A global comparison of the climatic niches of urban and native tree populations

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Abstract

Aim: Urban macroecology studies can provide important insights into the impacts of climate change and human intervention in ecosystems. Current theory predicts that urban trees are constrained by temperature in very cold climates but not in other climates. Here we predict the climatic niche variables of planted urban tree populations from the realised climatic niche of native populations, and explore whether niches are constrained across all temperatures.

Location: Global (182 cities across six continents).

Time period: Urban tree data: 1980-2016. Native tree data: 1950-2017.

Major taxa studied: 203 tree species.

Methods: We used urban tree inventory data and GBIF occurrence data to compare the realised climatic niches of native and urban tree populations. Realised climatic niches are calculated by combining bioclimatic data with native tree and urban tree occurrence data. Regression is used to predict the climatic niche of urban tree populations from the climatic niche of native populations.

Results: The realised climatic niche of native tree populations was a good predictor of the realised climatic niche of urban tree populations, although climatic niches are attenuated in urban populations. Urban tree niches were 38-90% wider than native tree niches, with the mean annual temperature niche breath of urban tree populations 3.3°C (52%) wider than native tree populations.

Main conclusions: Urban trees are planted in climates that are outside the realised climatic niche of native populations. Temperature remains a strong filter on urban tree populations across the full temperature range. Temperature increases due to the combined effect of the urban heat island and climate change are likely to have a substantial impact on urban tree populations around the globe. This is particularly true for temperate cities where cold climate trees are planted near the upper limits of their realised temperature niches.

Introduction

Temperature and rainfall are globally important determinants of the biogeographic distribution of tree species (Woodward & Williams, 1987). Current theory suggests that in urban areas, minimum annual temperatures limit the distribution of urban tree species while rainfall deficit can potentially be overcome by irrigation (Jenerette *et al.*, 2016). In all cities, the combined effect of the urban heat island and climate change is resulting in an increase in ambient temperatures (Peng *et al.*, 2012). This could lead to an expansion in the planted distribution of some tree species that will now be able to be survive in (formerly) colder cities (Jenerette *et al.*, 2016). However, it is currently unclear whether an increase in urban temperatures will also restrict the distribution of some cold-adapted tree species, or species close to their thermal maxima. A broader understanding of climatic limits to the distribution of urban tree species will help better predict the likely positive and negative effects of increasing temperatures on the world's urban trees. In turn, this will inform future tree selection by urban land managers to better withstand increasing temperatures, maintain the provision of urban ecosystem services and function of urban ecosystems.

A climate tolerance and trait choice (CTTC) hypothesis has been proposed to explain the distribution of urban trees (Jenerette *et al.*, 2016). This hypothesis states that in very cold climates, winter minimum temperature is a strong environmental filter, whereas in temperate climates, the temperature filter is weak (where irrigation is available) and species distribution is determined more by aesthetic traits (e.g. showy flowers) that influence human decision-making. While Jenerette *et al.* (2016) provide empirical evidence from North America to support their hypothesis, they call for a study of trees in globally distributed cities to extend macroecological theory. Other studies of urban vegetation suggest that temperature remains an important environmental filter of plant species across all climates (Kendal *et al.*, 2012; Ramage *et al.*, 2013). Similarly in natural forest ecosystems, plants respond to changes in temperature in all climates, not just at temperature extremes (Millar *et al.*, 2004; Danby & Hik, 2007; Fei *et al.*, 2017).

In natural forests, drought is a major cause of tree mortality, and interactions between increasing temperatures and drought are leading to rapid range shifts in the natural distributions of many tree species (Adams *et al.*, 2009; Park Williams *et al.*, 2012; Fei *et al.*, 2017). In urban forests, drought is also thought to be a major cause of poor tree health and mortality, although sustainability concerns are leading to demands for unirrigated landscapes (Vogt *et al.*, 2017). In response, research on climate change adaptation in urban forests has focussed on selecting drought tolerant species (e.g. Roloff *et al.*, 2009). Yet existing studies have found little effect of precipitation on urban tree distributions (e.g. Kendal *et al.*, 2012; Jenerette *et al.*, 2016), and the role of precipitation on the distribution of urban trees remains unclear.

