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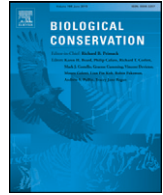
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# Out of the weeds? Reduced plant invasion risk with climate change in the continental United States

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# Out of the weeds? Reduced plant invasion risk with climate change in the continental United States



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## ABSTRACT

Identifying invasion risk is critical for regional prioritization of management and monitoring, however, we currently lack a comprehensive assessment of the invasion risk posed by plants for the United States. We aim to quantify geographic invasion risk for currently established terrestrial invasive plants in the continental U.S. under current and future climate. We assembled a comprehensive occurrence database for 896 terrestrial invasive plant species from 33 regional collections of field and museum data and projected species ranges using MaxEnt species distribution models based on current (1950–2000 average) and future (2040–2060 average) climate. We quantified geographic invasion risk as differences in species richness, invasion debt, range infilling, and identification of hotspots. Potential invasive plant richness was higher than observed richness, particularly in eastern temperate forests, where as many as 83% of species with suitable climate have not yet established. A small percentage (median = 0.22%) of species' potential ranges are currently occupied by them. With climate change, potential invasive plant richness declined by a median of 7.3% by 2050. About 80% of invasive plant hotspots were geographically stable with climate change, with the remaining 20% shifting northward. Invasion hotspots and current invasion debt reveal extensive, ongoing risk from existing invasive plants across the U.S., particularly in the Southeast. Climate change alters the spatial distributions of focal species for monitoring and is likely to reduce overall invasion risk in many areas. Early detection and rapid response programs could be most effective in stemming the spread of invasive plant species in areas with increased risk under climate change, while areas with persistent high risk are candidates for containment and control. The areas with reduced risk are prime locations for invasion of new imports from tropical and subtropical climates, highlighting the simultaneous need for prevention strategies.

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## 1. Introduction

Invasive species are a prominent threat to natural systems (Wilcove et al., 1998) and are both drivers of and responders to environmental change (Hellmann et al., 2008; MacDougall & Turkington, 2005). Invasive plant impacts include reduced native species diversity and abundance, altered community composition, and increased nutrient cycling (Hellmann et al., 2008; Kuebbing & Nuñez, 2015; Powell et al., 2013; Vilà et al., 2011). Like many species, invasive plants are also responding to climate change by shifting their geographic distributions (Hellmann et al., 2008; Walther et al., 2009). At the species level, climate change is expected to expand the ranges of many invasive plants (Bradley et al., 2009; Bradley et al., 2010), but for others it may lead to range contraction (Bradley et al., 2009).

Political boundaries are not ecological ones, but they delineate the allocation of conservation resources and policy. Given that conservation resources are limited, identifying relative invasion risk nationally can help to prioritize monitoring and management (Kuebbing & Simberloff, 2015). Early detection and rapid response programs, which aim to identify and eradicate new incursions shortly after arrival, are especially effective ecologically and economically for controlling early-stage invasions into new geographic areas (Hirzel et al., 2006; Leung et al., 2012; Sheley et al., 2015). Invasive plants within the continental U.S. that are moving into new geographic areas (e.g., a Southeastern species expanding into the Northeast) can be considered early-stage invaders in the new region, and handled in the context of early detection and rapid response programs. Containment and control programs aim to curb the spread of well-established species, and can be used to reduce invasion risk of plants present in part, but not all of a region (Hulme, 2006).

Within the continental U.S., selected species of invasive plants have shown both range expansions and contractions in response to climate change, suggesting that unexpected conservation opportunities could result from future climate change (Bradley et al., 2009). Hotspots of

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plant invasion with current and future climate have been identified in Australia for nationally important invasive plants (Gallagher et al., 2013; O'Donnell et al., 2012), but there has been no comprehensive assessment of the invasion risk posed by plants to the continental U.S. under current and future climates. Invasion risk can have many definitions; this analysis focuses on the geography of invasion risk through invasive plant range characteristics (range infilling) and aggregated range metrics (species richness, invasion debt, and identification of hotspots).

