



RESEARCH
PAPER

Space to invade? Comparative range infilling and potential range of invasive and native plants

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ABSTRACT

Aim Our understanding of potential ranges for native and non-native species is often based on their current geographic distributions. Non-native species have had less time than co-occurring native species to expand their ranges following introduction, so non-native ranges may under-represent suitable conditions. Therefore it is often assumed that species distribution models will predict disproportionately smaller potential ranges for non-natives than natives. We compare the distributions of native, endemic, alien and invasive plants to determine how the different range attributes of these groups might influence ecological forecasting.

Location Continental USA.

Methods We compared the geographic ranges of 13,575 plant species (9402 native, 2397 endemic, 1201 alien and 755 invasive) using (1) US only and (2) global distribution data from herbarium records. We calculated US longitudinal and latitudinal range extents as potential indicators of range-limiting factors, modelled potential range based on climate using principal components analysis, and calculated occupancy of potential ranges (range infilling).

Results Contrary to expectations, modelled potential ranges were significantly larger for non-natives than natives, even for species with few occurrences. Distributions of native species, not invasive species, appeared strongly limited longitudinally. However, invasive plants occupied substantially less area within their climatically suitable ranges than native plants (lower range infilling).

Main conclusions Invasive plant distributions were consistently broader, both climatically and geographically, than comparable native species. This suggests that invasive plant distribution models at regional scales are *not* underpredicting potential ranges relative to models for native species. In contrast, the comparatively limited longitudinal ranges of native species suggest a high degree of non-climatic limitation, which is likely to cause distribution models to underpredict the potential ranges of native species. Invasive plants have not achieved the degree of range infilling expected relative to natives. Thus, plants introduced to the US still have plenty of space to invade.

Keywords

Alien, bioclimatic envelope model, dispersal, ecological niche model, equilibrium, exotic, introduced, occupancy, plant invasion.

INTRODUCTION

Given the threat that biotic exchange poses to biodiversity and ecosystem services (Sala *et al.*, 2000), there is a strong need to

predict which invaders will attain the broadest geographic ranges and, thus, have some of the largest impacts (Parker *et al.*, 1999). The most common method used to estimate species environmental tolerances and predict their potential ranges is to

make statistical models of their distributions in relation to climatic variables ('species distribution models', SDMs) (Guisan & Zimmermann, 2000). SDMs that are based on climate assume that the occurrences of a species describe the entire climate space it can occupy ('climate equilibrium'). Low climate equilibrium causes models to underestimate potential range (Welk, 2004; Václavík & Meentemeyer, 2012). Underestimating the potential range of invasive species undermines assessments of invasion risk, prioritization of control efforts (Grice, 2009) and monitoring for early detection and rapid response to expanding invasions (Westbrooks, 2004). Additionally, the occurrences of a species could fully represent the climate space it could occupy but not fill all the geographic space it could occupy ('range equilibrium', e.g. Svenning & Sandel, 2013). Range equilibrium is related to occupancy of the potential range (hereafter, 'range infilling'). Comparatively low range infilling suggests that a species has a high potential for additional establishment.

The climate equilibrium assumption is likely to fail for species that are actively shifting their ranges, notably including tree species undergoing post-glacial migrations (e.g. in Europe; Svenning & Skov, 2004; Normand *et al.*, 2011) and non-native or invasive plants expanding into new terrain (Mack *et al.*, 2000; Williamson *et al.*, 2009; Essl *et al.*, 2011). For example, landscape-scale models created during the initial invasion stages of a forest pathogen (Václavík & Meentemeyer, 2012) and understory invasive plants (Jones, 2012) did a poor job of predicting the subsequent extents of these invasions because the initial invaded extents did not represent the full extent of these species environmental niches. Regionally, the ranges of non-native species tend to be more restricted than those of native species' (Williamson *et al.*, 2009), which suggests that non-natives have not had adequate time to attain climatic equilibrium and therefore models based on current non-native distributions are likely to underestimate their potential ranges. As actual and reported occurrences of invasive plants increase over time (e.g. Pyšek & Prach, 1995; Welk, 2004; Crawford & Hoagland, 2009) so too do the geographic extents of modelled potential range (Welk, 2004; Wang & Wang, 2006; Wilson *et al.*, 2007; Miller *et al.*, 2009).

Despite this general understanding that the relative climatic and range equilibrium of native and non-native species is likely to differ, the magnitude of this difference is unknown. Although there is no guarantee that native species are in climatic or range equilibrium (Svenning & Skov, 2004; Araújo & Pearson, 2005), they are thought to be closer than non-natives due to ample dispersal time. We take a comparative approach to examine the distributions of native and non-native species, including their modelled potential ranges, range infilling and overall geographic (longitudinal and latitudinal) extents. We expected that non-native plant distributions would show strong indications of dispersal limitation because they have not had sufficient time to spread into available habitat (Welk, 2004; Wilson *et al.*, 2007; Václavík & Meentemeyer, 2012).

Here, we compared the distributions of native, endemic, alien (non-native but not invasive, as defined below) and invasive plants in the continental USA to test two main hypotheses

related to the distributional patterns and, therefore, equilibrium of native versus non-native plants. First, we hypothesized that, after accounting for number of occurrences, non-native plants would have smaller potential ranges (modelled by SDMs) and overall geographic extents than native species (Fig. 1). We hypothesized that range infilling could differ between native and non-native species in two potential ways. First, after accounting for number of occurrences, range infilling could appear to be higher for non-native plants due to their limited geographic extents and smaller modelled potential ranges (Fig. 1). Alternatively, after accounting for number of occurrences, range infilling could be higher for native plants as they have had more time to achieve range equilibrium. Within the native groups, we predicted that endemic species would have higher range infilling than native species due to their relatively narrower geographic extents. Within the non-native groups, we predicted that invasive species would have larger potential ranges than alien species (e.g. due to broader physiological tolerance; Higgins & Richardson, 2014). This research represents the first comprehensive assessment of regional range extents, range infilling and comparative equilibrium for native and non-native plants.

