



# Plants' native distributions do not reflect climatic tolerance

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## ABSTRACT

**Aim** Biogeographers have long known that plant species do not fully encompass their fundamental niche. Nonetheless, in practice, species distribution modelling assumes that plant distributions represent a reasonable approximation of their environmental tolerance. For ecological forecasting, projections of habitat loss due to climate change assume that many species will be unable to tolerate climate conditions outside of those found within their current distributional ranges. We aim to test how well occurrences in the native range approximate the climatic conditions in which plant species can survive.

**Location** Continental USA.

**Methods** We compared the climatic conditions between occurrences in the US native versus US non-native ranges using 144 non-invasive plant species. We quantified differences in January minimum temperature, July maximum temperature and annual precipitation as indicators of climatic tolerance. We also compared modelled potential distributions throughout the US based on native and total ranges to test how expanded climatic tolerance translates into predicted geographical range.

**Results** Most species (86%) had non-native occurrences in climates outside those described by their native distributions. For the 80 species with lower minimum temperatures at non-native occurrences, the median expansion of minimum temperature tolerance was  $-2.9$  °C. Similarly, for the 90 species with lower precipitation at non-native occurrences, the median expansion of minimum annual precipitation was  $-23$  cm. Broader climatic conditions at non-native occurrences expanded the modelled potential geographical range by a median of 35%, with smaller range species showing larger expansions of potential geographical range.

**Main conclusions** Our results show that plants' native ranges strongly underestimate climatic tolerance, leading species distribution models to underpredict potential range. The climatic tolerance of species with narrow native ranges appears most prone to underestimation. These findings suggest that many plants will be able to persist *in situ* with climate change for far longer than projected by species distribution models.

## Keywords

climate tolerance, climatic suitability, dispersal, ecological niche, endemic plants, Maxent, range limits, range size, species distribution modelling.

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## INTRODUCTION

Species distributions identify only a portion of the environmental conditions where populations could potentially persist (Hutchinson, 1957; Wiens, 2011). Species distributions

are not only constrained by suitable abiotic conditions, but also by biotic interactions (Hutchinson, 1957; Sexton *et al.*, 2009; Wisz *et al.*, 2013) and dispersal ability (Pulliam, 2000; Soberón & Peterson, 2005). Although biogeographers recognize these limitations, regional niche models have historically

been built on an assumption that plant species distributions are near climatic equilibrium (Elith & Leathwick, 2009; Franklin, 2009). Thus, climate is the primary constraint on distributions at regional scales (Pearson & Dawson, 2003), and therefore, current ranges serve as good approximations of climatic tolerance.

This assumption has strong implications for conservation and management. Several ecological forecasting studies based on niche modelling have projected widespread extinctions and local extirpations of species with climate change (e.g., Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005a). Niche modelling has also been used commonly for reserve planning to maximize biodiversity conservation (e.g. Kremen *et al.*, 2008). Similarly, niche modelling has been applied widely to models of invasion risk under current and future climate conditions (e.g. Kriticos *et al.*, 2003; Thuiller *et al.*, 2005b; Bradley *et al.*, 2010). If species distributions indeed serve as good approximations of climatic tolerance, then ecological forecasting studies are more likely to capture all or most of the climate conditions in which the species can persist.

However, recent studies have raised concerns about the magnitude of influence of non-climatic factors on the regional distributions of species (Sexton *et al.*, 2009; Austin & Van Niel, 2011; Wiens, 2011; Wisz *et al.*, 2013). Several studies suggest that dispersal barriers in particular might prevent species from occupying climatically suitable habitat. For example, in the Northern Hemisphere, Pleistocene glaciation still exerts a strong influence on the distributions of many tree species (Svenning & Skov, 2007), forest herbs (Bellemare & Moeller, 2014) and beetles (Baselga *et al.*, 2012) after nearly 20,000 years. Likewise, plant distributions in recent geologic history show that climatic niches have shifted through time (Maiorano *et al.*, 2013), suggesting that distributions at any given time are a poor proxy of overall environmental tolerance. These sorts of non-equilibrium conditions, whereby species are still spreading into suitable habitat, may be widespread amongst native species (Bradley *et al.*, 2015).