Even under current climate conditions, the distributions of many invasive plants have yet to be fully realized due to the time lag between introduction and spread into recipient ecosystems. The potential for increased invasion due to these time lags has been termed invasion debt (Bennett et al., 2013; Essl et al., 2011; Gilbert & Levine, 2013; Rouget et al., 2016; Seabloom et al., 2006), which consists of four phases: introduction, establishment, spread, and impact (Rouget et al., 2016). Invasion debt in this analysis focuses on potential establishment within the continental U.S. based on the current invasive species pool, and can be generated by species that have not yet spread to the full extent of their potential range or low infilling of the potential range. A recent analysis of plant distributions in the continental U.S. suggests that non-natives have large ranges, but have low range infilling compared to natives (Bradley et al., 2015), therefore we expect low infilling to drive high invasion debt for many invasive plants in the continental U.S. Areas of high invasion debt and/or low infilling equate to areas at high risk of invasion because the species already exist in the larger geographic landscape. Invasive species richness is an aggregate metric that describes how many species have invaded a particular area, as opposed to focusing on the ranges of individual species. Species richness often correlates positively with area (Lomolino, 2000), whereas invasion debt and infilling are proportional diversity and species-level measures, so we view the two as distinct, but complimentary metrics for assessing invasion risk.

Here, we provide the first comprehensive assessment of the invasion risk posed to the continental U.S. by terrestrial invasive plants under current (1950–2000 average, hereafter termed 'current') and future (2040–2060 average, hereafter termed 'future' and '2050') climates. We specifically address changes in species richness, invasion debt, and invasion hotspots for all ecologically and economically important terrestrial plant invaders (896 species). Based on the aggregated output of species distribution models, we asked 1) what are the geographic patterns and magnitude of invasion debt with current climate? and 2) how will invasion risk shift in magnitude and geography under future climate? We expected that invasion debt would be highest in areas with many invasive plants due to the potential for low infilling across many species, and that invasion risk would increase throughout the continental U.S. with climate change. The results can serve as a baseline for tracking future invasion risk and can guide prioritization of conservation resources.

## 2. Materials and methods

### 2.1. Species list and occurrence data

We used the Federal Noxious Weed List (Executive Order 13112, 1999) and state noxious and invasive plant lists available from the USDA Plants database (USDA, NRCS, 2014), in addition to species listed in the Invasive Plant Atlas of the United States (Invasive Plant Atlas of the United States, 2014), to assemble a list of 1089 target species found in the continental U.S. (Alaska and Hawaii excluded). We excluded any species identified as native in the USDA Plants database (USDA, NRCS, 2014) as well as aquatic species. The species included on our source lists are known or expected to have ecological or environmental impacts in a range of settings, including agricultural and natural areas (Executive Order 13112, 1999; Invasive Plant Atlas of the United States, 2014). We searched a comprehensive set of 33 collections of field and museum data (Table S1 in Supporting Information) for each

of 1089 terrestrial invasive plant species and retained all records with geolocations. No occurrence data were available for 63 of the 1089 target species (~6% of species). Since some records may be entered into multiple databases (e.g., a regional herbarium might also contribute data to the Global Biodiversity Information Facility), we removed identical occurrence points. We removed all occurrence points that fell erroneously outside of the continental U.S. and excluded 130 species (~12% of species) with fewer than 10 total occurrence points. The majority (58%) of species had 100 or more occurrences (Fig. S1) and our final dataset included 896 species (Table S2). We also removed duplicates within each 5 km × 5 km climate grid cell for species distribution modeling (see Analysis below), which further reduced the number of occurrences used for modeling for some species (Table S2). Of the 896 species analyzed, the initial introduction dates are known for 206 species (Lehan et al., 2013).

Our distribution data focus on the invaded (continental U.S.) range only. We chose this approach because we had the highest quality data for the invasive range, and several studies have shown that invaded range data are appropriate for biogeographical analysis. Bradley et al. (Bradley et al., 2015) demonstrated that non-native plants in the continental U.S. have large introduced ranges, likely owing to large-scale human mediated dispersal as most invasive plants were deliberately introduced for horticultural purposes (Lehan et al., 2013; Reichard & White, 2001). Together, these papers suggest that dispersal limits range infilling, but does not limit overall range extents. In addition, invasive species can experience substantial climatic niche shifts between native and invaded ranges (Early & Sax, 2014; González-Moreno et al., 2015), which, if native range data are included, could lead to overestimates of invasion risk within the invasive range. Vastly overestimating invasion risk is arguably just as problematic for conservation applications as underestimating invasion risk (Bradley, 2013). Finally, there is only a single global database of plant distribution records (Global Biodiversity Information Facility; GBIF), which suffers from strong spatial biases due to inconsistent contributions between countries and regions (Beck et al., 2014). Because invasive plants are the focus of multiple data collection efforts in their invasive range (e.g., for management and monitoring programs), the spatial extent and number of occurrence points are larger in the invasive range relative to the global dataset. The underlying spatial collection bias is much more uneven at the global scale, which precludes quantifying sampling bias in a way comparable to what is possible within the continental U.S. (see Analysis). As such, we have focused on occurrence data from the invasive range of our study species because these data provide the highest quality dataset available across the large number of species, we can reasonably quantify sampling bias, and because we expect that the data for each species reasonably approximates the contiguous U.S. climate space in which it could persist.