Tree species are unlikely to fully occupy all of the areas they are climatically suitable for within their native (historically known) range for a variety of historical, biological and geographic reasons (Svenning & Skov, 2004). For example, while a location may be climatically suitable for a tree species, biotic interactions such as interspecific competition and herbivory, may limit the ability of that tree species to grow and reproduce. The climatic conditions within which a species is found is described as its realised climatic niche, and distinguished from its fundamental climatic niche, the climatic conditions that the species can tolerate (Hutchinson, 1957). The climatic niche can be conceptualised as an *n*-dimensional hypervolume, with axes mapped to particular climatic variables (e.g. mean annual temperature, annual rainfall, etc). Climatic niches can be characterised by values for position, breadth and limits (Thuiller *et al.*, 2005). Niche position is the average climatic conditions within the niche, niche limits are the upper and lower values of the climatic conditions within the niche, and niche breadth is the range (difference between upper and lower limits) of niche values, often calculated independently along each axes (Figure 1). A growing number of studies analysing species climatic niches or modelling habitat suitability have demonstrated that niche breadth and niche position can vary between native (historically known) populations and populations outside their native ranges (Gallagher *et al.*, 2010; Beaumont *et al.*, 2014; Bocsi *et al.*, 2016).

[FIGURE 1 HERE]

Urban trees are often cultivated in places that are geographically distant from their native range (Kendal *et al.*, 2012). Comparison of the climatic niches of native and urban tree populations provides a valuable opportunity for understanding differences between the realised and fundamental niches of tree species, and a better understanding of the climatic limits of urban tree species. Cultivating a given tree species within a city can overcome biotic constraints, biogeographic barriers to seed dispersal and ecological seed germination requirements (e.g. climate related seed dormancy, fire) that may restrict the native distribution of that species. As a consequence, we hypothesise that the realised climatic niches of urban tree populations will be broader than that of their native populations, and therefore provide a closer approximation of the species' fundamental ecological niche. It is less clear what the relationship between the niche position of native and urban tree populations will be, as this can vary with species-level factors limiting or skewing native distributions (Thuiller *et al.*, 2005) and historical and cultural factors influencing urban distributions (Kendal *et al.*, 2012). A better understanding of the climatic niche limits of urban tree populations will also provide useful information for the planning and selection of tree species that are better adapted to future urban climates.

In this study, we explore how the urban climatic niches of a global suite of urban tree species (*n* = 203 species) are shaped by the climatic niche of their native populations. In particular, we ask:

1) *How are the climatic niche positions of native and urban tree populations related?*
2) *How are the breadths and limits of climatic niches different between native and urban tree populations?*
3) *How are the climate niches of urban trees arrayed along a 0-30 °C mean annual temperature gradient?*

Methods

Datasets used

Urban tree species records were compiled from publicly available urban tree inventories (n = 433) of parks, streets and gardens from around the world (cities = 182, countries = 44, continents = 6; Figure 2; Appendix S3) published in journal articles, book chapters and government reports (Appendix S1). These were compiled over a 10-year period through review of the academic literature, grey literature, internet searches and through electronic news, forums and newsletters targeting the urban forestry industry. Studies that focussed on remnant (e.g. conservation) or spontaneous (e.g. invasive) species were not included in the analysis. While some remnant or spontaneous trees may have been recorded, the compiled dataset is largely comprised of deliberately planted trees occurring in urban streetscapes, parks and residential gardens. All native occurrences for the same suite of species were extracted from the Global Biodiversity Information Facility (GBIF) using the *dismo v1.1.4* package in R 3.3 (Hijmans & Elith, 2016) in January and February 2017. The GBIF database includes data a wide range of sources including herbarium records, scientific studies and citizen science projects, and includes both native and adventive populations (Franklin *et al.*, 2017).

[FIGURE 2 HERE]