One approach used to test how well plant distributions can be used to determine climatic limits is by comparing native and non-native ranges of invasive species (Guisan *et al.*, 2014). There is a considerable debate about whether shifts in the climatic niche are rare (Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013) versus common (Broennimann *et al.*, 2007; Gallagher *et al.*, 2010; Early & Sax, 2014; Li *et al.*, 2014; Fernández & Hamilton, 2015), where the latter could suggest underfilling of climatic niche space in the native range. However, non-overlapping climate conditions between ranges creates methodological challenges (Broennimann *et al.*, 2012), while ecological and evolutionary traits of invasive species (e.g. Pyšek & Richardson, 2007; Pearman *et al.*, 2008) might cause them to behave differently from non-invasive species, making them an imperfect study system.

More quantitative assessments are needed to illustrate how well geography reflects climatic limits for non-invasive

species. One group well suited for addressing this question is North American native plant species that have been cultivated and distributed for gardening purposes (Vetaas, 2002; Sax *et al.*, 2013). Ornamental plant species are often transported and established far beyond their native ranges (Van der Veken *et al.*, 2008), and many escape into natural ecosystems. Within a broadly geographically connected region such as North America, the introduction of regionally native ornamentals into non-native landscapes provides a unique opportunity to determine how well the native range can predict overall climatic tolerance limits. If regional distributions are primarily climatically limited, we would expect adventive occurrences (i.e. occurrences outside the native range) to occur within the same climatic conditions as native occurrences. Conversely, if climate does not strongly limit regional distributions, we would expect adventive occurrences to expand the climatic tolerance limits described by native occurrences.

Here, we compare the climate conditions associated with *native* occurrences to climatic conditions associated with *adventive* occurrences for 144 US endemic species that have been introduced as ornamentals in the continental USA. We estimate to what extent adventive occurrences can expand climatic tolerance limits estimated for species relative to native occurrences alone. We also test the effects of expanded climatic limits on estimated range size using species distribution modelling. This research quantifies how much non-invasive plant species distributions underestimate their climatically suitable habitat.

## METHODS

### Target species

We assessed US endemic plant species that are known to have at least one adventive occurrence somewhere in the USA and that are used as ornamentals. Adventive is defined here as the presence of a species outside of its native range, through the direct or indirect influence of human activity (Kartesz, 2014). Ornamentals are defined here as native plants used for planting or gardening purposes. Ornamentals were targeted specifically to increase the likelihood that their propagules would be broadly introduced, thereby creating ample opportunities for establishment in natural ecosystems. By focusing on US endemic species, we were better able to define the full geographical extents of the species native ranges. We used data from the Floristic Synthesis of North America (Kartesz, 2014) to identify plant species that are considered to be both endemic to the USA and adventive in at least one state. Floristic Synthesis data are derived from analyses of over 6 million county-level records by the Biota of North America Program (BONAP; Kartesz, 2014). The BONAP database was initiated in 1969 and integrates county records, herbarium vouchers, museum specimens and bibliographic references into the most comprehensive flora of the USA and North America. All records are verified by

taxonomic and floristic specialists. Species' native ranges prior to widespread introduction by humans are derived from early published state floras, species accounts and historical herbarium records dating to the 1700s from a variety of institutions across North America (see Appendix 1 for further details).

We used an Internet search to determine whether each target species could be considered ornamental, and therefore more likely to have been widely introduced outside of its native range. Our search used key words associated with use and commercial availability. For example, we searched for the genus and species + 'garden' or 'for sale' (Table 1). Species were identified as 'ornamental' if we found one or more websites that commented on garden uses or ornamental purposes for the species (e.g., cottage gardens, shrub borders, ornamental tree) and provided purchase options for seeds or live plants.

### Species occurrence data

We used occurrence records and associated geolocations for each target species from the Global Biodiversity Information Facility (GBIF) and several other online herbarium compendia in the USA, including CalFlora, the Consortium of California Herbaria, Consortium of Northeast Herbaria, Consortium of Pacific Northwest Herbaria, New York Botanical Garden, Southeast Regional Network of Expertise and Collections, and the Southwest Environmental Information Network. Herbarium data are commonly used to estimate climatic suitability and for modelling range limits in biogeographical studies (Lavoie, 2013). Herbarium collectors generally target species from natural areas, not gardens (e.g. Suarez & Tsutsui, 2004; Illinois State Museum 2015). Thus, we assume that although the targeted species are used as ornamentals, the herbarium occurrences represent escapes found in natural environments where climate is not directly manipulated. We divided the herbarium occurrence data for each species into points located within the native range

**Table 1** Key words associated with aesthetically purposed and commercially available plants were used to determine whether or not a species was considered ornamental.