METHODS

Species occurrence data

We compiled lists of plant species that are native, endemic, alien or invasive in the lower 48 US states using the USDA PLANTS database (USDA-NRCS, 2014). Native species are those listed on USDA PLANTS as 'Native' within a jurisdiction of the lower 48 states. Endemic species include any lower 48 natives identified by the Germplasm Resources Information Network (GRIN, 2013) as endemic to the USA. Endemic species were excluded from the native species list such that the native category does not include known endemics. Alien species are those listed on USDA PLANTS as 'Introduced' within a jurisdiction of the lower 48 states, excluding 'Native and introduced' species to focus only on non-natives. Invasive species are aliens listed as a state or federal noxious weeds (US Congress, 1974) or identified as impacting natural areas by the *Invasive Plant Atlas of the United States* (IPA, 2012). Invasive species were excluded from the alien species list such that the alien category does not include known invasives. Thus, our alien and invasive categories are similar to those defined by Richardson *et al.* (2000) as 'naturalized' and 'invasive', respectively.

We downloaded all global distribution data for the target plant species from the Global Biodiversity Information Facility (GBIF, 2014; accessed June, 2014). From these data, we created a subsample of all distribution points within the lower 48 states. In the USA many of the herbarium records were county centroids, so we converted all point data to a gridded resolution of 50 km, which approximates the area of an average county. Duplicate locations within any grid cell were discarded. We excluded from the analysis any species with fewer than five occurrence grid cells within the lower 48 states. Although other

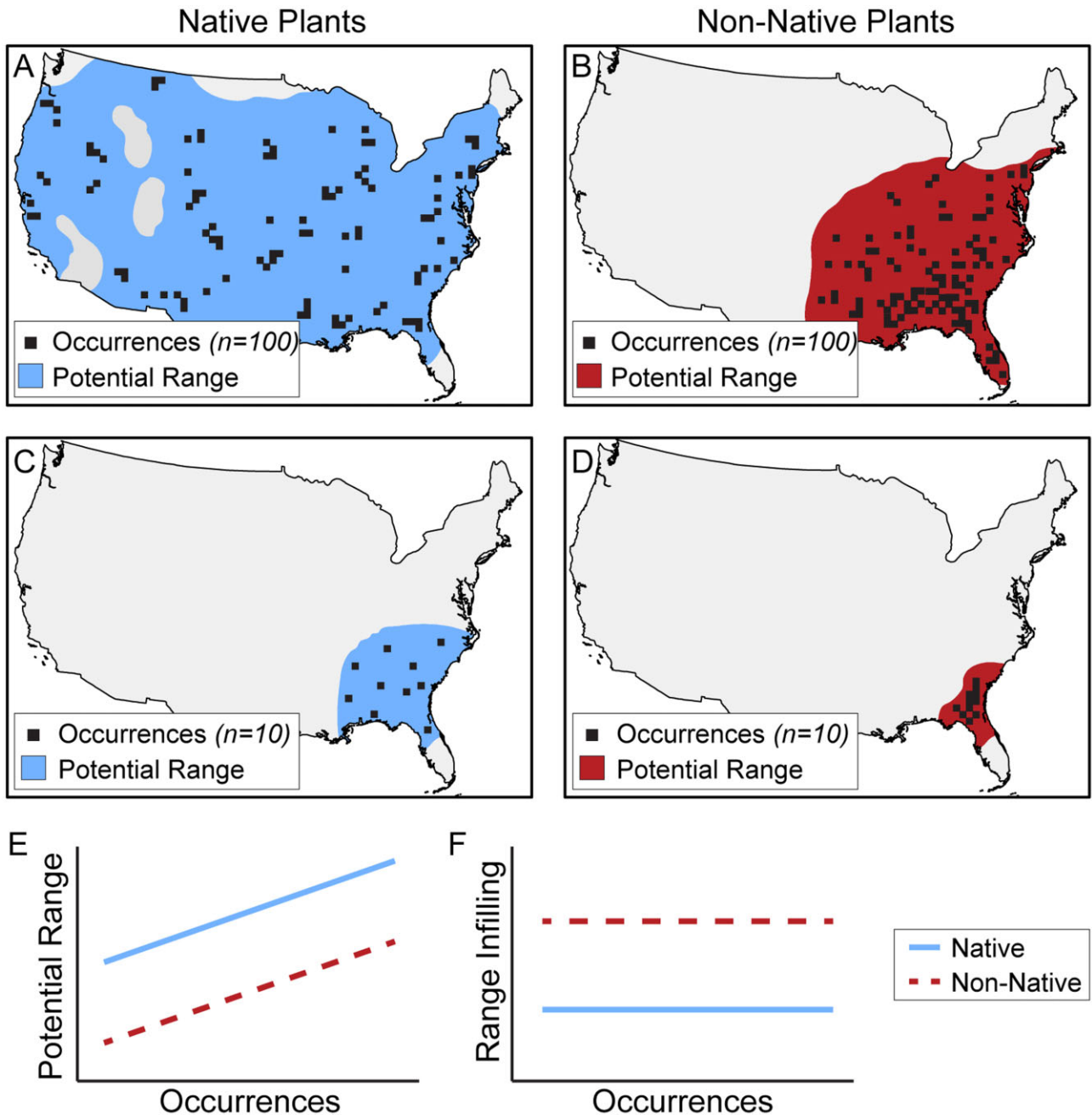


Figure 1 Schematic illustrations of hypotheses tested in this paper. Non-native plants are expected to have smaller geographic extents than native plants regardless of number of occurrences (A–D). This pattern would lead to non-natives having a lower modelled potential range (a proxy for climatic equilibrium, E). The pattern could also lead to a higher infilling of the current range for non-natives, making them appear to have higher range equilibrium than natives (F).

