

Research paper

Potential distributional shifts in North America of allelopathic invasive plant species under climate change models

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ABSTRACT

Predictive studies play a crucial role in the study of biological invasions of terrestrial plants under possible climate change scenarios. Invasive species are recognized for their ability to modify soil microbial communities and influence ecosystem dynamics. Here, we focused on six species of allelopathic flowering plants—*Ailanthus altissima*, *Casuarina equisetifolia*, *Centaurea stoebe* ssp. *micranthos*, *Dioscorea bulbifera*, *Lantana camara*, and *Schinus terebinthifolia*—that are invasive in North America and examined their potential to spread further during projected climate change. We used Species Distribution Models (SDMs) to predict future suitable areas for these species in North America under several proposed future climate models. ENMEval and Maxent were used to develop SDMs, estimate current distributions, and predict future areas of suitable climate for each species. Areas with the greatest predicted suitable climate in the future include the northeastern and the coastal northwestern regions of North America. Range size estimations demonstrate the possibility of extreme range loss for these invasives in the southeastern United States, while new areas may become suitable in the northeastern United States and southeastern Canada. These findings show an overall northward shift of suitable climate during the next few decades, given projected changes in temperature and precipitation. Our results can be utilized to analyze potential shifts in the distribution of these invasive species and may aid in the development of conservation and management plans to target and control dissemination in areas at higher risk for potential future invasion by these allelopathic species.

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1. Introduction

Invasion by exotic plants is considered a significant threat to the biodiversity of native communities, with environmental and economic costs of nearly \$1.3 trillion globally from 1970 to 2017 and exceeding \$162 billion in 2017 alone (Diagne et al., 2021). These non-natives may alter soil microbial communities and the structures of native ecosystems such that changes in energy flow, decomposition, and cycling of organic matter and nutrients drive

many natives to local extinction (Vilà et al., 2011; Ito and Reshi, 2013; Stefanowicz et al., 2017). A recent meta-analysis involving 1041 cases of plant invasion from 135 plant taxa found that invasive plants reduced the fitness and growth of native plants by 47.1% and 22.1%, respectively. Modifications to the plant community structure were further cited with diminished species diversity (50.7%) and abundance (43.5%; Vilà et al., 2011).

Various hypotheses have been proposed to explain the invasive success of exotics, but two predominate: “the natural enemies hypothesis” (i.e. enemy release) and “the evolution of increased competitive ability hypothesis” (EICA; Callaway and Ridenour, 2004; Hierro et al., 2005). According to the first hypothesis, invasives lack enemies in the new range. This also suggests that the presence status of invasive species (i.e. absent or incipient/in non-equilibrium expansion/in equilibrium) warrants different modeling parameters and management protocols (Suárez-Mota

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et al., 2016). The second hypothesis suggests that exotics have increased competitiveness in the novel range due to new selection pressures. Both hypotheses consider primarily consumer–plant interactions and lack substantive information on interplant interactions. Callaway and Ridenour (2004) proposed an alternative to explain the invasive success of many exotics. Rather than attributing the proliferation of exotics to a lack of predators/competitors or increased tolerance to various climates in invaded ranges, their “novel weapons hypothesis” posits that the augmented competitiveness of certain invasives is due to their production of harmful chemical compounds, or “novel weapons”, not experienced by the native flora (Callaway and Ridenour, 2004). Because natives are much more susceptible to the allelochemicals released by exotic invaders, allelopathy may contribute to successful biotic invasions via non-resource exchanges between plants (Callaway, 2002).

Effective management of invaders can be aided by predictions of potential distributional shifts under various bioclimatic variables through time. To develop long-term solutions, information from Ecological Niche Models (ENMs) and Species Distribution Models (SDMs) can provide possible future distributional scenarios and help minimize risks and maximize conservation results (Guisan and Zimmermann, 2000). Although modeling parameters may vary across studies (e.g. environmental data used or using fundamental vs. realized niches for predictions), there is consensus that ecological niche models provide useful information, illustrating possible future scenarios of shifts in suitable geographic areas (Pearson and Dawson, 2003; Soberon and Peterson, 2005).

Projecting species distributions based on environmental characteristics onto geographic space, whether a region within or outside the native range or in the present or future, can be challenging. The validity of correlative models forecasting invasiveness after introduction of exotic species is contingent on assumptions that (1) the niche of the species is conserved, and (2) species are in climatic equilibrium (i.e. their current distributions are reflective of their climate tolerance; Early and Sax, 2014). While some have discussed the possibility of niche shifts in some invasive species (Broennimann et al., 2007; Gallagher et al., 2010; Mukherjee et al., 2012; Goncalves et al., 2014), others have indicated that these cases are limited and niche conservatism may be assumed for most terrestrial plant invasions (Petitpierre et al., 2012). Even so, differences between fundamental and realized niches remain as challenges when modeling future distributions (Soberon and Peterson, 2005).