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#### Internet search steps to determine whether species is ornamental

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1. Scientific name (*Genus species*) to assess immediate and obvious results
  2. Scientific name and 'garden' to assess ornamental use
  3. Scientific name and 'for sale' to assess commercial availability
  4. Common name (according to the USDA PLANTS database) and 'garden' when search words in line 2 yielded no clear results
  5. Common name and 'for sale' when search words in line 3 yielded no clear results
  6. Scientific name and 'seeds' or 'seeds for sale' when search words in lines 2 and 3 yielded no clear results
  7. Common name and 'seeds' or 'seeds for sale' when search words in line 4 and 5 yielded no clear results
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(according to the Floristic Synthesis) versus adventive points located outside the native range (Fig. 1).

As is apparent from Fig. 1, a number of occurrence records fell just outside the borders of the native counties. It is likely that many of these occurrences are, in fact, part of the native range and that the BONAP data set underestimates some native counties. To test whether misclassifying neighbouring points as adventive rather than native influences the results, we performed a second test whereby we expanded BONAP's definition of the native range to include both native counties plus any county bordering a native county.

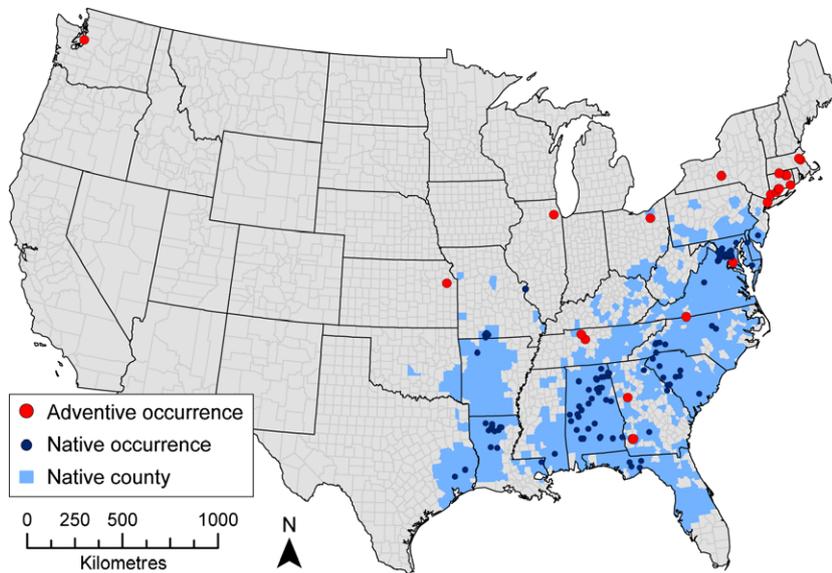
For both data sets, we removed duplicate species occurrences within any single climate grid cell (see below). To sufficiently describe the native climate space, we limited the analysis to species with at least 10 occurrence points (an occurrence in 10 unique climate grid cells) in the native range and at least one adventive occurrence.

### Climate comparison

We used interpolated climate data from Worldclim (Hijmans *et al.*, 2005) to test for differences in climatic tolerance limits between the native and adventive ranges of each species. Worldclim data were based on averaged conditions from 1950 to 2000 at a spatial resolution of 0.04166 decimal degrees (approximately 5-km grid cells for most of the USA). We extracted climatic conditions at native and adventive occurrences using climate predictors likely to limit plant growth: average annual precipitation, average January minimum temperature and average July maximum temperature. Using the extracted climate data, we then calculated minimum annual precipitation, minimum January minimum temperature, maximum January minimum temperature (important for winter chilling requirements; Primack *et al.*, 2009) and maximum July maximum temperature for each species based on the occurrence points located within the species' native range. Although other climate variables might be more important for individual species, this set is representative of average conditions that are indicative of climatic tolerance for plant species and are typically used in niche modelling. We compared the climatic tolerance limits suggested by the native range to the same values calculated using occurrences in the species' adventive range. For each climate variable, we measured how many species had adventive climate values outside the limits circumscribed by the native range. We also calculated how different the climatic limits in the native range were from those in the adventive range.

