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ORIGINAL PAPER

Plant migration due to winter climate change: range expansion of tropical invasive plants in response to warming winters

Michael J. Osland · Bogdan Chivoiu · Laura C. Feher · Leah L. Dale · Deah Lieurance · Wesley M. Daniel · Jessica E. Spencer

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Abstract Warming winters due to climate change can facilitate the range expansion of invasive non-native species. In the southeastern United States, the frequency and intensity of extreme winter temperatures determines the northern range limits of many tropical organisms including many species of invasive non-native plants. However, the effects of winter climate change on invasive species' range limits have been understudied. Here, we used temperature and species occurrence data to examine the sensitivity of invasive tropical plant species to freezing temperatures. We also examined the potential for northward range expansion of these species due to winter climate change. From an initial group of 81 invasive plant species selected due to their ability to transform native plant communities, our analyses identify and quantify species-specific temperature thresholds for 40 tropical, cold sensitive species. Future winter warming scenarios indicate that these tropical invasive plant species have the potential for northward range expansion across the southeastern United States in response to small changes in the severity of winter cold temperature extremes. The potential for range expansion is greatest in coastal areas, which typically have warmer temperatures than inland counterparts. Thus, coastal regions are likely to serve as biological invasion hotspots from which invasive species expand into inland areas. The state of Florida has become a global hotspot for biological invasions, with tens of millions of dollars (US) spent annually to control the ecological and societal impacts of invasive plants on publicly held conservation lands. Collectively, our results underscore the need to better anticipate and prepare for the northward range expansion of invasive plants from Florida into the southeastern United States in response to winter climate change.

Keywords Invasive plants · Non-native plants · Northward range expansion · Climate change · Winter warming · Tropicalization

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M. J. Osland (✉) · L. C. Feher
U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, USA
e-mail: mosland@usgs.gov

B. Chivoiu · L. L. Dale
Cherokee Nation System Solutions, Contracted to the U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, USA

D. Lieurance
Agronomy Department, University of Florida, Gainesville, FL, USA

W. M. Daniel
U.S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL, USA

J. E. Spencer
U.S. Army Corps of Engineers, Jacksonville, FL, USA

Introduction

Ecologists and natural resource managers are increasingly challenged to better anticipate the ecological effects of interactions between climate change and biological invasions (Bradley 2009; Early et al. 2016; Pyšek et al. 2020; Sage 2020; Lopez et al. 2022). In particular, there is a pressing need to advance understanding of how changes in the frequency and intensity of extreme climatic events (e.g., droughts, floods, heat waves, tropical cyclones, and winter storms) (USGCRP 2017; IPCC 2021) may alter the distribution and abundance of invasive non-native species (Smith 2011; Diez et al. 2012). Here, we investigated the potential for northward range expansion of tropical invasive plants in the southeastern United States due to warming winters, specifically decreases in the severity of extreme cold winter temperatures.

Near the transition zone between tropical and temperate climates in North America, the poleward range limits of many tropical species are governed by the frequency and intensity of extreme winter temperatures (Boucek et al. 2016; Cavanaugh et al. 2019; Osland et al. 2021). For example, extreme cold temperatures govern the northern range limits of terrestrial plants (Greller 1980; Box et al. 1993), insects (Ungerer et al. 1999; Johnson et al. 2017), amphibians (Glorioso et al. 2018), terrestrial and freshwater reptiles (Mazzotti et al. 2016; Card et al. 2018), coastal fishes (Boucek and Rehage 2014; Stevens et al. 2016; Purtlebaugh et al. 2020), coral reefs (Lirman et al. 2011; Toth et al. 2021), sea turtles (Foley et al. 2007; Lamont et al. 2018), manatees (Hardy et al. 2019; Cloyed et al. 2021), and coastal wetland plants (Cavanaugh et al. 2019; Osland et al. 2019a). Warming winters due to climate change are expected to lead to ecological tropicalization, which is the transformation of temperate ecosystems by poleward-moving tropical organisms (Vergés et al. 2014; Carter et al. 2018; Osland et al. 2021).