The goal of this research was to estimate potential geographic shifts in suitable climate and geographic areas at risk of invasion under possible climate change scenarios for six allelopathic and invasive flowering plants: *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae), *Casuarina equisetifolia* L. (Casuarinaceae), *Centaurea stoebe* ssp. *micranthos* (Gugler) Hayek (Asteraceae), *Dioscorea bulbifera* L. (Dioscoreaceae), *Lantana camara* L. (Verbenaceae), and *Schinus terebinthifolia* Raddi (Anacardiaceae) (Fig. 1). Allelochemical secretions by each of these species have detrimental impacts on native plant species and may include phytotoxicity, inhibition of seed germination, and reduced root length, among others (Heisey, 1996; Kong et al., 2006; Perry et al., 2007; Procópio et al., 2015; Eneh et al., 2016; Oksari et al., 2019). Other allelopathic mechanisms may act indirectly by influencing soil properties, altering nutrient status, and disrupting microbial symbiosis. Thus, allelopathic invasives have extensive effects in the ecosystems that they invade. In this study, we obtained plant occurrence and climatic data to develop SDMs of these allelopathic invaders to evaluate how areas of suitable climate may shift under climate change regimes.

2. Methods

2.1. Occurrence data acquisition and processing

Occurrence data for each species were obtained from the *Integrated Digitized Biocollections* (iDigBio) and *Global Biodiversity Information Facility* (GBIF) databases via the *spocc* package in R (Chamberlain et al., 2018; R Core Team, 2017). Spatial bias can reduce the predictive power of SDMs, which may be mitigated by subsampling the data and spatially filtering occurrence localities (Beck et al., 2014; Boria et al., 2014). Thus, our records were cleaned so that data with duplicates, incomplete coordinates, unlikely coordinates (e.g., 0,0), or those lacking environmental data were removed using the *scrubr* v.0.1.1 package in R (Chamberlain, 2016). Points falling outside of the respective training region for each species (see section 2.2 below) were also removed. After the cleaning process, 162 to 753 occurrence points remained for each species (*A. altissima* = 301, *C. equisetifolia* = 427, *C. stoebe* ssp. *micranthos* = 320, *D. bulbifera* = 319, *L. camara* = 753, *S. terebinthifolia* = 162). These presence points were then rarefied to 100 points using the *thin_max.R* script available at <http://enmtools.blogspot.com/>.

2.2. Climatic data processing and niche model training region delimitation

For four species, training regions were generated so that presence points from the native ranges of each species could be used to train models: *C. equisetifolia* (native to South Asia and Australia), *D. bulbifera* (native to Africa and Asia), *L. camara* (native to the American tropics), and *S. terebinthifolia* (native to South America; Barkley, 1944; Wilson and Johnson, 1989; Wilkin, 2001; Taylor et al., 2012). For *A. altissima* and *C. stoebe* ssp. *micranthos*, native to Asia and eastern Europe, respectively (Burch and Zedaker, 2003; Treier et al., 2009), the paucity of collection records obtained for the native ranges of these species precluded proper model development in those regions. Thus, models for these two species were trained on data from the United States, where the number of records was sufficient for model development. Due to evidence of possible niche shifts following invasion for *C. stoebe* ssp. *micranthos* (Broennimann et al., 2007), model training with invasive occurrences may also better capture new occupied niche parameters.

Worldclim V1 variables BIO1 through BIO19 at a 2.5 arc minute resolution (~5 km² at the equator) were used in model development (Hijmans et al., 2005). To delimit the training regions, we used *rgeos* v.0.4–2 in R (Bivand et al., 2018) to produce a convex hull around records that occurred within the native region and added a 0.25-degree buffer around the convex hull. This region corresponded to native ranges for each species, with the exceptions of *A. altissima* and *C. stoebe* ssp. *micranthos*, for which the introduced ranges were used due to a limited number of occurrences in the queried databases in the native ranges. The native region, rather than invaded range, was used in model training for *C. equisetifolia*, *D. bulbifera*, *L. camara*, and *S. terebinthifolia* following Beans et al. (2012), who indicated that superior distribution predictions are obtained while training with native occurrence data. The findings of Beans et al. (2012) are likely due to a need for environmental equilibrium within the training region, which invasive species in new areas have not yet reached (Václavík and Meentemeyer, 2012). Bioclimatic variables were then masked and clipped to these training regions with cropping functions in R package *raster* v.2.6–7 (Hijmans, 2017). A Multivariate Environmental Similarity Surfaces (MESS; Elith et al., 2010) analysis was performed using the R package *dismo* (Hijmans et al., 2017) for each species to compare the climates of the training region to the climates projected (e.g.,



Fig. 1. Photographs of plant species analyzed in this study: (A) *Ailanthus altissima*, (B) *Casuarina equisetifolia*, (C) *Centaurea stoebe* ssp. *micranthos*, (D) *Dioscorea bulbifera*, (E) *Lantana camara*, and (F) *Schinus terebinthifolia*.

climate of North America under the rcp4.5 model in the year 2050) onto for downstream analyses and identify regions where extrapolation may occur for predicting areas of suitable climate, thus reducing the reliability of the predictions.

