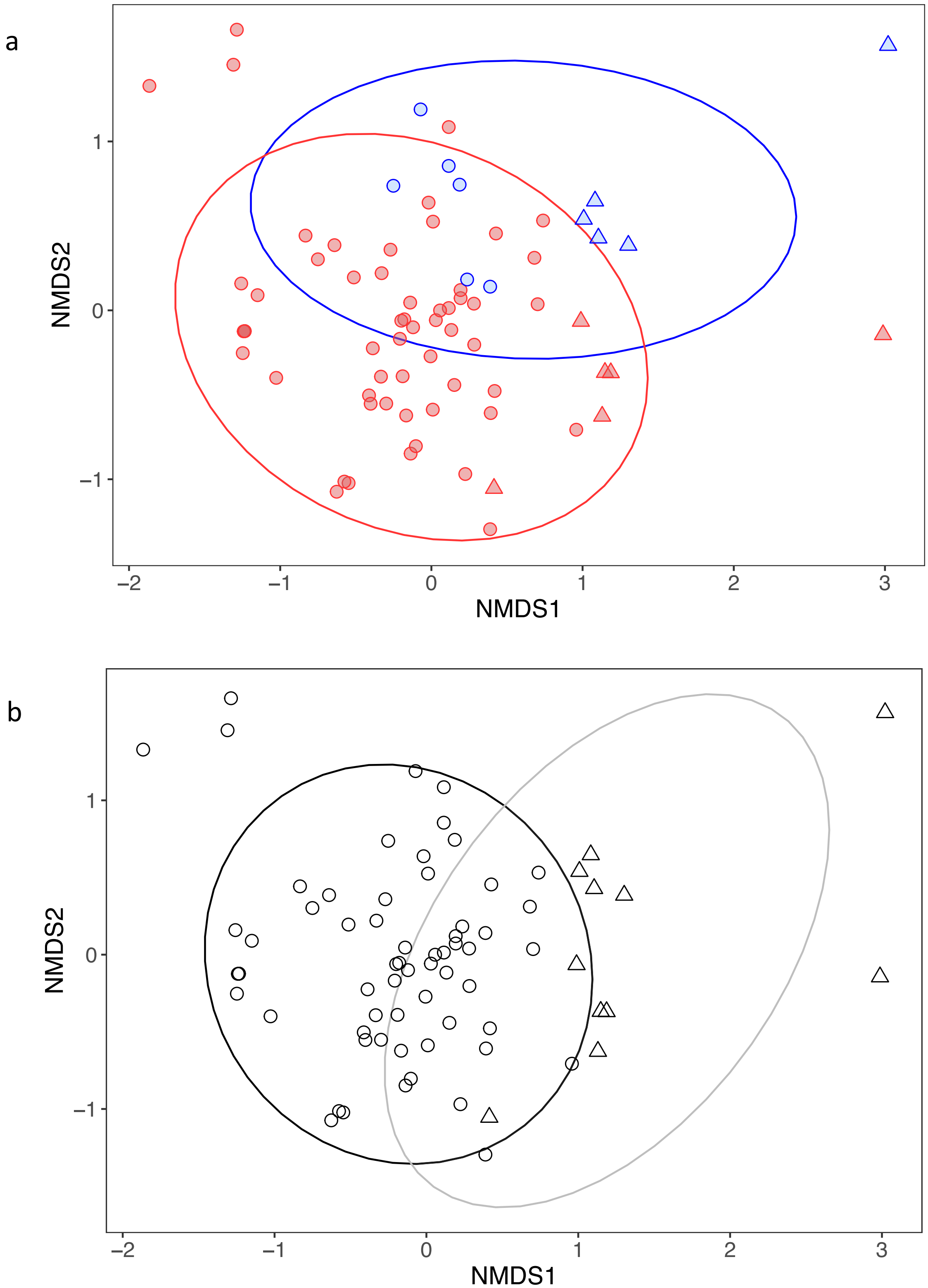


Fig. 3. (*a*) NMDS plots of native (blue) versus non-native (red) tree species clustered by their Lepidoptera associations ($p = 0.037$); (*b*) broadleaf (circles) or coniferous (triangles) tree species clustered by their Lepidoptera associations ($p < 0.0001$).



tebrate communities on nine native and seven non-native tree species in city parks in Malmö, Sweden, and they documented that native trees contained significantly more invertebrates than non-native trees. Mata et al. (2021) examined insect diversity on indigenous versus introduced plants in urban parks in Melbourne, Australia, and also found elevated

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numbers of indigenous insect species on indigenous plants. However, Helden et al. (2012) did not find significant differences between native and non-native trees with respect to the species richness or abundance of Hemiptera, another order of primarily phytophagous insects. Interestingly, Tallamy et al. (2021) suggested that because of their "sucking" feeding mode, Hemiptera should be better able to avoid consuming novel plant secondary metabolites (as compared to the "chewing" mouthparts of Lepidoptera caterpillars), so it is perhaps not surprising that there was no effect of plant origin on Hemiptera abundance or diversity. Together with previously published studies, there appears to be good evidence that native trees in urban environments, whether located in city parks or next to streets and sidewalks, support a higher number, greater diversity, and different communities of herbivorous insects.

