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Invasion Risk in a Warmer World: Modeling Range Expansion and Habitat Preferences of Three Nonnative Aquatic Invasive Plants

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Biological invasions and climate change pose two of the most important challenges facing global biodiversity. Of particular importance are aquatic invasive plants, which have caused extensive economic and environmental impacts by drastically altering native biodiversity and ecosystem services of freshwater wetlands. Here, we used the maximum entropy model, Maxent, to model the potential range expansion of three nonnative aquatic invasive plants: alligatorweed, limnophila, and giant salvinia, throughout the continental United States under current, 2030 to 2059 (2040), and 2070 to 2099 (2080) climate scenarios. Maxent is a popular method to model predicted current and future species distributions based on biogeography and climate. Alligatorweed, limnophila, and giant salvinia are noxious invaders of freshwater habitats in the southeastern United States and cause economic and ecological loss. In addition, we analyzed each species' habitat preference based on wetland type, occurrence in man-made habitats, and distance to the nearest stream to better understand what future habitats are at risk and how these species spread. Our results show that in 2040 and 2080 climate scenarios, all three species have the potential to increase their range throughout the northeastern United States and as far as New York and Massachusetts. The spatial distribution of alligatorweed was primarily determined by precipitation of the warmest quarter (15.8%), limnophila was primarily determined by precipitation of the warmest quarter (52.2%) and mean temperature of the coldest quarter (21.8%), and giant salvinia was primarily determined by the mean temperature of the coldest quarter (24.3%). All three species were found significantly more frequently in lakes and ponds than in other freshwater habits. Giant salvinia was found significantly more often in man-made wetland habitats. In order to reduce the detrimental impacts of these species, land managers in the northeastern United States should concentrate early detection and rapid response management in lakes, ponds and man-made wetland habitats.

Nomenclature: Alligatorweed, *Alternanthera philoxeroides* (Mart.) Griseb.; giant salvinia, *Salvinia molesta* Mitchell; limnophila, *Limnophila sessiliflora* (Vahl) Blume.

Key words: Aquatic invasions, climate change, freshwater wetlands, man-made habitats, Maxent.

Biological invasions and climate change pose two of the most important global challenges throughout the next century due to their extensive economic and environmental impacts (Pimentel et al. 2005; Thomas et al. 2004; Walther et al. 2009). Humans have greatly increased global biotic interchange of species in the last century via efficient modes of transportation and increased trade routes (Drake and Lodge 2004). From increased human movement there is a greater opportunity for intentional and unintentional introduction of nonnative species (Rahel and Olden 2008). With widespread globalization demands continuing, human-induced introductions will become more prevalent as a larger number of species are assisted in overcoming their previous natural barriers to travel to new locations and become invasive (Hulme 2009; Westbrooks 1998).

Biological invasions have caused negative environmental impacts on the individual, population, and landscape levels (Parker et al. 1999), which is why invasive species are considered the second greatest threat to native biodiversity (Wilcove et al. 1998). These impacts include outcompeting native species (Alvarez and Cushman 2002), altering nutrient cycling (Ehrenfeld 2003; Vitousek and Walker 1989), and decreasing biodiversity (McGeoch et al. 2010). In

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Management Implications

Aquatic invasive plant species are well known to have dramatic impacts on the habitats they invade. The impacts of these species include decreases in plant and animal biodiversity, altered nutrient cycling, and impact navigation and recreation of inland waterways. Climate change is expected to amplify the number of aquatic biological invasions by changing climatic conditions, particularly by warmer temperatures, increasing the likelihood that previously climatically restricted species will be successful in northern latitudes. Because of the serious consequences aquatic invasive plants pose to aquatic and wetland habitats, understanding the future range expansion of these species is imperative for early detection and management. Alligatorweed, limnophila, and giant salvinia are noxious invaders of freshwater habitats in the southeastern United States. In this study, we ask the following questions: What is the potential for range expansion of three highly invasive plant species in current and future climate scenarios? and What are the aquatic and wetland habitat preferences of these three species? Our results show that with future climate change, and consequently, warmer temperatures, these three species will have the potential to expand their ranges into the mid-Atlantic and northeastern United States. Lakes and ponds are at increased risk for future invasion because all three species were more frequently found in these habitats over other freshwater wetland types. Furthermore, giant salvinia was found significantly more often in man-made wetland habitats, which could increase its chance of flourishing in disturbed environments. The results of our study provide a first step in managing the future spread of alligatorweed, limnophila, and giant salvinia in the continental United States. In particular, land managers should concentrate early detection and rapid response management in lakes, ponds and man-made wetland habitats to effectively control the spread of these species and reduce overall costs of managing these species.

addition to detrimental environmental impacts, humans also spend an immense amount of time and resources on the removal, management, and prevention of invasive species (Courchamp et al. 2003; Daehler et al. 2004). In 2004, $120 billion dollars was spent in the United States on environmental damage caused by invasive species (Pimentel et al. 2005).

Climate change is expected to amplify the number of biological invasions by changing climatic conditions at every stage of the invasion process, increasing the likelihood that previously restricted species will be successful (Bradley et al. 2010; Walther et al. 2009). Hellmann et al. (2008) highlighted five potential influences that climate change could have on invasive species, which include assisting transport and introduction, increasing establishment of new invasives, altering the impacts of previously established invasive species, modifying range distributions, and altering management strategies. In addition, as climate change causes species to either adapt, migrate, or go extinct, ecological niches that were previously occupied can open, providing further opportunity for a nonnative invasive species to establish (Parmesan 2006). These alterations to current environments can create favorable conditions for invasive species to increase their ranges and establish in previously inadequate areas (Walther et al. 2009). Changes in average temperature and precipitation in higher latitudes, in particular, could provide an increased invasion risk from plant species that were previously limited from expanding poleward because suitable habitat was lacking (Bradley et al. 2010; Ibañez et al. 2009). As this happens, local environments will continue to be affected by decreasing biodiversity at even higher rates, thereby increasing the cost of management associated with invasive species (Jones and Reichard 2009).