### Potential range comparison

We created species distribution models (SDMs) based on annual precipitation, minimum January temperature and maximum July temperature using Maxent (Phillips *et al.*, 2006) for each species. We chose the same base climatic



**Figure 1** Native and adventive range of *Chionanthus virginicus* (white fringe tree) in the continental USA. Native counties according to BONAP are shown in light blue. *Chionanthus virginicus* has 132 total occurrence records with 109 located within the native range (dark blue points) and 23 located outside the native range ('adventive', red points).

predictor variables that we used in the climate comparison for comparability between the two analyses and because they are most closely associated with the climatic tolerance of an average plant species. We accounted for sampling bias by including a bias file in Maxent derived from the modelled relationship between all species occurrence points and human population density and road density across the continental USA (Merow *et al.*, 2013). The bias file represents a null expectation that a species is likely to be found in areas with high sampling. Our goal was to circumscribe the full range of climatic conditions in which each species could occur in the continental USA and to compare modelled ranges within and across species, so we chose to use the full study region as our background extent (Merow *et al.*, 2013). This choice facilitated the comparison of projected range sizes based on the native versus total range and conformed to our spatial domain of interest. In both the sampling bias model and species SDMs, we included only linear, quadratic and product features, used 10-fold cross-validation and left other settings at their default values. We calculated the average area under the curve (AUC) statistic for test samples in each model run.

For each species, potential range models were created for (1) only the points in the species' native range and (2) all available points (native + adventive). We used a threshold Maxent suitability value that encompassed 95% of the distribution points used to define potential range, and compared total land area of modelled potential range for native range points versus all available points for each species to calculate differences in overall range. The 95% threshold might lead us to underestimate expanded climatic suitability with all points because some adventive occurrences will be excluded. However, it also reduces the influence of any errors from amongst the adventive occurrences. We excluded the Venus flytrap (*Dionaea muscipula*) from all analyses of change in potential range because the species was an outlier, with a range expansion of over 14,000%.

### Range size versus expansion

Given that our criteria for including species was fairly liberal (10 native points and 1 adventive point), we also tested whether numbers of data points or native range size related to expansion of climatic tolerance. We calculated (1) number of points in the native range, (2) area of the native range based on BONAP county data and (3) number of points in the adventive range. We compared each of these three metrics to percentage change in potential range (native versus native + adventive) derived from the SDMs as well as to expanded climatic limits for each of the individual climate variables. We compared each of these three metrics to percentage change in potential range (native versus native + adventive) derived from the SDMs as well as to expanded climatic limits for each of the individual climate variables using generalized linear regression with square-root- and log-transformed response variables to account for overdispersion. We calculated  $D^2$  values to quantify variance explained using the modEVA package (Barbosa *et al.*, 2014).

### RESULTS

We identified 144 endemic, ornamental plants with at least 1 adventive occurrence and 10 or more native occurrences. Nearly all of these species were perennial (129 of 144). The average number of records located inside the native range was 105 (median: 64), while the average number of records located outside the native range was 11 (median: 7). The large majority of species had multiple adventive data points; only 12 species had a single adventive point. The average potential native range size based on the species distribution models was 1,970,000 km<sup>2</sup> (median: 1,800,000 km<sup>2</sup>). Additional summarised results for the target species are presented in Appendix 2.

One hundred and twenty-four of 144 species (86%) had one or more adventive occurrences that expanded the climatic

limits circumscribed by the native range occurrences for at least one of the four climate variables tested. For example, *Chionanthus virginicus* (white fringe tree) has a total of 109 native and 23 adventive occurrences. Ten of the adventive occurrences were below the minimum January temperature threshold of  $-7\text{ }^{\circ}\text{C}$  defined by occurrences in the native range and three were also below the minimum annual precipitation threshold of 96.2 cm (Fig. 2). These expanded climatic limits translated into a modelled potential range that was 29% larger (Fig. 2).

