Urbanisation, plant traits and the composition of urban floras

Running Title: Urbanisation and plant traits

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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.

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; Vesk 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 CO_2 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 numbers in relation to some analysis of urban floristic data. We took a broad-based approach to analyses of the effects of urbanisation on traits that included studies of extinction, invasion and variation in abundance, as described below. However, not all studies describing plant traits could be used. We did not include studies of intraspecific trait variation, trait responses to specific disturbances and processes within urban areas, or comparisons between different urban habitats. We also limited our review to terrestrial higher plants and where traits were used to predict abundance or occupancy. Where we encountered a study that did not formally analyse plant functional traits, but documented trends within the discussion, we included it in our analysis.

We used published papers as the unit of replication, although some papers included multiple analyses. We found 29 papers from which some information could be gleaned. We scored the response for each trait in each study as one of three possibilities: monotonically increasing with urbanisation, or decreasing, or neutral. An increase may be broadly interpreted as possession of the trait (or higher values of continuous traits) being advantageous to plants under urbanisation.

Neutral responses were recorded for cases where there was either no response detected, or where the response was clearly not monotonic.

Details of studies

Eight of the 29 studies that met our criteria analysed native species only. The majority studied naturalized exotics as well, with some papers separating the analyses. Sixteen studies reported change over time, with temporal extents ranging from 20-300 years. Eleven studies analysed extinction or persistence on flora lists from cities, towns or urbanised counties. Four of these also analysed the invasion of introduced species (Aronson et al., 2007; Chocholoušková and Pyšek, 2003; Dolan et al., 2011; Knapp et al., 2010). However, we have not chosen to distinguish between native and alien species as this focus can blur advantageous and disadvantageous trait responses (Thompson and Davis, 2011). One of the extinction studies, i.e. Duncan et al (2011), utilises data from eleven cities, six of which showed appreciable extinction rates and were analysed further for trait effects. Four studies analysed change over time at specific urban sites or in grid cells (Aronson et al., 2007; Godefroid and Koedam, 2007; Van der Veken et al., 2004; Williams et al., 2005). A further thirteen studies presented contemporary snapshots from datasets of quadrats or grid cells (sometimes aggregated from quadrats) ranging from 1 km^2 to 130 km^2. The spatial extent of these analyses ranges from approximately 50 km^2 to 350,000 km^2. Quadrat or grid cell studies can have responses and covariates at the level of the sampling unit and so may fit gradient design models of occurrence or, more frequently, multivariate methods (six studies).

Analyses ranged widely in complexity and approach. At the simple end were statements of the percentage of species expressing a trait that went extinct (e.g. Preston, 2000; Turner et al., 1996). Others provided information on the frequencies of trait states through time, to display the time course of change. Contingency tables were commonly used to analyse each of these two types of data. List data were also analysed with various regression approaches, for instance modelling the probability of extinction as a function of traits (among other covariates). Regression approaches were also commonly used for analyses of occupancy or abundance data from plots or grid cells (Knapp et al., 2008). Commonly, the trait distributions were the response variables and the landuse of the sites of cells used as explanatory variables. Occasionally, trait data served as covariates in analyses of species‟ indices, such as the urbanity index used by Thompson and McCarthy (2008). More often data were subjected to ordination approaches to recover gradients of urbanisation from species by sites, and sites by environment matrices. Subsequently, species‟ traits were related to these land use gradients.

The species‟ characteristics most commonly investigated in the 29 studies considered were Ellenberg indicator values and the closely related Landolt numbers. Strictly speaking these are not plant traits but indicate the realised ecological niche of plant species along gradients of light, temperature, moisture, nutrients and affinity to acid or base soils. As such they are a proxy for a suite of traits that adapt a species to a particular habitat or environmental condition through the action of multiple filters. Competitor-Stress tolerator-Ruderal (CSR) strategy categories by Grime et al (1988) are similar indicators that were also commonly investigated in the literature. CSR strategies reflect strategic variation between species and extensive screening has demonstrated relationships between measureable traits and the primary axis of competitors to stress tolerators (Grime et al., 1997). Whole-plant traits such as growth form and lifespan have also been frequently investigated. In contrast, traits that reflect plant resource allocation spectra such as specific leaf area (SLA), seed mass and plant height, which are potentially the most informative, have not been examined as consistently. Some traits commonly examined in response to disturbance or environmental gradients (e.g. leaf nitrogen content) have not been studied at all in urban areas. This may be because the data are more difficult to collect, but the availability of global databases and potential for traits such as leaf nitrogen content to reflect the novel urban environment should be an incentive for this to occur.