### 2.2. Climate data

We used interpolated climate data from WorldClim (Hijmans et al., 2005) for both current climate and future climate projections. Current climate data were based on averaged conditions from 1950 to 2000 at a spatial resolution of 0.04166 decimal degrees (approximately 5 km × 5 km grid cells for most of the continental U.S.). We used 13 downscaled climate model projections (Table S3) that spanned a range of predictive ability (Rupp et al., 2013; Sheffield et al., 2013) from CMIP5 for mid-century (average for 2041–2060, hereafter termed '2050') under Representative Concentration Pathway 4.5 (RCP 4.5) to create future projections at the same spatial scale (obtained from WorldClim). RCP 4.5 represents a target forcing of 4.5 W m<sup>-2</sup> above the pre-industrial baseline by 2100, with stabilization after that date, and is similar to the IPCC AR4 SRES B1 storyline (Collins et al., 2013). Expected global temperature increase with RCP 4.5 is 1.8 ± 0.5 °C by 2100, with greater increases expected over land (2.4 ± 0.6 °C) than oceans (1.5 ± 0.4 °C) (Collins et al., 2013). Despite longer-term differences in radiative and

temperature increases between RCP 4.5 and other more and less extreme RCPs, temperature increases are expected to be similar across RCPs by mid-century (Collins et al., 2013). We therefore focused our analysis on this intermediate RCP and a wide range of GCMs to efficiently capture variability in future projections.

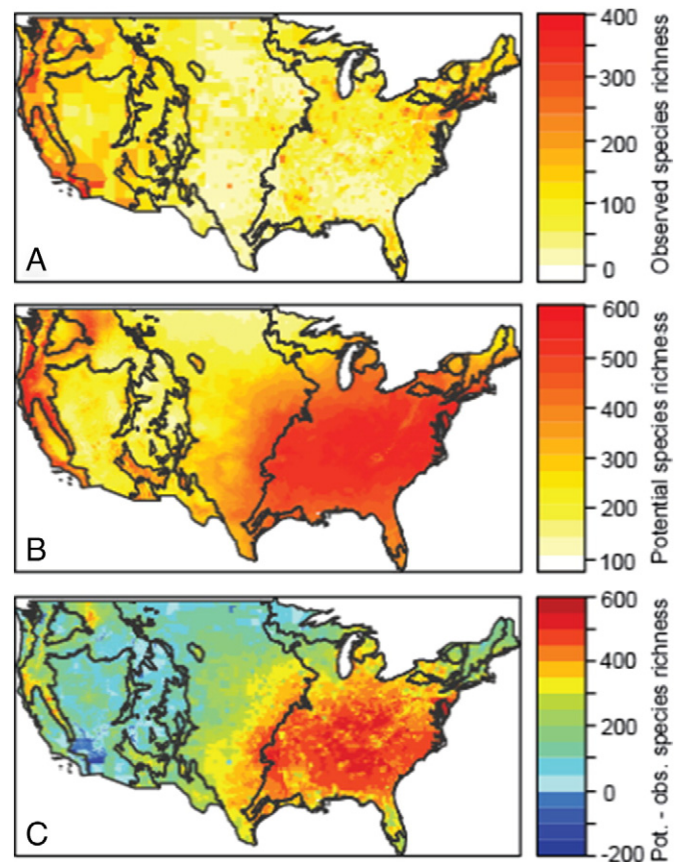
We included three climate predictors likely to limit plant growth across a range of ecoregions: average January minimum temperature (a proxy for cold tolerance), average maximum July temperature (a proxy for heat tolerance), and average annual precipitation (a proxy for water requirements). We chose these three predictors based on a priori expectations of how temperature and precipitation were likely to affect plant ranges, availability of future climate metrics (i.e., monthly maximum temperature, minimum temperature, and precipitation), and exploratory analysis of a subset of our target species (analysis not shown).

