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Linking herbivory and ecosystem services in urban forests

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Urban forests provide important benefits for humans. Species interactions, in particular herbivory, can alter their function and ultimately threaten their ecosystem service provisioning. We call for research that identifies herbivory drivers in urban forests and tests for links between herbivory and forest services. Knowledge gained can inform management of urban ecosystems.

Background and motivation

Urban forests (see Glossary) comprise woodlands, forests, tree stands, hedgerows, and individual trees located in urban and peri-urban areas, including naturalized vegetation, street trees, arboreta, parks, and gardens. These forests provide key benefits to urban populations, namely **ecosystem services**, ranging from pest control and biodiversity maintenance to recreational activities and human health [1]. Therefore, studying the ecological drivers of urban forest function and services represents a central task in order to enhance their provisioning of such services to humans and increase their resilience.

A rich set of species interactions unfolds within urban ecological communities, among which herbivory is one of the most common and important. Indeed, urban areas contain diverse herbivore communities which contribute importantly to urban biodiversity. At the same time, urban forests have highly modified biotic and abiotic conditions relative to **rural forests**, which strongly shape plant–herbivore interactions [2]. Observed herbivory patterns are characterized by striking variability. In some cases, urban forests exhibit considerably high herbivory rates relative to rural forests, often reaching outbreak levels (e.g., in the case of insects), whereas in other cases, herbivory is low or virtually absent [2]. Ecological research is starting to address the causes behind such variability, but much remains unknown.

There is good evidence from plant communities in natural areas (e.g., grasslands, forests) that herbivory exerts strong controls over forest **ecosystem functions** [3], which in turn underlie ecosystem services. Herbivory plays a pivotal role in energy transfer from plants to higher trophic levels and links green and brown (detritivore) food webs, for example, via subsidies to brown webs from the products of herbivore consumption (e.g., frass) or by changing plant chemistry (e.g., secondary metabolite levels) and thus leaf litter properties for detritivores [4]. As a result, herbivory plays a key role in shaping ecosystem functions such as nutrient cycling and **primary productivity**. In some cases, particularly when plant tissue loss is high, herbivory can degrade or weaken services, resulting in **ecosystem disservices**. However, despite the above evidence, links between herbivory and ecosystem functions and services have not yet been made in urban forests.

We argue that research linking herbivory to ecosystem processes is central to understanding biotic controls over urban forest function and can be achieved gradually. First, by conducting research aimed at identifying the ecological drivers of herbivory in urban forests. Second, by measuring urban forest ecosystem functions and assessing their relationships with herbivory patterns, either through correlational or manipulative approaches. And third, identifying urban forest ecosystem services of high priority and the functions they arise from, to then reach an integrative understanding that links herbivory (based on an understanding of its drivers), ecosystem processes, and services.

Glossary

Abiotic factors: a non-living part of an ecosystem that shapes its environment.
Bottom-up control: producer growth or other traits (e.g., defences) shape biomass and diversity at higher trophic levels.
Ecosystem disservices: the detrimental consequences of ecosystem changes or deficient ecosystem services. These include direct negative impacts on humans (e.g., diseases) and the disruption of services (e.g., cultural or provisioning).
Ecosystem function: physicochemical and biological processes that occur within the ecosystem to maintain terrestrial life (e.g., stocks of energy and materials, fluxes of energy or material processing, stability of rates or stocks over time).
Ecosystem services: many and varied benefits to humans provided by the natural environment and from healthy ecosystems which depend on the proper functioning of an ecosystem (e.g., nutrient cycling, carbon capture, pest regulation, conservation of charismatic species, biodiversity provisioning).
Primary productivity: the rate at which energy is converted to organic substances by photosynthetic producers.
Rural forests: wooded areas that are formally managed, shaped, transformed, or rebuilt by rural individuals or communities; that are fully integrated within farming systems; and that constitute an important structuring component of rural landscapes.
Top-down control: predation or parasitism by higher trophic levels reduces herbivore biomass and herbivory.
Urban forest: a forest, or a collection of trees, that grow within a city, town, or a suburb.
Urbanization: the process by which large numbers of people become permanently concentrated in relatively small areas, forming cities.