In particular, control of aquatic invasive plants is imperative because of their impacts on aquatic and wetland ecosystems. These ecosystems support high biodiversity (Hörnberg et al. 1998) and are crucial habitats for large numbers of endangered species, game species, migratory waterfowl, and others (Van Dyke 2008). Aquatic and wetland habitats also provide a variety of ecosystem services important for humans, including nutrient cycling, storm and flood protection, erosion control (Mitsch et al. 2009), irrigation, recreation, water filtration, waterways, and power generation (Kay and Hoyle 2001). These essential ecosystem services can be disrupted when aquatic invasive species invade. When some invasive aquatic plants colonize wetland ecosystems, mostly facilitated by humans, they reproduce rapidly through asexual and vegetative reproduction to form huge mats and dense stands along the water's surface (Van Dyke 2008; Villamagna and Murphy 2010). These mats lower native plant and animal biodiversity (Chambers et al. 1999; Julien and Broadbent 1980; Spencer and Coulson 1976), alter nutrient cycling (Windham and Ehrenfeld 2003), harbor disease (Oliver 1993), and inhibit waterway maneuverability (Julien et al. 1995; Langeland et al. 2008; OTA 1993; Villamanga and Murphy 2010). As climate change alters aquatic ecosystems by influencing streamflow, amount and duration of ice cover, water quality, and water chemistry, aquatic invasive species are predicted to invade to previously uninhabitable areas (Parmesan 2006; Rahel and Olden 2008).

Species distribution models (SDMs) are among the best ways to predict future potential ranges of invasive species because the extent and severity of climate change is still unknown. Understanding the potential spread of an invasive species is instrumental in properly managing ecosystems before the species decreases native biodiversity and removal becomes too expensive. Modeling is effective for large-scale assessment of future areas of invasion because the data do not take years to obtain, and models have accurately predicted future invasion areas in the past (Jarnevich et al. 2010). When modeling future climate, climate models are currently the most efficient way to simulate future climate scenarios (Beaumont et al. 2008). Until more reliable climate models are available to predict which species will cause the greatest threats to aquatic systems, conservation and preventative measures will only be able to respond after an invasion. It is crucial to link predicted ranges of species with climate change to assess where high-risk areas of invasions exist for better rapid response management.

In this study, we modeled the potential range expansion of *Alternanthera philoxeroides* (Mart.) Griseb. (alligatorweed), *Limnophila sessiliflora* (Vahl) Blume (limnophila), and *Salvinia molesta* Mitchell (giant salvinia). These three species are well known as noxious invaders of freshwater habitats in the southeastern United States as well as globally, and none are persistent in the northeastern United States. All three species appear to be limited to the southern United States because they require a warmer climate (Julien and Broadbent 1980; Ramey 2001; Shen et al. 2005; Spencer and Bowes 1985; Whiteman and Room 1991), but we lack a comprehensive study that looks at additional suitable areas in the continental United States under current and future climate change.

The objectives of this study were to determine the potential range expansions of *A. philoxeroides*, *L. sessiliflora*, and *S. molesta* under current and future climate to assess potential future invasions in the northeastern United States. Using the SDM Maxent, we modeled the potential range of each species under current, 2030 to 2059 (2040), and 2070 to 2099 (2080) climate conditions to assess further spread. We chose Maxent because of its high predictive power in modeling invasive species' spread (Beans et al. 2012; Jarnevich and Reynolds 2011; Medley 2010), habitat suitability of endangered species (Kumar and Stohlgren 2009), and species response to climate change (Elith et al. 2011). We then combined these species distribution models with an analysis of wetland habitat preferences of each species in order to identify specific freshwater wetland types at risk for all three species. The management strategies of these three species are most successful when populations of these species are at low densities; thus, understanding the potential range expansion and habitat preferences of these species ahead of the invasion will allow for early detection and rapid response. The results of this research will help inform managers of areas in the continental United States that should receive high priority to prevent or minimize the impacts of future aquatic invasions.

Materials and Methods

Study Species. *Alternanthera philoxeroides* is a highly invasive plant native to South America in the Paraná River region of southern Brazil, Paraguay, and Argentina (Sainty et al. 1998). *Alternanthera philoxeroides* is thought to have first invaded the United States in the late 1800s from ballast water from a South American ship. Since then, it has spread rapidly to wetlands throughout the southern United States (Csurhes and Markula 2010; Spencer and Coulson 1976), but appears to be limited from spreading farther north because of cooler winters.

Alternanthera philoxeroides is a stoloniferous and rhizomatous herb that has the ability to grow quickly in aquatic and terrestrial ecosystems. It grows more successfully in freshwater habitats, where its stems are thicker and taller with larger leaves compared to its terrestrial form (Julien and Broadbent 1980). Although the two morphologies (terrestrial and aquatic) of *A. philoxeroides* are recognized, they do not differ genetically. The aquatic form is rooted in soil or substrate near the water's edge, but has the ability to disperse free-floating mats more than 1 m thick (Csurhes and Markula 2010). The stems of the terrestrial form range from solid to semihollow; the aquatic plant's larger hollow stems provide buoyancy in self-sustaining dense mats (Julien et al. 1995). *Alternanthera philoxeroides* is polygamous and grows throughout the summer months through vegetative reproduction with growth generally ceasing or decreasing in the winter months (Julien and Broadbent 1980). Optimal growth occurs at a constant 30 C (86 F), whereas reduced growth has been seen below a constant 5 C (Shen et al. 2005). *Alternanthera philoxeroides* is restricted to moist habitats and cannot survive extended periods under water or a sustained winter frost (Julien and Broadbent 1980; Julien et al. 1992).

The ability of *A. philoxeroides* to proliferate in a wide range of habitats has made it very successful in invading new areas. Currently, it is considered one of the most problematic invasive plants, spanning thirty countries (Csurhes and Markula 2010; Geng et al. 2007). Areas invaded by *A. philoxeroides* contain dense monoculture stands, accelerating a decrease in native biodiversity (Julien and Broadbent 1980; Spencer and Coulson 1976). Other qualities of *A. philoxeroides*, such as its fast growth rate, tolerance for eutrophic high nutrient sediment habitats, and disturbed areas also gives it a competitive advantage over other native plants (Csurhes and Markula 2010). Additionally, *A. philoxeroides* restricts boating, impedes recreational fishing in streams, rivers, and lakes, and invades pastoral and agricultural lands (Julien et al. 1995; Langeland et al. 2008).

Limnophila sessiliflora is an invasive freshwater aquatic perennial herb native to Southeast Asia in Indochina and Malaysia. Its first introduction to the United States was suspected to be in the 1950s through the aquarium plant industry in Florida (Mahler 1980; Spencer and Bowes 1985). In 1961, this species was officially documented growing spontaneously in the United States in a canal in Tampa, Florida (Langeland et al. 2008).

