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Shifting hotspots: Climate change projected to drive contractions and expansions of invasive plant abundance habitats

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Abstract

Aim: Preventing the spread of range-shifting invasive species is a top priority for mitigating the impacts of climate change. Invasive plants become abundant and cause negative impacts in only a fraction of their introduced ranges, yet projections of invasion risk are almost exclusively derived from models built using all non-native occurrences and neglect abundance information.

Location: Eastern USA.

Methods: We compiled abundance records for 144 invasive plant species from five major growth forms. We fit over 600 species distribution models based on occurrences of abundant plant populations, thus projecting which areas in the eastern United States (U.S.) will be most susceptible to invasion under current and +2°C climate change.

Results: We identified current invasive plant hotspots in the Great Lakes region, mid-Atlantic region, and along the northeast coast of Florida and Georgia, each climatically suitable for abundant populations of over 30 invasive plant species. Under a +2°C climate change scenario, hotspots will shift an average of 213 km, predominantly towards the northeast U.S., where some areas are projected to become suitable for up to 21 new invasive plant species. Range shifting species could exacerbate impacts of up to 40 invasive species projected to sustain populations within existing hotspots. On the other hand, within the eastern U.S., 62% of species will experience decreased suitability for abundant populations with climate change. This trend is consistent across five plant growth forms.

Main Conclusions: We produced species range maps and state-specific watch lists from these analyses, which can inform proactive regulation, monitoring, and management of invasive plants most likely to cause future ecological impacts. Additionally, areas we identify as becoming less suitable for abundant populations could be prioritized for restoration of climate-adapted native species. This research provides a first comprehensive assessment of risk from abundant plant invasions across the eastern U.S.

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KEYWORDS

biogeography, habitat suitability, invasion hotspot, invasive plant, invasive species, proactive management, range shift, species distribution model

1 | INTRODUCTION

Invasive species – non-native species capable of reaching high abundances and causing ecological harm (Richardson et al., 2000) – are among the most ubiquitous threats to managed landscapes and native ecosystems, causing widespread ecological and economic impacts that include losses to biodiversity, ecosystem function, and crop yields (Pimentel et al., 2000, 2005; Pyšek & Richardson, 2010; Vilà et al., 2011). Climate change is projected to exacerbate these impacts by facilitating the spread of invasive species (Allen & Bradley, 2016; Bradley et al., 2010; Hellmann et al., 2008). Species distribution models based on invasive species occurrences (i.e., an observation of the species at any level of abundance) have been used to predict invasion risk under current and future climate conditions (e.g., Allen & Bradley, 2016; Hulme, 2006; O'Donnell et al., 2012). While risk of an invasive species occurrence can be useful for guiding management via early detection and rapid response (EDRR), the areas where species can occur are broader than areas that support abundant populations (Beaury et al., 2023; Bradley, 2013). Hence species distribution models using all species occurrences can overestimate invasion risk (Bradley, 2013). For management, overestimating invasion risk leads to hundreds of 'high risk' taxa in any given area – many more than are feasible to monitor and manage within time and monetary constraints (Beaury et al., 2020; Kuebbing & Simberloff, 2015). With limited management resources, identifying areas where invasive species can occur at *high abundance* is critical for informing proactive natural resource management as these are likely to be where ecological impacts are the greatest (Bradley et al., 2019; Parker et al., 1999; Pearse et al., 2019).

Invasive species that reach high abundance have a greater chance of maintaining their current distribution, have greater capacity to extend their ranges (Verberk, 2011), and have a greater potential to cause negative ecological and economic impacts (Bradley et al., 2019; Parker et al., 1999; Pearse et al., 2019). Larger populations also have greater evolutionary potential, and therefore may respond and adapt more rapidly to changing environmental conditions (Verberk, 2011). Despite the critical role of abundance in supporting existing and expanding invasions, species distribution models that incorporate abundance data remain rare in the literature – in part due to the lack of high-quality, georeferenced abundance records (Bradley et al., 2018; Johnston et al., 2015). Unfortunately, species distribution models based on all occurrences (hereafter occurrence-based models) often fail to accurately predict areas that can support abundant populations (O'Neill et al., 2021). Instead, species distribution models based on abundant occurrences (i.e., locations where populations of invasive species achieve high local abundance) may serve as a better proxy for invasion risk (Beaury et al., 2023; O'Neill et al., 2021). To better prioritize monitoring and management

decisions in a landscape with limited management resources, we need to leverage existing abundance data to understand the current and future distribution of habitats that can support abundant populations of invasive plants.

The more widespread or abundant a species is, the more expensive management actions like suppression and removal become (Latombe et al., 2022; Rejmánek & Pitcairn, 2002). If future changes result in more favourable habitat for species to establish or spread (Allen & Bradley, 2016; Bradley et al., 2009), these taxa likely pose expanded invasion risk and should be prioritized for proactive management (Westbrooks, 2004). However, climate change could induce species ranges to not just expand or persist, but also potentially contract (Allen & Bradley, 2016; Bezeng et al., 2017; Bradley et al., 2009). Highlighting contractions in invasion risk allows us to prioritize sites for restoration (Bradley et al., 2009). For a few taxa, distribution models that incorporate abundance have proved useful for refining geographic assessments of potential expansion and contraction of invasion risk (Beaury et al., 2023; Jarnevich et al., 2021). Yet, despite the management implications, how climate change may affect the distribution of abundant populations of invasive plants remains unknown for most species in the United States (U.S.).

Comparisons across models have also highlighted the complex relationship between the geographic distribution of abundant populations and environmental space (Catford et al., 2011, 2016; Ricciardi et al., 2021). Drivers of such species-specific variation are largely uncertain but may be associated with life history strategies, including plant growth form (Bonser & Geber, 2005; Rowe & Speck, 2005). Plants of different growth forms vary in morphological and physiological adaptations, and hence are likely to vary in their sensitivity and response to changes in environmental conditions (Bonser & Geber, 2005; Rowe & Speck, 2005). As a result, the geographic distributions of abundant populations likely differ between plant growth forms, which in turn will affect the structure and biodiversity of invaded native communities (Guerin et al., 2019) as well as the type and effectiveness of different management strategies (Weidlich et al., 2020).

Here, we compiled occurrences of abundant populations for invasive plants across the eastern U.S. We used these data to predict areas that are climatically suitable for abundant populations, (hereafter defined as a species' abundance habitat), under current and future climatic conditions. To support climate-informed management of invasive species we asked the following questions: (1) what areas are currently climatically suitable for abundant plant populations? (2) how are hotspots of abundance habitat (where the abundance habitat for multiple species overlaps) projected to shift with climate change? and (3) do current and future projections of abundance hotspots differ based on plant growth form? We predict that future areas that are climatically suitable for abundant populations will shift

northward, mirroring range shifts observed in previous distribution models (Allen & Bradley, 2016) as species track suitable climatic conditions. We also predict that abundance hotspots will differ between the major plant growth forms, with the greatest shifts in abundance hotspots will be observed in shorter-lived growth forms such as vines and herbs that are often able to produce seeds or propagules within one growing season, compared to more long-lived growth forms like trees that typically require several seasons to reproduce and spread (Giorgis et al., 2016). Using results from species distribution models, we created management products, including state watch lists of species projected to maintain or expand abundance habitat under a +2°C climate change scenario. By compiling and standardizing plant abundance data and using the subset of abundant occurrences to model areas climatically suitable for abundant populations for a large number of plant taxa, our study highlights areas at higher risk of invasive species spread and potential impact – a much better proxy for invasion risk than occurrence-based distribution models alone.