Freezing and chilling temperatures can lead to mortality and/or physiological damage for tropical native (Greller 1980; Myers 1986; Box et al. 1993; Olmsted et al. 1993) and non-native plants (Morton 1980; Simberloff 1996; Turner et al. 1997; Hutchinson and Langeland 2014; Osland and Feher 2020). However, the effects of winter climate change on the distributions of tropical invasive non-native plants have been understudied. Advancing understanding of the potential for invasive plant range expansion is especially important in the southeastern United States because Florida [i.e., the coastal, comparatively warmer, and more tropical/subtropical portion of this region (Hela 1952; Chen and Gerber 1990; Duever et al. 1994; Lugo et al. 1999)] has become a global hotspot for biological invasions (Dawson et al. 2017; Pyšek et al. 2017, 2020), with many species of tropical invasive plants that have a rich history of problematic and costly societal and ecological impacts (Simberloff et al. 1997; South Florida Ecosytem Restoration Task Force 2015; Rodgers et al. 2018). For example, approximately 45 million dollars (US) are spent annually by federal and state governmental agencies to manage invasive plants on publicly-held conservation lands in Florida (Hiatt et al. 2019). The northward range expansion of these plants presents a challenge for resource management in areas adjacent to and beyond current range limits. This study focuses on invasive plant species (sensu Iannone III et al. 2020), which are species that: (1) have been moved by humans to Florida from other parts of the world - often from other continents; and (2) are causing environmental and/or economic harm to humans (FLEPPC 2019; Lieurance and Flory 2020). Our study does not focus on native species that occur naturally in the region but are expanding their native distributions due to climate change.

In this study, we examined the influence of extreme cold winter temperatures and winter climate change on the northern range limits of terrestrial tropical invasive plants in the southeastern United States. We hypothesized that the northern range limits of tropical invasive plants would be governed by species-specific threshold responses to extreme cold winter temperatures (see generalized illustration in Fig. 1), which would mean that warming winters due to climate change could potentially facilitate the northward range expansion of these species. By threshold response, we mean that we expected that there would be strong positive nonlinear, sigmoidal relationships between winter cold temperature extremes and the presence of tropical invasive plant species. Such relationships would indicate that small changes in the intensity of winter temperature extremes could trigger large changes in species distributions (e.g., range expansions or contractions). Our research specifically addresses the following questions: (1) what is the sensitivity of the region's most problematic tropical invasive plant species to freezing temperatures; (2)

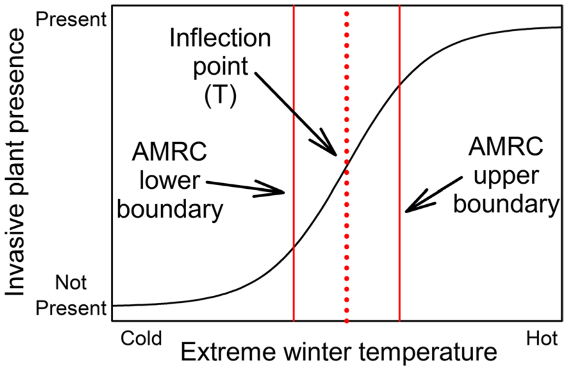

Fig. 1 A generalized illustration of the hypothesized non-linear sigmoidal relationship between extreme cold winter temperatures and the presence of tropical invasive non-native plants. The dotted vertical line represents the inflection point or discrete temperature threshold (T). The solid vertical lines depict the temperature threshold zone, which is defined by the lower and upper boundaries of the area of maximum rate of change (AMRC). For more information regarding the evaluation of ecological transitions and thresholds using sigmoidal models, inflection points, and AMRC threshold zones, see Wilson and Agnew (1992), Timoney et al. (1993), Hufkens et al. (2008), and Frazier and Wang (2013)

how does that sensitivity govern northern range limits; (3) what is the potential for northward range expansion of invasive species under alternative future climate scenarios; and (4) what is the areal coverage of protected lands that are potentially vulnerable to the northward range expansion of invasive species under alternative future climate scenarios? Our analyses focus on 81 species that the Florida (USA) Invasive Species Council has identified as Category I Invasive Plant Species, which are species that are altering native plant communities by displacing native species, changing community structures or ecological functions, or hybridizing with natives (FLEPPC 2019). We also incorporated information from the University of Florida Institute of Food and Agricultural Sciences' Assessment of Nonnative Plants (Lieurance and Flory 2020) to communicate the management and risk assessment implications of warming-induced range expansion.