The finding that broadleaf and coniferous trees differed in their associated Lepidoptera aligns with published literature on this topic (Holloway and Hebert 1979; Hatcher 1990). Although there are some Lepidoptera that can feed on both coniferous and broadleaf trees (Brown 2018), many species are limited to feeding on tree species that share similar chemical profiles (Menken et al. 2009). Coniferous foliage also tends to have higher water and fibre content and lower nitrogen content than broadleaf trees (Ricklefs and Matthew 1982; Hatcher 1990) and thus these two tree types constitute a very different food source.

Our approach of using databases and published literature to quantify known associations between street trees and Lepidoptera enabled us to compile data for 95 tree species simultaneously (pre-filtering). By filtering the dataset to include only associations between street trees and BC Lepidoptera, our results provide a good estimate for which street trees should be suitable hosts for native Lepidoptera. There are also limitations to this approach. Our results may underestimate Lepidoptera species richness for street trees for which there were very little published insect-association data. For example, *Tilia* × *euchlora* K.Koch, *Parrotia perisca* (DC.) C.A.Mey., and *Platanus* × *acerfolia* (Aiton) Willd. appear 4262, 2442, and 1832 times in the Vancouver street tree database but we were only able to find one Lepidoptera association for each of these tree species. We did not run a separate analysis on hybrid street trees but we hypothesize that many of the street trees for which there are little Lepidoptera association data are hybrid trees. Out of the 13 street trees for which we were unable to find Lepidoptera data, six were hybrids (Table S1). Although the database approach to compiling plant–insect associations is commonly employed (e.g., Tallamy and Shropshire 2009; Padovani et al. 2020), a follow-up study that actively samples the Lepidoptera–street tree associations documented here would be beneficial for confirming the overall accuracy of these results.

In conclusion, we have documented that in comparison to non-native species, native street trees are likely to support significantly more species of native Lepidoptera. As cities continue planting trees as part of their climate change mitigation strategies, we suggest that a greater consideration be placed on how cities can better support the growth and survival of native tree species. Alternatively, if a non-native tree species is more likely to survive in a specific urban area, we recommend choosing a non-native species that has been documented to be associated with at least some native insects. To aid decision makers in BC, we have assembled summary tables of street tree–Lepidoptera associations for this region (Tables S4–S6). Urbanization has destroyed large swaths of suitable habitat for countless plant and animal species. A greater focus on the provenance of street trees and the biodiversity these trees support may go a long way toward reducing insect declines worldwide.

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Data availability

All data used to generate the results in this manuscript are available on Dryad: DOI: 10.5061/dryad.3j9kd51r7.

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Competing interests

The authors declare no conflicts of interest.

Supplementary material

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References

Anderson, E.C., Locke, D.H., Pickett, S.T.A., and LaDeau, S.L. 2023. Just street trees? Street trees increase local biodiversity and biomass in higher income, denser neighborhoods. Ecosphere, **14**(2). doi:10.1002/ecs2.4389. PMID: 36762202.

Bell, J.R., Blumgart, D., and Shortall, C.R. 2020. Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. Insect Conserv. Divers. **13**(2): 115–126. doi:10.1111/icad.12412.

Beran, F., and Petschenka, G. 2022. Sequestration of plant defense compounds by insects: from mechanisms to insect–plant coevolution. Annu. Rev. Entomol. **67**(1): 163–180. doi:10.1146/annurev-ento-062821-062319. PMID: 34995091.

Brown, J.W. 2018. Patterns of Lepidoptera herbivory on conifers in the New World. J. Asia-Pac. Biodivers. **11**(1): 1–10. doi:10.1016/j.japb.2018.01.008.

Burner, R.C., Selås, V., Kobro, S., Jacobsen, R.M., and Sverdrup-Thygeson, A. 2021. Moth species richness and diversity decline in a 30-year time series in Norway, irrespective of species' latitudinal range extent and habitat. J. Insect Conserv. **25**(5): 887–896. doi:10.1007/s10841-021-00353-4.