2 | METHODS

2.1 | Data processing for candidate taxa

We compiled georeferenced records of plant species with abundance data (reported as percent cover) in the U.S. from 14 data sources (Appendix S1). These data repositories represent contributions from hundreds of natural resource managers and include manager reported observations (e.g., EDDMapS), standardized vegetation services (e.g., NPS, FIA), and state data depositories (e.g., CalFlora). From these sources, we used the USDA PLANTS database (USDA, NRCS, 2022) to identify plant species that were introduced to the contiguous (lower 48 states) United States. For each species we retained occurrences that included measures of plant percent cover or average plant cover class (a range of percentage cover values); replacing average cover class values with the median percentage cover value within the reported range (e.g., 15%–20% cover was replaced with 17.5%). We removed cover values that fell outside of 1%–100% range, locations outside of the contiguous U.S., and duplicate records across the pooled data sources. For most data sources, no additional information was available on the scale or methods used to collect plant cover data and few species had sufficient coverage of abundance values (i.e., 0%–100% cover across a range of habitats) to support models of continuous abundance. For these reasons, we did not aim to predict continuous abundance, electing instead to predict areas climatically suitable for abundant populations, defining an abundant population as any recorded occurrences of a species with $\geq 5\%$ plant percent cover (see reasoning below). This approach allowed us to include a large number of invasive plants with existing abundance data and provided an important refinement of existing, hotspot analyses based on non-native species occurrences. While plant abundance data span the contiguous U.S., we focused on the eastern U.S. due to biogeographic differences between the eastern and western regions, and hence likely differences in plant-climatic

associations (Bailey, 2009; Omernik & Griffith, 2014). Because we wanted to include as many species as possible, we included any species with at least one abundant population east of 100°W (Seager et al., 2018), assuming this indicated the species could establish and become abundant within the eastern U.S.

To define areas where species can become abundant, previous studies have selected abundance points associated with percent cover thresholds near or below 10% cover for defining populations/occurrences as abundant (Bradley, 2016; Jarnevich et al., 2021; O'Neill et al., 2021), but recent analyses suggested little difference between suitability predicted from 5% and 10% cover thresholds (Beaury et al., 2023). Therefore, we selected points with a $\geq 5\%$ cover or average cover class to define a species as having established an abundant population in a given location (hereafter, abundance record). To increase the likelihood of robust model performance, we only fitted models to species with over 100 abundance records or with 50 records after pre-processing (see below). This resulted in an initial set of 175 candidate taxa that had sufficient total abundance records and at least one record in the eastern U.S., with a total of 455,455 abundance records to use in species distribution models.

2.2 | Species background data

For each candidate species we predicted potential distributions of abundance populations under current and +2°C climate projections using the Software for Assisted Habitat Modelling library in the Vistrails (v. 2.2.3) scientific workflow system (sahm; Morisette et al., 2013). To reduce spatial bias in the abundance records and avoid pseudoreplication, we followed preprocessing steps outlined in Morisette et al. (2013), thinning each species' abundance data by 4km using the 'spThin' package (v.0.2.0; Aiello-Lammens et al., 2015) in R (v.4.1.2; R Core Team, 2021) to match the resolution of our predictors. Following methods outlined by Young et al. (2020) and Jarnevich et al. (2021), we used a target background approach (Phillips et al., 2009) to generate pseudo-absence data to mimic sampling biases in abundance location data (Appendix S1). The target background approach reduces the effect of spatially biased abundance records by drawing background points with the same sampling biases (Young et al., 2020). For each species we randomly selected up to 10,000 target background points from the full set of abundance records (e.g., Appendix S1), subset to the target species' growth form from within a 99% kernel density estimate isopleth (an isopleth is a line representing a constant value, as in a contour line on a topographical map) around the focal species' point locations. The number of background points varied based on the size of the isopleth and number of points found within it (sample size in Appendix S1).

Growth form data were assigned based on the USDA PLANTS database. For taxa with more than one growth form recorded (e.g., Subshrub/Vine), we chose the most representative growth form based on information from the primary literature on plant ecology. When generating background points, we grouped growth forms

likely to be searched for and recorded together to reduce spatial biases associated with small groups. We combined vines with forb/herbs to generate background points, assuming both would be found when searching understory communities. Likewise, we combined shrub, subshrub, and shrub/tree growth forms, assuming all three would be a focus of understory woody plant surveys. As a result, plants were grouped into one of four growth forms for targeted background sampling: tree, graminoid, vine/forb/herb, and shrub/subshrub/shrubtree (Appendix S1). For 11 candidate species, small sample sizes and/or disjunct distributions of points prevented us from generating background points; for these species, we extended the spatial extent of the kernel density estimate isopleth (Calenge, 2006) to ensure background point generation.

2.3 | Environmental variables

We selected eight environmental predictor variables from a candidate set of 78 variables created by Engelstad et al. (2022) that encompassed a suite of temperature and precipitation metrics that are known to influence the establishment and spread of invasive plant taxa. We based our environmental variable selection on the following criteria: (a) availability of future climate projections for the variable and (b) importance for explaining the spatial distributions of 62 invasive plants on our candidate list that were also examined in recent models based on invasive species occurrence (Engelstad et al., 2022). The final eight environmental variables included in our models were as follows: Minimum winter temperature, Mean diurnal temperature range, Maximum summer temperature, Precipitation seasonality, Mean summer potential water deficit, Mean evapotranspiration between April and October, Isothermality, and Mean annual precipitation (Appendix S2). These current climate variables are averaged over ~30 years of data spanning 1981–2018 and derived from BioClim and ClimateEngine (Appendix S2). Hence, our models focused on predicting areas with climatic suitability for invasive populations (abundance habitat), although other factors, such as forest cover and soil characteristics, may restrict distributions further (see Discussion).

For each variable, we downloaded +2°C future climate projections from TerraClimate (Abatzoglou et al., 2018) and used the 'terra' package (v. 1.5-21) (Hijmans et al., 2022) in R to create our future environmental variable output rasters. TerraClimate integrates 23 CMIP5 global climate models to create future projections (see Qin et al., 2020). The future climate variables are built on the current climate interpolations, making them directly comparable. For each climate dataset (current and +2°C), all environmental variables were processed to the same extent (contiguous U.S.), spatial resolution (4 km²) and coordinate reference system (Alber's Equal Area) using nearest neighbour resampling. To reduce collinearity among predictor variables, for each species we retained all environmental predictors with $\leq |0.7|$ correlation (Dormann et al., 2013), using the maximum absolute value across Pearson, Spearman, and Kendall coefficients. When a pair of variables exceeded a 0.7 correlation

coefficient, we retained only the variable with the highest variable importance in the model based on the amount of deviance explained by a univariate generalized additive model produced in sahm (Young et al., 2020).