### 2.3. Analysis

We modeled the potential distribution for each species under current and future climate using the maximum entropy modeling software package MaxEnt (Phillips et al., 2006). MaxEnt is a commonly-used and robust tool for species distribution modeling based on species-level occurrence data (Elith et al., 2011; Merow et al., 2013; Phillips et al., 2006). Accounting for sampling effort is important in MaxEnt modeling (Merow et al., 2013) and we created a sampling bias surface by summarizing the point occurrence data to species richness at the county level (i.e., using the all invasive species as a target group), then rasterizing the resulting surface to 5 km × 5 km grid cells that matched the climate data (Fig. 1a) (Merow et al., 2016; Rouget et al., 2016). We chose to use counties as our sampling unit for the bias surface because summarization to the 5 km × 5 km grid resulted in many zeros, which would require arbitrary reassignment to some small non-zero value for use as a bias surface. Each species was then modeled independently using its point occurrences, with all species having the same sampling bias surface. Our goal was to circumscribe the full range of climatic conditions in which each species could occur in the continental U.S., so we chose to use the entire continental U.S. as our background extent (Merow et al., 2013; Van Der Wal et al., 2009). To maintain consistency across species and balance complexity with biological reality (Merow et al., 2013; Moreno-Amat et al., 2015), we included only linear, quadratic, and product features, removed duplicate points within each climate grid cell, 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 across model runs as a metric of model fit. Despite its shortcomings (Lobo et al., 2008), AUC is highly correlated with other model performance metrics (Hirzel et al., 2006) and indicates how well presence points can be distinguished from background points for occurrence-based models (Fitzpatrick et al., 2013; Merow et al., 2013).

We used a threshold MaxEnt logistic suitability value that encompassed 95% of the fitting distribution points to define the potential range of each species (Bosci et al., 2016; Fitzpatrick et al., 2013) and summed the binary ranges across species to find potential species richness for each climate grid cell. The 95% threshold might lead us to underestimate the potential range because some occurrences are excluded, however, it also reduces the influence of any marginal or outlier occurrences. We projected the model fitted with current climate to each of the 13 future climate models and applied the same species-level thresholds and summation of binary ranges to those projections, then calculated the future ensemble average and standard deviation (to quantify uncertainty) at the pixel level. Our summation of species within each pixel is representative of aggregated range potential, but does not imply that all species can or do co-exist in local communities.

We quantified invasion risk in four ways: differences in species richness, invasion debt, range infilling, and identification of hotspots. For species richness, we calculated two pixel-level difference metrics, one



**Fig. 1.** Terrestrial invasive plant richness under current climate. Although invasive plants are already prevalent across the continental U.S. (a), modeled potential richness (b) reveals extensive invasion risk. The Southeastern U.S. in particular has much lower than expected observed invasive plant richness (c). All maps represent numbers of species at 5 km resolution and black lines delineate CEC level I ecoregions. Panels (a), (b), and (c) denote different scales.

between current climate potential and observed species richness and another between ensemble average future and current climate potential richness. Invasion debt was a richness metric that represented the proportion of species for which the climate is suitable that have yet to be recorded, calculated as  $1 - (\text{observed richness} / \text{potential richness})$  at the pixel level for both current and future climate projections. For additional comparison, we also averaged the pixel-level metrics (i.e., species richness, differences in species richness, and invasion debt) across Commission for Environmental Cooperation Level I ecoregions (Fig. S2) (Commission for Environmental Cooperation (CEC), 1997) and calculated Spearman rank correlations between ecoregion size, richness metrics (observed, current potential, and future potential), and invasion debt (current and future). Range infilling was a species-level metric that represented the proportion of the potential range that was occupied under current climate, calculated for each species as  $(\text{number of grid cells with observations}) / (\text{number of grid cells in potential range})$  (Bradley et al., 2015). We defined invasion hotspots as areas with potential richness in the top 25th percentile for current and ensemble future climate projections (O'Donnell et al., 2012). Analyses were conducted in R 3.2 (R Core Team, 2015), including the *raster* package (Hijmans et al., 2015).

We assessed whether introduction date affected potential range size estimates to evaluate our assumption that the invasive species in our dataset were widely dispersed. If species are not dispersal limited, we expect a non-significant slope for the regression  $\text{potential range size} = \text{introduction date} + \text{intercept}$ , suggesting that our study species are widely dispersed regardless of time since introduction. We fit the simple linear regression for the subset of 206 species with known introduction dates (Lehan et al., 2013) in R 3.2 (R Core Team, 2015). We also

restricted the data to the 168 species that were introduced 100+ years ago (e.g., introduced prior to 1915, representing the majority of species for which we have introduction date data) in a second analysis to test whether older introductions showed a similar pattern to the overall dataset.