To extract native occurrences only, we obtained published native range spatial polygons for a sample of urban tree species (Appendix S4) that occurred in at least three cities. Native range polygons were obtained for the USA (n = 107) from Little Jr. (2016) and Europe (n = 21) from the European Forest Genetic Resources Programme (2016). Native range spatial polygons were manually constructed for species (n = 75) from native range information available in published floras for Australian, South American, African and Asian species (e.g. Chippendale, 1988; Missouri Botanical Garden, 2017). The coordinates of GBIF points were standardised to the same 2.5 arcminute grid as the climate data (below), and all duplicate records removed. As there were many GBIF records from locations much hotter or colder than our cities, and some records from wetter or drier places, all GBIF records with a mean annual temperature warmer than our hottest city (Chennai, India 28.6 °C) or less than our coldest city (Nuuk, Greenland -1.2 °C), or with annual precipitation less than our driest city (San Juan, Argentina 96 mm/year) or more than our wettest city (Taipei, Taiwan 2720 mm/year), were removed. GBIF records prior to 1950 were also removed to better align the temporal extent of the data. Lastly, only GBIF records occurring within these native range polygons and outside urban areas (identified as those occurring within urban polygons derived from MODIS satellite imagery (Schneider *et al.*, 2009)), and urban tree inventory points occurring outside the native range polygons (72% of all records), were retained in the analysis. In total, 203 tree species were included in the final analysis, associated with 3,675 urban tree inventory species occurrence records, and 250,857 GBIF records.

To determine climatic niches, nineteen bioclimatic (BIOCLIM) variables were extracted for every city centre and species occurrence record from the WORLDCLIM database at a resolution of 2.5 arcminutes (Hijmans *et al.*, 2005). BIOCLIM data has been widely used in global studies of climatic drivers of natural and invasive plant species distribution (Jeschke *et al.*, 2008; Beaumont *et al.*, 2009; Booth *et al.*, 2014). BIOCLIM values for the 19 variables were extracted at all GBIF points recorded within native range polygons, and for urban populations at each city centre where the species had been recorded in an urban tree inventory. The distribution of BIOCLIM variables at GBIF points and in cities is in supplementary material (S5).

Data analyses

All data analyses were conducted in R 3.3 (R. Development Core Team, 2010). Taxonomy was standardised against The Plant List (www.theplantlist.org) using the *taxonstand v1.8* package (Cayuela & Oksanen, 2016). We calculated the range of each BIOCLIM variable across all urban environments sampled. Mean annual temperature (BIOCLIM1) and annual precipitation (BIOCLIM12) were selected as useful and widely used climatic measures in plant biogeography that are easily interpretable (Woodward & Williams, 1987). Other important climatic variables were determined using a PCA of all city BIOCLIM variables, and selecting a single variable loading heavily on each component (Appendix S2).

For each tree species, we calculated climatic niche position and breadth separately for native and urban populations, for each BIOCLIM variable of interest. Niche position was calculated as the mean value, lower niche limit as the 2.5th percentile, upper niche limit as the 97.5th percentile, and niche breadth as the distance between lower and upper limits (Figure 1). Native climatic niche values were then used to predict urban niche values using generalised linear regressions with a normal error distribution, separately for niche position, lower limit and upper limit, and niche breadth, for each BIOCLIM variable of interest. We note that these niche parameters are not independent; all temperature variables are correlated to some extent and niche parameters are likely to behave similarly. As there were large differences in the sample size of native and urban populations, for each species the larger sample was randomly subsampled to match the smaller sample size 999 times and mean niche values calculated across all permutations.

The spread of urban species occurrence across a mean annual temperature gradient was determined by assessing the overlap of each species' niche with 1 °C mean annual temperature bins (from 0 °C and 30 °C). Tree species were considered present at a mean annual temperature if their realised urban or native mean annual temperature niche overlapped the 1 °C bin. We measured turnover in species composition along this temperature gradient by calculating the number of tree species present, gained and lost for each 1 °C bin.

Results

Three components were chosen for the PCA as being both easily interpretable and able to explain a large proportion of the variation in the data (Appendix S2): mean temperature of the coldest quarter (BIOCLIM11) loaded heavily (0.95) on component 1, precipitation of the driest quarter (BIOCLIM17) loaded heavily (0.91) on component 2, and mean maximum temperature of hottest month (BIOCLIM5) loaded heavily (0.79) on component 3. Mean annual temperature (BIOCLIM1) and annual precipitation (BIOCLIM12) were relatively well correlated with components 1 (loading=0.93) and component 2 (loading=0.76), respectively.

How are the climatic niche positions of native and urban tree populations related?

The niche positions of native tree populations were good predictors of the niche positions of urban populations for all temperature variables (Figure 3; Table 1). There was collinearity within temperature and precipitation niche position variables and similar patterns were expected across the models. However, there were some differences in the strength of relationship for different temperature variables. Mean temperature of the coldest quarter had the strongest relationship, whilst the mean annual temperature also had a strong relationship. The mean maximum temperature of the hottest month, precipitation of the driest quarter and annual precipitation of native and urban tree populations had a moderate relationship. (Figures 3; Table 1).