2.3. Model development

Maxent v.3.3.3k (Phillips et al., 2006) was used to develop models for each species in R, using ENMEval v.0.3.0 (Muscarella et al., 2014). Feature-class (FC) combinations of Linear, Hinge, Linear + Quadratic, Linear + Hinge + Quadratic, and Linear + Quadratic + Product and eight specific regularization multiplier (RM) values beginning from 0.5 and increasing in increments of 0.5–4.0 were used to develop our models. Five FC combinations and eight RM values produced 40 models that were used to test and evaluate each species (Table A.1 contains features included in each model used in downstream analyses). This approach allowed us to test multiple models and minimize overfitting (i.e. reduce the number of features included in the model) while maintaining high predictive power.

We then conducted the “block” method to assess our models by applying longitudinal and latitudinal lines to split localities of occurrence into four bins, where the presence data were then partitioned. Although the area under the Receiver Operating Characteristic curve (AUC) has been used as the standard approach for model comparison in the past, it can be misleading and easily biased. Models could be overfit, which would make model assessment inaccurate (Lobo et al., 2008; Jiménez-Valverde, 2012). Instead, we evaluated our models using ΔAICc (Akaike information criterion with sample size correction) scores, such that models scoring zero were converted into a logistic output format. These were then projected onto the respective training region for each species, as well as current and future climate models for North America, which were accordingly used for further analyses. For projections under future climate scenarios, three models were selected for evaluation: MIROC5 (Model for Interdisciplinary Research On Climate), CCSM4 (Community Climate System Model), and GFDL-CM3 (Geophysical Fluid Dynamics Laboratory Climate Model). Models were projected onto areas using each climate model for North America for the current climate and the predicted climates of 2050 and 2070 under two representative concentration pathways (rcp), rcp4.5 and rcp8.5. These represent two models of carbon emissions: predicted atmospheric carbon concentrations under current, intermediate emissions scenario, rcp4.5, and an extreme emissions scenario, rcp8.5.

2.4. Analyses

A composite prediction map for future climate scenarios was built in R by taking the mean of the suitability scores for each future climate projection for a given year and rcp for each species. While the

composite prediction may be more conservative in nature, each selected climate change model has unique parameters that allow greater accuracy at different levels of regional and continental climate (Sheffield et al., 2013). CMIP5 models of North America, in general, perform well in predicting broad-scale climates, although specific biases are present for different variables (e.g. temperature, precipitation, soil, regional climatic features such as monsoons, extratropical cyclones, and Great Plains low-level jet—a rapidly moving stream of air in the lower atmosphere). The average projection would take into consideration the strengths of each climate model.

Binary predicted occurrence rasters were generated to compare the sizes of geographic areas of suitable climate in the present and the future for each species. For each species, suitability scores from the present climate prediction raster were sampled at all presence points. Cells with a predicted suitability score that met or surpassed the threshold of minimum predicted suitability at an occurrence point for a given species, or the minimum training presence (MTP), were converted into a predicted presence for current and composite future predictions. Cells that failed to meet the threshold were converted into a predicted absence.

Calculation of area in km² for each SDM was conducted in R through biomod2 v.3.3–7 (Thuiller et al., 2016). To assess changes in ranges from present to future projections, biomod2's RangeSize command was used to give quantitative trends in regions where a species has already established presence and in regions that are currently unoccupied. We compiled the composite prediction maps for each species under 2050 rcp4.5, 2050 rcp8.5, 2070 rcp4.5, and 2070 rcp8.5 climatic conditions and generated at-risk heat maps by overlapping SDMs for all six species for each climatic scenario in QGIS v.2.18.13. The heat maps, ranging from 0 to 6, with 0 being no predicted presence for the included species and 6 being predicted presences for all included species within a cell, allowed us to determine regions potentially threatened by multiple species analyzed within our study.