Climate outside of current conditions is possible with climate change (called non-analog climate), so we assessed this possibility in our study region with multivariate environmental similarity surfaces (MESS) (Elith et al., 2011; O'Donnell et al., 2012). MESS analysis measures similarity by comparing the value of each climate variable in each pixel in current climate to the minimum and maximum of future climate for that variable across the continental U.S. (Elith et al., 2010). Negative similarity index values indicate non-analog climate. We conducted the analysis for each of the 13 future climate models, identified non-analog climate pixels in each comparison, and summed the number of future climate models that predicted non-analog climate in each pixel (thus values ranged from 0 to 13 in the aggregated analysis). MESS analysis was conducted in R with the *ecospat* package (Broennimann et al., 2015).

**3. Results**

Observed invasive plant richness (Fig. 1a) is substantially lower than potential richness under current climate (Fig. 1b). The current richness underestimate is most pronounced in the Southeastern U.S., where observed richness is as much as 566 species lower than potential richness according to climate niche models (Fig. 1c). The climatic niche models fit most species well, though a small area had under-predicted richness in the Southwestern U.S. (Fig. 1c), with an average test AUC of 0.86 and median of 0.87 (Table S2). AUC values ranged from 0.51 to 1.00, with 1.2% of species having an AUC below 0.60 and 8.9% of species with an AUC greater than 0.99 (Table S2). Range infilling was low, with a median of 0.22% and range of 0.003–44.46%.

Of the 206 species (23% of our total species) for which we had introduction dates, potential range size was only weakly predicted by introduction date (slope = -10,242 km<sup>2</sup>/year, P = 0.0001, R<sup>2</sup> = 0.07). When the analysis was restricted to species introduced 100+ years ago (i.e., prior to 1915; 168 species), the relationship between introduction date and range size was even weaker (slope = -7397 km<sup>2</sup>/year, P = 0.024, R<sup>2</sup> = 0.03). Hence, very recently introduced species had somewhat smaller potential range sizes, but introduction date was generally a poor predictor of potential range size. Thus, our models of invasion risk appear to well represent the potential invasive range across all species.

At the ecoregion level, Eastern Temperate Forests, which constitute about 20% of the continental U.S., had an average of 401 fewer recorded species than expected, an invasion debt of 83% of invasive species (Table 1). Observed and potential richness were not simply a function of ecoregion size. The largest ecoregions (e.g., Great Plains, Eastern

Temperate Forests) had low observed richness and high projected richness, but small ecoregions had similarly low observed richness (e.g., Southern Semiarid Highlands) and/or high projected richness (e.g., Marine West Coast Forest) (Table 1).

A striking pattern emerged for future projections, with lower potential invasive species richness (up to a 50% decline in some areas) compared to current potential richness across the majority of the continental U.S. (Fig. 2a). The median percentage decline in pixel-level invasive species richness across the continental U.S. was 7.3%. The magnitude of changes in invasive plant richness averaged across ecoregions was less dramatic due to smoothing of small-scale variation, but projections were lower in 8 out of 10 ecoregions with climate change (Table 1). Southern Semiarid Highlands and Mediterranean California had the greatest decrease in invasion debt, with an average of 7–8% fewer invasive plant species expected there by 2050 (Table 1). Northern latitude locations were the only areas with increased invasion risk (Fig. 2a), but the magnitude of increase at the pixel-level is quite large (up to 175% increase). The ecoregions associated with increase in invasion risk, Northern Forests and Northwestern Forested Mountains, showed 2 and 7% higher average invasion debt by mid-century (Table 1). Unlike all other ecoregion-level summary metrics, the ecoregion-level change in invasion debt from current to 2050 was positively correlated with ecoregion size (Spearman r = 0.67, P = 0.04). The majority of hotspot areas (80.5%) is the same under current and projected future climate and is centered in the Eastern Temperate Forest ecoregion (Fig. 3). The remaining ~20% of hotspot area shifts northward in the Eastern Temperate Forest and Northern Forest ecoregions with climate change.

Uncertainty in future invasive richness projections ranged from 1 to 43 species and was highest in the western mountains, north-central U.S., and northern parts of the Northeast (Fig. 2b) corresponding to areas of high uncertainty in the climate model ensemble (Fig. S3). However, most areas with projected loss of invasive plant richness had relatively low uncertainty, whereas projected areas of increased invasion risk had relatively high uncertainty (Fig. 2). The magnitude of uncertainty was much smaller than the magnitude of change across the continental U.S. Future projected non-analog climate was rare; based on the MESS analyses, future projected climate was within current conditions for 99.6% of the continental U.S.