Limnophila sessiliflora is a rooted herb, with both submersed and immersed plant parts, that can form a dense mat up to 3 m (9.8 ft) in depth (Langeland et al. 2008; Spencer and Bowes 1985). *Limnophila sessiliflora* has the ability to reproduce sexually, with each flower able to produce as many as 300 seeds with up to a 96% germination rate (Spencer and Bowes 1985). In addition to sexual reproduction, it can reproduce through stem fragmentation (Hall et al. 1991). It thrives in shallow freshwater as well as in turbid and high-nutrient conditions (Gilbert 1984). The growth of *L. sessiliflora* slows during the winter and early spring (Spencer and Bowes 1985). Optimal growth temperatures occur between 20 to 26 C, but it can tolerate temperatures as low as 15 C and as high as 28 C (Ramey 2001). This species has also exhibited sensitivity to lower temperatures by a reduced photosynthetic rate (Spencer and Bowes 1985).

Listed as a federally noxious weed in the United States and prohibited in Australia, *L. sessiliflora* is an invasive threat to freshwater ecosystems worldwide. Areas commonly invaded by *L. sessiliflora* are slow-moving freshwater ecosystems such as lakes, ponds, swamps, streams, ditches, and canals. *Limnophila sessiliflora* has restricted navigation in invaded waters because the mats can be extremely dense at the water's surface. This dense vegetative surface also allows the *L. sessiliflora* to outcompete native benthic submersed aquatic macrophytes (Spencer and Bowes 1985). Specifically, *L. sessiliflora* has been shown to displace native water lilies (Gilbert 1984).

Salvinia molesta is a highly invasive rootless perennial fern originally native to Brazil (Oliver 1993; Room 1983). Introduction of *S. molesta* to the United States was most likely from the aquarium and plant trade industry (Nelson et al. 2001). The first recorded location of an established population in the United States occurred in South Carolina in 1995 (Johnson 1995).

Salvinia molesta is primarily found in freshwater wetlands and has a low tolerance for saline and dry environments (Oliver 1993). Reproduction is exclusively vegetative; *S. molesta* does not reproduce sexually or produce viable spores (Barrett 1989). Vegetative reproduction is highly successful because five serial lateral buds have the ability to sprout from each mature node (Lemon and Posluszny 1997). For this reason, whole stands of *S. molesta* are thought to be clones of one another (Barrett 1989). Additionally, *S. molesta* can grow in a mat up to 1 m thick, consisting of an interwoven, rapidly growing vegetative stand (Barrett 1989; Mitchell and Tur 1975). *Salvinia molesta* can double its biomass in 2.2 d in its preferred slow moving water habitats such as flood canals, rice paddies, artificial lakes, and hydroelectric facilities, as well as undisturbed freshwater wetlands (Barrett 1989; Oliver 1993). Whiteman and Room (1991) revealed that fatality occurred when *S. molesta* was exposed to temperatures lower than −3 C or greater than 43 C for more than 2 to 3 h or in the event of ice formation.

The known detrimental environmental and economic impacts of *S. molesta* have caused it to be prohibited in the United States, and the U.S. Department of Agriculture has deemed it as one of the most noxious weeds in the country (Oliver 1993). The fast growth rate of *S. molesta* reduces the abundance of native plants as they compete for space and light (Sharma and Goel 1986). Additionally, slow decomposition rates reduce oxygen for young fish and other organisms (Hattingh 1961). Necessary economic expenditure has occurred as waterways invaded by *S. molesta* have become impassable by boat (Barrett 1989). Other negative worldwide economic impacts attributed to the presence of *S. molesta* include rice paddy invasion and increased human health risk by providing a favorable habitat for mosquitoes carrying diseases such as elephantiasis, encephalitis, malaria, and dengue fever (Oliver 1993).

Model. We used the species distribution model Maxent, Version 3.3.3e, to model the potential range expansion of *A. philoxeroides*, *L. sessiliflora*, and *S. molesta* with climate change. We chose Maxent because it has performed well with high predictive power compared to similar SDMs (Elith et al. 2006; Phillips et al. 2006). Maxent is a maximum-entropy, machine-learning model that uses presence-only data and corresponding environmental parameters to model potential climatically suitable environments for a species. This quality is beneficial because presence points are usually the most readily available (Elith et al. 2011). In addition, Maxent uses background data points as a null model to calculate each species' probability distribution. These points represent locations where the species has had an opportunity to disperse but might or might not occupy (Elith et al. 2011; Phillips et al. 2004). True absence points are increasingly difficult to determine for invasive species' ranges because most of these species are not at equilibrium with their environment (Elith et al. 2010). To run Maxent, we used the current location points, climate, and altitude data sets to model each species' current probability range. We chose to use the invaded, instead of the native range, to model each species because invaded ranges can be climatically distinct from their native ranges (Broennimann et al. 2007). We used these data sets, substituting current for future climate, to model each species' future potential range.

We used auto features for each model run, so the model used the number of occurrence points to determine what feature type was appropriate for each respective species. We also kept default values for the maximum number of points at 10,000 (Elith et al. 2010; Phillips and Dudik 2008) and the replicate run type was set to cross validation with 10 replicate runs for each species. The percentage of points used to split up the data into training and test data sets were 90% for training and 10% for testing.

We calculated model performance using the area under the receiver operating characteristic curve (AUC). We evaluated the model performance of each run by withholding a different 10% of each species' occurrence points to use as test data. The subsequent 90% of the occurrence points were used to train the model. In addition, we ran each of the simulations 10 times, using the cross-validation option in Maxent, to reduce an inflated model performance from just one run (Elith et al. 2010, 2011). Cross validation split up the occurrence data into 10 equal groups and withheld one of the 10 groupings for each of the 10 runs to be used to train the model. Each of the separate groupings are more commonly referred to as folds in Maxent. Cross validation used a different fold to train and test the model so as not to give one grouping of points more weight than the other. Maxent calculates the AUC values for each model run for the training and testing data (Phillips et al. 2006). AUC values range from 0.5 to 1.0, where a score of 0.5 signifies a model that is not any better than random and AUC values closer to 1.0 are models with higher performance predictability (Young et al. 2011).

Modeling Current Invasion. We obtained latitude and longitude occurrence points for *A. philoxeroides*, *L. sessiliflora,* and *S. molesta* from the Global Biodiversity Information Facility (GBIF) database (2011). The GBIF database is a compilation of present point records from data sets around the world. Data sets for all three species were collected and compiled from the GBIF database. The data collected for all three species came from 2 to 11 data providers. Each of the downloaded data sets were used as the current occurrence points for each species. Data sets were only filtered down to remove duplicate points and points that fell outside of the United States. These presence points, excluding duplicates and points overlapping areas with incomplete climatic data, were used to capture the climate suitability based on the invaded range in the continental United States. This resulted in 844 points for *A. philoxeroides*, 66 points for *L. sessiliflora*, and 171 points for *S. molesta* used in model generation.