There were some consistent differences between the climatic niche position of native and urban tree populations (Figure 3). All niche position relationships had a slope <1 and a positive intercept, indicating a shift away from climatic extremes in urban tree populations. Tree species whose native populations are found in colder climates can be commonly found in cities whose temperatures are up to 5 °C warmer than native populations. This shift away from temperature extremes is also present in hotter climates, although model relationships were relatively weak.

Niche positions for precipitation variables among urban populations were also consistently different to native populations of the same species. A shift away from precipitation extremes was identified; species with native populations from very dry areas are found in somewhat wetter cities, while species with native populations from wet areas found in much drier cities. This is strongly related to total precipitation, i.e. species from wetter climates (annual precipitation >1000 mm/year or driest quarter > 150 mm/qtr) are found in much drier cities, while species from drier climates (annual precipitation <500 mm/yr or driest quarter <100 mm/qtr) are generally found in cities with similar or slightly higher precipitation levels.

[FIGURE 3 HERE]

[TABLE 1 HERE]

Are the breadths and limits of climatic niches different between native and urban tree populations?

The climatic niche breadths (as measured by the difference between the 97.5th-2.5th percentiles, calculated separately for each BIOCLIM variable) of urban tree populations are consistently and substantially wider than those of native populations (Figure 3; Table 2). Niche breadth was on average 51% wider along the mean annual temperature axis of urban than native populations, 64% wider for temperature of the coldest quarter, and 90% wider for maximum temperature of the hottest month. Similarly, the mean niche breadth was 38% wider along the annual precipitation axis of urban than rural populations, and 47% wider along the precipitation of the driest quarter axis. Again, due to collinearity within temperature and precipitation niche breadth variables, similar patterns were expected across the models.

The relationship between the niche breadths of rural and urban tree populations varied along a gradient of niche breadth (Figure 3). With the exception of mean temperature of the coldest quarter, species whose native populations have narrow climatic niches tended to have urban populations with broader climatic niches. In contrast, species whose native populations have very broad climatic niches tended to have urban populations with similar climatic niche breadth. There were few species whose urban tree populations had smaller niche breadths than their native populations (i.e. there were few points below the 1:1 line in Figure 3).

[TABLE 2 HERE]

Unsurprisingly, the temperature niche limits (upper limit = 97.5th percentile, lower limit = 2.5th percentile) of native and urban tree populations followed similar patterns to niche position and breadth for each BIOCLIM variable. Limits of mean temperature of the coldest quarter and mean annual temperature had the strongest relationship (Figures 3; Table 1). There was a weaker relationship with mean maximum temperature of the hottest month. The limits of precipitation variables also had weaker relationships between native and urban populations. Temperature and precipitation niche limits were less extreme in urban tree populations than in native populations. While mean minimum of the coldest quarter of native tree populations remained the best predictor of the lower limit of urban tree populations, mean annual temperature was a slightly better predictor of upper niche limits.

How are the climate niches of urban trees arrayed along a 0-30 °C mean annual temperature gradient?

There are few tree species that occur in very cold temperatures; only 13% of species had a mean annual temperature niche that overlaps 3 °C (Figure 4a). As mean annual temperatures increase, more species start to occur as temperatures move past their lower niche limits (Figure 4b). Above 11°C, some species started to reach their upper niche limits and no longer occur. Most urban tree species (83%) in this study have climatic niches that include a mean annual temperature bin of 14 °C. Between 13 °C and 16 °C, there is a rapid turnover of species as colder climate species begin to drop out, and warmer climate species start to occur. Above 16 °C colder climate species continue to reach their upper niche limits, and relatively few new species start to occur. There are few species that occur in very hot temperatures; 23 °C is warmer than the upper limit of the mean annual temperature niche of 89% of species in this study.