Methods

Study area

To identify temperature thresholds and quantify relationships between extreme cold winter temperatures and the distribution of tropical invasive plants, we selected a study area within the southeastern United States that includes the states of Florida, Georgia, and South Carolina (Fig. 2). This area was selected because it spans a tropical-temperate transition zone (Hela 1952; Chen and Gerber 1990; Duever et al. 1994; Lugo et al. 1999), where tropical, cold sensitive species are abundant in the warmer, more tropical/subtropical south (i.e., Florida) but not present in the colder, more temperate north (i.e., South Carolina) (Greller 1980; Myers 1986; Box et al. 1993; Olmsted et al. 1993). The frequency and intensity of winter cold temperature extremes governs the northern range limits of many tropical, cold sensitive plant and animal species in this region (Sakai and Larcher 1987; Box et al. 1993; Osland et al. 2021). We divided the study area into a grid of ¼ degree cells for acquiring temperature and plant distribution data. Our ¼ degree study grid was developed to match the location and size of the ¼ degree converted gridded temperature data. To avoid cells that were predominantly water, we removed cells from the initial dataset that contained less than 1% land. Collectively, these steps produced a dataset for subsequent analyses that contained 670 cells—281 cells in Florida, 254 cells in Georgia, and 135 cells in South Carolina. For the future projections, we utilized a grid of 2.5-arcmin resolution cells that extended across the entire conterminous United States.

Winter minimum temperature data

We obtained continuous gridded daily minimum temperature data (2.5-arcmin resolution) produced by the PRISM Climate Group (Oregon State University; prism.oregonstate.edu) using the PRISM (Parameter-elevation Relationship on Independent Slopes Model) interpolation method (Daly et al. 2008). These data were used to determine the absolute minimum temperature (i.e., the coldest temperature recorded) for each grid cell for the 30-year period extending from 1981 to 2010. This 30-year period was selected because it includes several plant-relevant extreme