Drivers of herbivory in urban forests

Bottom-up drivers of herbivory in urban forests include variation in plant traits at the individual tree level (arrow A in Figure 1), including physical and chemical defences and nutritional quality [5,6]. At broader spatial scales, there are tree stand-level features that can strongly affect herbivory (arrow B in Figure 1). For example, low diversity of tree species, which includes planting of monospecific stands, increases the chance of herbivores locating host plants and reside and reproduce in those patches, thus increasing herbivory rates and the risk of insect pest outbreaks

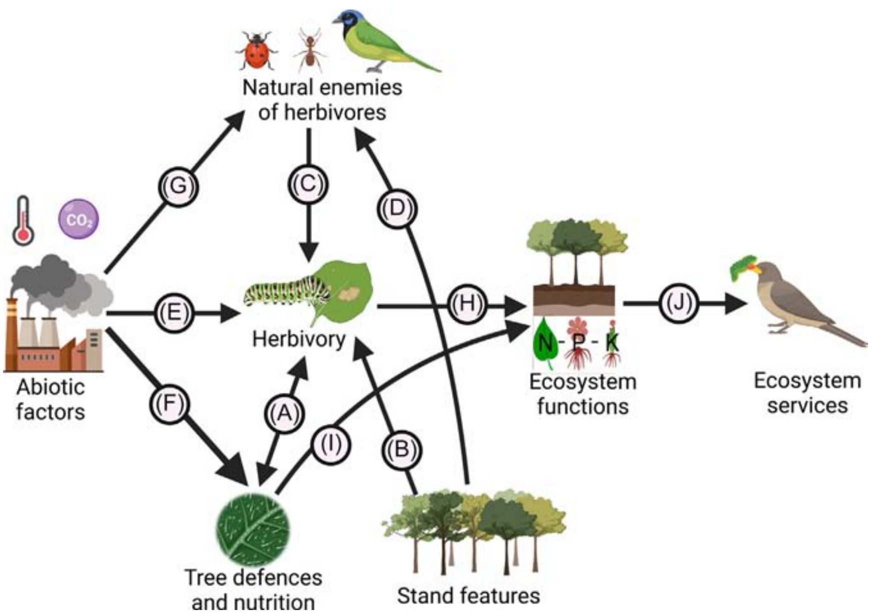

Figure 1. Conceptual diagram showing proposed ecological drivers of herbivory in urban forests and the link between herbivory and ecosystem functions and services. (A) Bottom-up effects of tree-level traits on herbivory and vice versa via induced plant defences; (B) effect of tree stand-level features on herbivory (including spatial features, e.g., connectivity and stand size); (C) top-down effects of predators on herbivory; (D) effect of stand-level features on natural enemies [these features can also favor predation and promote feedbacks impacting herbivory and plants (D+C+A)]; (E) effect of abiotic forcing (e.g., contaminants, nutrient deposition, artificial light, etc.) on herbivory, as well as via bottom-up (F+A) and top-down (G+C) drivers of herbivory; (H) effects of herbivory on ecosystem functions due to plant tissue consumption (e.g., on primary productivity); (I) effects of plant traits on ecosystem functions (e.g., recalcitrant compounds on decomposition rates), including indirect effects of herbivory on ecosystem functions via changes in plant traits [e.g. induced defences (A+I)]; (J) ecosystem services (carbon sequestration, pest regulation) emerge from ecosystem functions. Pathways depicted highlight examples given in the text, but additional ones involving herbivory (e.g, natural enemy effects on herbivores influencing herbivory and/or plant traits and in turn ecosystem functions) are equally plausible but not shown for simplicity. Likewise, other pathways not involving herbivory (e.g. abiotic factors and stand-level features directly affecting ecosystem function) are not shown either given the herbivory-focused arguments. Figure created with BioRender.com.

in urban forests [7]. In addition, spatial features such as connectivity and patch size likely also play important roles in shaping herbivory patterns, as shown recently for tree pathogens in cities [8].

Herbivory in urban forests can also be shaped by changes in **top-down control** by natural enemies of herbivores (arrow C in Figure 1). Carnivore effects are nonetheless highly variable in urban forests and in many cases are species or guild specific [9]. For instance, parasitoid and bird attack can be higher, lower, or not differ between urban and rural forests [9], whereas predation by ants has been found to be greater in urban forests [5]. In addition, bottom-up drivers such as stand-level features (e.g., tree diversity or composition) can promote feedbacks between trees and predation which shape herbivory and plant traits or biomass (arrows D+C+A in Figure 1), as shown in rural forests [10]. To date, however, these dynamics have not been studied in urban forests.