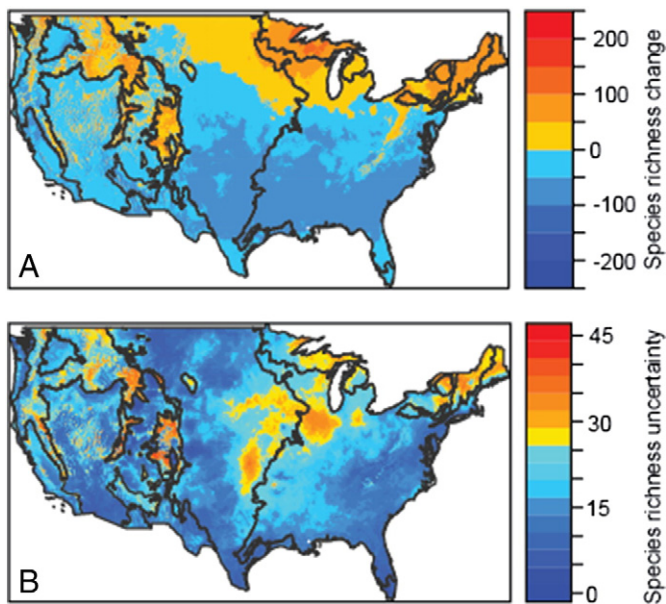
**4. Discussion**

Under current climate, invasion debt is apparent throughout the continental U.S., and is consistent with the low range infilling calculated for many species. Our observed richness map shows political boundaries in some data poor regions (Fig. 1a), suggesting that invasions have not been recorded or that records have not been reported to regional collections. However, invasion debt is evident even in areas with extensive survey effort, such as the Northeast (Bois et al., 2011)

**Table 1**

Observed and potential invasive plant richness and invasion debt averaged by continental U.S. ecoregions under current and future climate (RCP 4.5, 2050). Negative values represent reductions in invasive plant richness and invasion debt, respectively, with climate change.

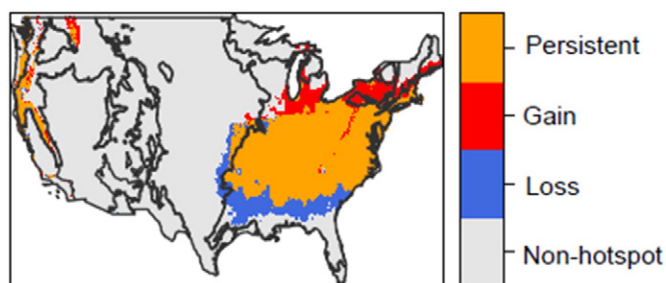
Ecoregion	Current					Future				
	Area (km <sup>2</sup> )	Land area percent	Average observed richness	Average potential richness	Potential-observed current richness	Average invasion debt	Average potential richness	Future-current potential richness	Average future invasion debt	Average invasion debt change
Eastern temperate forests	2,711,530	20.3	80	481	401	0.83	452	-29	0.82	-0.01
Marine west coast forest	394,155	3.0	210	414	204	0.49	395	-19	0.47	-0.02
Tropical wet forests	22,576	0.2	106	377	272	0.72	356	-21	0.70	-0.02
Mediterranean California	189,420	1.4	229	374	145	0.39	328	-46	0.30	-0.08
Temperate Sierras	108,867	0.8	109	340	231	0.68	296	-44	0.63	-0.05
Southern semiarid highlands	271,698	2.0	114	318	205	0.64	264	-54	0.57	-0.07
Northwestern forested mountains	1,944,770	14.6	140	307	167	0.55	323	16	0.57	0.02
Northern forests	2,879,820	21.6	98	286	188	0.66	360	74	0.73	0.07
Great plains	2,801,110	21.0	49	285	236	0.83	263	-22	0.81	-0.01
North American deserts	2,006,780	15.1	112	225	114	0.50	206	-20	0.46	-0.05



**Fig. 2.** Future changes and uncertainty in species richness. Potential terrestrial invasive plant richness is considerably lower with climate change across much of the continental U.S. (a). Uncertainty in species richness model projections is highest in areas with increased species richness and uncertainty in climate change projections (b). Estimates are based on a 13-model ensemble richness mean (a) and standard deviation (b) for mid-century (2050) under RCP 4.5 at 5 km resolution. All maps represent numbers of species at 5 km resolution and black lines delineate CEC level I ecoregions. Panels (a) and (b) denote different scales.