3. Results

3.1. Contributions of bioclimatic variables

Patterns in percent contribution and permutation importance from our model statistics indicate several small contributions from different variables across all six species, with two or three major variable contributions for each species. Of the six invasive species investigated, *S. terebinthifolia* was more influenced by precipitation variables than any other species studied here, yielding greater percent contributions and permutation importance for layers BIO12 through BIO19 (Table A.2). In fact, it was one of two cases, the other being *D. bulbifera*, for which contributions of data relating to precipitation surpassed those of temperature in our model development. The other four species were correspondingly more

dependent on temperature predictions (BIO1 through BIO11). We note that while temperature and precipitation play a crucial role in forming species distribution projections, there are other excluded factors, such as soil type and land cover, that also influence invasion by alien species. Nonetheless, most of our species exhibit a wide tolerance of soil and nutrient conditions, which may help alleviate related limitations of the models.

3.2. Assessing reliability of future climate projections

MESS outputs for each species indicated that the future climates within the projection region largely resided within the parameters of our training region, demonstrating sufficient reliability for model transferability (Fig. A.1–A.6). However, a few special cases must be independently assessed. For *Centaurea stoebe* ssp. *micranthos*, our models displayed a large overlap of parameters corresponding to the training region because the species was both trained in and projected onto North America. *A. altissima*, the other species for which this model prediction method was used, did not exhibit such trends, likely as a result of a training region that encompassed lower latitudinal regions than *C. stoebe* ssp. *micranthos*. This observation would skew the climatic variables and training parameters such that some northern regions would no longer fall within reliable interpolative boundaries. For the remaining four species, SDMs were trained in regions with appropriate ranges of parameters to allow for interpolation within the projection region.

3.3. Evaluation of distribution trends under future climate scenarios

Our models analyzing climatic suitability for the six species studied here corresponded well to their respective current distributions as presented by the Biota of North America Program (BONAP; www.bonap.org). The results of our study showed that regions at greatest risk of multi-species invasion are primarily in the northeastern United States. These areas are distinguished by the heat maps (Fig. 2) of overlapping binary SDMs and suggest prospective expansion of suitable climate into southern Canada. Comparisons of map B to map C and of map D to map E (Fig. 2) indicate a northward shift in maps C and E, corresponding to more extreme bioclimatic predictions underlying C and D. Similarly, comparisons of B to D and of C to E show that the projected northward trend (under both rcp4.5 and rcp8.5) increases with time, from 2050 to 2070.

Quantitative results for changes in the size of predicted ranges exhibited predominantly positive values for all six species (Table 2; Fig. A.7–A.12). Positive values for range change indicate greater predicted gains in unoccupied sites than losses in occupied sites. Species distribution areas also correspond with range change values, exhibiting overall increases in area through time and with extremity of bioclimatic variables.

Centaurea stoebe ssp. *micranthos* and *D. bulbifera* also appeared to display the smallest expansions/largest contractions relative to their estimated present distributions within the United States. Both species fluctuated between –7% and 21% in range change percentages respective to years (2050 or 2070) and their extremity (rcp4.5 or rcp8.5; Table 2). Despite similar net changes in their predicted areas of suitable climate, however, the predicted northward shift in distribution of *C. stoebe* ssp. *micranthos* appears to occur more rapidly than that of *D. bulbifera*, which is supported by comparatively larger values for areas lost and areas gained (Table 2). In fact, the predicted changes in the distribution of *D. bulbifera* may occur more slowly than any of the other species examined.

In contrast, the species that is predicted to show the fastest change in distribution of suitable habitat is *A. altissima*. The range

change percentages for *A. altissima* far exceed those for any other species in our study. In addition, *A. altissima* exhibited values predicting gains in habitat suitability in new regions that surpassed predicted loss in suitable habitat by a substantial margin (Table 2).

4. Discussion

The goal of this research was to estimate potential geographic shifts in suitable climate and geographic areas at risk of invasion under possible climate change scenarios for six allelopathic invasive angiosperm species in North America. We developed SDMs using climatic data to predict possible shifts in the distribution of suitable climatic conditions for these allelopathic invaders, but recognize that biotic factors excluded from our model development, including allelopathy itself and other biotic interactions, also play crucial roles in shaping current and potential future distributions. As is the case in many current applications of ecological niche models, considerations of species traits and other organismal interactions would enhance the models and help further determine potential rates and extents of invasions into existing plant communities (Chen et al., 2011).