Finally, **abiotic factors** also influence herbivory in urban forests (arrow E in Figure 1), including pollution, altered water regimes (artificial irrigation vs. increased runoff), artificial light from lamps, warming in heat islands, increased CO_2 emissions, among others, which can directly affect herbivory by causing changes in herbivore movement or survival [2]. In addition, abiotic factors can affect herbivory in urban forests via changes in plant traits (arrows F+A in Figure 1) or natural enemy pressure (arrow G+C in Figure 1). For example, in a recent study we found that increased CO_2 emissions were correlated with lowered levels of leaf defences in oak (*Quercus robur*) trees growing in European cities, but insect leaf damage was not associated with leaf defences, thus rejecting the idea of indirect **bottom-up controls** on herbivory via CO_2 [6]. Nonetheless, mechanisms linking abiotic conditions and herbivory via these indirect pathways remain virtually unstudied in urban forests.

Herbivory and urban forest function: integrating herbivory drivers

Herbivory exerts important controls over ecosystem functions. For example, plant tissue loss due to herbivore consumption can drive reductions in primary productivity of up to 25% in forests, grasslands, and agricultural systems [11]. Likewise, variation in herbivory could also lead to (in some cases predictable) changes in ecosystem properties in urban forests (arrow H in Figure 1). In addition, indirect mechanisms could also take place whereby, for example, herbivory affects nutrient cycling through changes in plant chemistry (arrows A+I in Figure 1) [4]. In addition, greater resource availability (e.g., nitrogen deposition) boosts plant growth, favoring increases in herbivory which in turn drives reductions in primary productivity. Other abiotic drivers such as greater water runoff or soil compaction can instead lead to reduced forest productivity but similarly drive higher rates of herbivory due to lower tree defences [12], similarly driving decreases in primary productivity. Alternatively, there could also be cases where herbivory is lower in urban forests (mentioned previously) and potentially lead to opposing outcomes [5,6,13].

By addressing herbivory drivers and links to ecosystem processes, we can understand how variation in herbivory impacts urban forest ecosystem function and also detect commonalities across urban systems. To this end, observational studies relating herbivory rates measured on site with city databases on biotic (tree density, sizes; [8]) or abiotic (e.g., CO_2 emissions, nitrogen deposition; [6]) factors coupled with methods to quantify ecosystem functions (e.g., stem diameter measurements to estimate productivity) can be of great value. Likewise, when possible, experimental studies are also desirable, including, for example, leaf litter manipulations, predator exclusions, and warming experiments. To this end, baseline information on insect and vertebrate communities is indispensable to robustly link focal (and ecologically important) plant–herbivore interactions with herbivory patterns and ecosystem processes. A valuable opportunity for studying herbivore communities as well as measuring herbivory and ecosystem processes lies ahead in urban citizen science efforts and increasing availability of city databases to extract information on herbivory drivers.

Linking herbivory and urban forest services

Ecosystem functions affected by herbivory in turn underlie ecosystem services which affect humans in urban settings (arrow J in Figure 1), including conservation of charismatic species, recreation, and mental well-being, as well as carbon capture and regulation of pollinator services, pests, or diseases within urban or peri-urban forests and gardens. For example, carbon sequestration can be estimated based on carbon density values obtained from ground data or through forest inventories and maps obtained by remotely sensed data (e.g., aerial images with LiDAR or satellite images) [14]. Data on herbivory and its underlying drivers can in turn be correlated to test mechanisms involving herbivory impacts on carbon stocks in urban forests. Likewise, pest regulation, for example, can be assessed with surveys of abundance and damage by focal insect pests in urban forests for which tree- and stand-level features as well as predator pressure are concomitantly measured (or previously known from databases) in order to identify drivers of pest abundance and achieve a predictive understanding of outbreaks. In this case, herbivory itself is the ecosystem disservice rather than a driver of services, but a similar rationale and methods can be followed to assess ecological drivers.

Future outlook

Understanding the links between herbivory and bottom-up and top-down controls, and, in turn, ecosystem processes can provide key insight into urban forest functions and resulting services. Similar efforts can be made to study other plant–enemy interactions, such as disease dynamics by plant pathogens. Knowledge gained can be used to develop urban forest management solutions aimed at promoting urban biodiversity conservation and ecosystem services. This also includes the design of urban forests that are more resilient and are better at buffering the effects of stressors within urban systems, as well as reduce **urbanization** effects on adjacent rural areas.

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Declaration of interests

None declared by authors.

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