independent distribution datasets exist for both native and non-native species, which probably provide more complete information than the GBIF alone (Beck *et al.*, 2013), the GBIF is the only source that could consistently provide distributional data for all of our target species at a global scale. We assumed that data limitations and sampling biases associated with GBIF records, while unavoidable, were consistent between groups and, thus, did not influence the overall comparison between groups. However, we tested for the influence of sampling bias by com-

paring GBIF occurrences with state-level occurrences identified by the USDA Plants website, which aims to accurately list all states in which a species is established (USDA-NRCS, 2014). We repeated the analyses for each species group using only the subset of species whose GBIF records occurred in at least 80% of the states it occupies as identified by USDA Plants (a ‘high geographical consistency’ subset of species).

The inclusion of global distribution data is likely to create better estimates of species climatic tolerances and improve

models of potential ranges within the USA (Broennimann & Guisan, 2008). As a result, we analysed potential range and range infilling based on the continental US distribution as well as based on the global distributions for all groups, using only species with one or more occurrences outside the USA in the second analysis. The inclusion of global distribution data is likely to bias the *comparative* analysis because, by definition, non-natives are found outside the USA and are therefore likely to have non-US records, whereas US natives might not have been introduced globally. This will lead to a smaller modelled potential range and larger modelled range infilling for natives relative to non-natives. However, the potential range and range infilling estimates are likely to be more accurate when based on global data because they use more complete data to approximate climatic tolerances.

Potential range and infilling

For each species we recorded the total number of grid cells occupied (O) and the latitudinal and longitudinal ranges (in decimal degrees) of those occupied grid cells within the continental USA. We calculated potential range (P) based on climatic conditions in the occupied grid cells (using the US and the global distribution in separate analyses). Potential range was calculated using the following climatic variables, which were derived from the Climatic Research Unit (CRU) dataset at 10' resolution from 1961–90 (New *et al.*, 2002) and were averaged within each 50-km grid cell of a global climate grid: mean temperature of the coldest month, mean temperature of the warmest month, growing degree days above 5 °C, seasonality of precipitation (coefficient of variance of mean monthly values), the summed precipitation of the three wettest months and the summed precipitation of the three driest months. We conducted a principal components analysis (PCA) for these climate variables using the *ade4* package in R. We used the first two axes of this PCA (which explain 83% of the variability in climate conditions) to construct a two-dimensional global climate space, onto which we plotted the distribution of each species based on: (1) the 50-km grid cells the species occupies in the USA only and (2) the 50-km grid cells the species occupies globally. For each species, we then calculated the minimum convex hull polygon that included 95% of the species' occurrences. This 95% threshold was chosen to reduce the influence of outliers, which might not represent the climatic tolerances of the species and could artificially increase the modelled potential range. The grid cells with climatic conditions that fell inside this polygon were considered as the species' potential climatic range, which we then projected onto the USA to identify potential range geographically.

A presence-only approach such as this, rather than a presence/pseudo-absence approach such as Maxent or boosted regression trees, was necessary, given the suspected dispersal limitation of some groups. Sampling pseudo-absence data from locations that are climatically suitable for a species but which the species does not occupy would artificially shrink estimates of the species' climatic tolerances. This effect would be strongest for species

with a low degree of range infilling (e.g., non-native species that are still expanding their range), for which large geographic areas may be suitable but unoccupied. The potential range for these species would be underpredicted. In contrast, the climatic tolerances measured by a presence-only approach are driven solely by the species' observed distribution. Thus, although the presence-only approach we used may overestimate a species' potential range, it reduces the likelihood of a systematic bias occurring between species with different degrees of range infilling.

Additionally, plotting each species' distribution in a climatic space that is obtained from the entire region across which species occurrences were gathered (i.e. the global climate grid) is an approach that was developed to allow fair comparisons of potential ranges between different species, particularly those with different range sizes (Broennimann *et al.*, 2012). We selected the PCA approach in order to follow the principles of Broennimann *et al.* (2012). However, to test our results with a more traditional presence-only approach we repeated the analyses using BIOCLIM (Busby, 1991), applying a presence-absence threshold that was calibrated to include 95% of the distribution points for each species.

We created contingency tables based on the occupied and potential maps to identify correctly identified occupied/unoccupied grid cells as well as false positive and false negative rates. We used these data to calculate Cohen's kappa (Cohen, 1960) for each species, a measure of overall map accuracy (and, thus, preferable to the area under the curve in this case). Kappa statistics are likely to be inversely related to range infilling because they are sensitive to the false positive rate (i.e. climatically suitable pixels that contain no occurrence record for the species).

We used the number of occupied (O) and potential (P) grid cells to calculate range infilling for each species. Typically, range infilling is calculated as O/P (e.g., Svenning & Skov, 2004; Munguía *et al.*, 2012; Sánchez-Fernández *et al.*, 2012). However, for any geographic area there is a fixed maximum potential range (P_{\max}) defined by the total available pixels in the region (for the continental USA at a 50-km grid resolution, P_{\max} was 3327 pixels). The existence of a fixed maximum potential range creates a minimum boundary of O/P_{\max} . For comparative studies where groups have different distributions of O , the standard measure of O/P would skew the final calculation: species with high numbers of occupied grid cells (e.g. invasive species, in this study) would have higher calculated O/P (e.g., than endemics), and equal levels of range infilling would appear as greater infilling for these species. Hence, we used a normalized measure of range infilling to compare between groups such that:

$$\text{Range infilling} = (O/P) - (O/P_{\max}). \quad (1)$$

Estimated values of potential range and range infilling

In order to compare the distributions of native and non-native species, we calculated the average values of potential range (P),