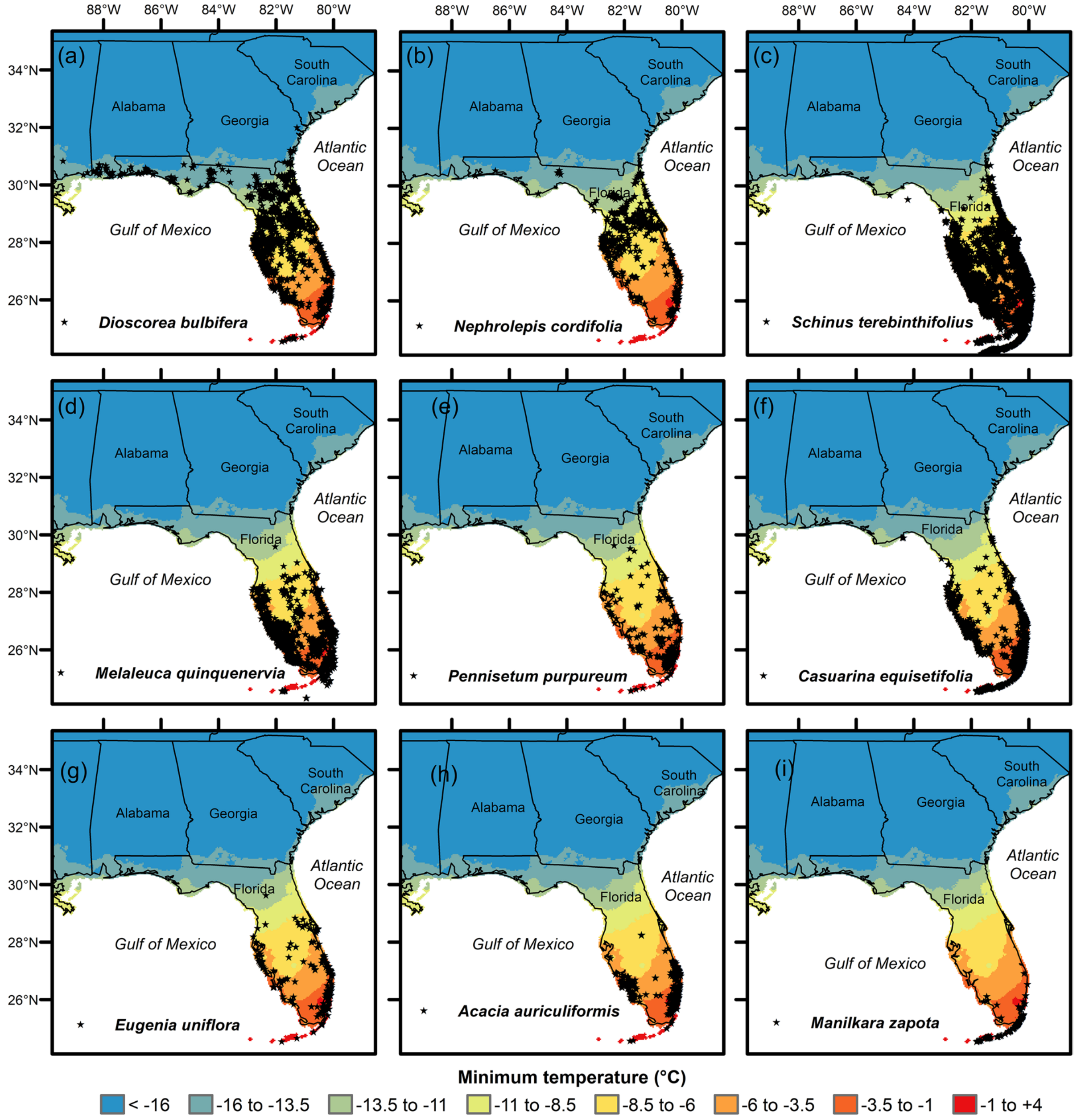

Fig. 2 Maps of minimum air temperatures and the occurrence of nine tropical invasive non-native plants species: (**a**) *Dioscorea bulbifera* (air potato); (**b**) *Nephrolepis cordifolia* (narrow swordfern); (**c**) *Schinus terebinthifolius* (Brazilian pepper); (**d**) *Melaleuca quinquenervia* (Melaleuca); (**e**) *Pennisetum purpureum* (elephant grass); (**f**) *Casuarina equisetifolia* (Australian pine); (**g**) *Eugenia uniflora* (Surinam cherry); (**h**) *Acacia auriculiformis* (earleaf acacia); and (**i**) *Manilkara zapota* (sapodilla). We selected these nine species due their abundance and notoriety in the region and because they illustrate the variation in cold-tolerance in the region from more-to-less cold tolerant, respectively. Minimum temperatures represent the absolute coldest temperature recorded for the period extending from 1981 to 2010, which were obtained from data produced by PRISM climate group (prism.oregonstate.edu). The species occurrence data were obtained from the Early Detection & Distribution Mapping System (EDDMapS)

freeze events that occurred in the 1980s (Attaway 1997; Osland et al. 2017; Cavanaugh et al. 2019). For the threshold analyses, we averaged the 2.5-arcmin minimum temperature data to convert it to the ¼ degree resolution data of that study grid.

Plant distribution data

We used the Early Detection & Distribution Mapping System database (EDDMapS 2020) to obtain plant distribution data for the 81 species on the FLEPPC's (2019) Category I Invasive Plant Species List (FLEPPC 2019) (Additional file 1: Table S1). EDDMapS is a web-based mapping system that combines data from various sources to create a national network of invasive species distribution data for the United States (Bargeron and Moorhead 2007). For each plant species, we obtained point and polygon-based occurrence data from EDDMapS, which we integrated to assign a binary code to each study grid cell to indicate species presence or absence. Species presence designation was based upon point or polygon presence within a cell. We used the USDA PLANTS Database (USDA NRCS 2023) to check and refine species nomenclature.