2.4 | Modelling climatically suitable abundance habitat

For each species and climate dataset, we predicted potential abundance habitat using five species distribution modelling algorithms: Boosted Regression Trees (BRT), Generalized Linear Model (GLM), Multivariate Adaptive Regression Splines (MARS), Maxent (v. 3.4.4), and Random Forests (RF). To maximize the amount of data for model fitting for each candidate taxa we used all abundance records in the contiguous U.S. All models were fit using the default parameters within SAHM outlined in Young et al. (2020). For each species, we randomly split abundance records into a training data set (70%) and testing data set (30%). Models were internally evaluated on the training dataset using 10-fold cross validation (Young et al., 2020). Despite the utility of spatial cross validation for overcoming potential modelling problems associated with spatial autocorrelation between training and testing datasets, we did not use spatial cross-validation splits in this study. This is because we have encountered issues with spatial splits when modelling invasive taxa with highly disjunct populations (e.g., species occurring primarily in the northeastern and northwestern U.S.) when using SAHM for modelling. We checked for overfitting by examining differences in area under the receiver operating characteristic curve (AUC-ROC) values between training and average cross-validation split datasets, using an a priori criteria of $> \pm 0.05$ and visual inspection of response curve complexity. When overfitting was identified, we adjusted model-specific parameters (e.g., Maxent beta multiplier value, MARS penalty, BRT learning rate, etc.; see Appendix S2) to improve model fit. We excluded the output of individual model algorithms when the null model (no environmental predictor variables) was selected ($n=1$). We evaluated the final model fit for each algorithm using the True Skill Statistic (TSS), AUC-ROC value, and Boyce Index (Hirzel et al., 2006). We checked model fit and selected the best fit model for each algorithm prior to applying the models to our future climate variables. Of our 175 candidate species, we excluded 30 species that had fewer than 50 abundance records following pre-preprocessing and spatial thinning as we have encountered issues with model fit when modelling invasive taxa with fewer than 50 records post-thinning and previous studies have suggested 50 data points as a minimum for species distribution models (Santini et al., 2021; Wisz et al., 2008). We also excluded one species (*Anthoxanthum odoratum*) because three of the five model algorithms were substantially overfit and unable to be optimized. As a result, we modelled the current and future projections of climatic suitability for abundant populations across the contiguous U.S. for 144 of our initial 175 candidate species. Details of climate variables retained, model optimization parameters, and model fit statistics for the final 144 taxa are reported in Appendices S2 and S3.

2.5 | Abundance hotspot analysis

To identify current and future hotspots where the abundance habitat for multiple species overlaps, we employed an ensemble approach. We opted for an ensemble approach over individual model outputs as recent work comparing models from several algorithms for species found that ensembles of carefully constructed models can outperform single algorithms (Valavi et al., 2022). In our study, we carefully constructed models by evaluating each individual model contributing to the ensemble and revised model algorithm parameters as needed, hence our methods closely resemble those of Valavi et al. (2022). For our ensemble approach, for each species ($n = 144$), we binned the five algorithms' continuous mapped outputs using three thresholding measures (first percentile [threshold that classifies the 1 percent of training data with the lowest suitability predictions as unsuitable], tenth percentile [threshold that classifies the 10 percent of training data with the lowest suitability predictions as unsuitable], and the maximum of sensitivity-specificity (Freeman & Moisen, 2008) where sensitivity is the true positive rate and specificity is the true negative rate. The resulting binary maps for each algorithm and threshold were summed to create an ensemble map with model agreement values ranging from 0 (no predicted climatic suitability for abundant populations) to 15 (all five model algorithms \times three threshold measures predicted climatic suitability for abundant populations). Each ensemble was geographically reduced by a Multivariate Environmental Similarity Surface (MESS; Elith et al., 2010) to limit the effect of environmental extrapolation, where locations with environmental conditions outside the range of those found in the model training data are masked out. We used an additional threshold of ≥ 11 of 15 model agreement to identify the areas with the highest climatic potential for supporting abundant populations for each species (i.e., 'abundance habitat').

We summed the maps of abundance habitat for each species to create a map of abundance hotspots across the eastern U.S. for both current and future climate conditions. The values of these hotspot maps ranged from 0 to 144, reflecting the total number of candidate taxa with abundance habitat projected for each map pixel. We also created aggregated hotspot maps for individual growth forms (Forb/Herb, Graminoid, Shrub, Tree, and Vine). While several of the modelled species have abundant populations in the western U.S., we limited our hotspot analysis to east of 100°W because species with abundant populations only in the west were excluded from our initial species selection, creating an incomplete picture of invasion hotspots in the western U.S. We used these hotspot maps to generate watchlists for eastern U.S. states, listing the species with predicted abundance habitat under current and future climate scenarios (Appendix S4). We then compared the area of abundant habitat under current and $+2^\circ\text{C}$ climate predictions and categorized the differences based on whether habitat is maintained (areas predicted as climatically suitable in both current and future climate conditions), increases (currently climatically unsuitable areas predicted to be climatically suitable in the future) or decreases (currently climatically suitable areas that are predicted to be climatically unsuitable in the

future) given projected climate change. To further explore the differences in shifts of abundance habitat, we calculated the distance and direction of geographic shift based on the shift in the centroid (mean latitude and longitude of abundance habitat) between the current and future areas climatically suitable for abundant populations for each species. The direction of geographic shift measurement was described as shifting towards northeast (bearing $0^\circ \geq 90^\circ$), southeast (bearing $90^\circ \geq 180^\circ$), northwest (bearing $180^\circ \geq 270^\circ$), or southwest (bearing $270^\circ \geq 360^\circ$). We used two-way analysis of variance (ANOVA) to test whether distances between current and future centroid locations differed significantly between plant growth forms, direction of geographic shift, or the interaction between the two. We also employed circular one-way ANOVA using the package 'circular' (v. 0.4-95; Lund et al., 2017) to test whether plant growth forms differ in the direction of geographic shift.

3 | RESULTS

Across the 144 invasive plants modelled here, the areas climatically suitable for abundant populations (i.e., 'abundance habitat'; classified as suitable by $\geq 11/15$ models) varied from $14,560\text{ km}^2$ to $4,394,738\text{ km}^2$ (mean $1,292,743\text{ km}^2$, analogous to $\sim 13\%$ of U.S. land area; Appendices S5 and S6). Silktree (*Neyraudia reynaudiana* (Kunth) Keng ex Hitchc.) had the smallest area of abundance habitat and tree of heaven (*Ailanthus altissima* [Mill.] Swingle) had the largest, which covered roughly 45% of the land area in the contiguous U.S. Given the inherent variance in species distribution model projections, and our additional, conservative 11/15 model threshold cutoff for classifying climatically suitable habitat it is possible for that species with few eastern U.S. records that the models could predict no abundance habitat in the eastern U.S. at the $4\text{ km} \times 4\text{ km}$ scale of our study. Indeed, for six species, all future abundance habitat was west of 100°W longitude while for four species (*Colocasia esculenta*, *Paederia foetida*, *Paulownia tomentosa*, and *Sansevieria hyacinthoidea*), there were no projected areas of future abundance habitat in the contiguous U.S. (Appendix S5). For the remaining 134 species, under current climate conditions abundance habitat in the eastern U.S. varied from 0 km^2 to $2,675,763\text{ km}^2$ (mean $794,371\text{ km}^2$) and future eastern abundance habitat varied from 215 km^2 to $2,916,080\text{ km}^2$ (mean $755,574\text{ km}^2$) (Appendix S5). One of these species (*Brassica nigra*) had future abundance habitat but no current abundance habitat projected for the eastern U.S. On average, abundance habitat in the eastern U.S. is projected to decrease slightly with a $+2^\circ\text{C}$ climate scenario (Appendix S5). However, our analysis reveals numerous invasion hotspots that are largely maintained.