(Fig. 1c), suggesting that other processes such as dispersal limitation or biotic resistance are preventing invasive species from infilling into more climatically suitable habitats. Some well-sampled areas at the extremes of the climate gradient within the continental U.S., such as the south-eastern corner of California in the North American Desert ecoregion, are under-predicted by our models, suggesting that some plants in hot, dry climates may perform better than expected. The low range infilling found here suggests that many species have ample space for expansion within their current distributions.

There was a weak relationship between introduction date and potential range size. Although continued expansion of invasive species is a concern for modeling environmental relationships at landscape scales (e.g., (Václavík & Meentemeyer, 2012)), poor climatic equilibrium does not appear to be a major concern at regional scales (Bradley et al., 2015). The broad regional extents of even recently arrived plants with few occurrences can be attributed to widespread human introduction, such as



**Fig. 3.** Change in invasion hotspots with climate change. The top 25th percentile of invasive plant richness is identified as hotspot area in current and future climate. Gold areas show invasion hotspot areas that are persistent with climate change projections, blue areas are current climate invasion hotspots that are no longer in the top 25th percentile under future climate, and red areas are invasion hotspots that are newly identified with future climate projections. Estimates are based on a 13-model ensemble average invasive richness for mid-century (2050) under RCP 4.5 at 5 km resolution. Black lines delineate CEC level I ecoregions.

deliberate planting through horticulture (Lehan et al., 2013; Reichard & White, 2001). Climate is a dominant driver of species distributions at landscape to regional scales (Pearson & Dawson, 2003), but land use and land cover can also be important (Bellard et al., 2013). However, we expect some suitable land use/land cover within each climatically suitable grid cell given the relatively coarse spatial resolution (5 km × 5 km grid cells) of this analysis. As a result, the distribution models reported here should provide a reasonable proxy for invasion risk.

Potential invasive plant richness depends on the invasion history (e.g., number of species introduced, dispersal by humans across large geographic extents) and survey effort. Invasion history and survey effort may be independent of ecoregion size and each other, leading to potential invasive plant richness estimates that are uncorrelated with ecoregion size. Change in invasion debt was the only characteristic related to ecoregion size, suggesting that larger ecoregions stand to gain proportionally more species than smaller ecoregions with climate change by 2050. However, the largest ecoregions also have either large latitudinal extents (e.g., Northwestern Forested Mountains) or large longitudinal extents in northern latitudes (e.g., Northern Forests). Therefore, climatic range, rather than ecoregion size, is more predictive of changes in geographic invasion risk.

With climate change, the majority of invasion hotspot area is projected to remain geographically stable in the continental U.S. through 2050. Global analyses of 99 highly problematic invasive species (plants and animals), have also identified the eastern U.S. as an invasion hotspot with climate change in 2100, with similar northern locations of increased invasion risk (Bellard et al., 2013). Invasion hotspot assessment in Australia showed similar geographic stability despite the differences in species listed (O'Donnell et al., 2012). Together, these studies suggest that the apparent stability in invasion hotspots may be a general pattern with 21st century climate change. Within the continental U.S., Eastern Temperate Forests have many invasive plant species (Iannone et al., 2015; Oswalt et al., 2015) with long introduction histories (Lehan et al., 2013) that are widespread with low infilling. This subset of species may explain the large invasion debt found in the Eastern Temperate Forest ecoregion, as well as the invasion hotspot centered there.

Our analyses showed very little no-analog climate within the continental U.S. This was similar, but slightly less than Williams and Jackson (Williams & Jackson, 2007), who found some no-analog climate along the southern (Gulf) and western (Pacific) coasts. The differences between the analyses are likely due to our focus on 2050 (vs. 2100) climate, the updated CMIP5 climate models with a new emissions scenario, and a different set of climate predictors for identifying non-analog climate. Nonetheless, the ensemble of climate models used to project future climate created uncertainty. Uncertainty in future (2040–2060) richness projections was highest in areas with the highest uncertainty in the climate models. Uncertainty in future species richness projections in the Northeast and central-western U.S. was linked to uncertainty in January minimum temperature projections, in the north-central U.S. linked to maximum July temperature, and in the West Coast to annual precipitation (Fig. S3). Areas with the highest uncertainty in warming January minimum temperatures, such as the Northeastern U.S., also have the highest projected mean increases in invasive species richness, which is likely due to reduced cold-limitation in these areas with climate change. The connection between uncertainty in invasion risk and plant physiology is beyond what occurrence data can provide, but these results suggest that cold tolerance may be important for explaining range expansions in northern areas of the continental U.S.