With projected climate change scenarios, we should expect to see shifts of current species distributions per BONAP (Biota of North America Program, www.bonap.org) and Kartesz (2015), in accordance with changes in temperature and precipitation patterns. Species with tolerance for a wider range of climatic conditions may be more competitive than those limited by narrow tolerance (Higgins and Richardson, 2014). For example, species that have broad native ranges often occur in a variety of habitats in a broader range of climatic regimes (Pyšek et al., 2004, 2009). *A. altissima* and *L. camara* have considerable tolerance to extreme temperatures and varying precipitation levels (Burch and Zedaker, 2003; Taylor et al., 2012). Other species, such as *S. terebinthifolia*, exhibit moderate tolerance for climatic extremes (e.g., low temperatures and high precipitation), while *C. equisetifolia* and *D. bulbifera* are less tolerant of such conditions (Barkley, 1944; Wilson and Johnson, 1989; Wilkin, 2001). Nonetheless, there are attributes that also enhance the competitive success of a species. Nitrogen-fixing symbiosis with the actinomycete *Frankia* in *C. equisetifolia* allows occupation of nutrient-poor soils (Danso et al., 1992). *C. stoebe* ssp. *micranthos* similarly thrives on dry and coarse soils that limit many competitors from establishing presence (Treier et al., 2009). However, all six species studied here flourish in warm environments (Barkley, 1944; Chicoine et al., 1986; Wilson and Johnson, 1989; Wilkin, 2001; Burch and Zedaker, 2003; Taylor et al., 2012), suggesting expansion of future distributions as the climate in North America continues to warm.

The trends reported here appear to be influenced by both time and rcp, with rates of carbon emissions being correlating with changes in temperature and precipitation patterns. Range contractions and spread generally correspond to temperature and/or hydrologic constraints as a result of warming and altered precipitation patterns (Hellmann et al., 2008). As climate changes, many areas that are currently occupied by a given species may become unsuitable, causing loss of distribution area (Table 1). Conversely, areas that were once unsuitable may become climatically suitable, leading to expansion into new geographic ranges.

The relative contribution of each bioclimatic variable used in model development varied with respect to each species (Table A.2). Changes in climate such as increases in temperature and precipitation have been shown to increase the performance of invasive species relative to native species, under the conditions of global warming and enriched atmospheric CO₂ (Liu et al., 2017). The effects of temperature, nitrogen, CO₂, precipitation, and burn conditions on *Centaurea solstitialis*, for instance, have been discovered to

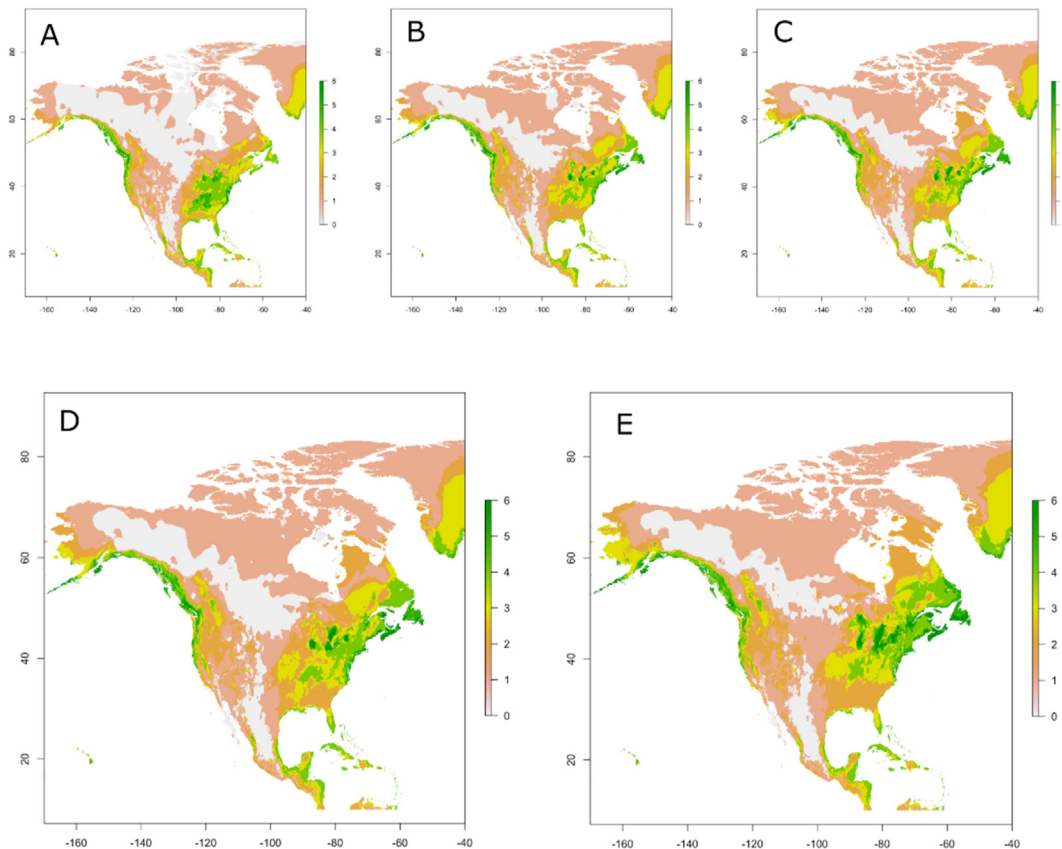


Fig. 2. Heat maps showing areas at risk constructed by combining projections of the six species. Projections are (A) current, (B) 2050 rcp4.5, (C) 2050 rcp8.5, (D) 2070 rcp4.5, and (E) 2070 rcp8.5. Species occupation of an area can range from 0 to 6, with 0 representing no suitable climate for any of the six species investigated present and 6 representing predicted suitable climate for all six species.

impact above-ground shoot biomass. A study conducted in California, an introduced range, showed that elevated CO₂ concentrations increased the biomass of *C. solstitialis* more than six-fold, whereas nitrate deposition increased biomass by over three-fold. The remaining variables—temperature, precipitation, and burn condition—influenced shoot biomass less dramatically and more variably (Dukes et al., 2011). Temperature and precipitation were the key considerations from which our models were developed.