To be as ecologically relevant as possible, we limited the area of interest, also known as the background in Maxent, because an invading species is usually not at its full distribution potential (Elith 2011). For this reason, we limited the background data to states with known occurrences for all three invasive aquatic species. Maxent is sensitive to modeling species not in equilibrium. We determined each species' background by compiling states with known occurrence data from GBIF database presence points and the Biota of North America Program (BONAP) database (Kartesz 2011). Maxent can be limited to only use background data from a subset of the region in question by utilizing a mask defined by the modeler (Elith et al. 2011). In our case, each mask consisted of the states with known occurrences for each respected species. This limited Maxent to training the model only using areas where we suspected each species has had the ability to spread to (Jarnevich and Reynolds 2011).

We collected current climate data from the Worldclim database at a 30 arc-second (~ 1-km [~ 0.62 mi] grid) resolution. This database includes data from 1950 to 2000 from weather stations around the world (Hijmans et al. 2005). We used altitude and the ecologically relevant bioclimatic variables because they capture a wide array of environmental trends and have been frequently used in ecological modeling (Ibañez et al. 2009; Jarnevich and Reynolds 2011; Medley 2010). We calculated the pairwise Pearson correlation for each of the 10 raster files using ENMTools v. 1.3. (Warren et al. 2010). Based on the Pearson correlation matrix, we eliminated annual mean temperature (BIO1) and minimum temperature of the coldest month (BIO6) out of the ten ecologically significant variables because they covaried with other variables (see Supplemental Table S1; http://dx.doi.org/10.1614/IPSM-D-15-00020.S1). The eight most ecologically relevant variables (Elith et al. 2010; Jarnevich and Reynolds 2011), that we retained were: altitude (Alt), temperature seasonality (BIO4), maximum temperature of warmest month (BIO5), mean temperature of coldest quarter (BIO11), annual precipitation (BIO12), precipitation of driest month (BIO14), precipitation seasonality (BIO15), and precipitation of warmest quarter (BIO18).

After training the model with the environmental layers clipped to each state with known occurrences, we projected the model onto the entire continental United States. This was to test whether other areas exist that have comparable climate conditions and could therefore be suitable locations given the environmental parameters. We created an additional mask variable of the entire continental United States with environmental layers of the same extent to project the model to new locations not used in the original model.

Modeling Invasion with Climate Change. We used seven future atmosphere-ocean general circulation models (AOGCMs; CCCMA_CGCM31, CSIRO_MK30, IPSL_CM4, MPI_ECHAM5, NCAR_CCSM30, UKMO_HADCM3, UKMO_HADGEM1) to run simulations modeling future climate change throughout the continental United States. These seven models were developed for the 4th Intergovernmental Panel on Climate Change Assessment Report using a thin-plate spline-smoothing spatial interpolation to create worldwide climate surfaces based on current climate data from the Worldclim database to project future climate conditions based on various carbon dioxide levels at different times into the future (Hijmans et al. 2005; IPCC 2007; Ramirez and Jarvis 2008). We chose the Special Report on Emission Scenarios (SRES) A1B model scenario because it assumes future energy production around the world will be balanced across energy sources, instead of relying on one type exclusively (IPCC 2007). This scenario predicts global atmospheric carbon dioxide concentrations to reach 720 ppm by 2100, which forecasts future concentrations in the middle compared to other SRES model scenarios (Bradley et al. 2010; Nakicenovic and Swart 2000).

We ran seven AOGCMs under 2030 to 2059 (2040) and 2070 to 2099 (2080) projections to evaluate the range of suitability of each species through time. With each future projection, we used the same eight environmental variables under current climate to project the Maxent output to future climate conditions. This manipulation instructs the model to use its training under current climate conditions to project those results using future climate conditions (Phillips 2012). Although there is no consensus as to which climate model is the most accurate in predicting future climate conditions (Beaumont et al. 2008), locations that have been predicted suitable by multiple models are concluded as future high-risk areas of invasion (Bradley et al. 2010). After running all seven future AOGCMs in Maxent in 2040 and 2080 scenarios, we identified the areas at high-risk by the degree of overlap between the different models. Areas with the most overlap were predicted to have the highest probability of invasion.

Threshold Evaluation. We used the 10 percentile-training presence logistic threshold to evaluate suitable and unsuitable areas for each species. This threshold classified suitable areas as those that exist above the probability value where 90% of the training locations were classified. Any probability below the 10% lowest probability threshold was deemed unsuitable. This is a more conservative threshold and it has been widely used by others modeling species distributions (Jarnevich and Reynolds 2011; Pearson et al. 2007; Young et al. 2011).

Wetland Habitat Preferences. We also used habitat preference as another variable to assess current and future high-risk areas of invasion. Understanding each species' wetland preferences allowed us to determine whether certain wetland habitats had a higher risk of being invaded, not just regions as Maxent allowed us to predict. We used wetland shapefiles from the U.S. Fish and Wildlife Wetlands Mapper that were designated into eight distinct wetland categories: freshwater-forested and shrub wetland, freshwater emergent wetland, freshwater pond, estuarine and marine wetland, riverine, lake, estuarine and marine deepwater, and other freshwater wetlands (U.S. Fish and Wildlife Service 2011). We used the Geospatial Modeling Environment (GME tools) (Beyer 2009–2012), in ArcGIS 10, to evaluate the types of wetlands in which each species was found by calculating the intersection of each species' presence points and the wetland shapefiles. All presence points that intersected a specific wetland were assumed to inhabit that wetland type. Points that did not overlap with a U.S. Fish and Wildlife wetland type were investigated further to see whether the locality description from the GBIF database gave any further indication of wetland type. Any points that were not designated as a specific type of wetland by the U.S. Fish and Wildlife Wetlands Mapper or the GBIF locality description were dropped from the analysis. This procedure resulted in 616 points for *A. philoxeroides,* 58 points for *L. sessiliflora,* and 176 points for *S. molesta.* Chi-squared goodness of fit tests (SPSS v. 18.0.0) were used to assess the preferred habitat type of each species.

After compiling all of the points with designated wetland types, we also analyzed the locality description from the GBIF database to determine how many of the points fell into man-made habitats (e.g., canals, dams, ditches, man-made lakes and ponds, reservoirs, retention ponds). This analysis tested whether any one of the species were found more frequently in man-made habitats. This output was analyzed using a chi-square test of independence (SPSS v. 18.0.0).