Analyses

The numerous different response variables, multiple modes of analyses and diversity of study types prevented the intended formal meta-analysis. Instead we used a vote counting approach, and although it is not ideal for evaluating evidence, it can be used when parameter estimates are highly heterogeneous or absent (Gurevitch and Hedges, 1999; Hedges and Olkin, 1980; Stewart, 2010). Two concerns predominate with this approach: vote counting provides no information about the magnitude of the effect, nor of the uncertainty of that effect. Mindful of these concerns, we proceed with our aim to synthesize the heterogeneous information available and to promote more consistent approaches to analyses.

PLANT TRAIT RESPONSES TO URBANISATION – RESULTS AND SYNTHESIS

The results of our synthesis are presented by indicator below. The traits which have received the most research attention are the Ellenberg Nutrient (16 studies), moisture (14 studies) and soil alkalinity (14 studies) indicators. Broadly, niche indicators revealed stronger relationships with urbanisation (Figure 1) than did the functional traits (Figures 2, 3).

Niche indicators

Light niche

Thirteen studies examined the response of urban plant species to light using light indicators (Figure 1). Five studies found that light-loving plants were more common in urban areas, five found a neutral response while three found a negative response. The inconsistency of this summary may reflect nonlinear changes that our summary hides, due to differential effects between habitats and possibly between plants of remnant habitats and the urban matrix. For example, the urbanisation of the London area has caused both light-loving and shade-tolerant species to go extinct although light-loving species had a higher proportional extinction rate (Preston, 2000). In Zurich, light-demanding species had high extinction rates in forests and erosion slopes but low extinction rates in meadows (Stehlik et al., 2007). Other studies, which could not be included in this analysis because they did not utilise Ellenberg indicators, have also found responses to light. Turner et al. (1996) found that shade tolerant understorey shrubs had high extinction rates in an isolated urban rainforest remnant in Singapore due to increased light levels caused by edge effects and Burton et al.. (2005) studying riparian forest found that shade tolerant species were negatively associated with increasing urbanisation.

Temperature niche

European researchers identified long ago that temperature increases due to the UHI alter plant distributions enabling thermophilous species, typically Mediterranean archaeophytes or aliens from North America or Asia (Pyšek, 1998), to colonise cities outside their natural geographic range (Godde and Wittig, 1983; Henke and Sukopp, 1986; Kowarik, 1990; Sukopp and Wurzel, 2003). Recent studies have generalised the earlier city- and plant-specific findings at a broader scale. Eleven studies we examined used Ellenberg or Landolt temperature indicators to investigate urban plant traits. Six found thermophilic species are favoured in urban areas and five found no clear trend (Figure 1).

Moisture niche

Seven of the fourteen studies that examined Ellenberg or Landolt indicators of plant affinity for moisture, found that urban floras are more tolerant to drought that those of the surrounding area or that plants with higher soil moisture requirements had greater extinction risks (Figure 1). This could be partially due to the high rate of wetland loss in urban areas (Dolan et al., 2011; Preston et al., 2003; Stehlik et al., 2007). However, the response is probably more complex because two of the six studies (coded as having a neutral response) found that the effect of urbanisation on plant moisture preference varied with habitat or landscape type. In Zurich, Stehlik et al. (2007) found that the moisture indicator had a significant effect on extinction rates, but the direction of the effect varied by habitat affiliation. Dry adapted species had the highest extinction rates in forests, in wetlands moisture-loving species had the highest rate of loss, while in meadows there was a unimodal response with those species at either end of the Landolt moisture scale lost. In Brussels, Ellenberg moisture niche was only a significant explanatory variable of vegetation composition in the most densely built up areas, where it decreased, and in open built-up areas with plantations where it increased (Godefroid and Koedam, 2007). The only study that found that urbanisation promoted species of wetter habitats found that native species colonising urban walls had higher moisture requirements than rock-outcrop species in natural areas (Lososová and Láníková, 2010).