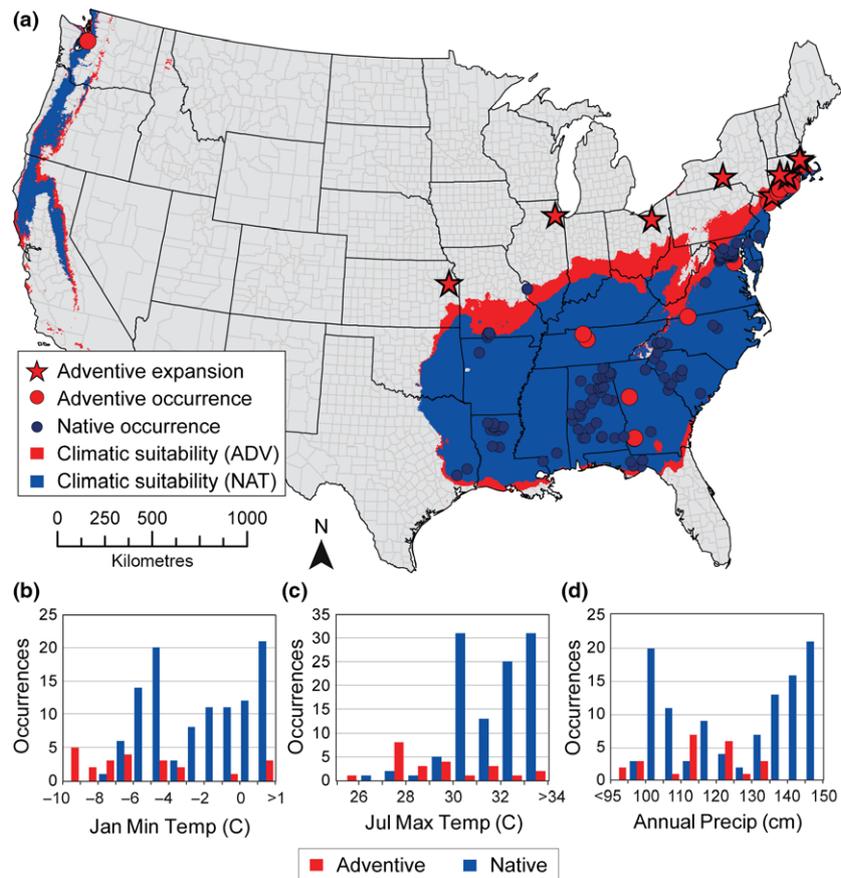
Adventive occurrences greatly expanded the observed climatic limits. Ninety of 144 (62%) had adventive occurrences with average annual precipitation values lower than occurrences in the native range, and the median reduction of precipitation tolerance was 23 cm per year (Fig. 3a), comparable to the total annual rainfall of Albuquerque, NM. Fifty-six of 144 (39%) species showed an increased limit of maximum July temperature by a median of  $1.2\text{ }^{\circ}\text{C}$ , while 51 of 144 (35%) species showed an increased limit of minimum January temperature by a median of  $3.4\text{ }^{\circ}\text{C}$  (Fig. 3b,c). Lastly, 80 of 144 (55%) species had adventive occurrences that lowered the limit of minimum January temperature by a median of  $2.9\text{ }^{\circ}\text{C}$  (Fig. 3d), or roughly the average temperature difference between Philadelphia and Boston.

One hundred and twenty-eight of 144 species (89%) showed an expansion of suitable climatic range when adven-

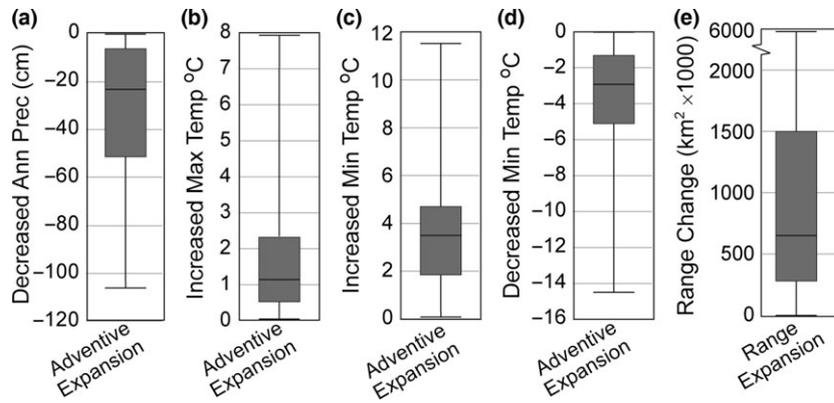
tive points were included in the species distribution models (e.g., Fig. 2). All of the models had test AUC values above 0.8, with median test AUCs of 0.95 and 0.93 for the native and native + adventive models, respectively (Appendix 3). SDMs were more likely to show a range expansion when a species also had a climatic expansion. Of the 124 species with a climatic expansion, 116 (94%) also showed an SDM range expansion. Conversely, of the 20 species with no climatic expansion, only 12 (60%) also showed an SDM range expansion.