Current hotspots of abundance habitat center around three locations in the eastern U.S.: the northeast coast of Florida and Georgia, the Great Lakes region, and the mid-Atlantic region of the U.S. (Figure 1a); habitat in each of these regions is predicted to be climatically suitable for abundant populations of at least 30 of the 144 modelled species. Future hotspots of abundance habitat show an

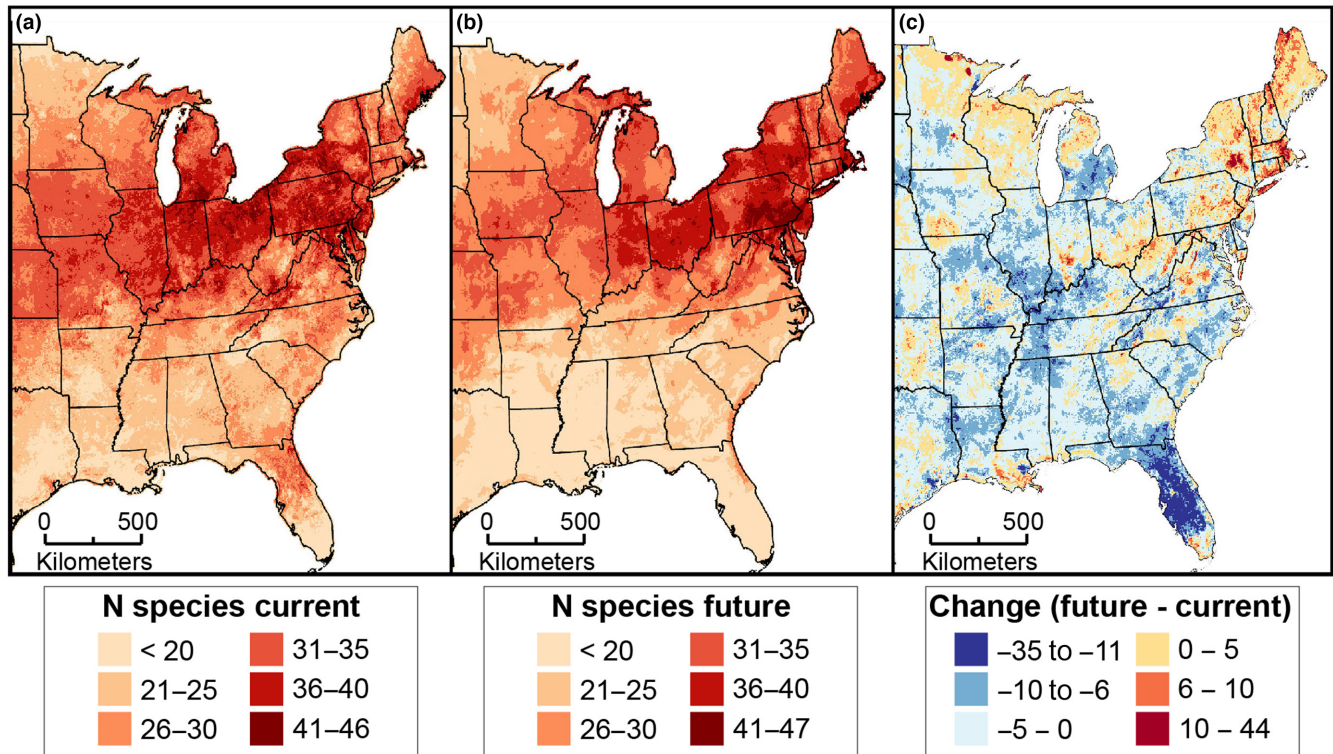


FIGURE 1 The number (N) of invasive plant species with habitat identified as climatically suitable for abundant populations ($\geq 5\%$ cover) in the eastern contiguous United States given (a) current climatic conditions, (b) $+2^\circ\text{C}$ climate warming scenario and (c) the difference between $+2^\circ\text{C}$ and current climatic conditions.

overall shift northward, with $+2^\circ\text{C}$ hotspots concentrated along the eastern Georgia coastline, the upper mid-Atlantic region, and in the lower New England area (Figure 1b). Given 2°C climate change projections, areas in the eastern U.S. are projected to become climatically suitable for abundant populations of an average of four new invasive species, with New England states becoming climatically suitable for abundant populations of up to 21 new invasive plant species (Figure 3a). On average, 18 invasive plants per 4 km^2 grid cell will maintain abundant populations in the eastern U.S., with up to 40 species projected to maintain abundance habitat in the northeast regions off the Great Lakes and New England (Figure 3b). In contrast, across the eastern U.S. conditions are projected to become climatically unsuitable for an average of five species with abundant populations, with regions such as the eastern Midwest projected to become climatically unsuitable for up to 22 invasive species due to climate change (Figure 3c).

The centers of abundance habitats for the 134 invasive plant species with abundance habitat east of 100°W longitude are projected to move between 17.5 and 1585.5 km, (average of 212.5 km, Figure 2, Appendix S5). For these 134 species, the centroids of abundance habitat are projected to show a significant directional geographic shift (Rayleigh t -statistic = 0.521, $p < .001$), shifting predominantly towards the Northeast ($n = 65$ species, 49%) or Northwest ($n = 45$ species, 34%) region of the U.S. In contrast, relatively few species show centroid shifts towards the Southeast (19 species, 14%) and Southwest (five species, 4%) (Table 1, Figure 2). Species moving towards the Northwest tend to experience the

furthest shift in abundance habitat centroids – moving an average of 243.6 km ($\text{SD} = 258.9$ km), followed by species shifting towards the Northeast (204.8 km, $\text{SD} = 158.4$ km), Southeast (183.8 km, $\text{SD} = 113.9$ km), and Southwest (142.0 km, $\text{SD} = 71.3$ km) (Figure 2, Appendix S5). Actual evapo-transpiration between April and October was most frequently included as a predictor variable – being included in 97% (139/144) of species models – and was also the most frequently included predictor variable for all directional shifts, particularly Northeast range shifting taxa. Precipitation seasonality was also important for species with abundance habitat shifting towards the Southeast and Southwest while maximum summer temperature and minimum winter temperature were frequently included in models for species shifting towards the Northwest (Appendix S2).