Species classification

Prior to quantitative analyses, we used a three-step process to identify and classify species for inclusion in subsequent data analyses. The first step was to clarify the criteria for inclusion, which were implemented in the second and third steps. The second step was to assess species for inclusion based on distribution size or plant life history. The third step was to assess species for inclusion based on their northern distribution relative to the tropical-temperate transition zone. We used the plant distribution data and life history information to classify the 81 plant species into the following groups: (1) "Insufficient distribution"; (2) "Floating aquatic plant"; (3) "Clearly not tropical"; and (4) "Potentially tropical" (Additional file 1: Table S1). The "Insufficient distribution" group included eleven species whose distributions were too restricted or detections too few for subsequent analyses. These were species that were reported in less than four grid cells and were therefore excluded from subsequent analyses. The "Floating aquatic plant" group included five species that were excluded from the temperature threshold analyses because the biophysical processes that govern aquatic plant species vulnerability to cold temperature extremes are mechanistically different than for terrestrial and emergent wetland plants. For example, due to the buffering effects of water, floating and submerged aquatic plant species are less vulnerable to mortality induced by short-term (i.e., single or multiple day) air temperature extremes compared to terrestrial and emergent wetland plants. The "Clearly not tropical" group included eleven species whose distributions extended far beyond the tropical-temperate transition zone (i.e., at least 400 km north of the Florida-Georgia border; five of these species extended more than 1000 km north of the Florida-Georgia border), indicating that these species' northern range limits are governed by factors not targeted in this study. Collectively, these three filtering steps identified 54 species in the "Potentially tropical" category, which were species that were included in subsequent temperature threshold analyses.

Data analyses: temperature controls on species range limits

For each of the 54 species selected for threshold analyses (i.e., species within the "Potentially tropical" group), we used nonlinear logistic regression analyses to quantify thresholds and evaluate the sigmoidal relationships between minimum temperature and plant presence. This approach has been effectively used to quantify winter temperature thresholds for tropical, cold-sensitive plant species in the southeastern United States (Osland et al. 2013, 2020a; Osland and Feher 2020). Near the tropical-temperate transition zone in this region, there is often an abrupt temperature-driven northern range limit for tropical cold-sensitive species where species are present in warmer areas to the south but absent from colder areas to the north. Thus, species presence patterns across this transition zone typically reflect a sigmoidal relationship, and the thresholds identified from sigmoidal models often correspond well with field-based observations of freeze damage and mortality (Osland et al. 2013, 2020a; Osland and Feher 2020).

We used first and second derivatives of the sigmoidal models to identify thresholds differentiating between species presence and absence. More specifically, we determined (a) the inflection point, which represents the location of maximum rate of change

(T) and is the local maxima of the first derivative; and (b) the area of maximum rate of change (AMRC), which is the area between the local maxima and minima peaks of the second derivative. Whereas the AMRC represents a threshold zone where the rate of change in plant presence is greatest, T represents a discrete threshold and the absolute location of the largest rate of change (for more info and examples, see: Osland et al. 2013; Osland et al. 2014; Osland and Feher 2020). For more general information regarding the evaluation of ecological transitions and thresholds using sigmoidal models, inflection points, and AMRC threshold zones, see Wilson and Agnew (1992), Timoney et al. (1993), Hufkens et al. (2008), and Frazier and Wang (2013). All data analyses were performed in R version 4.1.2 (R Core Team 2021). Nonlinear logistic regression analyses were conducted using the nlstools package (Baty et al. 2015; Baty and Delignette-Muller 2021). Maxima and minima peaks of derivative equations were identified using the RootSolve package (Soetaert and Herman 2009; Soetaert 2021). Spatial analyses were conducted in Esri ArcGIS 10.7.1 (Environmental Systems Research Institute). For all analyses, statistically significant relationships were defined as those with a p value < 0.05. The symbols * and *** are used to denote p values of less than 0.05 and 0.001, respectively.