For the species with range expansion, the median range expansion was 709,000 km<sup>2</sup> (about the size of the state of Texas; Fig. 3e) corresponding to an increase in suitable area of 35%. Species distribution models are presented in Appendix 4. Across all species, ranges generally expanded into cooler climates, as indicated by shifts in climatic limits (Appendix 4). When we repeated the above analyses using the expanded definition of native range (native counties identified by BONAP plus all adjacent counties), we found comparable or stronger relationships in all cases. This analysis is presented in Appendix 5.

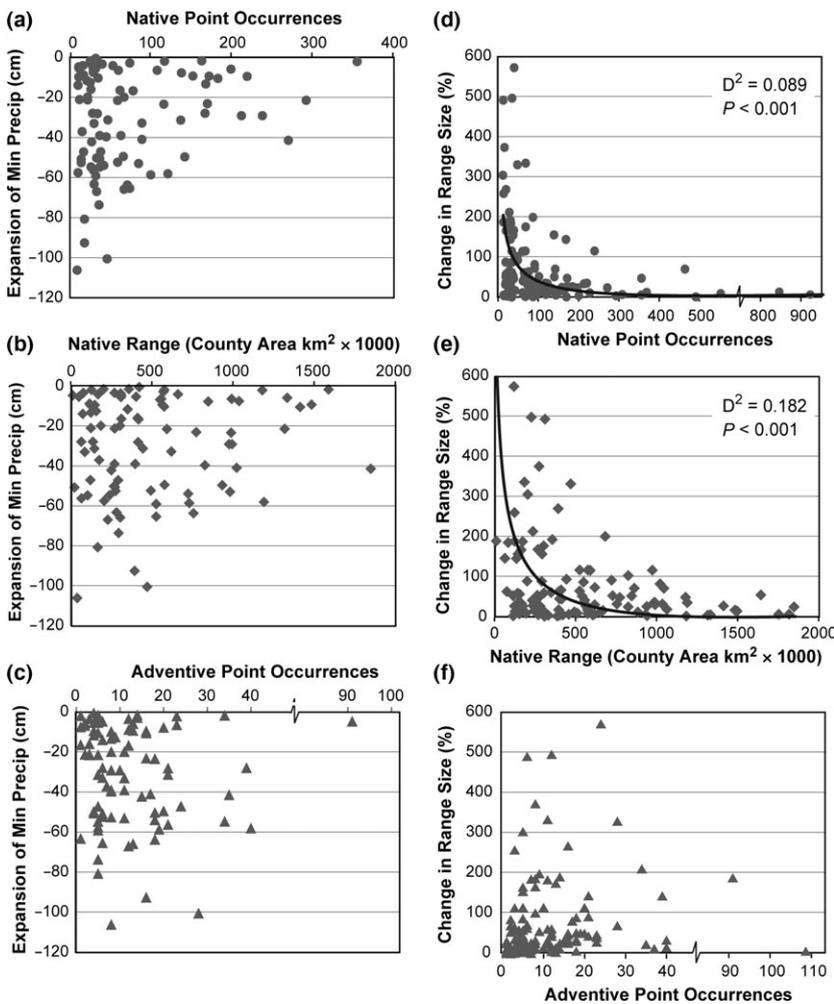
There appears to be a negative relationship between the size of the native range and the amount of expansion of the niche (Fig. 4). The relationship between native range size (based on BONAP county area) and change in SDM modelled range was statistically significant ( $D^2 = 0.18$ ,  $P < 0.001$ ;



**Figure 2** Species distribution models from Maxent show that including adventive occurrences of *C. virginicus* (white fringe tree) expands the projected range of climatic suitability. (a) Ten adventive occurrences (red stars) expand the species' climatic tolerance limits inferred from native range occurrences (dark blue), while 13 adventive occurrences (red circles) fall within the climatic limits described by native occurrences. (b–d) Adventive occurrences primarily lower inferred minimum temperature tolerance, while three occurrences also lower minimum precipitation tolerance.