We also analyzed the distance of each species' location to the nearest stream. Because these species are water-dispersed, we hypothesized that species found closer to streams might spread faster due to their proximity to moving bodies of water. After dropping duplicate records, 954 points for *A. philoxeroides*, 71 for *L. sessiliflora*, and 203 for *S. molesta* were analyzed. A shapefile of all the streams in the continental United States was obtained from the National Weather Service (National Weather Service 1999). We calculated the distance from each presence point to the nearest stream using the near-analyst tool in ArcGIS 10. Species-specific distance results were further analyzed using the Kruskal-Wallis test and ANOVA (because the data were not normally distributed; SPSS v. 18.0.0), to determine if there was a significant difference among the distance of each species to streams. The species locations did not have equal variances; therefore, we performed the post-hoc Games-Howell and Tukey HSD test to assess which species' distance to the nearest stream was significantly different from the others.

Results

Current and Future Suitability Ranges. Currently, *A. philoxeroides* has invaded a much larger range than *L. sessiliflora* and *S. molesta* with 844 presence points compared to 66 points from *L. sessiliflora* and 171 from *S. molesta* (Supplemental Figure S1; http://dx.doi.org/10.1614/IPSM-D-15-00020.S1). Most of the invaded range of *A. philoxeroides* was concentrated in the Southeast, Texas, and California (see Supplemental Figure S1a; http://dx.doi.org/10.1614/IPSM-D-15-00020.S1). *Limnophila sessiliflora* had the smallest invaded range with presence locations only in Florida, Georgia, and Texas with the majority occurring in Florida alone (see Supplemental Figure S1b; http://dx.doi.org/10.1614/IPSM-D-15-00020.S1). The current distribution of *S. molesta* was similar to *A. philoxeroides,* with invaded ranges throughout the Southeast, Texas, and California, and the highest concentration of presence points in Louisiana and Texas (see Supplemental Figure S1c; http://dx.doi.org/10.1614/IPSM-D-15-00020.S1).

Of 844 total occurrence points for *A. philoxeroides,* 759 presence records were used for training and 85 were used for testing the model. All of the 10-fold cross-validation runs for *L. sessiliflora* split up the total 66 points into 59 presence records used for training and 7 presence records used for testing the model. The runs of *S. molesta* split up the total 171 into 153 presence points for training and 18 for testing. Mean AUC values of *A. philoxeroides*, *L. sessiliflora*, and *S. molesta* for the current climate model were 0.872, 0.945, 0.925 for training data and 0.861, 0.928, 0.892 for testing data.

Our results indicated that under current climate conditions, areas as far north as New Jersey were currently climatically suitable for *A. philoxeroides* (Figure 1a). Areas in Louisiana, Alabama, and Mississippi were also climatically suitable for *L. sessiliflora* to extend its invasion range (Figure 1b). The suitable habitat for *S. molesta* did not extend much farther into additional locations compared to its current state occurrence probability distribution (Figure 1c) except in northern Montana, North Dakota, and Minnesota. Further Maxent analysis was conducted for *S. molesta's* current climate model runs to evaluate if any locations existed where one or more environmental variables fell outside the training data range, therefore limiting the model's predictability. Maxent refers to this as clamping (Phillips 2012). Based on additional Maxent analysis, clamping exhibited the largest influence on *S. molesta's* current climate runs in these northern areas of the United States, and therefore the predication of suitable climate in this area should be interpreted with caution (see Figure 2).

Based on the current distribution analysis, all three species were limited from expanding throughout the Northeast based on climate. Specifically, the spatial distribution of *A. philoxeroides* was determined mainly by precipitation of the warmest quarter at 15.8% and annual precipitation at 14.9% (Table 1). The spatial distribution of *L. sessiliflora* was mostly affected by precipitation of the warmest quarter with a 52.2% contribution, followed by mean temperature of the coldest quarter at 21.8%. The mean temperature of the coldest quarter (24.3%) primarily determined the distribution of *S. molesta*.

Future distribution models for all three species indicate that the climate will become suitable for northern expansion of these species (Figure 3). For *A. philoxeroides* in the 2040 scenario, inland areas of California, Georgia, South Carolina, North Carolina, and New Jersey had increased invasion risk, and areas of New York and southern New England were predicted to be at medium to high-risk for invasion (Figure 3a). In the 2080 scenario, there were much larger sections of the Northeast and Southwest suitable for *A. philoxeroides* to invade (Figure 3b). In addition, there were fewer areas with future invasion predictions consistent among all seven models in 2080. This resulted in larger portions of predicted areas at risk designated by orange, yellow, and light blue.

For *L. sessiliflora* in the 2040 scenario, there were much larger sections of Georgia, Alabama, Mississippi, Louisiana, and Texas at high risk compared to current climate predictions (Figure 3c). Additionally, South Carolina was predicted to have suitable conditions by 2040. By the 2080 scenario, the invasion opportunities for *L. sessiliflora* were predicted to increase to Oklahoma, Missouri, Tennessee, and North Carolina and states previously threatened were projected to continue to experience even larger areas at high risk (Figure 3d).

The 2040 scenario predicted suitable climate for *S. molesta* extending as far north as New Jersey (Figure 3e). In the 2080 scenario, high-risk areas for *S. molesta* were predicted to increase even farther north to Massachusetts and New York (Figure 3f). Additionally, under the 2080 climate scenario, greater portions of California, Arizona, Nevada, Tennessee, Kentucky, North Carolina, Virginia, Illinois, Indiana, Ohio, Pennsylvania, Maryland, Delaware and New Jersey will be suitable for *S. molesta*.

Wetland Habitat Preferences. All three species demonstrated significant habitat associations with one or more wetland types. *Alternanthera philoxeroides* was found more often in lakes (chi-square goodness of fit test = 5988.88, df = 8, $P < 0.0001$; Table 2). *Limnophila sessiliflora* was also found more often in lakes (chi-square goodness of fit test = 155.14, df = 6, $P < 0.0001$), and *S. molesta* was found more often in ponds and lakes than other wetland habitat types (chi-square goodness of fit test = 294.83, df = 9, $P < 0.0001$). *Salvinia molesta* was found significantly more often in man-made habitats (chi-square test for independence$_{(2,n=850)}$ = 63.26, $P < 0.0001$) (28.98% of locations were man-made) compared to *A. philoxeroides* (chi-square test for independence$_{(1,n=792)}$ = 63.32, $P < 0.0001$) (6.98% of locations were man-made), and *L. sessiliflora* (chi-square test for independence$_{(1,n=234)}$ = 6.69, P = 0.010) (12.07% of locations were man-made).

The average distance each species was found from a stream was significantly different among species (Kruskal-Wallis test = 10.87, df = 2, P = 0.004; ANOVA, F = 15.65, df = 2, $P < 0.0001$). *Limnophila sessiliflora* was found farther from streams (Mean: 127.01 m ± 35.57 m standard error [SE]), than *A. philoxeroides* (Mean: 44.17 m ± 2.77 m SE), and *S. molesta* (Mean: 50.82 m ± 10.47 m SE). Distances to the nearest stream were significantly different between *A. philoxeroides* and *L. sessiliflora* (Tukey HSD post-hoc test, $P < 0.0001$) and *S. molesta* and *L. sessiliflora* (Tukey HSD post-hoc test, $P < 0.0001$), but not for *A. philoxeroides* and *S. molesta* (Tukey HSD post-hoc test, P = 0.755).