Current and future abundance habitat projected by $\geq 11/15$ models varied substantially across taxa and across the eastern U.S. region (Figure 3e,f). On average, 16% (range 0%–63%) of current abundance habitat will remain climatically suitable for abundant populations of our candidate taxa under future climatic conditions (Appendix S5). In contrast, an average of 3.9% of the eastern U.S. is reclassified from either unsuitable or unknown (masked) to suitable for abundant populations given 2°C warming, while 5.6% of the eastern U.S. is reclassified from suitable to unsuitable under future conditions. The majority of species (81%, $n = 109/134$) are projected to maintain at least 1% of their current abundance habitat east of 100°W (range: 1%–63%, average: 19%), and 38 species are projected to maintain at least 25% of their current abundance

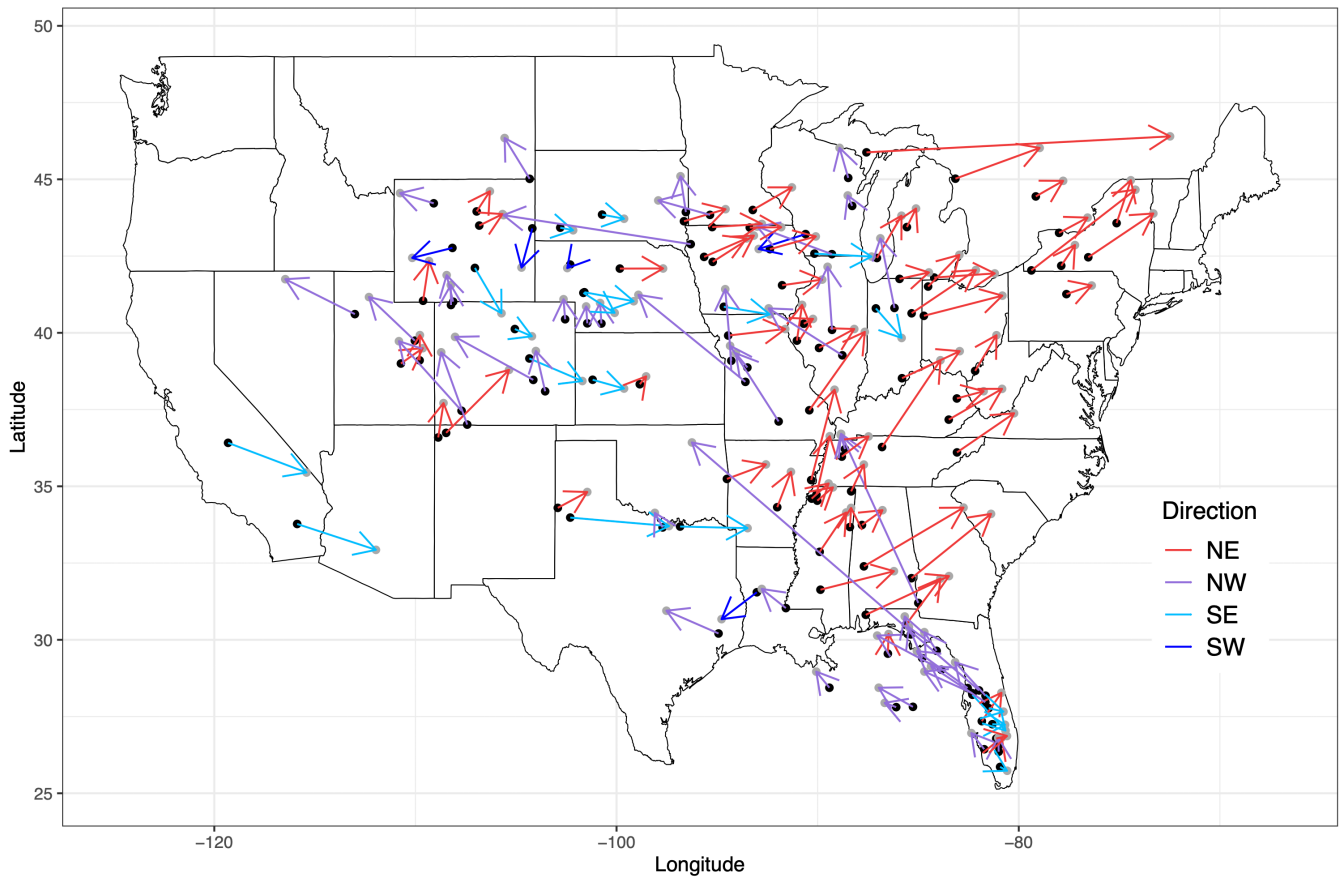


FIGURE 2 Direction of change in the centroids of abundance habitat identified for 134 invasive species with future eastern United States (U.S.) distributions. Arrows are drawn from the current centroid location (black dots) to the future centroid location (grey dots) given predictions from a +2°C warming scenario. Centroid locations display the mean latitude and longitude value calculated from the latitude and longitude values for all pixels of abundance habitat identified for each species within each climate scenario. For this reason, some average centroid locations appear located outside of the bounds of the contiguous U.S. landmass.

TABLE 1 The number and proportion (percentage) of the 134 invasive plant species with climatically suitable abundance habitat east of 100°W longitude, categorized by growth form, that are projected to shift the centroid of their abundance habitat towards the Northwest (NW), Northeast (NE), Southeast (SE), and Southwest (SW) given a +2°C warming scenario. Mean and standard deviation (SD) of range shift distance (in kilometres) is based on change in centroid location between current and future abundance habitat for taxa within each growth form.

Growth form	NW (%)	NE (%)	SE (%)	SW (%)	Mean distance (SD)	Species total
Forb/herb	15 (27)	28 (50)	10 (18)	3 (5)	215.8 (161.6)	56
Graminoid	8 (29)	13 (50)	5 (18)	1 (4)	170.1 (145.6)	28
Shrub	13 (45)	13 (45)	2 (7)	1 (3)	195.8 (115.1)	29
Tree	5 (56)	4 (44)	0 (0)	0 (0)	256.8 (211.3)	9
Vine	4 (33)	6 (50)	2 (17)	0 (0)	303.4 (424.6)	12
Total	45 (34)	65 (49)	19 (14)	5 (4)	212.5 (191.9)	134

habitat given the +2°C warming scenario. As a result, one third of species (51/134) will see an overall increase in abundance habitat in the eastern U.S., with the area identified as climatically suitable projected to increase between 215 and 786,463 km² (mean 164,922 km²). In contrast, 83 species (62%) are projected to experience a decline in abundance habitat, with the overall area of abundance habitat decreasing by an average of 163,973 km² (reductions

range from 1752 to 577,118 km²) (Appendix S5). Across the 134 species, an average of 35% of land in the eastern U.S. was masked due to climate dissimilarity, meaning predicting climatic suitability under future conditions would require extrapolating beyond the environmental space covered by the model training for a species. For individual states, Missouri is projected to become climatically suitable for abundant populations of the most novel plants ($n = 86$).