Soil alkalinity niche

There is good support for the proposition that urbanisation favours species of alkaline substrates. Of 14 studies investigating responses to soil alkalinity niches, eight reported increases, there were four neutral or non-significant responses and one found a decrease. The anomalous study was from Turnhout, a town in the Flanders region of Belgium, which has extremely high rates of atmospheric nitrogen deposition and it is suggested that the extensive loss of basidophilious species is due to widespread eutrophication of the area‟s poorly buffered sandy soils (Van der Veken et al., 2004). Other studies have reported high extinction rates in species from calcareous habitats but these are from urban areas where these habitats were rare and have been largely transformed (Bertin, 2002; Preston, 2000). Most studies investigating the soil alkalinity niche were from central Europe where species tolerant of high alkalinity are typically from calcareous habitats (Knapp et al., 2009; Tautenhahn et al., 2008). Consequently, in these areas there may be a natural environmental niche that supports species that are thus pre-adapted to urban conditions.

Nutrient niche

A number of studies have shown that plants characteristic of urban areas are tolerant of or favoured by high soil fertility (Hill et al., 2002; Pyšek, 1995; Roy et al., 1999). Our synthesis has found strong support for the hypothesis that urbanisation favours species with an affinity to high nutrient environments with twelve of the sixteen studies investigating Ellenberg or Landolt N indicators concurring. Studies of frequency or abundance found that nutrient-loving plants were more common in urban areas, while of four studies of plant extinction in urban areas, two found species of nutrient-poor habitats such as heathlands (Preston, 2000) meadows and fens (Stehlik et al., 2007) were more likely to go extinct. Other non-trait based studies have also reported the extensive loss of species from nutrient poor habitats, especially wetlands (Dickson et al., 2000; Preston et al., 2003), which, due to their topographic position, are particularly susceptible to drainage and eutrophication. Three studies found no response while one study, which focused on spontaneous herbaceous vegetation in man-made or heavily disturbed habitats, found that the nutrient indicator status of some phytosociological associations decreased (Pyšek et al., 2004). The authors attributed this to a reduction in moisture which leads to lower nutrient uptake and the loss of nitrogen-rich habitats such as garbage holes and rubbish tips (Pyšek et al., 2004).

Grime's CSR

We were only able to document the primary strategies C, S and R, as the secondary and tertiary strategies (ie CS, SR etc), where perhaps more information is contained, were not often reported. This and the variety of analyses (i.e. relative vs absolute frequencies) made synthesis difficult. Consequently, our results are inconsistent and do not support the general increase in competitors in urban floras that has been reported elsewhere (Chocholoušková and Pyšek, 2003). However, there was a tendency for stress tolerators to decrease (Figure 1), which has been associated with a reduction of stressful, low-nutrient habitats (Preston, 2000). Interpreting the response of Grime"s CSR categories as indicators is difficult because they can be the product of multiple filters that may be operating in different directions.

Vegetative traits

Lifeform / growth form

Many studies have reported the abundance or relative extinction rates of different plant lifeforms. Multiple classification schemes make interpretation of trends difficult, particularly for woody plants. However, in total, more studies found that there was an increase in woody plants (trees and shrubs) relative to other lifeforms (Figure 2). Explanations proposed for this include an increase in the number of invasive shrubs and trees „escaping" from gardens (Dolan et al., 2011; Godefroid and Koedam, 2007), and the fact that trees, due to their longer lifespan, are less likely to be entirely extirpated from cities. For example half of the tree species present in a lowland rainforest remnant in urban Singapore survived as one or two individuals (Turner et al., 1996). There is evidence to suggest that geophytes may be disadvantaged by urbanisation while therophytes are favoured. Geophytes have been reported as having high extinction rates and being less common in urban areas due to competition from taller alien species that may be favoured by increased nitrogen levels (Preston, 2000; Williams et al., 2005). Therophytes are associated with high levels of disturbance and soil fertility, and are typically thought to increase in cities due to the prevalence of disturbance in urban areas that creates brownfields suitable for colonisation by introduced species (Knapp et al., 2008). However, two studies found that therophytes were more prone to extinction than other lifeforms (Preston, 2000; Stehlik et al., 2007) indicating that there may be different responses between native and alien annual species.

Plant height

Our synthesis indicates that urbanisation favours taller plant species. Six studies investigated plant height. Three of the four studies that examined extinction found that shorter plants were more likely to go extinct; the other result was non-significant. The other two studies looked at frequency. Thompson and McCarthy (2008) found that taller plants were more common in urban areas, while Knapp et al.. (2009) found that shorter species had high urbanity, probably because urban floras contain many short-lived ruderal species. The near consistency of the response of plant height to urbanisation in different studies (Figure 3) and across cities (e.g. Duncan et al., 2011) is likely to be because plant height is expected to respond positively to many of the effects of urbanisation (e.g. UHI, higher nutrients) while negative impacts may be hidden by an urban extinction debt as taller species are generally longer lived (Hahs et al., 2009).