Discussion

In this study, we showed that under current, 2040, and 2080 climate scenarios, areas farther north than currently inhabited are climatically suitable for *A. philoxeroides*, *L. sessiliflora*, and *S. molesta* to invade. These results support our

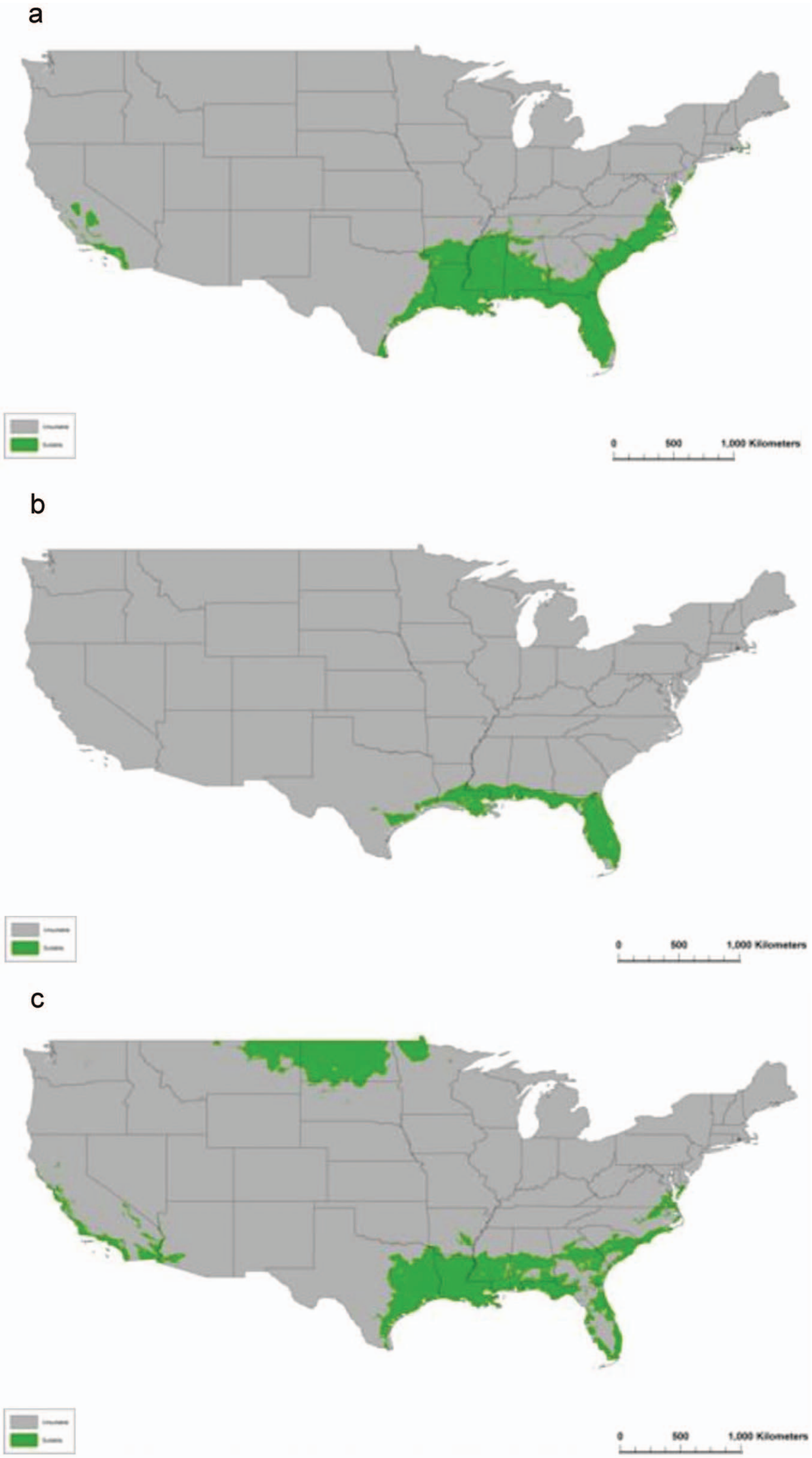

Figure 1. Species distribution models of (a) alligatorweed (*Alternanthera philoxeroides*), (b) limnophila (*Limnophila sessiliflora*), and (c) giant salvinia (*Salvinia molesta*) calculated in Maxent under current climate conditions in the continental United States using 10 percentile training-presence logistic threshold. Areas with high model congruency, and therefore suitable climate, are indicated in green, whereas gray areas represent low or no model overlap and are climatically unsuitable for invasion. (Color for this figure is available in the online version of this article.)

Figure 2. Map of *Salvinia molesta* exhibiting the influence clamping has on the current climate model runs and then projected to the rest of the continental United States. The 0 to 1 values indicate the absolute difference between predictions with or without clamping, where dark blue values closer to zero show low areas where clamping had an effect and red values closer to one show high areas where clamping had an effect on model output. (Color for this figure is available in the online version of this article.)

initial hypothesis that under climate change, and subsequently warmer temperatures, there could be a large expansion of each species' invasion range. However, modeling range expansion demonstrates potential limitations of the Maxent model and accurately modeling future climate scenarios. We also found that lakes and ponds are at increased risk for invasion because all three species occur preferentially in these habitats. To reduce detrimental impacts of these species, land managers in the northeastern United States should plan early detection and rapid response management scenarios in these habitats.

The three invasive species we studied here are not reported in all locations where current climate models indicate they could exist. First, not enough time might have passed since the initial invasion for each species to disperse to each appropriate location. Second, incomplete and biased sampling efforts could have missed some occupied areas. We limited our background data only to states with presence records to limit the effect of bias, but concern over biased sampling can still be important (Elith 2011; Jarnevich and Reynolds 2011). A more thorough sampling effort will be needed to determine whether these high-risk areas are not occupied by these species. For this reason, our study highlights the regions where further studies are needed to evaluate current local invasion risk.

We found the results of the spatial distribution percentages consistent with the ecological preferences of each species. Specifically, altitude contributed greatly to model generation for all three species' spatial distribution based on the preference of each species to inhabit locations at lower elevations. In addition, temperature and precipitation parameters that controlled the spatial distribution of the models, such as precipitation of the warmest quarter, annual precipitation, and mean temperature of the coldest quarter, were expected because they are all aquatic species that require warm temperatures in wet habitats.