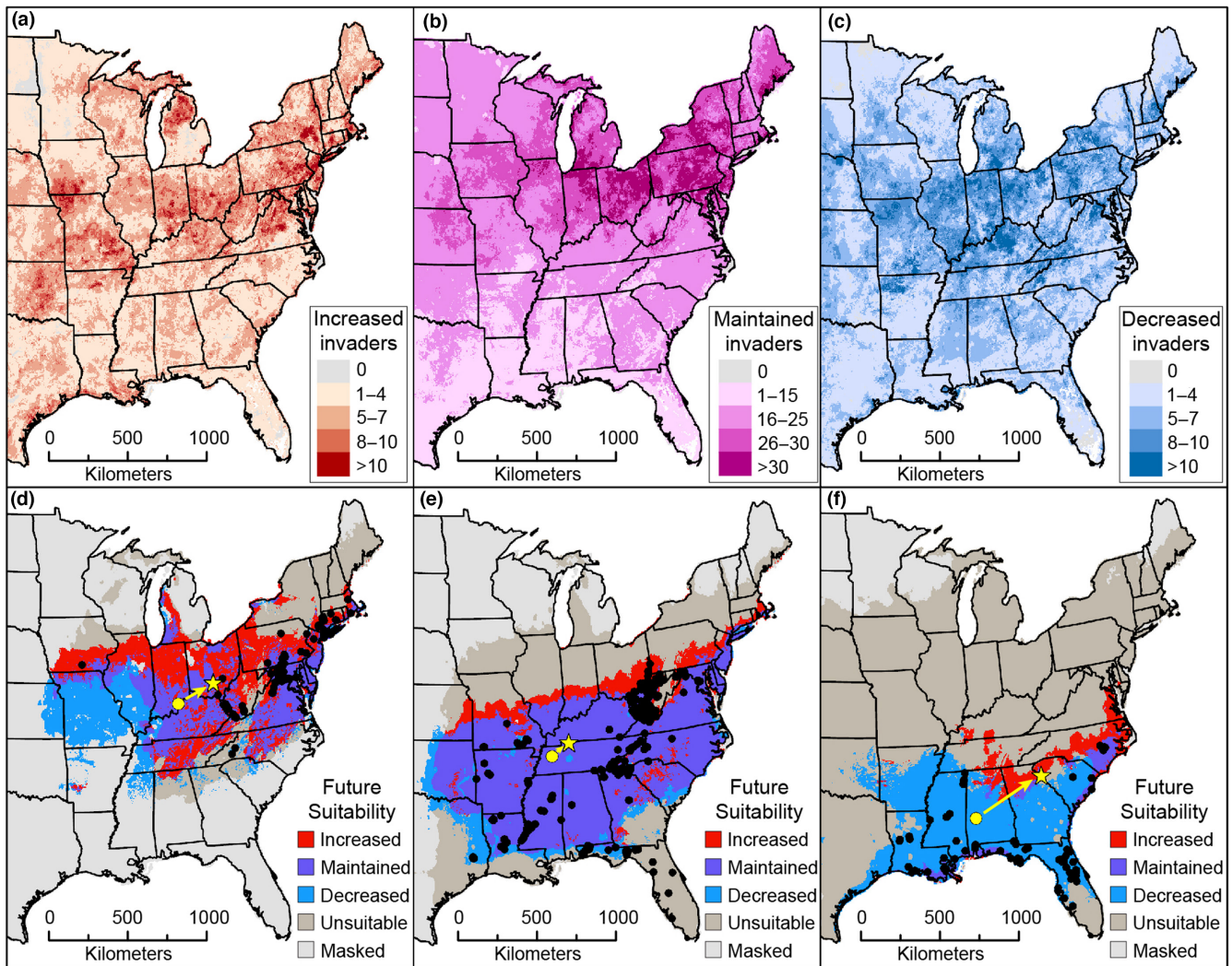


FIGURE 3 The number of invasive plant species across the eastern United States that (a) increase, (b) are maintained, or (c) decrease abundance habitat with +2°C climate warming. The amount of abundance habitat for invasive plants also changes in the eastern United States given +2°C climate warming. Distribution models may predict (d) range expansion (wine berry, *Rubus phoenicolasius* Maxim.), (e) range maintenance (kudzu, *Pueraria montana* [Lour.] Merr.), or (f) range contraction (alligatorweed, *Alternanthera philoxeroides* [Mart.] Griseb.). Abundance data points shown by black dots. Arrow indicates the average direction of abundance range shift from the centroid of current abundance habitat (yellow circle) to the centroid of future abundance habitat (yellow star).

North Carolina will become climatically suitable for abundant populations of the largest total number of plants ($n=127$); this includes species that currently have abundant populations in the state (Appendix S4).

Most models showed moderate to high performance with TSS values >0.4 for 84% of models based on train data and 80% of models based on test data, and AUC values ≥ 0.7 for 93% of models based on train data and 88% of models based on test data (Appendices S2 and S3). The Boyce Rho values for training data were all positive, indicating model predictions of abundance habitat matched abundance records. Three eastern U.S. species (*Imperata cylindrica* [IMCY], *Xanthosoma sagittifolium* [XASA2], *Pastinaca sativa* [PASA2]) had Boyce Rho values close to or below 0 for based on testing data, indicating poor model predictive performance for these taxa (Appendix S2).

3.1 | Plant growth forms

Across the contiguous U.S., current abundance habitat varied substantially across growth forms; the 10 invasive trees covered an average of 791,962 km² (range 39,069–4,394,738 km²) while the 28 graminoids covered an average of 1,573,319 km² (range 14,560–3,797,870 km²) (Appendix S5). Current and future abundance hotspots also varied by plant growth form (Figure 4). Current abundance hotspots for forb/herbs and graminoids are located in the Great Lakes and northeastern regions of the U.S. whereas hotspots for shrubs, trees, and vines are located in the lower Midwest and southeastern U.S. (Figure 4). The overall directional shift in abundance habitat towards the Northeast and Northwest was consistent across growth forms ($F_{4,135}=1.454$, $p=.220$, Table 1, Appendix S7). The mean shift in the centers of abundance habitat