Leaf traits

Five studies reported SLA in relation to abundance. Two found that high SLA species were more common in more urban areas, two found no significant effect of urbanisation on SLA, and Thompson and McCarthy (2008) found that intermediate SLA was consistently favoured by urbanisation. They noted that other studies may have failed to detect the unimodal relationship by not including quadratic terms in their analysis and assuming all relationships were linear. Given the contrasting expected effects on SLA of some of the most prevalent filters in urban environments, with the UHI, drought and heavy metals acting to decrease SLA, while high nutrient soils, increased light levels and disturbance increase SLA, perhaps a unimodal response is not surprising. A potential consequence is functional homogenisation with plants with both high and low SLA values being disadvantaged by urbanisation. However, there is an obvious need for further research on the response of SLA to urbanisation as it is a fundamental expression of plant resource allocation (Poorter et al., 2009) and has not been investigated in many urban ecology studies.

A series of studies by Knapp et al. (2009; 2008) examined the frequency of different leaf types, that characterise a SLA gradient, in the urban floras of Germany. At a national scale scleromorphic, mesomorphic and succulent leaf types were more frequent than hygromorphic (shade and semi-shade) leaves in urban grid cells compared to semi-natural or agricultural grid cells suggesting that high SLA was a disadvantage (Knapp et al., 2008). In Halle, species with mesomorphic and hygromorphic leaves increased and species with helomorphic (species of swampy areas with aeration tissue in the root) and hydromorphic leaves had high extinction rates due to loss of habitat (Knapp et al., 2010). SLA is negatively related to leaf lifespan, which was examined in five studies but results were again inconsistent. Burton et al. (2009) found that evergreens were more common in urban riparian areas, but Aronson et al. (2007) found that deciduous species were more likely to increase and less likely to decrease than evergreens over time. Three studies showed no significant response of evergreens but varied response among species with various short-lived leaf phenologies.

Reproductive and regenerative traits

Pollination strategy

Pollination mode was investigated in nine separate studies (Figure 3). Although some found that urbanisation favours wind pollination and disadvantages animal pollinated species (Knapp et al., 2010; Knapp et al., 2008; Lososová et al., 2006; Sodhi et al., 2008), five studies found that it was not a significant predictor variable. This may reflect the complexity of plant reproductive systems, their interaction with particular pollinator mutualisms, and how those pollinators respond to fragmentation and urban effects. Clear patterns may not emerge until there are enough studies to allow the analysis of the ability of species to self-pollinate as a co-variable. This would limit the analyses to those species that require a pollination mode that requires transport of the pollen beyond the plant.

Seed mass and seed bank longevity

Heavier seeds appear to be associated with plant persistence in urban areas (Figure 3). Of the six studies that reported seed mass, heavier seeded species were favoured in four of these, including the meta-analysis of extinction in six cities by Duncan et al.. (2011). Species with greater seed mass perform better in hazardous environments that are subject to drought, competition, deep shade or burial (Westoby et al., 2002). Many of these conditions are present in urban areas where the probability of a seed landing in a favourable environment may be reduced due to abundant impervious surfaces and soil compaction. An alternative explanation is that increased seed mass in urban areas is an artefact of urbanisation favouring taller species, as plant height is positively related to seed mass (Thompson and McCarthy, 2008). It has been proposed that frequent disturbance commonly associated with urban areas may favour species with small seeds that persist (Gilbert, 1989), but there was not consistent evidence to support this.

Clonality

Clonality can give plants competitive vigour, the ability to exploit patchy resources and can promote persistence after disturbance (Cornelissen et al., 2003), all traits potentially useful in urban landscapes. Our synthesis suggested no clear trends across the eight studies that investigated this trait. Perhaps because clonality can take many forms (e.g., tubers, rhizomes, branch layering, root suckering) the trait in its broadest sense may not have been specific enough to be meaningful in the urban context.

Dispersal strategy

Dispersal strategy was commonly investigated in urban plant trait studies but different categorizations made it difficult to synthesise results, and only wind dispersal was examined frequently enough to draw any conclusions. Three (Knapp et al., 2010; Sodhi et al., 2008; Williams et al., 2005) of the four studies that used extinction rates found that wind-dispersed species were more likely to disappear than those with other dispersal modes (Figure 3). However, studies that examined frequency of dispersal modes across all species did not show a consistent pattern. This suggests that different filters may operate on the native species present in remnants compared to those in the broader urban landscape.