There are potential limitations of Maxent for projecting future species' distributions. Maxent is unable to make accurate predictions in areas outside of its clamped values, those areas outside of the range of the training data. Evidence of this was seen in the current climate predictions for *S. molesta* in which our results predicted suitability into northern Montana and Wyoming unreliably (Figure 2).

Table 1. Average percent contribution of each environmental variable for the spatial distribution of alligatorweed (*Alternanthera philoxeroides*), limnophilia (*Limnophila sessiliflora*), and giant salvinia (*Salvinia molesta*) used to train the model.[a]

Variable	Alligatorweed	Limnophila	Giant salvinia
Alt	47	15	50.1
BIO4	8.8	5.6	1.4
BIO5	2.2	0.1	5.3
BIO11	7.5	21.8	24.3
BIO12	14.9	1.2	3.6
BIO14	2.9	3.4	4.6
BIO15	0.8	0.7	6.1
BIO18	15.8	52.2	4.6

[a] Abbreviations: Alt, altitude; BIO4, temperature seasonality; BIO5, maximum temperature of warmest month; BIO11, mean temperature of coldest quarter; BIO12, annual precipitation; BIO14, precipitation of driest month; BIO15, precipitation seasonality; BIO18, precipitation of warmest quarter.

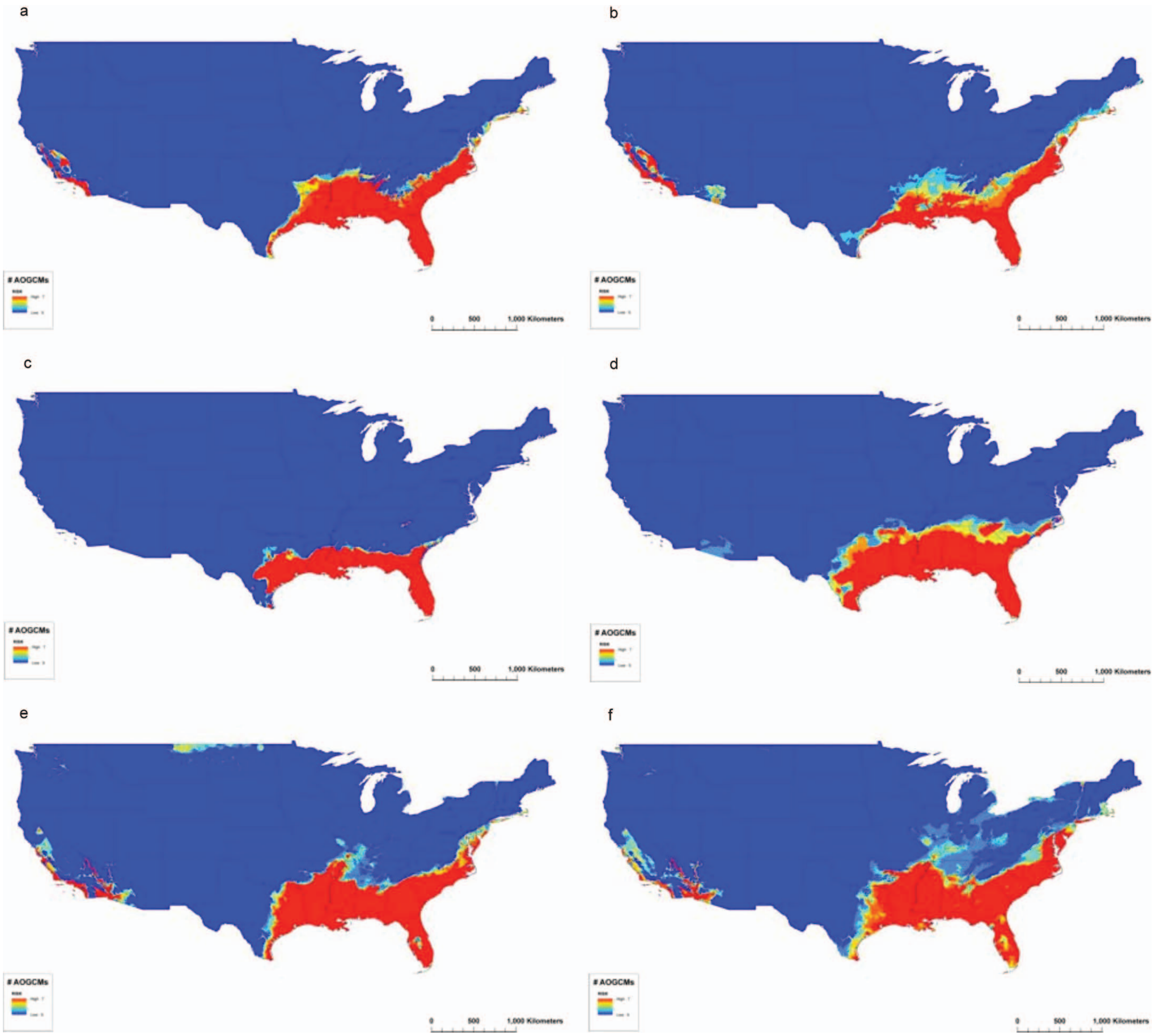

Figure 3. Species distribution models of (a,b) alligatorweed (*Alternanthera philoxeroides*), (c,d) limnophila (*Limnophila sessiliflora*), and (e,f) giant salvinia (*Salvinia molesta*) calculated in Maxent under 2040 (a,c,e) and 2080 (b,d,f) climate-change scenarios using a 10 percentile training-presence logistic threshold. All thresholds maps were calculated for all of the seven future climate models and then summed to evaluate model agreement. Areas with high model congruency, and therefore high risk, are indicated in red, whereas blue areas represent low or no model overlap and are thereby low- to no-risk areas of future invasion. (Color for this figure is available in the online version of this article.)

Another limitation is that 2080 climate models predict precipitation and temperature values ranging both well above and below the values used to train the model (Supplemental Table S2; http://dx.doi.org/10.1614/IPSM-D-15-00020.S1). For this reason, Maxent was unable to make predictions of species' probability occurrences at these locations. This characteristic of Maxent is referred to as the "problem of novel climate conditions" in which variables projected into new periods of time and areas are outside the range used to train the model (Phillips 2012). It is especially difficult to predict how species will respond as climate change continues to alter temperature and precipitation in the continental United States outside current ranges.

Our model results were generated from A1B middle-of-the-road climate scenarios. The A1B models are conservative

Table 2. Frequency (%) of occurrence of alligatorweed (*Alternanthera philoxeroides*), limnophila (*Limnophila sessiliflora*), and giant salvinia (*Salvinia molesta*) in freshwater wetland types. Wetland types are based on U.S. Fish and Wildlife wetland categories and the Global Biodiversity Information Facility (GBIF) locality descriptions.