**Figure 3** Box plots illustrate the degree to which adventive occurrences expand the inferred climatic tolerance limits and potential geographical range for US endemic species. Plots show median, quartiles and extremes for species with adventive occurrences outside the native range climate conditions. (a) Expansion of lowest annual precipitation ( $n$  expanders = 90), (b) expansion of highest July maximum temperature ( $n$  expanders = 56), (c) expansion of highest January minimum temperature ( $n$  expanders = 51), (d) expansion of lowest January minimum temperature ( $n$  expanders = 80), (e) expansion of modelled climatically suitable range ( $n$  expanders = 128).



**Figure 4** Plant species with small native range sizes are more likely to underestimate their potential range, but larger numbers of adventive points does not increase likelihood of range expansion. Scatter plots show the relationship between expanded minimum precipitation and native point occurrences, native range size and adventive point occurrences (panels a–c, respectively). None of the relationships were significant. In contrast, relationships between change in range size and native point occurrences or native range size (panels d–e, respectively) were both significant. Generalized linear model fits and associated deviance explained ( $D^2$ ) are presented for both relationships. Change in range size was not related to adventive point occurrences (panel f). Four points with range expansion  $\gg$  1000% are not shown in panels d, e and f, but support the patterns of a negative relationship with native occurrences and no relationship with adventive occurrences.

Fig. 4e), as was the relationship between native point occurrences and change in SDM modelled range ( $D^2 = 0.09$ ,  $P < 0.001$ ; Fig. 4d). The same pattern is not evident for adventive occurrences. Adding few adventive occurrences

seems just as likely to expand a plants' niche as adding many adventive occurrences (Fig. 4c,f). There were no significant or near-significant relationships with any of the other climate variables.

## DISCUSSION

Most species have not been broadly introduced outside of their native ranges. As a result, our understanding of climatic tolerance limits for the bulk of species can only be inferred from occurrences within their native ranges. Accordingly, ecological forecasting studies assessing extinction risk and supporting conservation planning are typically based on native occurrences (e.g., Peterson *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005a; Kremen *et al.*, 2008). Our results show that native range data strongly underestimate the climatic conditions where many species could occur (Fig. 3). The vast majority (86%) of species had adventive occurrences in climate conditions that were not encompassed by native range distribution data. Range models expanded substantially when adventive occurrences were included, and particularly when those adventive occurrences had novel climate conditions. Thus, the broader range models are likely due to expansion of the realized niche rather than a model response to the addition of more data points. The corresponding expansion of niche models by 35% geographically suggests that an assumption of climatic equilibrium in the native range (Elith & Leathwick, 2009; Franklin, 2009) may be optimistic for many native species.

Our results support previous evidence of strong non-climatic limitations on plants' native ranges (Vetaas, 2002; Svenning & Skov, 2007; Bellemare & Moeller, 2014; Early & Sax, 2014; Bradley *et al.*, 2015). Previous studies have shown niche shifts for invasive species between native and non-native ranges (Broennimann *et al.*, 2007; Gallagher *et al.*, 2010; Li *et al.*, 2014; Fernández & Hamilton, 2015) and suggest that niche shifts are particularly likely when invasive species are introduced as ornamentals (Donaldson *et al.*, 2014). This study supports the findings of Early & Sax (2014) that niche shifts are similarly prevalent amongst non-invasive species. This accumulation of evidence strongly suggests that the native distribution of a species is a poor proxy for climatic tolerance.

Moreover, our results suggest a pattern of greater niche expansion amongst plant species with smaller native range sizes (Fig. 4). This pattern has previously been observed for plants introduced to the USA from Europe (Early & Sax, 2014) as well as for reptiles and amphibians introduced globally (Li *et al.*, 2014). This pattern suggests that climate data are poor predictors of the potential distribution for narrowly distributed species (e.g., rare and endangered species). It is possible that non-climatic factors, such as dispersal limitations and biotic interactions, are instead limiting rare species distributions. The pattern could also be explained by under-sampling of distributions for rare species, or by model over-fitting for narrow range species leading to smaller extents of climatic suitability (e.g., Harrell *et al.*, 1984). In either case, adding available data from outside the native range could improve estimates of climatic suitability. Pooling global occurrences to approximate climatic tolerance is common for invasive species (e.g., Broennimann & Guisan, 2008).

Where non-native distribution data exist, this approach could also inform potential range estimates for non-invasive species.

