

ON THE NATURE OF THINGS: ESSAYS

New Ideas and Directions in Botany

Plant evolution in the urban jungle¹

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A hallmark of the Anthropocene is the rise of urban centers and their effects on the environment. Urban areas cover 3–5% of the total land surface yet more than half of Earth's human population lives in cities, suburbs, and towns (Seto et al., 2010). Urbanization is happening faster today than ever before, and this rapid development dramatically changes the physical environment, ecological communities, as well as local and global ecosystems (Seto et al., 2010; Alberti, 2015). Several decades of urban ecology have identified a syndrome of environmental changes associated with urbanization (Fig. 1). Despite these advances, we know little about how urbanization affects the evolution of organisms in general and plants in particular. Studying plant evolution within urban areas will facilitate a better understanding of evolution and could provide insight into problems related to conservation, environmental stability, and human health.

Why might urbanization influence plant evolution? Clearly, urban development changes both the biotic and abiotic environment (Fig. 1) in ways that could alter natural selection and adaptive evolution within plant populations. Urbanization may also influence nonadaptive evolution due to altered gene flow, genetic drift, or nonrandom mating (Donihue and Lambert, 2014). For example, urban development causes habitat fragmentation given that buildings and roads are a common feature to every city, where extensive pavement, concrete, and alteration of natural habitats is the rule rather than the exception (Bettencourt, 2013). This fragmentation can limit dispersal and gene flow, leading to greater genetic differentiation between populations. It can also influence the size of populations and thus the importance of neutral evolution because genetic drift will be greater in smaller populations. Finally, urban areas can alter mating patterns (e.g., increased selfing) through changes in pollinator communities (Eckert et al., 2010), which can

subsequently affect the distribution and fitness of plant genotypes. All of these factors may contribute to distinctive evolutionary dynamics in urban plant populations (see the section on Predictions).

The strongest evidence that urbanization can influence evolutionary processes and patterns comes from a small number of studies on animals. For example, the blackening of urban surfaces by pollution favors the development of darker moths that are better camouflaged against predators (Kettlewell, 1955). Urban pollution has resulted in evolution of tolerance to toxic chemicals among fish and mice (Whitehead et al., 2012; Harris et al., 2013). Changes in the physical environment associated with urbanization are also credited with causing the evolution of sexually selected traits in bird populations (Yeh, 2004). Even fewer studies have examined the effects of urbanization on plant evolution. Perhaps the best example is a study of dispersal traits in urban populations of *Crepis sancta* (Cheptou et al., 2008). This species produces both dispersing and nondispersing seeds, and plants within urban Montpellier, France, have evolved to produce a greater proportion of nondispersing seeds than plants from less urban areas. This adaptive evolution is consistent with the observation that dispersing seeds tend to scatter onto pavement within cities where they cannot germinate, whereas nondispersing seeds remain within patches favorable for germination. Urban areas can also influence the genetic structure of plant populations, as shown in *Linaria vulgaris*, which exhibits lower genetic diversity and fitness in urban populations than rural ones (Bartlewicz et al., 2015). These botanical studies, combined with those on animals, suggest that urban areas may frequently alter evolutionary dynamics in natural populations.

PREDICTING THE EFFECTS OF URBANIZATION ON PLANT EVOLUTION

Concepts and theory from evolutionary biology, coupled with an understanding of abiotic and biotic changes along urban–rural gradients (Fig. 1), lead to several general predictions about how urbanization is expected to affect plant evolution. These predictions

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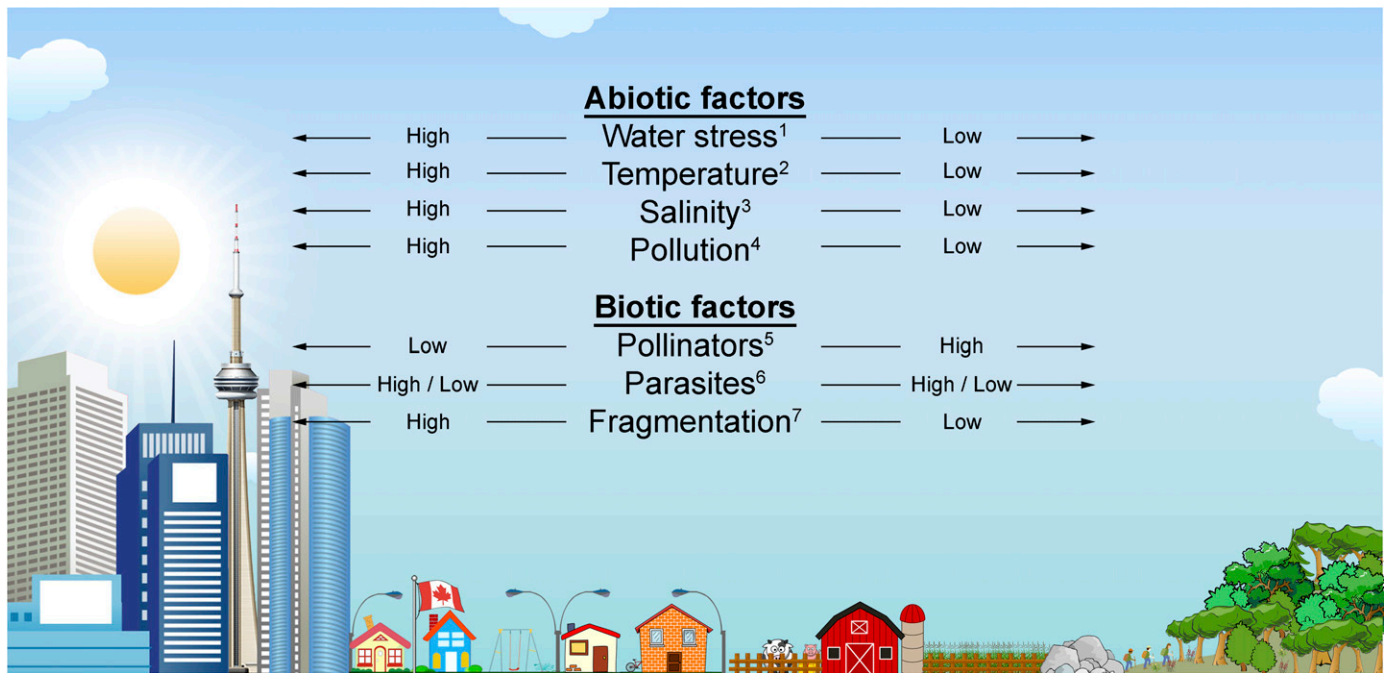