The results of our study and predicted distributions show important trends (Fig. 2). By juxtaposing regions of greater species density in the heat maps for 2050 and 2070, we observed a distinct northward shift in suitable climate, particularly to the northwestern and northeastern parts of North America (Fig. 2; Fig. A.7–A.12). This pattern is more extreme for rcp8.5 than for rcp4.5. Likewise, individual SDMs also exhibit this northward shift (Fig. A.7–A.12), while species distribution areas and range size outputs (Tables 1 and 2) indicate greater numerical values for 2070

and rcp8.5 in terms of distribution areas and range change percentages.

The northward shift of the species examined here agrees well with findings for other species (non-allelopathic) examined to date across North America and the Northern Hemisphere. Many studies have projected a northern movement of plants in the coming decades with climate change (Walther, 2003; McKenney et al., 2007; Bradley et al., 2010). In a climate suitability modelling study on 387 invasive species, a group found evidence for greater invasion risk for coastal biomes and high-latitude areas across multiple continents, including North America. As a result, several terrestrial and aquatic ecoregions (e.g. temperate broadleaf and mixed forests, temperate conifer forests, temperate coastal rivers, etc.), including northwestern and northeastern North America, may be expected to experience a significant risk for invasion and loss of biodiversity in the near future (Wang et al., 2019). Other studies conducted in regions in the Southern Hemisphere have identified correlates to

Table 1

Predicted species distribution areas obtained from each species corresponding to the year and extremity of the bioclimatic variables utilized for the projections. All values are given in km².

Climatic condition under future scenarios	<i>Ailanthus altissima</i>	<i>Casuarina equisetifolia</i>	<i>Centaurea stoebe</i> ssp. <i>maculosa</i>	<i>Dioscorea bulbifera</i>	<i>Lantana camara</i>	<i>Schinus terebinthifolia</i>
Training	3473394.1	2359210.9	4145633.5	14785943.7	8220509.7	952140.7
Current (in North America)	3870914.2	1578802.7	6384496.2	7497471.8	8005275.4	7081753.6
2050 rcp4.5	5457996.3	1573399.2	5552314.1	7900264	10341260.1	8483122.5
2070 rcp4.5	5907973.4	1688880.1	5933793	7852218.5	10524067.3	8541709.2
2050 rcp8.5	5582031.5	1910488.6	5821603.2	7996914.6	10644485.3	8534661.4
2070 rcp8.5	7156489.1	2057113.9	6460208.2	8098976.4	10868319.7	9474404.7

Table 2

Range size outputs for 2050 and 2070 under current (rcp4.5) and extreme (rcp8.5) climate scenarios. Stable0* represents unoccupied area that is predicted to be unoccupied in the future. Stable1** represents occupied area that is predicted to be occupied in the future.