Current invasive plants will certainly not disappear with climate change, but reduction in invasion risk for large portions of the country point to spatially-extensive conservation and restoration opportunities in the intermediate future. Importantly, reduced invasion risk is projected with no intervention from land managers or conservation professionals, leaving those resources and time to be spent on other priorities. Areas no longer suitable for particular invasive plants can be

restored with native communities likely to persist or develop in new climatic conditions if active management is desired (i.e., transformative restoration) (Bradley et al., 2009). However, invasive plants can alter their environments and climate change will continue to alter climatic conditions, so native plant restoration may not be as straightforward as replanting formerly invaded sites with locally occurring native species. Land management occurs at the local scale, so our results will be most useful when coupled with parcel-level knowledge of local plant communities. Our results represent the first step in restoration planning by identifying candidate geographic areas for restoration; the next step is to identify target timescales for planning (i.e., are we restoring communities to persist 10 years into the future, or longer with climate change in mind?) and to develop candidate restoration species lists that fit those timescales.

Our invasion debt estimates are a function of the species pool already introduced to North America (Reichard & White, 2001; Lehan et al., 2013). For example, Eastern Temperate Forests have a long history of introduced ornamental plants that have become invasive, and potential richness is accordingly high. In contrast, Tropical Wet Forests in the Southeast have a shorter history of ornamental introduction, and the lag time between introduction and invasion likely means that species currently being cultivated may go on to become invasive. Preventing new potential invasive plants from being introduced is key to capitalizing on broader national scale conservation opportunities identified by our models. Species adapted to tropical and subtropical climates, climates that will become more prevalent in areas “vacated” by the current pool of invasive plants, are already becoming more common in the ornamental plant trade and are prime candidates for monitoring (Bradley et al., 2012). Assessment of the potential invasiveness of new imported species (Koop et al., 2011; Leung et al., 2012) and early detection rapid response programs (EDRR) to eliminate new invaders (Leung et al., 2002; Sheley et al., 2015) are vital to prevent the introduction and establishment of new invasive species.

Given the distribution of invasion hotspots and the magnitude of both current and future invasion debt, management programs should be supported in all ecoregions. EDRR programs monitor areas of interest and quickly control any new populations of potentially invasive species before they become widespread and/or abundant. While typically applied to newly introduced species at the continental scale, EDRR programs could also be used at the leading range margin of range shifting species to curb spread into new regions. The ecoregions with increased potential richness (Northwestern Forests and Northwestern Forested Mountains) are obvious candidates for EDRR programs focused on species new to those ecoregions. Containment and control programs are typically applied within the range of established invasives (Hulme, 2006), and can be used to curb range infilling in ecoregions with high debt under current climate conditions, such as Eastern Temperate Forests (Table 1). Effective management of national invasions is contingent on communication and cooperation of local and regional land managers, presenting a challenge and opportunity to foster regional invasive plant management networks such as the Southeast Exotic Pest Plant Council and the Midwest Invasive Plant Network. Some invasive plants are listed only at the state or regional level, so the large-scale models that we developed can produce species watch lists for areas that are likely to receive range-shifting plants to aid EDRR programs and regional invasive plant networks as climate continues to change.

We have focused on invasive plant richness and invasion debt as risk metrics, but species abundance also drives impact (Parker et al., 1999). Occurrence data, even with their spatial heterogeneity (Fig. 1a), are more readily available than abundance data and enable this type of multi-species, broad-scale assessment. Greater availability of abundance data, in addition to occurrence data, will open new avenues to assess invasion risk and refine priority areas for monitoring and active management. Modeling frameworks are already available to create such forecasts (Ibáñez et al., 2009), yet data to parameterize such models across many species and at large spatial scales are lacking (but

see Iannone et al., 2015; Oswalt et al., 2015) for continental U.S. forest invasive plants). Continued collection and more robust sharing of invasive plant distribution data would aid in directing near-term management at landscape and local scales. Our assessment suggests that widespread conservation opportunities in the context of current invasive plants will emerge with climate change, but will be effective only with vigilant monitoring, management, and regional cooperation.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.09.015>.

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