FIGURE 1 A syndrome of changes to the abiotic and biotic environment associated with rural to urban gradients. References: (1) Whitlow et al. (1992); (2) Oke (1973); (3) Cunningham et al. (2008); (4) Lovett et al. (2000); (5) Bates et al. (2011); (6) Raupp et al. (2010); (7) Alberti (2005).

are likely to explain evolutionary processes and patterns in many species, but exceptions will exist and the predictions offered here can provide a framework to examine alternative hypotheses. We propose the following five predictions that relate to fundamental evolutionary patterns and processes:

Prediction 1. Urban and non-urban populations will differ in the amount of genetic diversity—Many plant species colonize urban areas from surrounding non-urban areas. This process is expected to cause a population bottleneck and smaller population sizes due to reduced suitable habitat, which will result in lower genetic diversity within urban populations (Bartlewicz et al., 2015). Note that some exotic ruderal plant species thrive in urban environments (e.g., *Capsella bursa-pastoris*, *Taraxicum officinale*, and *Polygonum aviculare*), and in such cases, opposite patterns in genetic diversity are expected between urban and non-urban environments.

Prediction 2. Urbanization will alter natural selection on populations—Changes in the biotic and abiotic environment (Fig. 1) lead to the expectation that natural selection will differ between urban and non-urban populations. When this altered selection is associated with increased stress in urban areas (e.g., road salt), faster adaptive evolution will occur given sufficient genetic variation. When altered selection leads to less stress in urban environments (e.g., decreased herbivory or reduced competition), adaptive evolution will not necessarily be faster, but the evolutionary optima for particular traits (e.g., investment in antiherbivore defenses) will differ between urban and non-urban populations.

Prediction 3. Neutral evolution will be greater in urban areas—When urban areas result in smaller population sizes and reduced genetic diversity (see Prediction 1), genetic drift and population bottlenecks will increase the rate of neutral evolution. These neutral processes may prevent urban populations from adapting to novel

conditions despite altered selection. Such neutral evolutionary processes would become less frequent for species that respond positively to urbanization.

Prediction 4. Genetic divergence between urban and non-urban populations will be proportional to the size of urban areas—Gene flow can counteract genetic divergence between urban and non-urban environments. When a plant species is most common in non-urban areas, the proportion of the urban population comprised of immigrants from non-urban populations will be higher in small compared with large urban areas. Accordingly, genetic divergence between urban and non-urban populations should be positively related to city size. Interestingly, the opposite prediction can be made when plant species are more abundant in urban areas, such as in ruderal introduced species. In these species, genetic divergence will decrease as cities increase in size because dispersal will mainly occur from urban populations to non-urban populations.

Prediction 5. Insect-pollinated plants will evolve greater self-pollination or clonal growth in urban areas—Urbanization frequently reduces the abundance and diversity of pollinators (Bates et al., 2011). Following such a decrease, self-compatible populations are expected to evolve increased selfing as a mechanism of reproductive assurance, so long as there is genetic variation in selfing rates and inbreeding depression is not too large (Eckert et al., 2010). Other taxa may invest in greater clonality if it does not result in costs associated with geitonogamy.

WHY IS PLANT EVOLUTION IN URBAN ENVIRONMENTS IMPORTANT?

While understanding the evolution of plants in an urban context will improve our knowledge of evolutionary processes, one might

reasonably ask whether a deeper understanding of evolution in urban environments can also help address practical socioeconomic issues. Does the understanding of evolution in urban areas contribute something substantive to applied problems in the development, operation, and maintenance of cities? Can it positively influence the health and welfare of people living in urban areas? Can we use an understanding of urban population biology to forecast how populations will be impacted by anthropogenic environmental change? The few studies that exist demonstrate that principles from urban evolutionary ecology can be used to design greener cities (Tanner et al., 2014), that evolution in urban areas can affect human health and welfare (Alberti, 2015), and that cities themselves can provide a “real-world” scenario for testing hypotheses about climate change (Youngsteadt et al., 2014). Accordingly, we view the study of plant evolution in urban areas as an important and largely untapped frontier in biology and an exciting and important area for future research.

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