Discussion

We found that temperature continues to constrain the distribution of all urban trees studied, not just those occurring in very cold cities. Minimum and mean annual temperatures of native tree populations are good predictors of the urban climates where those trees are planted. This is particularly important as the combined effect of the urban heat island and global climate change is likely to lead to temperature increases of at least 3-5 °C in many cities (Peng *et al.*, 2012), which is half the mean annual temperature niche breadth of the species included in this study. Temperature niches are broader in urban tree populations than in native tree populations, but niche positions are attenuated at temperature extremes; trees from very cold places tend to be planted in warmer cities, while trees from very hot places tend to be planted in cooler cities. Many cold climate trees start to disappear in temperate cities. These findings have important implications for the future vulnerability of some urban tree species to increasing temperatures due to global environmental change in all climates.

Our results are partially consistent with the proposed climate tolerance and trait choice (CTTC) theory to explain the distribution of urban trees (Jenerette *et al.* 2016). Minimum temperatures are important; however, our results also demonstrate that this temperature filter continues to be a powerful influence on the distribution of urban trees across all climates, not just cold ones. The difference in these findings may be due to the larger global dataset of 196 cities across a wide range of temperatures as compared to the North American dataset of 20 cities used by Jenerette *et al.* (2016). The findings of our study do not invalidate the trait choice hypothesis in moderate climates, as people in temperate cities have a larger pool of suitable tree species to choose from which would allow greater consideration of aesthetic traits.

The temperature niche position of native tree populations was a good predictor of the niche position of urban populations of the same species. In particular, mean temperature of the coldest quarter and mean annual temperature of urban tree populations were similar to native populations. Minimum temperatures have been identified as a key driver of the distribution of urban trees (Ramage *et al.*, 2013; Jenerette *et al.*, 2016), as it directly relates to tolerance of freezing temperatures and strongly influences plant growth and survival in colder areas. However, mean annual temperature may be a good proxy for a wide range of other climate-related mechanisms that continue to limit the distribution of urban trees in all climates. Physiological responses such as dehydration, xylem cavitation, heat damage and carbohydrate exhaustion can vary among species along temperature gradients (Allen *et al.*, 2010). Higher temperatures may also influence the distribution and abundance of pests and diseases, increasing these threats for some urban tree species (Tubby & Webber, 2010). As higher temperatures often contribute to tree moisture stress, this can further influence the susceptibility of trees to herbivory or pathogens (Dale and Frank 2014). Interestingly, there was no evidence that urban tree distributions have responded to urban heat, which should allow urban trees to be planted in cities that are colder than natural populations.

Climatic niche breadths were consistently and substantially wider in urban tree populations. Species with very narrow niche breadths among their natural populations had urban populations with much wider temperature and precipitation niches, while species with very large native niche breadths had similarly wide niche breadths in urban populations. This is consistent with the assumption that cultivation overcomes some of the limitations to dispersal in natural populations, and allow species to occupy a greater extent of their fundamental niche.

The upper and lower niche limits for temperature and precipitation were also attenuated in urban tree populations (Figure 2). Tree species naturally occurring in cold areas are more often planted in cities that are warmer than their natural temperature niche. Similarly, although with more uncertainty, tree species naturally occurring in hot areas are more often planted in cities that are cooler than their native temperature niche. Perhaps counterintuitively, these data suggest that the current urban forest populations found in cool-temperate cities could be more vulnerable to increasing temperatures than the urban forests of warmer climate cities. While it is true that more tree species may start to fall within the temperature niche of cooler cities as their temperatures increase, many of the cold climate tree species currently planted in these cities are at, or close to, the upper limit of their known temperature niche. In contrast, tree species from warmer areas tend to be planted closer to the lower limits of their temperature niche of their native range, and thus may have more capacity to tolerate future temperatures increases.

Precipitation is often discounted as a useful predictor of urban tree distributions (Kendal *et al.*, 2012; Jenerette *et al.*, 2016). Our findings provide further empirical support for this. We found that the precipitation niche position, breadth and limits of native tree populations were weak predictors of the precipitation niche variables of urban tree populations. Urban trees are regularly planted in cities that are much drier than their native populations. This could be explained by the use of irrigation. While irrigation data are not currently available to test this at a global scale, much of the urban tree data used in the study are from locations that are less likely to receive irrigation. Irrigation may be common in drier cities in affluent countries e.g. south west USA (Jenerette *et al.*, 2016), but is less likely in the areas contributing to the inventory data used in this analysis, including land uses such as street trees, in cooler climates, and in developing countries.