DISCUSSION

Our synthesis both confirms and generalises some previously reported trends and highlights the complexity of plant-environment interactions in urban systems. There was consistent support for the specific hypotheses that urbanisation shifts the ecological niche of floras towards a niche that is warmer and more characteristic of alkaline and/or nutrient rich soils. There is also evidence that urban floras may be more drought tolerant and more light loving that those of other areas. The strong response of niche indicators (Ellenberg and Landolt numbers) to urban environments is expected, given that they are an expression of tolerance to specific environmental conditions and reflect the response of multiple traits to environmental conditions. Unfortunately, their utility is limited to Europe where the ecology of the flora is well known and Ellenberg values are widely available, which restricts global generalisations. It is encouraging that niche indicators are responsive to urbanisation and that those responses relate to the changes in conditions and resources due to urbanisation. Yet this is sufficient neither for generalised understanding of *why* it is that plants respond in observed ways nor for the prediction to new floras where the niches of species are not well characterised. For this, we suggest, individual traits need to be examined.

We suggest three possible explanations for the varying consistency of the effect of urban environmental filters on plant traits which may assist efforts to develop a general understanding (Figure 4). First, when a single urban stressor acts upon a trait (Figure 4a), or multiple stressors are all predicted to act on a single trait in the same direction (Figure 4b), we would expect consistent directional changes in the trait along an urban gradient. Our results suggest that seed mass, plant height and the number of annual species increase in urban areas. Notably, in each case multiple potential drivers, with different strengths, but similar directions, may contribute to the consistent trait responses seen. While a particular trait may respond strongly to urbanisation the mechanism responsible is sometimes unclear and highlights the need to test potential relationships experimentally to confirm causality of mechanistic drivers.

Second, if multiple urban stressors are predicted to act upon a single trait in different directions (Figure 4c), we would expect inconsistent outcomes for that trait, unless one stressor was clearly stronger than the others. For example, as described above, the response of specific leaf area (SLA) to urbanisation is likely to be unclear as urban abiotic stressors are likely to act on the trait in different directions. In this case, future research should either attempt to untangle the relative strength and direction of the competing filters, or suites of complementary traits should be investigated, as they may de-confound of the effects of multiple filters, thereby advancing our understanding of mechanistic relationships.

Third, stressors vary in their strength and consistency between and within cities due to numerous factors and this would be expected to impact on the consistency of the trait signal observed. For instance, the urban heat island occurs in all cities and thus would be expected to have strong, consistent trait signals. In contrast, more complex stressors that operate through biological and biophysical interactions, such as changes to dispersal vectors, would be expected to vary depending on local factors including the biotic composition and its spatial distribution. Therefore consistent trait signals would be less likely to be observed. For example Aronson et al. (2007) found that broad-leafed deciduous alien shrubs with bird-dispersed fruit increased their range sizes in New York City but native, evergreen shrubs with fleshy fruit decreased. In isolation these results suggest that urbanisation is not consistently impacting bird dispersed or evergreen versus deciduous shrubs. However, the true effect on these traits may be being masked by the fact the native shrubs that Aronson et al (2007) cite as particularly affected by urbanisation grow on acidic soil habitats that have been strongly affected by habitat loss and eutrophication. If these effects could be accounted for, bird-dispersed shrubs may be responding positively to urbanisation as they have in other studies (e.g. Rogers et al., 2009).

There are two broad categories of studies in our synthesis; studies examining the extinction of native species and studies of vegetation frequency or abundance across the urban landscape. The extinction studies are effectively reporting the trait response of vegetation from remnant habitats only, while the studies of frequency and abundance often include alien and native species from remnant, or spontaneous and other non-cultivated urban vegetation. This distinction is important because the filters of habitat transformation and fragmentation operate most strongly on the former, which is why some trait response patterns (e.g. dispersal strategy) may be clearer when extinction studies are considered in isolation. Including exotic species may be unhelpful in some instances (Thompson and Davis, 2011) because their response to urbanisation is driven by a different set of traits (cf. Aronson et al. 2007. example described above). The response of a number of characteristics (e.g. light niche) also appears to be habitat dependent and may reflect trait divergence. This is not surprising as specific habitats have selected for particular traits that may respond similarly to changed environmental conditions within a habitat but differently when compared across habitats. Trait responses may also be missed or be seen as inconsistent because studies fail to capture these habitat specific responses. For example if plants with particular niche indicators or traits are prevalent in a habitat which is preferentially lost due to urbanisation, the trait response may be missed if the they are studied at a city wide scale because it is too coarse a scale. As the number of urban traits studies increase, analyses that distinguish between the response of vegetation of remnant patches versus all vegetation and across specific habitats (i.e. forests) may provide insights not currently discernible.