Clem, C.S., and Held, D.W. 2018. Associational interactions between urban trees: are native neighbors better than non-natives? Environ. Entomol. **47**(4): 881–889. doi:10.1093/ee/nvy071. PMID: 29771321.

FC, M., and Davis, T. 2022. _ggpattern: 'ggplot2' Pattern Geoms_. R package version 1.0.1. Available from https://CRAN.R-project.org/package=ggpattern.

Fernández-Juricic, E. 2000. Avifaunal use of wooded streets in an urban landscape. Conserv. Biol. **14**(2): 513–521. doi:10.1046/j.1523-1739.2000.98600.x.

Frank, S.D., Backe, K.M., McDaniel, C., Green, M., Widney, S., and Dunn, R.R. 2019. Exotic urban trees conserve similar natural enemy communities to native congeners but have fewer pests. PeerJ, **7**: e6531. doi:10.7717/peerj.6531.

Green, K., Caley, P., Baker, M., Dreyer, D., Wallace, J., and Warrant, E. 2021. Australian Bogong moths *Agrotis infusa* (Lepidoptera: Noctuidae), 1951–2020: decline and crash. Austral Entomol. **60**(1): 66–81. doi:10.1111/aen.12517.

Grunzweig, L., Spiering, D.J., Labatore, A., and Warren, R.J. 2015. Non-native plant invader renders suitable habitat unsuitable. Arthropod Plant Interact. **9**(6): 577–583. doi:10.1007/s11829-015-9402-z.

Hartley, M.K., Rogers, W.E., and Siemann, E. 2010. Comparisons of arthropod assemblages on an invasive and native trees: abundance, diversity and damage. Arthropod Plant Interact. **4**(4): 237–245. doi:10.1007/s11829-010-9105-4.

Hatcher, P.E. 1990. Seasonal and age-related variation in the needle quality of five conifer species. Oecologia, **85**(2): 200–212. doi:10.1007/BF00319402.

Helden, A.J., Stamp, G.C., and Leather, S.R. 2012. Urban biodiversity: comparison of insect assemblages on native and non-native trees. Urban Ecosyst. **15**(3): 611–624. doi:10.1007/s11252-012-0231-x.

Holloway, J.D., and Hebert, P.D.N. 1979. Ecological and taxonomic trends in macrolepidopteran host plant selection. Biol. J. Linn. Soc. **11**(3): 229–251. doi:10.1111/j.1095-8312.1979.tb00036.x.

Iungman, T., Cirach, M., Marando, F., Pereira Barboza, E., Khomenko, S., Masselot, P., et al. 2023. Cooling cities through urban green infrastructure: a health impact assessment of European cities. Lancet, **401**(10376): 577–589. doi:10.1016/S0140-6736(22)02585-5.

Jensen, J.K., Ekroos, J., Watson, H., Salmón, P., Olsson, P., and Isaksson, C. 2023. Urban tree composition is associated with breeding success of a passerine bird, but effects vary within and between years. Oecologia, **201**(3): 585–597. doi:10.1007/s00442-023-05319-8.

Jensen, J.K., Jayousi, S., von Post, M., Isaksson, C., and Persson, A.S. 2022. Contrasting effects of tree origin and urbanization on invertebrate abundance and tree phenology. Ecol. Appl. **32**(2): 1–17. doi:10.1002/eap.2491.

Laussmann, T., Dahl, A., and Radtke, A. 2021. Lost and found: 160 years of Lepidoptera observations in Wuppertal (Germany). J. Insect Conserv. **25**(2): 273–285. doi:10.1007/s10841-021-00296-w.

Lewinsohn, T.M., Agostini, K., Lucci Freitas, A.V., and Melo, A.S. 2022. Insect decline in Brazil: an appraisal of current evidence. Biol. Lett. **18**(8): 20220219. doi:10.1098/rsbl.2022.0219.

Liu, J., and Slik, F. 2022. Are street trees friendly to biodiversity? Landsc. Urban Plan. **218**: 104304. doi:10.1016/j.landurbplan.2021.104304.

Majewska, A.A., and Altizer, S. 2020. Planting gardens to support insect pollinators. Conserv. Biol. **34**(1): 15–25. doi:10.1111/cobi.13271.

Marando, F., Heris, M.P., Zulian, G., Udías, A., Mentaschi, L., Chrysoulakis, N., et al. 2022. Urban heat island mitigation by green infrastructure in European functional urban areas. Sustain. Cities Soc. **77**: 103564. doi:10.1016/j.scs.2021.103564.