range infilling (as described above), kappa the and longitudinal and latitudinal extent for each of the four groups. Some groups have more species with few occurrences, while other groups have more species with many occurrences, which could skew the comparison of average values. To account for number of occurrences and the resulting skewed data, we also regressed the above variables against number of occupied grid cells using generalized additive model (GAM) functions. This allowed us to compare calculated estimates for each group based on hypothetical species occupying a given number of grid cells. The modelled relationships between number of occurrences and potential range, longitudinal range and latitudinal range were based on a GAM function with a log link and gamma data distribution. The basis dimension 'k', was increased to 180 in order to increase smoothness and decrease overfitting, which caused large wiggles in the original model fit. The relationships between occurrences and range infilling and between occurrences and kappa were fitted using a GAM function with an inverse link and a gamma data distribution, and *k* was increased to 25 for GAMs using US distribution data alone. We used the GAM models to estimate potential range, range infilling and their 95% confidence intervals for hypothetical species that we defined as rare (using the median number of occurrences across all species), intermediate (using the mean number of occurrences across all species), and common (averaging the 95th percentile of number of occurrences across all species). We compared range infilling and potential range between groups of species based on the confidence intervals for each of these three representative modelled species. Analyses were conducted in R (version 3.0.2).

RESULTS

Species occurrence data

Our dataset included a total of 13,575 species that occupied at least five 50-km pixels in the lower 48 states. Of these, 9402 were native (but not known to be endemic), 2397 were endemic, 1021 were alien (but not invasive) and 755 were invasive. Species names and USDA PLANTS symbols are catalogued in Appendix S1 in the Supporting Information along with summary statistics for each group. There were a total of 3327 available pixels (P_{max}) in the lower 48 states. Across all species, the median number of US occurrence pixels was 37 (this value was used to represent rare species), the mean number of occurrence pixels was 118 (intermediate species) and the upper 95th percentile number of occurrence pixels was 533 (common species). Endemic and alien plant groups occupied fewer pixels (median of 35 and 21, respectively), while the invasive plant group was skewed towards higher numbers of occurrences (median of 90 pixels).

Range infilling

Range infilling of both invasive and alien plants was significantly lower than for native and especially endemic plants (Table 1, Fig. 2). Using PCA models of potential range based on distribution data from the continental USA only and averaged across all species, range infilling of native plants was 14.5% (95% CI 14.2–14.9%). In contrast, invasive plants had an average range infilling of only 9.8% (95% CI 8.5–11.0%). This difference was also significant for rare and intermediate species. Rare native plants

Table 1 Range infilling (per cent normalized occupied/potential range, equation 1) in the continental USA and 95% confidence interval for each group of species. Calculations are based on potential range modelled using principal components analysis from US-only occurrences (top) and global occurrences (bottom). Average range infilling is the mean for all species in the group. Estimated range infilling for rare, intermediate and common species is based on generalized additive models fitted to the data distributions for the median, mean and 95th percentile occurrences, respectively. Using the average across all species to compare groups of species may not be as instructive due to the different skew in occurrence frequencies (see for example Fig. 2).

Group	Average for all species	Rare species (occurrences = 37)	Intermediate species (occurrences = 118)	Common species (occurrences = 533)
Estimated range infilling (per cent) modelled from <i>US-only</i> occurrences:				
Natives	14.5 (14.2–14.9)	10.2 (9.7–10.8)	9.7 (8.9–10.7)	15.6 (12.7–20.5)
Endemics	16.5 (15.8–17.3)*	10.5 (9.7–11.4)	15.4 (13.3–18.4)*	27.3 (18.7–20.8)
Aliens	12.4 (10.8–14.0)†	7.1 (6.2–8.5)†	7.5 (5.6–11.0)	5.5 (3.1–23.5)
Invasives	9.8 (8.5–11.0)†	7.5 (6.8–8.4)†	7.2 (6.2–8.6)†	8.6 (6.5–13.0)
Estimated range infilling (per cent) modelled from global occurrences:				
Natives	6.2 (5.9–6.4)	6.4 (6.0–6.9)	6.2 (5.8–6.7)	13.6 (11.8–16.1)
Endemics	13.1 (12.3–14.0)*	6.5 (5.9–7.4)	10.6 (9.4–12.1)*	22.1 (17.6–29.6)*
Aliens	1.3 (1.0–1.5)†	1.2 (1.1–1.4)†	1.3 (1.1–1.6)†	1.6 (1.1–2.5)†
Invasives	1.8 (1.6–2.0)†	1.5 (1.3–1.8)†	2.0 (1.6–2.6)†	1.5 (1.0–2.5)†

All values are mean (95% CI).

*Significantly greater than natives.

†Significantly less than natives.