Another reason for the inconsistencies in the response of plant traits that act through biotic interactions may be the intentional cultivation of plants in urban areas by humans. This has greatly facilitated the spread of many species and their distribution across urban landscapes cannot be understood without taking human behaviour into account (Pyšek et al., 2010). Cultivation by humans may give plants traits like seed size, pollination strategy and dispersal syndromes limited explanatory power in urban environments because fundamental biological trade-offs such as seed size versus establishment success are overcome or modified. While beyond the scope of our review, human preference has been shown to favour particular traits (Kendal et al., 2012) and shift the trait distribution of urban floras through increased propagule pressure originating from planted species. This has led to an increase in the phanerophyte (tree and shrub) lifeform in many urban areas due to escaped woody ornamentals and has been reported for Rome (Celesti-Grapow and Blasi, 1998), Hamburg (Kowarik, 2005) and Plzen in the Czech Republic where the contribution of shrubs and trees to the city flora increased from 5% to 15% between 1910 and 1990 (Chocholoušková and Pyšek, 2003). Gardeners are also likely to select species that are insect-pollinated as a consequence of preferring larger flowers (Knapp et al., 2010).

CONCLUSIONS AND WAYS FORWARD

The robustness of our analyses was constrained by our inability to undertake a formal meta-analysis due to the variable nature of existing urban plant trait studies. Consequently, we echo the calls of others urging researchers to more fully present their data to encourage meta-analytical thinking (Gurevitch and Hedges, 1999). Understanding that meta-analysis proceeds from measures of effect sizes, which present direction and magnitude of an effect and need to be accompanied with sample sizes or other statistics to reflect the uncertainty in them is important. So, while authors are encouraged to present P-values in support of hypothesis testing, this should be accompanied by parameter estimates with uncertainty. We also highlight the limitations of the multivariate analyses using eigenvector methods (such as RLQ analyses) frequently used in urban plant trait studies for meta-analyses. First, such methods lack an explicit model that can be linked to a biological process, and extracted and applied somewhere else. Second, such ordinations are optimised for the dataset and the covariates being analysed, which will vary between studies and between research questions, making their generality uncertain. Attempts to resolve the complex causality of trait-urban environment interactions through experimentation involving putative causal factors or by modelling methods such as generalised linear models structural equation modelling (Grace, 2006) or probabilistic networks will be particularly useful.

While our review has developed a better understanding of how urbanisation may assemble urban floras, the lack of generality found could have various explanations. Firstly, urban ecology and comparative ecology are both relatively young fields of research, and the specific use of functional traits in the investigation of urbanisation is very recent; 29 studies is not a large sample. By highlighting the traits studied frequently and synthesizing study results, we seek to hasten the descriptive, exploratory phase of this research worldwide so that research can proceed more quickly to addressing the mechanistic relationships between urban environments and plant assemblages. Secondly, as urbanisation comprises a complex suite of drivers that may interact in their filtering effects on plant traits, variations in the relative strengths of those drivers may contribute to variability in trait responses to urbanisation. Further insights can be gained by focusing on specific urbanisation processes, measurement of plant functional trait responses, and analyses and reporting methods that allow comparative generalizations of results (McDonnell and Hahs, 2013). The investigation of simple types of data across many places (e.g. urban flora lists) will continue to be useful, but targeted studies and the experimental measurement of relevant traits are needed to confirm the causal processes structuring urban floras. In addition, analyses capable of detecting non-linear effects on trait means and effects on trait variances, not just means, may prove important in unpicking the complex interactions of multiple urban effects on plant traits.

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Figure Captions

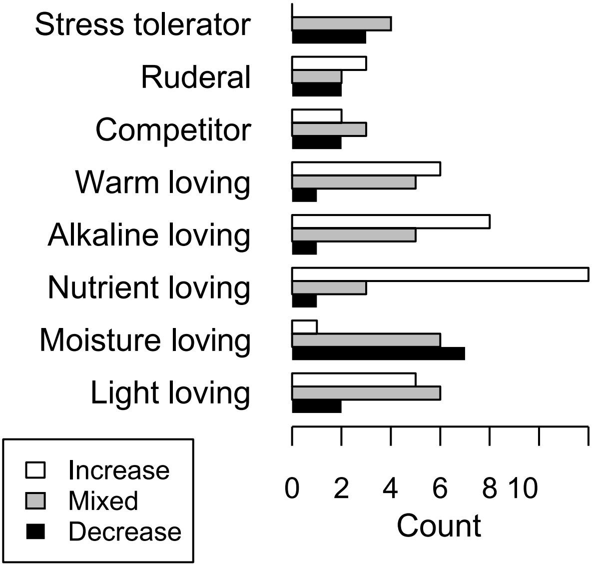
Figure 1. Literature support for relations between urbanisation and plant strategy and niche indicators. Count is number of papers with data supporting an increase, decrease or mixed responses with urbanisation.