Wetland Type	Alligatorweed	Limnophila	Giant salvinia
Estuarine and marine deep water	2.76	5.17	1.70
Estuarine and marine wetland	1.14	0.00	2.84
Freshwater emergent wetland	2.11	0.00	1.70
Freshwater forested/ shrub wetland	14.94	13.79	9.09
Freshwater pond	5.03	12.07	32.95
Lake	56.82	46.55	32.95
Other	0.00	0.00	0.57
Riverine	17.21	22.41	18.18

predictions because there is little evidence that greenhouse gas emissions are substantially decreasing globally, and therefore, we might predict even larger areas to be suitable for *A. philoxeroides*, *L. sessiliflora*, and *S. molesta*. In addition, consensus is still lacking regarding which climate model most accurately represents future climates (Araújo and New 2006; Bradley et al. 2010), making it necessary to use multiple models to prevent making unrealistic conclusions from one model alone. These reasons will continue to limit future predictions until there is greater consensus among the models.

Our methods only identify suitability locations that are climatically suitable, and do not definitively identify areas that will be inhabited by these species. Instead, the purpose of this research, and similar studies using species distribution models, is to make broad predictions of a species' suitable climate envelopes (Elith 2011). Guisan and Thuiller (2005) stress the constraints of species-distribution models such as Maxent that do not take into account crucial biological and ecological interactions. To fully understand the future risks and opportunities of species under current and future climate scenarios, more thorough studies of the species' biology (e.g., nutrient and habitat requirements) and ecology (e.g., dispersal and competitive interactions) need to be understood.

Although some studies have shown invaded ranges shrinking with climate change, providing positive restoration opportunities locally (Bradley et al. 2009), areas with predicted invaded range expansion, as in our study, increase management concerns from the potential negative impacts local ecosystem will face and how we will respond (Rogers and McCarty 2000). Specifically, the future large increase in suitable climate for all three invasive species will increase the region of concern, resulting in more time and resources spent in prevention and management at locations previously not at risk. Additional invasions could also cause negative environmental impacts similar to those effects where each species has already invaded. This could result in the reduction of native species either by climate change altering climatic conditions and making previous habitat no longer suitable, or by being outcompeted by these new invaders (Parmesan 2006).

The results of this study, and other model-based analyses (Jarnevich et al. 2010), are meant to provide managers with a better understanding of where each one of these species will have the highest probability of occurring. These results will allow more thorough early detection and rapid response management, which is now common practice in managing invasive plant species in the United States (Westbrooks 2004). Our 2080 scenarios indicate that *A. philoxeroides* and *S. molesta* will be climatically able to invade areas in the Northeast that they were unable to reach under current climate conditions. Not only will new areas be under increased invasion risk, but lakes and ponds will be more vulnerable, based on each species' habitat preference. Specifically, our analyses demonstrate the need for lakes to receive the highest priority to prevent *A. philoxeroides* invasions and lakes and ponds to prevent future *S. molesta* invasions in these high-risk probability areas. *Salvinia molesta* is significantly associated with man-made habitats more than the other two species, which could result in an increased threat of proliferation in more disturbed sites. Even though we predicted that *L. sessiliflora* would not expand as far north as the other species, areas as far north as North Carolina should be aware of the potential risk of future expansion throughout the next century. In these areas, lakes are at greatest risk of invasion by *L. sessiliflora*.

The fact that *S. molesta* was found most often in man-made habitats might provide additional invasion opportunities in future landscapes. The ability for *S. molesta* to invade more-disturbed habitats could result in the species spreading much faster as these habitats increase with human development. This quality could assist the species in establishing and spreading faster across the landscape and also into remnant wetland habitats compared to the other species that were not as closely associated with man-made habitats.

Limnophila sessiliflora has currently invaded a smaller range throughout the continental United States compared to *A. philoxeroides* and *S. molesta* in the current model runs (see Supplemental Figure S1; http://dx.doi.org/10.1614/IPSM-D-15-00020.S1), even though its proposed introduction was earlier than *S. molesta* (Johnson 1995). The distance to the nearest stream analyses suggest that although *L. sessiliflora* is found frequently in riparian habitats, this species inhabits areas much farther from streams than *A. philoxeroides* and *S. molesta*. The inability of *L. sessiliflora* to establish in the habitats closest to streams could limit how rapidly it will disperse to nearby locations. Previous studies have indicated that rivers can be important conduits for dispersal for species that have a high capacity to float and reproduce vegetatively (Johansson et al. 1996). However, species with other dispersal mechanisms can travel long distances across riparian habitats in a single flood event; studies have observed that diaspores spread up to 230 km in 2.5 d (Andersson 2000; Nilsson et al. 1994). The ability of rivers to disperse seeds has also helped invasive species' spread (Jacquemyn et al. 2010; Rahlao et al. 2010; Säumel and Kowarik 2010).

The results of our research could help in successfully managing these species in the future to lessen their economic and environmental impacts. Currently, the biological control of *A. philoxeroides* has been a successful management strategy in the United States. The flea beetle, *Agasicles hygrophila,* has reduced populations of *A. philoxeroides* in approximately 3 mo by consuming the plants' stored food, inhibiting photosynthesis, and reducing leaf biomass (Center et al. 2009). *Amynothrips anderson*i, a thrip, thrives on new growth of rooted *A. philoxeroides,* which is not as common for the flea beetle to predate, thereby reducing the functionality of the plant (Center et al. 2010). Management of *L. sessiliflora* has been virtually unsuccessful because no current management strategies have significantly reduced plant populations, and aquatic herbicides have resulted in minimal reduction of the plant (Mahler 1980). Management strategies controlling *S. molesta* depend on the location and severity of the invasion. Examples of successful forms of management include biological control with weevils, herbicides, and mechanical and manual removal of the plant (van Oosterhout 2006). Many of these management strategies are the most successful when the invasive species is at low densities, and for that reason, our results might help to control more intense spread if newly invaded locations are detected early.

The results of our study provide a first step in managing the future spread of *A. philoxeroides*, *L. sessiliflora*, and *S. molesta* in the continental United States. Our results offer additional tools to highlight areas that should be sampled more intensively to assess the best form of management to limit additional established populations under current and future climate. Future species distribution models, such as Maxent, are one of the best ways to make predictions across environmental space and time, but additional biological and ecological experimentation should still be tested locally. Thorough site-specific evaluation is still needed to determine the ways in which prevention and management will be the most successful and attainable.

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