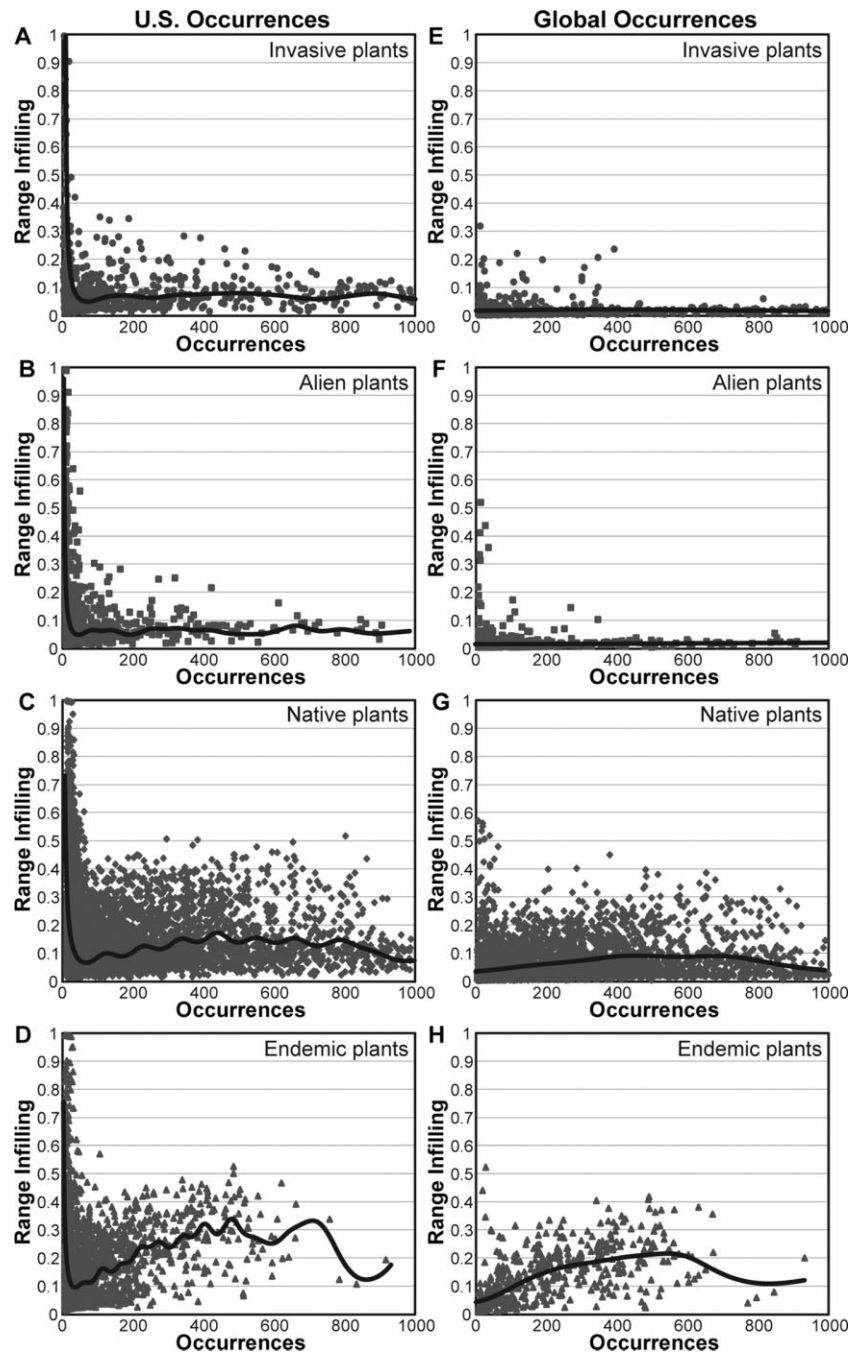


Figure 2 Invasive and alien plants have lower range infilling for any given number of occurrences than native and endemic plants. This pattern is evident regardless of whether potential range is calculated from continental US occurrences (A–D) or from global occurrences (E–H). The black line shows the generalized additive model regression fit.

had range infilling values of 10.2% (95% CI 9.7–10.8%), while rare invasive plants had range infilling values of only an estimated 7.5% (95% CI 6.8–8.4%) (Table 1). Endemic species had consistently higher range infilling than all other species groups, regardless of number of occurrences. The comparison based on a BIOCLIM modelling approach produced very similar results (Appendix S2).

The difference in range infilling between groups is even more evident when using models of potential range based on global distribution data. Averaged across all species, range infilling of native plants was 6.2% (95% CI 5.9–6.4%), while range infilling for invasive plants was only 1.8% (95% CI 1.6–2.0%). All levels

of occurrence were significant, but the difference was particularly evident for common species. Common native plants had range infilling values of 13.6% (95% CI 11.8–16.1%), while common invasive plants had range infilling values of only an estimated 1.5% (95% CI 1.0–2.5%) (Table 1).

Potential range

The modelled potential range for invasive plants was consistently higher than for native plants (Table 2, Fig. 3). This finding was consistent when models were based only on US occurrences or based on global occurrences, and BIOCLIM models

Table 2 Potential range (number of 50-km pixels) and 95% confidence interval for each group of species. Calculations are based on potential range modelled using principal components analysis from US-only occurrences (top) and global occurrences (bottom). Average potential range is the mean for all species in the group. Estimated potential range for rare, intermediate and common species is based on generalized additive models fitted to the data distributions for the median, mean and 95th percentile occurrences, respectively. Using the average across all species to compare groups of species may not be as instructive due to the different skew in occurrence frequencies.

Group	Average for all species	Rare species (occurrences = 37)	Intermediate species (occurrences = 118)	Common species (occurrences = 533)
Estimated potential range modelled from <i>US-only</i> occurrences:				
Natives	757 (743–772)	575 (543–609)	1192 (1079–1316)	1816 (1437–2294)
Endemics	536 (518–555)†	543 (487–605)	843 (696–1020)†	1396 (865–2253)
Aliens	747 (700–794)	767 (656–897)*	1389 (1008–1916)	2486 (1027–6014)
Invasives	1265 (1200–1330)*	769 (688–860)*	1312 (1010–1551)	2256 (1634–3115)
Estimated potential range modelled from global occurrences:				
Natives	1734 (1706–2028)	1118 (1080–1157)	1656 (1591–1724)	2272 (2123–2433)
Endemics	1007 (956–1057)†	674 (621–731)†	998 (906–1100)†	1488 (1268–1747)†
Aliens	2056 (2001–2111)	2039 (1935–2148)*	2600 (2359–2865)*	3023 (2363–3868)
Invasives	2261 (2416–2556)*	1816 (1699–1941)*	2498 (2265–2755)*	3045 (2514–3687)*

All values are mean (95% CI).

*Significantly greater than natives.