<i>Ailanthus altissima</i>							
Climatic Condition Under Future Scenarios	Loss (pixels)	Stable0* (pixels)	Stable1** (pixels)	Gain (pixels)	Percent Loss of Occupied Sites (%)	Percent Gain of New Sites (%)	Species Range Change (%)
2050 rcp4.5	44958	1635775	184993	157600	19.551	68.536	48.985
2070 rcp4.5	53149	1592659	176802	200716	23.113	87.286	64.173
2050 rcp8.5	57155	1609423	172796	183952	24.855	79.996	55.141
2070 rcp8.5	70286	1476802	159665	316573	30.566	137.67	107.104
<i>Casuarina equisetifolia</i>							
2050 rcp4.5	24556	1906134	63884	28752	27.766	32.51	4.744
2070 rcp4.5	25965	1896038	62475	38848	29.359	43.926	14.567
2050 rcp8.5	17489	1892562	70951	42324	19.775	47.856	28.081
2070 rcp8.5	31723	1865072	56717	69814	35.87	78.939	43.07
<i>Centaurea stoebe ssp. maculosa</i>							
2050 rcp4.5	102292	1523444	321815	75775	24.119	17.867	-6.252
2070 rcp4.5	115870	1465776	308237	133443	27.321	31.464	4.144
2050 rcp8.5	123629	1466032	300478	133187	29.15	31.404	2.254
2070 rcp8.5	155663	1356862	268444	242357	36.704	57.145	20.442
<i>Dioscorea bulbifera</i>							
2050 rcp4.5	5273	1498234	481154	38665	1.084	7.949	6.865
2070 rcp4.5	10824	1493560	475603	43339	2.225	8.91	6.684
2050 rcp8.5	4204	1492092	482223	44807	0.864	9.211	8.347
2070 rcp8.5	11497	1472641	474930	64258	2.364	13.21	10.847
<i>Lantana camara</i>							
2050 rcp4.5	20632	898904	803481	300309	2.504	36.44	33.937
2070 rcp4.5	27040	868435	797073	330778	3.281	40.137	36.856
2050 rcp8.5	23223	863179	800890	336034	2.818	40.775	37.957
2070 rcp8.5	29643	830464	794470	368749	3.597	44.745	41.148
<i>Schinus terebinthifolia</i>							
2050 rcp4.5	23625	1419229	456237	124235	4.923	25.89	20.966
2070 rcp4.5	28550	1409802	451312	133662	5.95	27.854	21.905
2050 rcp8.5	31298	1408541	448564	134923	6.522	28.117	21.595
2070 rcp8.5	18288	1350861	461574	192603	3.811	40.137	36.326

these observations. For instance, a modelling study on invasive plants in Australia concluded a poleward shift towards southern regions of the country by 2050 (O'Donnell et al., 2012). Together, these results suggest that invasion hotspots are likely to shift towards the poles as climate change progresses. Furthermore, in some cases, plants are projected to move upslope in mountain ranges to escape warmer and drier projected climates (Liang et al., 2018). These findings support the identification of potential invasion hotspots that are consistent with our results discussed herein.

Under future climate scenarios, each species evaluated in our study poses a possible strong threat to the biodiversity of existing natural communities (i.e. localities in which these species are predicted to have suitable climate). Two species that are of particular concern are *A. altissima* (species with the greatest potential range shifts) and *C. equisetifolia* (species with a rapid expansion potential), according to range shift data (Table 2). An important factor for consideration in exotic plant invasions is dispersal mechanisms. Of the six species we studied, *A. altissima*, *C. stoebe ssp. micranthos*, and *C. equisetifolia* are all known to disperse primarily by wind. *A. altissima* and *C. equisetifolia* both produce relatively small samaras, varying in size from 2 to 3 cm for *A. altissima* and from 0.5 to 1 cm for *C. equisetifolia* (Shiels, 2011; Planchuelo et al., 2016). Kaproth and McGraw (2008) also found that secondary dispersal mechanisms, such as water, play a significant role in the dispersal success of *A. altissima*. Seed dispersal for *C. stoebe ssp. micranthos*, although similarly facilitated by wind, is structurally different with fruits that are achenes. These fruits

may be disseminated through human disturbance, consistent with high abundance of the species in urban areas (Duncan et al., 2017).

In contrast, *S. terebinthifolia* and *L. camara* have biotic seed dispersal mechanisms. Small fruits are often eaten by animals, primarily birds, and may be dispersed vast distances (Shiels, 2011; Dlamini et al., 2018). Seeds from *S. terebinthifolia* also exhibit interactions with insects, such as ants, which further augment their dispersal success. Because wind-dependent and animal-dependent dispersal mechanisms both have great range expansion potential, we may expect these species to be more widely disseminated than *D. bulbifera*. As dispersal of *D. bulbifera* takes place in the form of bulbils, gravity plays a dominant but limiting role for the dispersal of this species, while secondary mechanisms such as water- or animal-mediated dispersal facilitate greater dispersal distances (Rayamajhi et al., 2016). When *D. bulbifera* is compared to the other five allelopathic invasives in this study, we may expect its distributional shifts to be more moderate. Although dispersal mechanism was not a factor included in the development of our models, the dispersal capabilities that would affect distributional shifts generally reflect changes in suitable climate for each species, as in the case of *D. bulbifera*, which exhibits some of the smallest numerical values among the six species.