Figure 2. Literature support for relations between urbanisation and plant functional types. Count is number of papers with data supporting an increase, decrease or mixed responses with urbanization.

Figure 3. Literature support for relations between urbanisation and plant functional traits. Count is number of papers with data supporting an increase, decrease or mixed responses with urbanization.

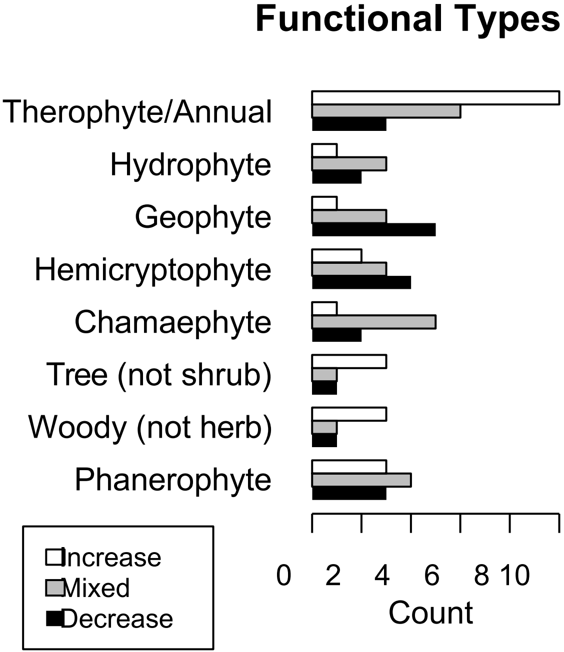
Figure 4. Conceptual diagram illustrating three potential scenarios for how urban environmental stressors act to shift the trait frequency distribution (Freq.) for Trait X from an initial distribution (T0; solid line) to a new distribution (T1; dashed line). A single stressor acting on a trait should broaden or shift the distribution in a predictable direction (a). Multiple stressors acting in a consistent direction should also broaden or shift the distribution in a predictable direction (b). However, when multiple stressors are acting in inconsistent directions, the distribution is likely to broaden or change unpredictably, making it difficult to record a shift in the new trait distribution (c).

Figure



Strategy and Niche Indicators

Figure


Functional Types
Therophyte/Annual
Hydrophyte
Geophyte
Hemicryptophyte
Chamaephyte
Tree (not shrub)
Woody (not herb)
Phanerophyte
☐ Increase
▨ Mixed
■ Decrease
0
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4
6
8
10
Count