Plant traits, habitat preferences, threshold groups, and risk categories

For each of the species with significant temperature threshold results, we consulted the literature to determine the plant's: (1) growth form [i.e., tree, shrub, vine, grass, forb (i.e., herbaceous but not grass), or fern]; (2) habitat preference (i.e., uplands, wetlands, or both uplands and wetlands); (3) documented sensitivity to cold temperature extremes (i.e., reports of cold-induced damage or mortality); and (4) ability to resprout following disturbance. For communication purposes and range expansion analyses, we used the temperature threshold results to group the species into the following three temperature threshold categories: North Group (-16 °C to -11 °C), Mid Group (-11 °C to -6 °C), and South Group (-6 °C to -1 °C).

To communicate the management and risk assessment implications of warming-induced range expansion, we incorporated information from the University of Florida (UF) Institute of Food and Agricultural Sciences' (IFAS) Assessment of Nonnative Plants, which uses literature-based risk assessment tools to predict invasion risk within Florida of non-native plant species as well as plant species proposed for introduction (Lieurance and Flory 2020). These risk assessments are conducted for three regions of Florida (South, Central, and North), where invasive non-native species are typically assigned one of the following five region-specific categories: (1) "prohibited" (i.e., prohibited from use in Florida according to the Federal Noxious Weed List, the Florida Department of Agriculture and Consumer Services (FDACS) 5B-64.011 Prohibited Aquatic Plants, or FDACS 5B-57.007 Noxious Weed List); (2) "invasive" (i.e., invasive and not recommend for use); (3) "high invasion risk" (i.e., predicted to be invasive and not recommended for use); (4) "caution" (i.e., recommended for management to prevent escape); or (5) "not considered a problem" (i.e., not considered a problem species at the time within this region). For each of the species with significant temperature threshold results, we acquired the region-specific risk assessment categories from the UF/IFAS Assessment of Nonnative Plants.

Range expansion under alternative future winter warming scenarios

We used a six-step process to evaluate the potential range expansion of tropical invasive plants under the following three alternative future warming scenarios: a +2 °C, +4 °C, and +6 °C increase in winter cold temperature extremes. First, we acquired recent climate data, which consisted of a national scale grid of 2.5-arcmin resolution minimum temperature data (i.e., the same 1981–2010 PRISM data, but for the entire conterminous United States). Second, we developed the +2 °C, +4 °C, and +6 °C future warming scenarios, where we added 2 °C, 4 °C, or 6 °C, respectively, to the 1981–2010 minimum temperature data for each study grid cell. Third, we used the temperature thresholds for species groups North, Mid, and South to predict the position of these group range limits under the three scenarios. Fourth, we used the species-specific temperature threshold results in combination with the future climate data to predict species presence under the three scenarios. In the fifth step, we compiled those species-specific results to predict the potential total number of species present within each cell under each of the three scenarios. Finally, we used Global Aridity Index data (Zomer et al. 2022) to add a transparent mask to our future projection maps that denotes areas that may be too arid (i.e., Hyper Arid, Arid, or Semi-Arid climatic zones) to support the range expansion of our focal plants. Due to water availability constraints, we expect that the potential for range expansion of our focal tropical invasive species is most likely within Humid and Dry sub-humid climates.

Protected lands vulnerable to range expansion

To quantify the area of protected lands that are vulnerable to the northward range expansion of invasive species under the three alternative future climate scenarios, we used data obtained from the U.S. Geological Survey (USGS) Protected Areas Database of the United States (USGS Gap Analysis Project 2022). We specifically used the Gap Analysis Project (GAP) Status Codes 1, 2, and 3, which include lands owned by federal, state, local, or private institutions with a complete or partial permanent protection from natural land cover conversion. We used the group-specific range expansion data (i.e., data for the three species groups: North, Mid, and South) to quantify the area of protected lands that are vulnerable to the northward range expansion under the three scenarios for each of these three groups.