†Significantly less than natives.

produced even more significant results (Appendix S2). Invasive plants had a larger estimated potential range than native plants regardless of number of occurrences using global distributions, although the difference was only significant for rare species using US-only distributions. Similar to invasive plants, potential range estimates for rare alien plants were also significantly higher than rare native plants (Table 2). Endemic species typically had smaller potential ranges than other species groups, but the difference was not always significant.

Model accuracy

The accuracy of alien and invasive distribution models was lower than native and endemic distribution models, regardless of number of occurrences, and was significantly lower for rare occurrences (Table 3). Map accuracy, based on the kappa statistic, reflects both correctly identified occurrences as well as incorrectly identified occurrences (i.e. the false positive rate; in this case calculated by treating non-occurrences as 'pseudo-absences'). The patterns described above of low range infilling but high potential range for invasive and alien species also creates a high false positive rate and a correspondingly low kappa statistic. Conversely, endemic species, which have the highest range infilling (Table 1) and smallest potential range (Table 2) also had the highest overall map accuracy (Table 3).

Longitudinal and latitudinal range

Consistent with their overall broader potential ranges, invasive and alien plants also had significantly broader longitudinal and latitudinal extents than native and endemic plants (Fig. 4). For

rare species (the median value of 37 occurrences), invasive plants had an estimated longitudinal range of 32.8° (95% CI 30.3–35.5°), while rare native plants have an estimated range of only 12.8° (95% CI 12.3–13.2°). The estimated longitudinal range of invasive plants was higher than native plants regardless of number of occurrences (Appendix S3), although this difference was not significant for common species. Latitudinal ranges also differed significantly for rare species: rare invasive plants had an estimated latitudinal range of 11.6° [95% CI 11.0–12.3°], while rare native plants had an estimated range of only 8.0° (95% CI 7.8–8.3°). At higher numbers of occurrences, latitudinal differences between groups were no longer significant, with common species showing similar latitudinal extents (Appendix S3).

Our recalculation of all of the above distribution variables based on the subset of species with the highest geographical consistency [i.e. species whose GBIF records had at least 80% overlap with USDA Plants (USDA-NRCS, 2014) occurrence records] showed no difference in the observed pattern. Those results are presented in Appendix S4. Based on this analysis, biases associated with incomplete or inaccurate records in GBIF do not appear to influence the comparative results.

DISCUSSION

Based on this first comprehensive comparison of range attributes for native and non-native plants in the USA, non-natives had lower range infilling and larger potential ranges than native species. Regional range infilling for both alien and invasive plants was significantly lower than for either native or endemic plants. For common species, estimated range infilling for invasive plants was about half that of comparable native plants (this

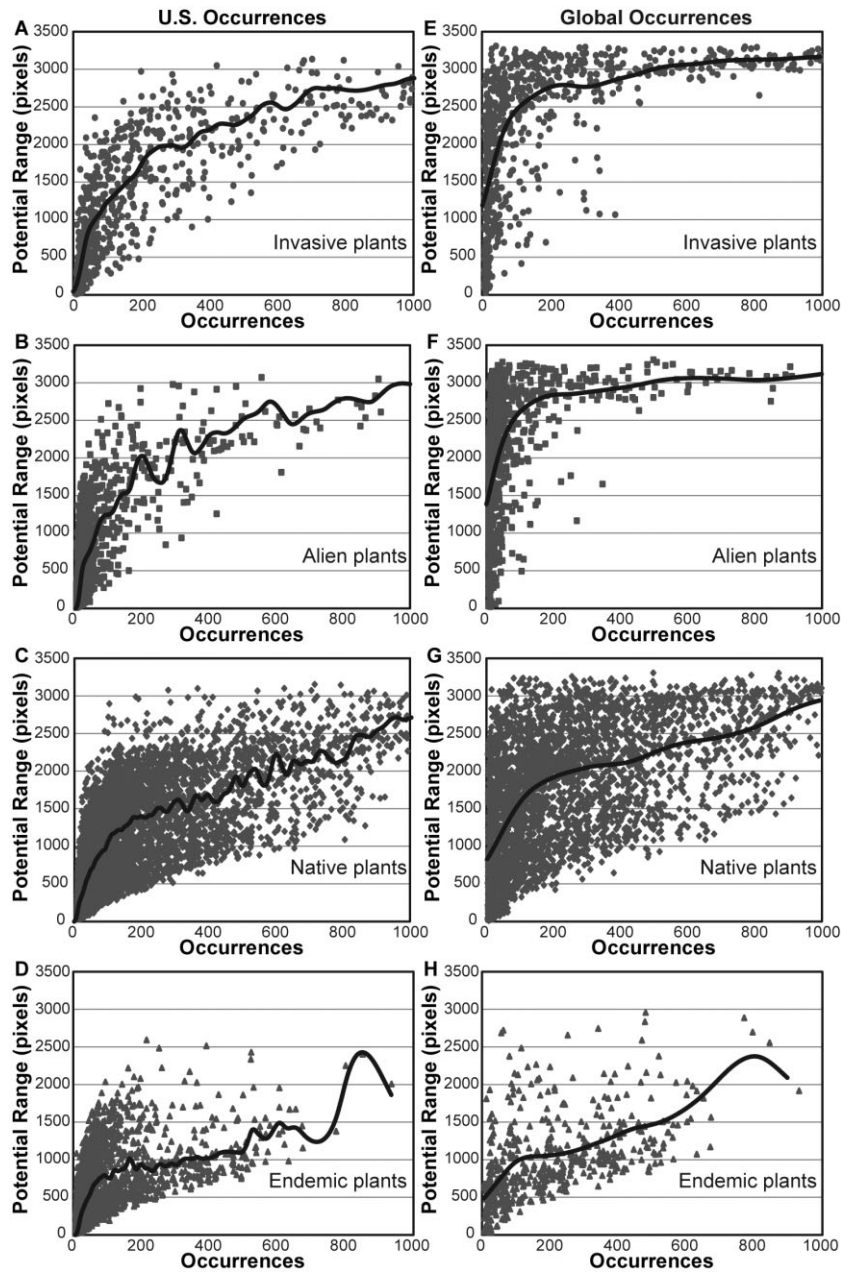


Figure 3 Invasive and alien plants have a larger potential range for any given number of occurrences than native and endemic plants. This pattern is evident regardless of whether potential range is calculated from continental US occurrences (A–D) or from global occurrences (E–H). The black line shows the generalized additive model regression fit.