In combination, these findings are consistent with a growing body of research demonstrating that the realised climatic niches of species can change when they are introduced to new environments (Gallagher *et al.*, 2010; Beaumont *et al.*, 2014). Many of the potential barriers that restrict native trees from fully occupying their fundamental climatic niche are alleviated through cultivation in urban tree populations: they are actively dispersed by people around the globe, germination barriers are overcome by nursery propagation, and the importance of species competitive interactions are often diminished. However, while niche breadths were clearly wider, the realised climatic niches of native tree populations continue to be useful predictors of the realised niches of urban populations. While some tree species may thrive in urban environments that are dramatically different from their native environments, these results show that the vast majority of urban tree species are constrained to climatic environments that are related to their native ranges.

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Biosketch: Dave Kendal is a Senior Lecturer in Environmental Management at the University of Tasmania. Dave's research aims to increase understanding of why and how we create and manage the landscapes we do, and what the ecological outcomes of that management are: mostly in the context of green space in cities, and more generally around human engagement with different kinds of nature in cities and beyond.

Data Accessibility: Urban tree occurrence data can be obtained for the species listed in Appendix S4 from the list of publications in Appendix S1. Native species occurrence data can be obtained for the species listed in Appendix S1 from the publically accessible Global Biodiversity Information Facility.

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Supplementary material

Appendix S1 – Urban tree inventory data sources

Appendix S2 – Climatic variable PCA

Appendix S3 - Urban areas included in this study

Appendix S4 - Species included in this study

Appendix S5- Climatic variable envelopes

Appendix S6 – Niche widths of urban and native tree populations

TABLES

Table 1 - Regression parameters for BIOCLIM variables when predicting urban population niche values from native population niche values. All values significant at $P < 0.001$ *except ~ n.s.* D^2 *is the proportion of deviance explained* $D^2 = (D_{null}-D_{model})/D_{null}$

	Name	BIO1	BIO11	BIO5	BIO12	BIO17
niche	intercept	7.00	3.11	20.8	519	57.1
position	intercept.se	0.39	0.25	1.08	41.9	7.57
	coefficient	0.47	0.57	0.25	0.23	0.30
	coefficient.se	0.03	0.03	0.04	0.04	0.05
	D^2	0.56	0.64	0.18	0.14	0.17
niche	intercept	5.13	6.69	7.8	615	136
breadth	intercept.se	0.47	0.66	0.53	55.4	10.1
	coefficient	0.70	0.86	0.62	0.41	0.42
	coefficient.se	0.07	0.07	0.08	0.08	0.07
	D^2	0.35	0.44	0.24	0.12	0.16
niche	intercept	4.03	-0.98	15.1	225	~1.16
lower.limit	intercept.se	0.30	0.27	0.83	27.7	3.40
	coefficient	0.53	0.71	0.27	0.18	0.19
	coefficient.se	0.03	0.03	0.03	0.04	0.03
	D^2	0.64	0.71	0.25	0.11	0.16
niche	intercept	10.1	8.57	18.9	806	149
upper.limit	intercept.se	0.67	0.39	1.55	78.5	12.0
	coefficient	0.54	0.52	0.48	0.31	0.27
	coefficient.se	0.04	0.04	0.05	0.05	0.05
	D^2	0.46	0.50	0.31	0.14	0.12

Table 2 – Mean climatic niche breadths (97.5th percentile – 2.5th percentile) for selected BIOCLIM variables. Standard deviations are shown.

	Natural populations	Urban populations	% species where urban niche is wider
Mean annual temperature (BIOCLIM 1)	6.3 °C ±3.2	9.6 °C ±3.7	82%
Minimum temperature of the coldest quarter (BIOCLIM 11)	8.6 °C ±4.6	14.0 °C ±6.0	88%
Maximum temperature of the hottest month (BIOCLIM 5)	6.1 °C ±3.0	11.6 °C ±3.8	94%

Annual precipitation (BIOCLIM 12)	636 mm/yr ±326	875 mm/yr ±382	77%
Precipitation of the driest quarter (BIOCLIM 17)	129 mm/yr ±68	190 mm/yr ±73	79%

FIGURES

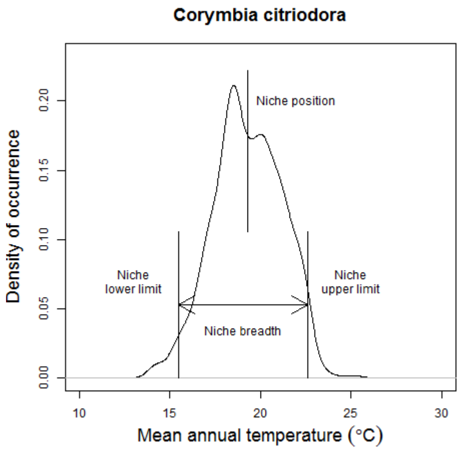

Figure 1 – Climatic niche values for mean annual temperature of native populations of Corymbia citriodora.