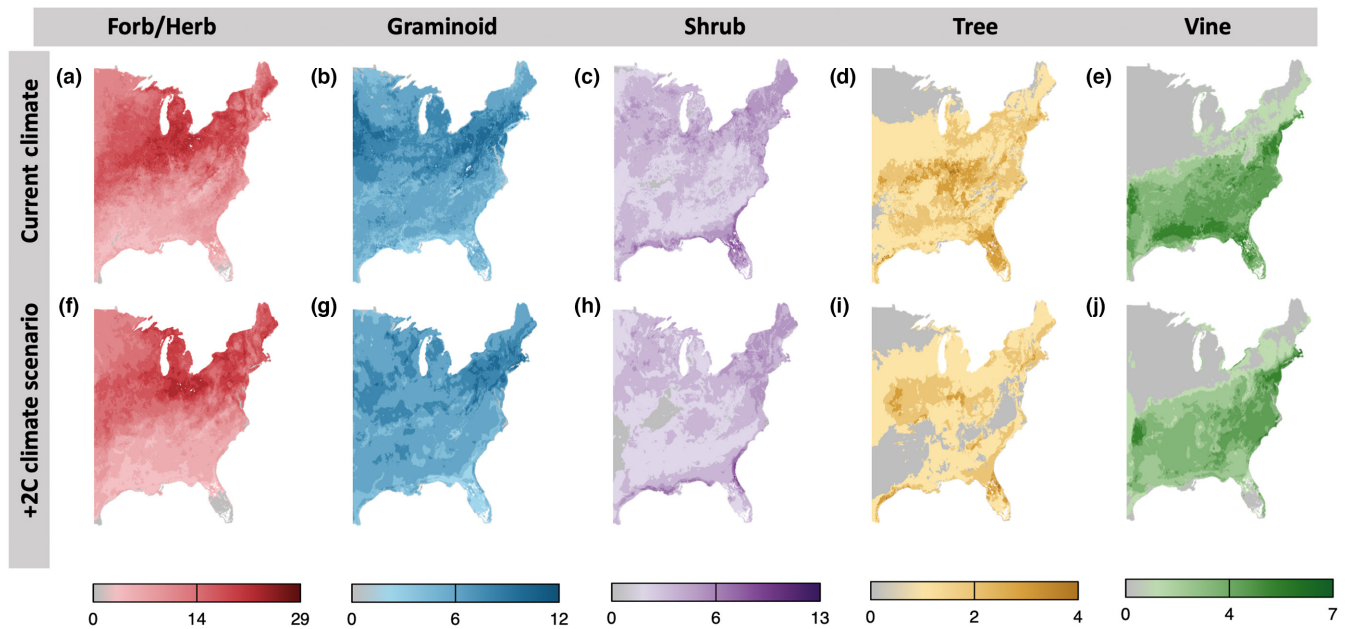


FIGURE 4 The number of invasive plants per location likely to have habitat suitable for abundant populations ($\geq 5\%$ cover) given current climatic conditions (a–e) and $+2^\circ\text{C}$ warming climate scenario (f–j) for each of five major plant growth forms.

also did not significantly differ between growth forms ($F_{4,123} = 1.216$, $p = .308$), despite average shifts in abundance habitat varying from 170 km ($SD = 146$ km) in graminoids to 303 km ($SD = 425$ km) in vines (Table 1). The interaction between the distance and direction of abundance habitat shifts was significantly different across plant growth forms ($F_{9,123} = 2.576$, $p = .009$). The overall greatest directional shift in distance between current and future abundance habitat centroids was observed in vines with an average shift of 651 km ($SD = 624$ km) towards the Northwest. This trend appears largely driven by one species (*Dioscorea bulbifera*; DIBU), which is projected to shift 1585.6 km towards the Northwest under our $+2^\circ\text{C}$ climate scenario (Appendix S5).

Across growth forms, we observed similar trends in the projected change in the area that is climatically suitable for abundant populations (Appendix S5). Graminoids had the largest mean area maintained as abundance habitat under both current and future conditions (768,347 km²; 19.8%), followed by forbs/herbs (716,011 km²; 18.4%). The mean overlap in current and future abundance habitat for trees, shrubs, and vines was less than 12%, meaning these growth forms maintain the least amount of current abundance habitat given projected climate change. Trees, in particular, have the lowest overlap between climate scenarios (285,948 km²; 7.4%). Approximately half (55%) of forbs/herbs species showed an overall decrease in abundance habitat, which was slightly lower than the relative proportion (66%–68%) of species observed across the other growth forms (Appendix S5).

4 | DISCUSSION

Invasive species movement and range expansion are a top threat to successful adaptation of ecological communities to climate change

(Mainka & Howard, 2010; Peters et al., 2018; Walther et al., 2009). Our study uses occurrences of abundant populations in species distribution models to refine spatial projections of invasion risk and proactively identify potential shifts in abundance habitat with climate change. Under current environmental conditions, we identified three regional abundance hotspots: (1) the northeast region of Florida and Georgia, (2) the Great Lakes region, and (3) the mid-Atlantic region of the eastern U.S. These areas could support abundant populations of up to 40 different invasive plant species, with the centroids of these hotspots projected to shift by hundreds of kilometres with climate change. By modelling abundance habitat under current and future climate, our study provides targeted species lists that can be used by managers to focus limited resources for early detection and rapid response on areas where invasive species have the greatest potential to reach high abundance and have the greatest impacts (O'Neill et al., 2021; Vander Zanden & Olden, 2008; Yokomizo et al., 2009).

Proportionally the number of range shifting taxa identified in our study (15%, $n = 21/144$ taxa) is similar (11%, $n = 100/896$ taxa) to that identified in models using occurrence-only data by a previous hotspot analysis, conducted at a similar spatial scale (5 km \times 5 km) by Allen and Bradley (2016). Our use of abundance rather than occurrence-only data allows us to focus on a smaller number of species of potentially high impact because abundance is correlated with ecological impact (Bradley et al., 2019). This may explain why the number of range shifting abundant taxa identified by our study (up to 21 novel species with abundance habitat) is substantially smaller than the number of range shifting taxa (up to 100 novel species) identified by Allen and Bradley (2016). Different modelling approaches could influence the differences between observed hotspots in this study versus Allen and Bradley (2016), who mainly identified invasion hotspots in northeastern U.S.

states. However, O'Neill et al. (2021) found distinct hotspots for occurrence versus abundance habitat under current climate, suggesting that the different hotspots are not simply a modelling artefact. The taxa in our study represent those commonly reported as abundant in the eastern U.S. by natural resource managers via online repositories. Leveraging information on abundance habitat will prevent both the overinvestment of management resources on areas or species unlikely to become abundant as well as the underinvestment on areas or species likely to increase in abundance and lead to the greatest future impact (Bradley et al., 2019; Pearse et al., 2019). For example, areas projected to gain abundance habitat could contain 'sleeper' populations of species that are currently limited by climate but could become invasive with climate change (Spear et al., 2021); these existing populations are priority targets for eradication. Previous studies that focus on non-native occurrence data alone cannot predict potential changes in the areas climatically suitable for abundant populations (Bradley, 2016; Jarnevich et al., 2021; O'Neill et al., 2021) and therefore would fail to identify sleeper populations. Similarly, abundance habitat provides a more targeted estimate of risk from range-shifting invasive species, – information that could be used to build more proactive state regulations against the continued propagation of high-risk species as ornamentals (Beaury, Patrick, & Bradley, 2021). Expanded efforts to collect and use abundance data as part of current invasive species monitoring would improve our ability to inform risk for management activities (Bradley et al., 2018). We consider species already well established within the U.S., yet there may be novel invaders previously excluded by climate that may be able to establish in southern regions. Currently, only 10% of land managers in eastern North America monitor for new invasive taxa (Beaury et al., 2020) due to lack of funding and personnel (Beaury et al., 2020; Kuebbing & Simberloff, 2015). Proactively managing novel range-shifting taxa via early detection and rapid response will require managers to split time and resources between both current and future invasive taxa. This task will be more feasible given the narrower list of range-shifting invasive plants (average of four per 4 km² grid cell) – a resource commonly requested by invasive species practitioners to inform prevention and management within jurisdictions ranging from protected areas to states. Additionally, the data from abundance habitat projections available in Appendices S4 and S6 of this study have been incorporated into county-based mapping tools by Early Detection and Distribution Mapping Systems (EDDMapS; Wallace & Barger, 2014) to facilitate access and utilization by practitioners. Given that observations of novel establishment and spread of invasive taxa are typically reported by the general public, practitioners could use these species watchlists and interactive online maps to develop educational materials for high-risk taxa to facilitate public involvement in early detection and rapid response efforts.