Mata, L., Andersen, A.N., Morán-Ordóñez, A., Hahs, A.K., Backstrom, A., Ives, C.D., et al. 2021. Indigenous plants promote insect biodiversity in urban greenspaces. Ecol. Appl. **31**(4). doi:10.1002/eap.2309.

McCoy, D.E., Goulet-Scott, B., Meng, W., Atahan, B.F., Kiros, H., Nishino, M., and Kartesz, J. 2022. Species clustering, climate effects, and introduced species in 5 million city trees across 63 US cities. eLife, **11**: e77891. doi:10.7554/eLife.77891.

Menken, S.B.J., Boomsma, J.J., and Van Nieukerken, E.J. 2009. Large-scale evolutionary patterns of host plant associations in the Lepidoptera: host plant use in the Lepidoptera. Evolution, **64**(4): 1098–1119. doi:10.1111/j.1558-5646.2009.00889.x.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., et al. 2022. vegan: Community ecology package. Available from https://cran.r-project.org/web/packages/vegan/index.html [accessed 30 June 2023].

Ossola, A., Locke, D., Lin, B., and Minor, E. 2019. Yards increase forest connectivity in urban landscapes. Landsc. Ecol. **34**(12): 2935–2948. doi:10.1007/s10980-019-00923-7.

Ozanne, C.M.P. 1999. A comparison of the canopy arthropod communities of coniferous and broad-leaved trees in the United Kingdom. Selbyana, **20**(2): 290–298.

Padovani, R.J., Salisbury, A., Bostock, H., Roy, D.B., and Thomas, C.D. 2020. Introduced plants as novel Anthropocene habitats for insects. Global Change Biol. **26**(2): 971–988. doi:10.1111/gcb.14915.

Panigaj, L., and Panigaj, M. 2008. Changes in lepidopteran assemblages in Temnosmrečinská dolina valley (the High Tatra Mts, Slovakia) over the last 55 years. Biologia, **63**(4): 582–587. doi:10.2478/s11756-008-0081-4.

Pohl, G.R., Cannings, R.A., Landry, J.-F., Holden, D.G., and Scudder, G.G.E. 2015. Checklist of the Lepidoptera of British Columbia, Canada. J. Entomol. Soc. B.C.(3). Available from https://journal.entsocbc.ca/index.php/journal/article/view/917 [accessed 30 June 2023].

R Core Team. 2023. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Ricklefs, R.E., and Matthew, K.K. 1982. Chemical characteristics of the foliage of some deciduous trees in southeastern Ontario. Can. J. Bot. **60**(10): 2037–2045. doi:10.1139/b82-251.

Robinson, G.S., Ackery, P.R., Kitching, I., Beccaloni, G.W., and Hernández, L.M. 2023. HOSTS—a database of the world's lepidopteran hostplants. Nat. Hist. Mus. doi:10.5519/HAVT50XW.

Schlaepfer, M.A., Guinaudeau, B.P., Martin, P., and Wyler, N. 2020. Quantifying the contributions of native and non-native trees to a city's biodiversity and ecosystem services. Urban For. Urban Green. **56**: 126861. doi:10.1016/j.ufug.2020.126861.

Sjöman, H., Morgenroth, J., Sjöman, J.D., Sæbø, A., and Kowarik, I. 2016. Diversification of the urban forest—can we afford to exclude exotic tree species? Urban For. Urban Green. **18**: 237–241. doi:10.1016/j.ufug.2016.06.011.

Somme, L., Moquet, L., Quinet, M., Vanderplanck, M., Michez, D., Lognay, G., and Jacquemart, A.-L. 2016. Food in a row: urban trees offer valuable floral resources to pollinating insects. Urban Ecosyst. **19**(3): 1149–1161. doi:10.1007/s11252-016-0555-z.

Tallamy, D.W., and Shropshire, K.J. 2009. Ranking Lepidopteran use of native versus introduced plants. Conserv. Biol. **23**(4): 941–947. doi:10.1111/j.1523-1739.2009.01202.x.

Tallamy, D.W., Narango, D.L., and Mitchell, A.B. 2021. Do non-native plants contribute to insect declines? Ecol. Entomol. **46**(4): 729–742. doi:10.1111/een.12973.

Wagner, D.L. 2020. Insect declines in the Anthropocene. Annu. Rev. Entomol. **65**(1): 1–24. doi:10.1146/annurev-ento-011019-025151.

Wickham, H., and Seidel, D.,RStudio. 2022. August 20. scales: scale functions for visualization. Available from https://cran.r-project.org/web/packages/scales/index.html [accessed 30 June 2023].

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., et al. 2019. Welcome to the Tidyverse. JOSS, **4**(43): 1686. doi:10.21105/joss.01686.