It is unclear from our analyses whether species are under-filling climatically suitable habitat due to dispersal barriers, biotic interactions (e.g., Wiens, 2011; Wisz *et al.*, 2013) or some combination of both. The plants we analysed were more likely to tolerate colder temperatures (median expansion  $-2.9$  °C) in their adventive ranges than warmer temperatures (median expansion  $+1.2$  °C). This difference suggests that dispersal limitations associated with the last glaciation (Bellemare & Moeller, 2014) could be affecting distributions. However, the warmer and drier conditions in the southern USA also reduce the availability of moisture, which may be more significant than temperature in determining distribution. The difference may also reflect increased propagule pressure from human preferences and more widespread planting of ornamentals in northern populated areas of the USA. Additional investigation into particular species with alternative modelling strategies could help to tease these differences apart.

Importantly, point occurrence data derived from herbarium records do not identify whether those plants exist as part of established populations. The majority of the species in our data set were perennial forbs, shrubs and trees, suggesting that occurrences reflect climatic conditions that the plant could tolerate over multiple years. However, herbarium records in both the native and adventive ranges could include transient individuals or populations able to tolerate climatic conditions, but not establish self-sustaining populations in the long term (Pulliam, 2000; Sax *et al.*, 2013). Some records may also represent misidentifications or misapplication of collection location. Further, the  $\sim 5$  km spatial resolution of the climate data precludes identification of local microclimates, which could modify the average climate conditions derived from Worldclim (e.g., Slavich *et al.*, 2014) and lead to both over- and underestimates of climatic niche expansion. Ornamental plants may also be artificially selected for species or varieties with broader tolerance and could behave differently from non-ornamentals. Experimental studies are needed to determine whether the expanded climatic tolerance limits inferred based on geography truly reflect potential for an average plant to establish viable populations.

Even if some adventive occurrences overestimate long-term population success, the overall pattern emerging from these results still suggests much broader climatic tolerance for most species. One implication is that plant species may be able to tolerate some level of climate change *in situ*, beyond what would be predicted by current conditions in the native range. It also appears that many species would already be able to successfully establish outside of their native ranges, even before climate changes. The latter finding could support conservation strategies like managed relocation (Richardson *et al.*, 2009), particularly for slow-growing, long-lived species like trees that might require planting well in advance of shifting climate conditions (Sax *et al.*, 2013). Given that many plant species appear limited by dispersal

ability (Svenning & Skov, 2007), it is unlikely that they will be able to keep up with climate change unaided. The broader climatic tolerances observed here suggest that eventual range contraction might take longer than previously expected, but direct human intervention will still be needed to relocate and conserve vulnerable species. Promoting regionally native, non-invasive plants in lieu of non-natives could provide long-term benefits for conservation.

In an era of rapid climate change, conservation biogeography often focuses in particular on risks to rare native species. Our analyses suggest that species native ranges often underestimate their climatic tolerance, and climate is especially unlikely to constrain the ranges of rare species. As a result, projections of species' climatic suitability in current and future climate are likely to underpredict potential habitat. The vast majority of the plants studied here could survive outside of climate conditions described by their native ranges and are likely to persist *in situ* under climate change for longer than species distribution models would predict. While climate change is clearly an important threat to species, near-term projections of habitat loss associated with climate change, particularly for rare species, should be interpreted with caution.

## ACKNOWLEDGEMENTS

We thank C. Curtis, R. Early, E. Fusco, B. Petitpierre and two anonymous referees for helpful comments on earlier drafts of this manuscript. This research was supported by the National Institute of Food and Agriculture, US Department of Agriculture, the Massachusetts Agricultural Experiment Station and the Department of Environmental Conservation under Projects No. MAS00016 and MAS00410.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Description of the Biota of North America (BONAP) data set.

**Appendix S2** Summary information on the target species.

**Appendix S3** Area under the curve (AUC) statistics for all species distribution models.

**Appendix S4** Species distribution models for all species based on native range and native + adventive ranges.

**Appendix S5** Analysis of inferred climatic tolerance using broader definition of 'native' counties.

## BIOSKETCH

The authors' research focuses on how well biological processes can be inferred from geographical distributions, with an overarching interest in differences between invasive and non-invasive plant species. TB, JB and BAB conceived of the idea. TB collected the data and extracted climate information. JMA performed the distribution modelling. JK and MN contributed BONAP data. BAB and JMA analysed the data. BAB led the writing with participation from all co-authors.

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Editor: Wilfried Thuiller