fraction was even smaller, only 10%, based on global distribution data; Table 1, Appendix S2). This difference was even more evident for species with high geographic consistency with the USDA PLANTS database (USDA-NRCS, 2014; Appendix S4), suggesting that sampling biases do not cause the observed pattern. If we assume that invasive plants will eventually achieve similar infilling to natives, then these results suggest considerable ongoing invasion risk – even from some of the most widespread invaders. Meanwhile, the broad longitudinal and latitudinal distribution of rare invasive plants (Fig. 4, Appendix S3) suggests that there are plenty of nascent foci from which these species can spread in the future (Moody & Mack, 1988).

Two results suggest that the broad modelled potential ranges of invasive plants could be due to their widespread introduction

into suitable habitats across the USA (enabling them to achieve higher climatic equilibrium than native species; Fig. 4, Appendix S3), and not simply because invasive species have intrinsically broad niches (Hufbauer *et al.*, 2012; Higgins & Richardson, 2014). First, whereas we expected to find non-native plants with few occurrences clustered near one or two locations of initial establishment, the distribution data instead suggest that even rare non-native plants are widely established across the lower 48 states (Table 2), presumably introduced as either ornamentals or seed contaminants (Mack & Erneberg, 2002; Lehan *et al.*, 2013). Second, we found no significant difference between invasive and alien (non-invasive) species in terms of modelled potential range. This lack of difference suggests that broader climatic niches are *not* the sole driver of the observed broader potential

Table 3 Map accuracy based on the mean kappa statistic and 95% confidence interval for each group of species. Average kappa is the mean for all species in the group. Estimated kappa for rare, intermediate and common species is based on generalized additive models fitted to the data distributions for the median, mean and 95th percentile occurrences, respectively. Using the average across all species to compare groups of species may not be as instructive due to the different skew in occurrence frequencies.

Group	Average for all species	Rare species (occurrences = 37)	Intermediate species (occurrences = 118)	Common species (occurrences = 533)
Estimated kappa based on potential range from <i>US only</i> occurrences:				
Natives	0.227 (0.223–0.231)	0.179 (0.175–0.184)	0.161 (0.154–0.168)	0.259 (0.231–0.295)
Endemics	0.254 (0.245–0.262)*	0.167 (0.158–0.177)	0.251 (0.224–0.285)*	0.479 (0.353–0.743)*
Aliens	0.180 (0.170–0.190)†	0.111 (0.102–0.124)†	0.137 (0.112–0.179)	0.118 (0.076–0.264)
Invasives	0.159 (0.148–0.170)†	0.132 (0.121–0.146)†	0.132 (0.115–0.157)	0.167 (0.127–0.245)
Estimated kappa based on potential range from <i>global</i> occurrences:				
Natives	0.111 (0.107–0.115)	0.187 (0.183–0.192)	0.166 (0.159–0.174)	0.248 (0.222–0.282)
Endemics	0.229 (0.214–0.243)*	0.172 (0.164–0.182)	0.248 (0.223–0.281)*	0.472 (0.351–0.723)*
Aliens	0.027 (0.022–0.031)†	0.031 (0.027–0.036)†	0.032 (0.028–0.037)†	0.039 (0.028–0.065)†
Invasives	0.028 (0.024–0.032)†	0.029 (0.025–0.035)†	0.037 (0.029–0.051)†	0.023 (0.015–0.043)†

All values are mean (95% CI).

*Significantly greater than natives.

†Significantly less than natives.

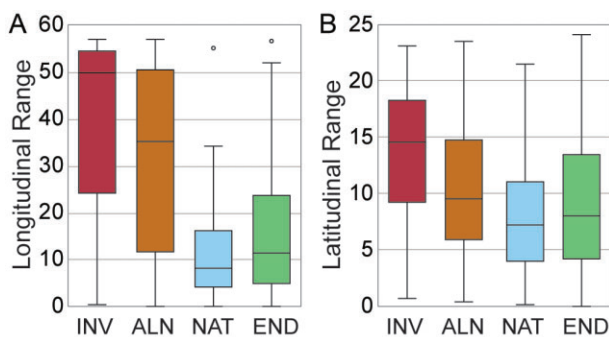


Figure 4 Distributional extents based on occupancy data for invasive (INV), alien (ALN), native (NAT) and endemic (END) plants relative to (A) longitudinal range and (B) latitudinal range in the USA. The maximum available longitudinal and latitudinal range for the lower 48 states is 58° and 25°, respectively. Boxes show the lower and upper quartiles and the median value. Whiskers show either the maximum and minimum values or 1.5 times the interquartile range (whichever is closer to the mean). Dots represent values outside the range of 1.5 times the interquartile range. All groups are significantly different, and comparisons for group averages, rare, intermediate and common species are shown in Appendix S3.

ranges of invasive species. Instead, human dispersal is likely to play a strong role in the observed differences in potential range between invasive and native species (Fig. 3).