Our analyses highlight substantial potential shifts in the distributional patterns of abundant invasive plant populations across the eastern U.S. with changing climate. Such changes lead to markedly different management strategies. For example, species with

maintained abundance habitat in a given area are likely already being managed and these efforts will need to continue, although some aspects such as the timing of management and efficacy of control measures are likely to be affected by climate change (Bradley et al., 2010; Hellmann et al., 2008). Species with expanded abundance habitat in a given area will require either a new focus on monitoring for range-shifting invasions and/or a new focus on eradicating sleeper populations (Spear et al., 2021). Areas with predicted future contractions in non-native species abundances could be further screened for microhabitat features, such as soil type and topography, which may allow them to become candidate sites for restoration. This will likely require developing climate-informed restoration practices focused on warm-adapted, fast developing, and functionally diverse native plants that can resist further invasion (Hess et al., 2019; Yannelli et al., 2020).

Variation in species abundances reflect variation in underlying population dynamics, which are driven by both demographic and environmental processes (Waldock et al., 2022). While not feasible without information on community biodiversity and structure, other analytical approaches such as joint species distribution models and mechanistic distribution models could improve future predictions for species or areas. These alternative modelling approaches could refine predictions of abundance habitat by accounting for traits and interspecific interactions, which may enable or prevent taxa from maintaining abundant populations despite potentially suitable environmental conditions (O'Reilly-Nugent et al., 2020). Similarly, other important predictors, which can influence invasive plant distributions, such as forest cover or human landscape modifications, were unaccounted for in our study (Mod et al., 2016). Baer and Gray (2022) showed that biotic predictors improve the performance of species distribution models at finer spatial scales (1 km), and in the eastern U.S., the majority of management efforts occur at relatively small spatial scales – either within single or a network of properties within a single state (Beaury et al., 2020). Yet, future projections for biotic and many abiotic predictors at this scale are currently lacking. While many modelling improvements are possible, outputs from correlative climate models in our study serve as an important first step in assessing current and future invasion risks using existing abundance data. For example, by combining correlative mapping products with site-specific knowledge on field conditions and processes that affect invasion success, such as the magnitude and type of human activities, distance to roads, dispersal pathways, and soil characteristics (Catford et al., 2011), managers and researchers can tailor broad lists of range shifting taxa to local or regional scales at which early detection and rapid response management actions are undertaken.

Abundance hotspots may pose even greater risk if native and invasive plants are shifting their ranges at different rates. Most native plants are moving more slowly, at about half the pace of climate change. For example, Beckage et al. (2008) found that forest trees in Vermont's Green Mountains had shifted about 100 m up slope between 1964 and 2005, whereas climate warming would predict an upward shift of over 200 m. Similarly, Ash et al. (2017) showed that understory plants in Wisconsin had shifted 49 km northward

between 1950 and 2000, whereas climate warming would predict a northward shift of 90 km. In contrast, invasive plants are more likely to keep up with our projections of a northward expansion of abundance habitat centers of 213 km (Table 1). Invasive plants benefit from human-mediated dispersal, as many continue to be deliberately planted and spread through the ornamental plant trade into warmer climate conditions (Beaury, Patrick, & Bradley, 2021; Van der Veken et al., 2008). Indeed, 91% (123 of 134) of the species in our study are ornamental species that were deliberately introduced to the U.S. (Lehan et al., 2013). With the growth of relatively unregulated online plant sales (Beaury, Patrick, & Bradley, 2021; Humair et al., 2015), coupled with inconsistent regulations of invasive plants across state borders (Beaury, Fusco, et al., 2021; Lakoba et al., 2020), human activities will likely continue to facilitate long distance dispersal of invasive plants, which may enhance the invasion success of these species, particularly long-lived, slow growing taxa such as trees, by enabling them to better track suitable climatic conditions and realize larger portions of their abundance habitat. Ornamental introduced plants projected to remain or become abundant with climate change are prime candidates for state regulation.

Invasion success varies across plant growth forms (Ni et al., 2021) and differential invasion success of growth forms alters the composition and structure of native invaded communities (Guerin et al., 2019). Forbs/herbs represent the dominant growth form of abundant invasive plants in the eastern U.S., making up 42% of our dataset. Similarly, they are also the dominant growth form of established invasive plants in the U.S., contributing 51% (452/896) of species in Allen and Bradley (2016)'s analysis of occurrence hotspots. Fast-growing growth forms, such as forbs/herbs and grasses are associated with shifts in native communities away from woody growth forms, potentially as these invasives suppress native seedling regeneration (Guerin et al., 2019). This suggests that eradication and control of forbs/herb species will remain a high priority for mitigating negative effects of these invasive species on native ecosystems across the U.S. The other growth forms in our study make up similar proportions of the occurrence versus abundance species assemblages observed by Allen and Bradley (2016) with the notable exception of vines. Vines are proportionally rare when we focus on occurrences alone (3% or 30/896 species) but are proportionately more common when we focus on abundance data (9% or 12/144 species). Our analyses show vines are also projected to have the largest average climate-driven shift in abundance habitat centers of 300 km (Table 1). Vines often have functional traits important to invasion success and impact, including high relative growth rate or above-ground biomass, which in turn correlates with higher fecundity or competitive ability (Díaz & Cabido, 1997; Giorgis et al., 2016; Ni et al., 2021). For example, the air potato vine (*D. bulbifera* L.), which our study projected to have the greatest average shift in the center of current and future abundance habitat, can grow up to 25 cm per day, producing vines up to 51 m in length (Rayamajhi et al., 2016). In comparison to Allen and Bradley (2016), our results suggest that vines might have a proportionally higher risk of becoming abundant and hence invasive in new areas than other growth forms.

Given the caveats associated with correlative distribution models (Jarnevich et al., 2015), the spatial predictions of abundance habitat expansions or contractions reported here should be treated as hypotheses, particularly for species projected to show large reductions in abundance habitat and those with fewer abundance records. Previous work by Sofaer et al. (2018), showed that despite good model performance metrics, multi-taxa occurrence distribution models were highly variable and often failed to accurately predict future range expansions and contractions among taxa. This uncertainty also extended to metrics of changes in the magnitude and direction of abundance habitat, although models showed more accurate predictions of habitat that was always or never suitable for a species (Sofaer et al., 2018). The extent to which this uncertainty affects our results remains unknown; however, our conservative threshold approach for assessing climatically suitable abundance habitat (based on $\geq 11/15$ model agreement), combined with our ensemble approach that aggregated a large number of species distribution models, may reduce some of these projection inaccuracies (Naimi et al., 2022).

5 | CONCLUSIONS

Spatial analyses of invasive plant range shifts can inform proactive management (Allen & Bradley, 2016; Bellard et al., 2013). However, with limited management resources and hundreds of invasive species potentially shifting into new areas, it is imperative that we find ways to identify and prioritize the range shifting species likely to have the greatest impacts on native ecosystems. Using species distribution models, we show that current abundance hotspots in the eastern U.S. are projected to shift an average of 213 km predominantly towards the northeast. Our results suggest that changes in climate suitability could facilitate the establishment of abundant populations of up to 21 new invasive plants, with forbs/herbs remaining the most common invasive plants in the eastern U.S. Our study provides the first comprehensive assessment of changing invasive plant risk for the eastern U.S. across a large number of abundant taxa. By identifying areas of high potential risk and impact, our abundance habitat maps can inform early detection and rapid response in areas where invasive plants are expanding as well as identify candidate sites for restoration in areas where invasive plants are contracting.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The abundance data that supports the findings of this study are available in the supplementary material of this article (Evans et al., 2022).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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