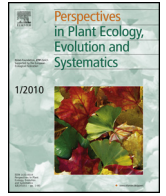




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Review

Urbanisation, plant traits and the composition of urban floras



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ABSTRACT

Given the increasing prevalence of cities, a better mechanistic and functional understanding of plant responses to urbanisation will assist biodiversity conservation and the provision of ecosystem services. Plant functional traits offer an opportunity to do this. To explore the relationship between plant traits and the urban environment, we synthesised the results of 29 studies that specifically examined plant traits or niche indicators (e.g. Ellenberg numbers) of urban floras. Niche indicators for nutrients, temperature and alkalinity were found to consistently increase across many studies. Some plant traits (e.g. woodiness, seed mass and height) tended to increase in response to urbanisation, while other traits have mixed responses and many other traits are understudied. We propose that variability in the observed responses is linked to the consistency and strength of urban stressors acting on those traits, and the importance of local factors. Our synthesis highlights the complexity of urban plant–environment interactions with many traits influenced by multiple abiotic, biotic and disturbance effects of urbanisation. Multiple stressors make it difficult to detect trends in urban plant trait signatures unless one urban stressor drives a particularly strong response or multiple stressors act on the response in the same direction. While our review has developed a better understanding of how urbanisation may assemble urban floras, further advances can be gained through studies that focus on specific urbanisation processes, measurable morphological traits and data curation and analyses that facilitate meta-analysis.

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Introduction

Urbanisation is rapidly transforming our world. Over the 20th century, the world's urban population grew from 220 million people to 2.8 billion, and since 2008, over half of the world's population has lived in urban areas (UNFPA, 2007). Within the next 20 years, the world's urban population is expected to reach 5 billion. Consequently, for the foreseeable future, cities will continue to expand, changing and fragmenting landscapes from agricultural and native vegetation cover to areas covered by impervious surfaces. In these altered landscapes vegetation is often restricted to much smaller patches and is subject to changed environmental conditions associated with urban environments (Sukopp, 2004; Williams et al., 2009). These changes can lead to reduced frequency and abundances of native plant species and increased prevalence of introduced alien flora, ultimately leading to the local extinction of many native plant species from cities (Hahs et al., 2009; Thompson and Jones, 1999) and the creation of new urban plant communities. Understanding which plant species are likely to benefit and those likely to be detrimentally impacted will be important for biodiversity conservation and the provision of ecosystem services in an increasingly urbanised world.

Urbanisation can be considered both as a generalised ecological gradient (McDonnell and Pickett, 1990) and as a characteristic suite of disturbances (Sukopp, 2004), for which plant functional traits are a useful investigative tool. Plant functional traits facilitate generalisation of ecological knowledge across species and floras (Keddy, 1992) and help elucidate mechanisms within plant ecological strategies (Grime, 2001; Westoby et al., 2002). Further, traits aid process-based understanding of vegetation response to environmental gradients, such as soil nutrients and rainfall (McDonald et al., 2003; Pollock et al., 2012), and to disturbances such as grazing (Diaz et al., 2007; Dorrough and Scroggie, 2008; Veski et al., 2004) and fire (McIntyre et al., 1999; Pausas and Bradstock, 2007). Crucially, the use of standardised measures of plant structure and function independent of taxonomy means results can be examined for generality worldwide.

Urban habitats around the world are increasingly similar in their structure and composition, and exhibit consistent changes in physical and biological parameters along urbanisation gradients (Grimm et al., 2008; Pickett et al., 2001; Seto et al., 2010). Urbanisation creates distinct meso- and local-scale environments in cities where the key abiotic conditions and resources that influence plant performance (i.e. temperature, light intensity, water and CO₂ availability, physical and chemical properties of soil) are altered compared to the surrounding non-urban landscape. Common environmental changes due to urbanisation include warmer climates due to the urban heat island (UHI), and drier, more nutrient-rich and alkaline soils due to the combined effect of impervious surfaces and aerial nutrient deposition. Through local extinctions and the introduction of new organisms, urbanisation can also alter biotic interactions and disturbance regimes. Each of these changes could potentially

act as a biotic environmental filter or stressor differentially impacting plant species depending on their environmental niche and the traits they have evolved to exploit it (Williams et al., 2009).

Urban environmental stressors are sometimes unidirectional, for example air pollution and temperature in urban areas nearly always increase relative to the surrounding landscape due to industrial activity and the urban heat island, but some such as soil moisture and light are variable within urban landscapes and can be higher or lower than the pre-urbanisation state. Other stressors such as altered or new disturbance regimes may be context dependent. Therefore, the actions of an environmental stressor may affect plant functional traits with different degrees of consistency and predictability, depending upon the nature of the stressor and its degree of influence on plant functional traits.

To explore the current state of knowledge about how urban environmental filters have been acting upon plant functional traits, we reviewed the published literature to determine (a) which traits have received the greatest research attention, and (b) how consistent the responses have been between studies. Williams et al. (2009) proposed four filters of urban floras: (i) habitat transformation, (ii) fragmentation, (iii) the urban environment and (iv) human preferences. The scope of this review is largely restricted to the effects of the urban environment filter. This is because although urban habitat transformation often leads to the consistent loss of particular habitats (e.g. wetlands), which may alter trait distributions by eliminating resident species with consistent trait combinations, the impact is habitat- and city-specific (Williams et al., 2009). In addition, the traits that make species susceptible to habitat fragmentation have already been reviewed elsewhere (Ewers and Didham, 2006; Henle et al., 2004), so we only consider how urbanisation may interact with habitat fragmentation to influence plant traits. We also restrict ourselves to natural and spontaneous vegetation of urban areas and deliberately exclude cultivated vegetation, because the impact of human preference on the traits of urban vegetation is a new research field with few studies (but see Kendal et al., 2012; Knapp et al., 2010). Based on the findings of our review, we identify some of the potential obstacles that hamper current efforts to develop a consistent understanding of the effect of urban environmental filters on plant traits, and propose some pressing areas for future research.

Methods

We searched Web of Science and Scopus using the terms “urban” AND “plant” AND “trait”, and collated all relevant papers published in the English language. We then sourced additional papers from the references listed, and studies that later cited them. We also included relevant studies that we uncovered when performing literature searches on particular traits, such as lifespan, lifeform, and pollination. Our criterion for inclusion was that the study had to have reported traits and/or niche indicators such as Ellenberg

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