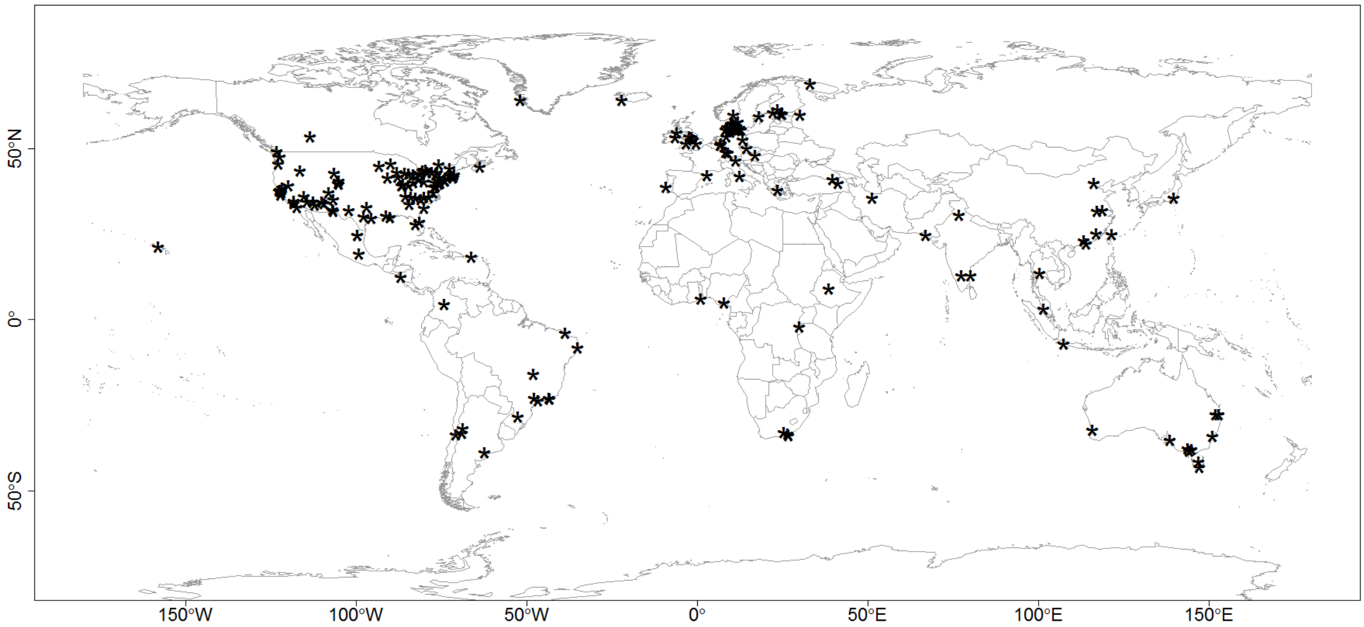

Figure 2 – A map of the cities included in the study.