Advantageous dispersal mechanisms not only enable invasives, such as *A. altissima* and *C. equisetifolia*, to expand into new ranges faster than natives, but may also confer greater competitive advantage over native populations in terms of acquiring resources (Gioria and Osborne, 2014; Guzzetti et al., 2017). If the natives and

invasives continue to co-occur, these differences may result in local extinction of natives, warranting strategic control initiatives to prevent the spread of invasive species (Catford et al., 2018). With our results, agencies for plant conservation and land management can develop cost-effective methods of containment that prioritize areas at greatest risk of invasion for these six species investigated here. Establishing Early Detection and Rapid Response (EDRR) protocols may allow land managers to establish monitoring programs that detect populations when they are small. In the past, management was primarily accomplished through chemical, biological, and mechanical strategies in restoring natural disturbance regimes (Hellmann et al., 2008). While success rates vary among these methods, advances in biotechnology call for novel techniques in regulating invasive species. One study conducted on compounds extracted from three invasive plant species in the Po plain of northern Italy, *Lonicera japonica*, *Phytolacca americana*, and *Prunus serotina*, proposed exploitation of fruits via bioprospecting to prevent seed dispersal and limit invasion (Guzzetti et al., 2017). This approach would not only benefit industries requiring commercially valuable compounds but might also provide a unique solution to the complex dilemma of invasion. For allelopathic species rich in biochemical compounds, such as those investigated here, the proposition of using bioprospecting appears viable. *D. bulbifera*, for instance, provides a folk remedy used in treating cancer (Sharma et al., 2017). In a recent study, bulbils of *D. bulbifera* were isolated and purified to produce mannose-binding lectin, which could influence cancer and HIV treatment regimens (Sharma et al., 2017). *S. terebinthifolia*, another species with anticancer properties, similarly exhibits potentially valuable applications (Oliveira et al., 2018). Extracts of other species, such as *C. equisetifolia* and *L. camara*, may play a role in antibiotic research (Swamy, 2017; Shriniwas, 2017), while *A. altissima* may be utilized as a potential herbicide to control unwanted vegetation (Meng et al., 2015). Nevertheless, further analyses must be conducted regarding the effects of allelochemicals, the plausibility of their commercial integration, and seed/fruit collection strategies (to limit dispersal) before developing feasible programs.

There is evidence indicating detrimental impacts to other plants due to the secretion of allelochemicals by the six species in our study. Available data suggest that allelopathy may influence invasive success of the species studied here within invaded ranges (Achhireddy and Singh, 1984; Gordon, 1998; Morgan and Overholt, 2005; Mummey and Rillig, 2006; Gómez-Aparicio and Canham, 2008; Usman et al., 2014). Extracts from *C. equisetifolia*, *D. bulbifera*, and *S. terebinthifolia* have been found to contain compounds associated with phytotoxic effects in other species (Procópio et al., 2015; Eneh et al., 2016; Oksari et al., 2019). Allelochemicals in *A. altissima* (ailanthone; Heisey, 1996), *C. stoebe* ssp. *micranthos* (racemic (\pm)-catechin; Perry et al., 2007), and *L. camara* (lantadene A and B; Kong et al., 2006) similarly result in inhibition of seed germination, reduction of root length, and herbicidal activities on neighboring species. Other evidence suggests that changes in climatic conditions may enhance the toxicity of allelochemicals through higher concentrations of allelochemical secretion (Pedrol et al., 2006; Šežienė et al., 2012). This chemical enhancement may suggest an even greater future threat by allelopathic invasives, with impacts on a new suite of native species. Although incorporating the role of these biochemicals into our modeling analyses is beyond the feasibility of the current study, it remains a possible rich area of future research modeling. For example, these chemical characteristics might alter the predictions of future distributional shifts when incorporated into more complex models. Despite such limitations, we have identified geographic regions that will likely experience dramatic increases in risk for invasion by six allelopathic invasives, under two models of

future climate for 2050 and 2070: current climate trends (rcp4.5) and extreme climate conditions (rcp8.5). The results should be useful for management and control of these species as climate change alters potential species distributions.

Stemming the distribution shifts of these six invasive species, exacerbated by changes in climate, necessitates quick, large-scale responses coordinating research and management. Although our results can provide assistance, there are other limitations. Most notably, the modelling performed in this study does not account for biotic interactions between allelopathic and native species. Future research should examine how natives are chemically affected by compounds synthesized by allelopathic species and the extent of range contractions experienced by natives in invaded ranges. Another limitation is that our models and projections to predicted future climates are static and do not take into account niche evolution over the timeframe assessed in this study (present to 2050 or 2070). Our analyses are best considered as a first approximation of the future distributional trends of six highly invasive species having allelopathic traits. Subsequent investigations should employ novel models that might better assess the role of allelopathy, as well as determine which native species in a newly invaded region may be most severely impacted by the invasives studied here. Finally, the results obtained here are likely relevant to other allelopathic invasives and provide predictions for their responses to ongoing climate change.

Author contributions

A.W. and A.E.M. designed the study, performed the modelling, and analyzed the data. A.W. wrote the initial draft of the manuscript, and all authors contributed in interpretation/discussions of the data and revisions of the manuscript. All authors approved the final manuscript for publication.

Data statement

The cleaned occurrence data used in ecological niche model development are available at 10.5281/zenodo.4989053.

Declaration of competing interest

The authors have no conflict of interest.

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Appendix A Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pld.2021.06.010>.

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