The climate in the USA varies more consistently along a latitudinal gradient than a longitudinal gradient. Thus, a narrow longitudinal range is more likely to represent dispersal or other non-climatic range limitations, whereas a narrow latitudinal range is more likely to represent climatic range limitation. Across latitudinal gradients, rare non-native plants are significantly more broadly dispersed than rare native plants (endemic

or not), suggesting that rare non-natives are better poised for future latitudinal range shifts, for example in response to climate warming (Van Der Veken *et al.*, 2008). Climate change could therefore cause even greater reassembly of biodiversity than currently expected, as non-native species may shift their distributions in advance of natives, pre-empting niche space and preventing native species from colonizing newly suitable locations ('priority effects'; Hortal *et al.*, 2011). However, this non-native dispersal advantage disappears for intermediate and common plants, suggesting that the latitudinal distributions of common natives are not dispersal limited.

Conversely, across longitudinal gradients, where there are more abrupt physical (e.g. mountain ranges) and climatic (e.g. deserts) dispersal barriers in the USA, non-native plants have a significantly broader range than natives regardless of number of occurrences (Fig. 4, Appendix S3). The extents of the longitudinal ranges of non-natives suggests that introduction by humans has enabled these plants to bypass long-distance dispersal barriers that natives have not been able to overcome (Ricciardi, 2007). This pattern is not limited to those plants considered invasive, but is equally true of non-invasive aliens. Hence, it cannot be attributed solely to broader climatic tolerances of invasive species. Given equivalent human introduction opportunities, it seems likely that native species would also be capable of establishing across longitudinal dispersal barriers and into climate conditions not represented within their current ranges. Although we initially hypothesized that limited dispersal time would lead to smaller modelled potential ranges for *non-native* species, we instead found evidence for range restriction in *native* species which had smaller longitudinal extents regardless of the number of occurrences. These data suggest that longitudinal dispersal barriers in the continental USA play a more important role than climate in limiting the current distributions of native plants, a finding that merits additional empirical research. If

native plant ranges are strongly dispersal limited, then ecological forecasting of climatic habitat for native species (e.g. Thomas *et al.*, 2004) might underestimate future ranges. Indeed, our results suggest that most native species could survive in climatic conditions well outside of their native range.

Previous studies of relative species traits and invasion time series suggest that invasive plants will continue to spread (e.g. Pyšek & Prach, 1995; Welk, 2004), and may eventually meet or exceed typical levels of range infilling for native plants. The overall opportunity for range infilling depends on the size of the realized niche, which is a combination of abiotic and biotic conditions and dispersal limitations (Soberón & Nakamura, 2009). Compared with native species, invasive plants tend to have broader abiotic tolerances (Cadotte *et al.*, 2006; Higgins & Richardson, 2014), be better competitors (Pyšek & Richardson, 2007) and be dispersed more broadly (e.g. as ornamentals; Mack & Erneberg, 2002). Hence, it is reasonable to hypothesize that the overall regional range infilling of invasives could eventually be higher than for natives. Further, empirical evidence supports the expectation that invasive plants are infilling through time. Non-native plants introduced earlier in time have more occurrence records, and time since introduction is positively correlated with non-native abundance and range infilling (Pyšek *et al.*, 2003; Wilson *et al.*, 2007; Williamson *et al.*, 2009). All of these findings suggest that there are more problems from plant invasions on the horizon, and incorporating 'time since introduction' would be a logical next step for projecting ultimate levels of range infilling for these invasive species.

Treating potential range as a proxy for relative climatic equilibrium, our results suggest that non-native species are filling comparatively more of their *climatic* space than native species, even when considering only non-native range distributions. At the regional scale, modelled potential range for US alien and invasive plants was significantly larger than potential range for native plants, particularly for species with few occurrences (Table 2, Fig. 3). Thus, the oft-cited concern that SDMs for non-native species underestimate potential range because the species are not at climatic equilibrium (for examples see Elith *et al.*, 2010) might not apply at regional scales. This finding differs from the results of studies at landscape scales, which indicated that models based on early stages of invasion strongly underestimated future invasion risk (Jones, 2012; Václavík & Meentemeyer, 2012).

Although regional models predict relatively large potential ranges of non-natives, even at low occurrence numbers, predictions of invasion risk based on these data should still be treated with caution. First, GBIF records do not differentiate casual occurrences (*sensu* Richardson *et al.*, 2000) from established populations, nor do they differentiate locations where invasive species are established, but not invasive. By combining all three types of occurrences, distribution models are likely to overestimate potential ranges of non-native species due to casual occurrences (Sax *et al.*, 2013) and overestimate invasion potential by including established but not invasive populations (Bradley, 2013). Second, our analyses reveal a strong influence of scale on relative equilibrium. At regional scales, the broad potential range

and longitudinal extents of non-natives suggests that human introduction has caused non-natives to fill more of their climatic niche than comparable natives. At regional scales, non-natives therefore appear closer to climatic equilibrium. In contrast, the comparatively small estimates of range infilling observed for non-native species suggests that they are farther from geographic 'range' equilibrium (Svenning & Sandel, 2013). Range equilibrium is more likely to be observed at a landscape scale, and is a function of the local dispersal capabilities of the individual species, which could take a long time to achieve (Essi *et al.*, 2012).

In conclusion, our results show that potential ranges of alien and invasive plants are much larger than those of native species in the USA. Regionally, human actions are likely to help non-natives overcome dispersal barriers that limit the distributions of natives. At the same time, our results indicate that alien and invasive plants have lower range infilling than native species. If the range attributes of invasive species increasingly approximate those of natives, then the average invasive plant is currently occupying only half of the range that we would ultimately expect. Given their significant impacts to date, we would predict increasing threats to native biodiversity based on our findings that non-native plants in the USA have plenty of space to invade.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Spreadsheet list of target species and numbers of occurrences.

Appendix S2 Analysis based on a BIOCLIM model.

Appendix S3 Additional results for latitude and longitude ranges.

Appendix S4 Comparative analysis for subset of species with highest geographical consistency.

BIOSKETCHES

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