Figure

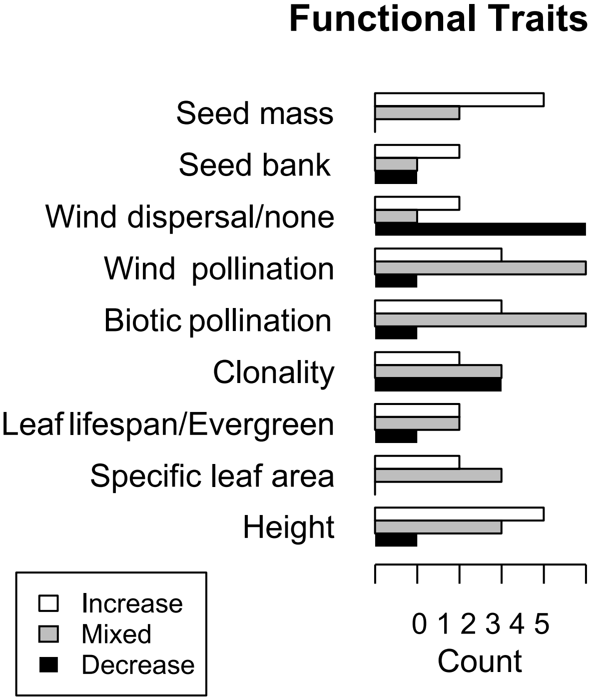
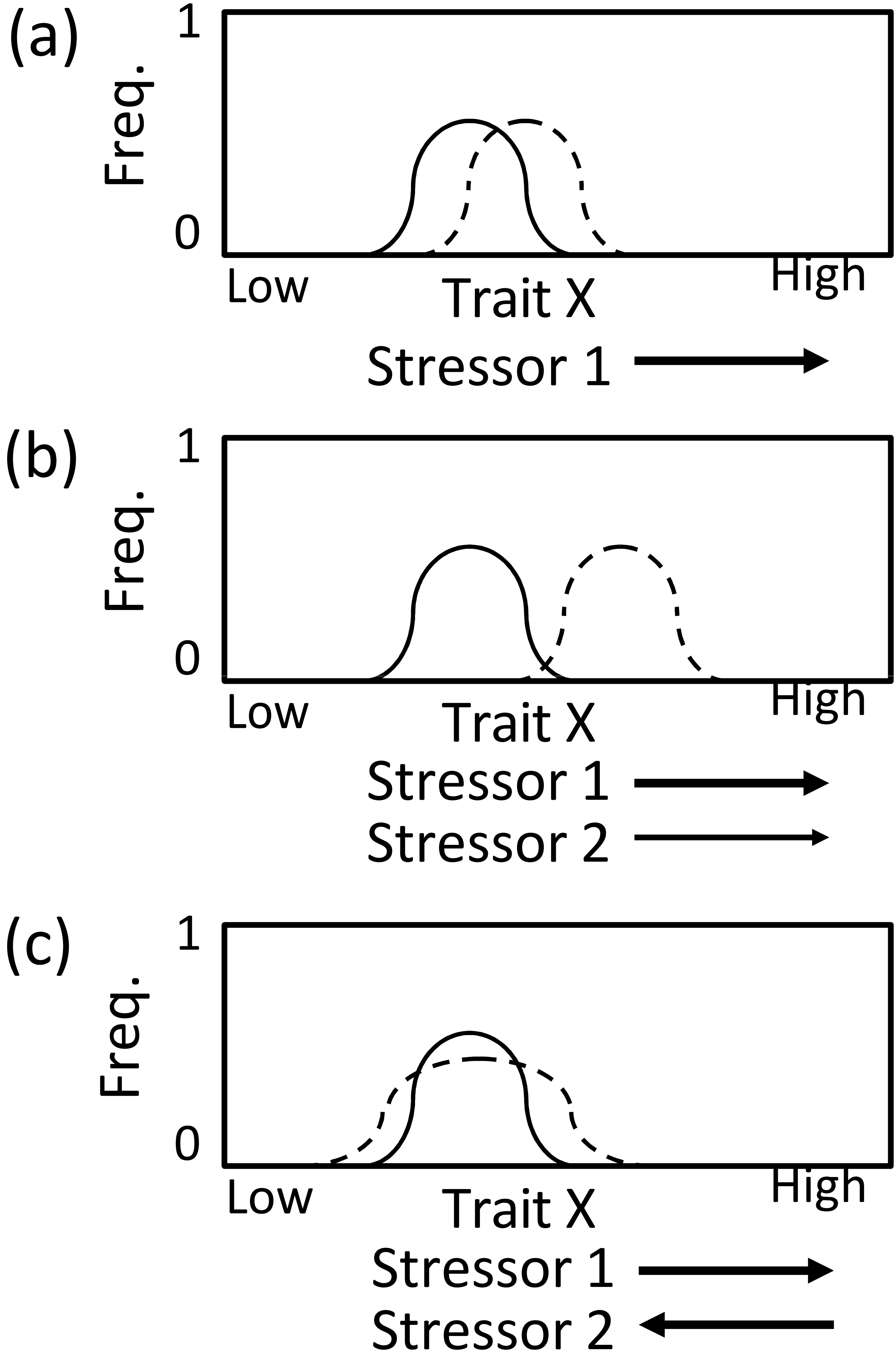

Functional Traits
Seed mass
Seed bank
Wind dispersal/none
Wind pollination
Biotic pollination
Clonality
Leaf lifespan/Evergreen
Specific leaf area
Height
0 1 2 3 4 5
Count
☐ Increase
▨ Mixed
■ Decrease

Figure 4


(a)
1
Freq.
0
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Stressor 1
(b)
1
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Trait X
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Stressor 1
Stressor 2
(c)
1
Freq.
0
Low
Trait X
High
Stressor 1
Stressor 2

References Used