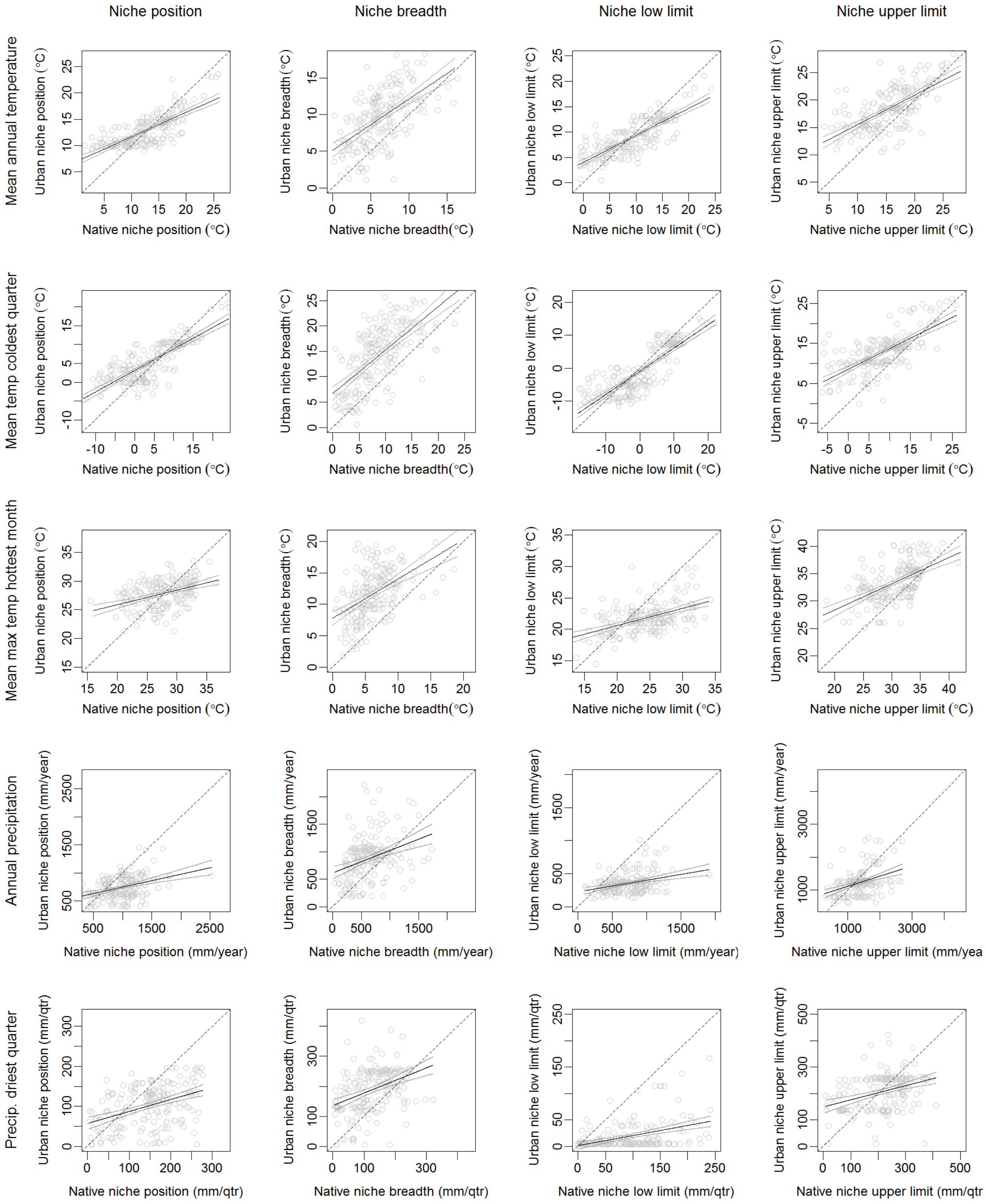

Figure 3 - Relationships between native and urban niche position for climatic variables. 95% confidence interval of the mean is shown, and a one-to-one relationship is shown as a dashed line.

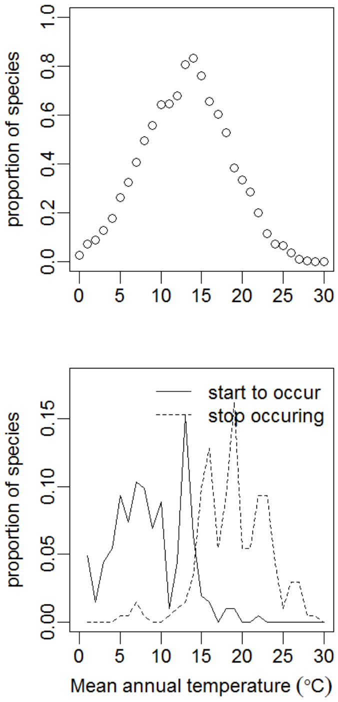

Figure 4 – The proportion of species in 1 °C mean annual temperature bins that a) are known to occur (combined native and urban niche) and b) start to occur (enters niche) or stops occurring (leaves niche) in urban plantings.