Results

Temperature controls on species range limits

Of the 54 species that we classified in the "Potentially tropical" group (Additional file 1: Table S1), we identified temperature thresholds for 40 species (Table 1). For each of the 40 species, we quantified significant nonlinear sigmoidal relationships between minimum temperature and species presence as hypothesized in Fig. 1. As examples, we include graphical depictions of the sigmoidal temperature-presence relationships and thresholds for nine species: *Dioscorea bulbifera* (air potato), *Nephrolepis cordifolia* (narrow swordfern), *Schinus terebinthifolius* (Brazilian peppertree), *Melaleuca quinquenervia* (melaleuca), *Pennisetum purpureum* (elephant grass), *Casuarina equisetifolia* (Australian-pine), *Eugenia uniflora* (Surinam cherry), *Acacia auriculiformis* (earleaf acacia), and *Manilkara zapota* (sapodilla). (Fig. 3a-i). We selected these nine species due their abundance and notoriety in the region and because they illustrate the variation in cold-tolerance in the region from more-to-less cold tolerant, respectively. For the forty species, temperature thresholds ranged from -16 °C to -1 °C (Table 1). Fifteen species had temperature thresholds between -16 °C and -11 °C (North Group); eleven species had temperature thresholds between -11 °C and -6 °C (Mid Group); and fourteen species had temperature thresholds between -6 °C and -1 °C (South Group) (Table 1).

Plant traits, habitat preference, and risk assessment categories

Of the 40 species identified in the temperature threshold analyses (Table 1), 15 are trees (37.5%), 9 are shrubs (22.5%), 6 are grasses (15%), 5 are forbs (12.5%), 3 are vines (7.5%), and 2 are ferns (5%) (Additional file 1: Table S2). Our literature review indicates that all 40 species have the ability to resprout following disturbance and 39 of the species have a documented sensitivity to cold temperature extremes (i.e., reports of cold-induced damage or mortality) (Additional file 1: Table S2). Based on habitat preference information, 16 species are predominantly found in uplands (i.e., terrestrial areas that are not wetlands), 3 species are predominantly found in wetlands, and 21 species are found in both upland and wetland ecosystems (Additional file 1: Table S2). The UF/IFAS Assessment of Nonnative Species indicates that of the 40 species identified in the temperature threshold analyses: (1) 12 species are in the prohibited category in all three IFAS regions; (2) 18 species are in the invasive category in at least one IFAS region; (3) 2 species are in the high invasion risk category in at least one IFAS region; (4) 7 species are in the caution category in at least one IFAS region; and (5) 1 species is in the assessment in process category in all three regions (Additional file 1: Table S3). Note that these region-specific classifications are sometimes reflective of cold sensitivity constraints on species distribution. For example, there are several cold-sensitive species that are classified as invasive in the IFAS South and/or IFAS Central

Table 1 Temperature thresholds governing the presence of 40 tropical invasive non-native plant species whose northern range limits are determined by extreme cold winter temperatures. This table includes results from the nonlinear logistic regression analyses. Group indicates species group, which was assigned using the temperature threshold results as follows: North Group (-16 °C to -11 °C), Mid Group (-11 °C to -6 °C), and South Group (-6 °C to -1 °C). T represents the inflection point or discrete temperature threshold. Area of maximum rate of change (AMRC) represents the upper and lower boundaries of the temperature threshold zone. RSE is the residual standard error from the regression analyses. The symbols * and *** denote *p* values of less than 0.05 and 0.001, respectively

Group	Scientific name	Common name	T (°C)	AMRC (°C)	RSE
NORTH	*Ardisia crenata*	Coral ardisia	-15.8***	-17 to -14.5	0.32
NORTH	*Cinnamomum camphora*	Camphortree	-15.7***	-16.4 to -15.1	0.23
NORTH	*Colocasia esculenta*	Coco yam	-15.0***	-16.5 to -13.4	0.35
NORTH	*Panicum repens*	Torpedograss	-14.8***	-16.1 to -13.6	0.17
NORTH	*Tradescantia fluminensis*	Small-leaf spiderwort	-14.3***	-15.3 to -13.2	0.26
NORTH	*Dioscorea bulbifera*	Air potato	-13.9***	-15.3 to -12.6	0.15
NORTH	*Lantana camara*	Lantana	-13.8***	-15.3 to -12.3	0.16
NORTH	*Solanum viarum*	Tropical soda apple	-13.2***	-14.7 to -11.7	0.31
NORTH	*Ludwigia peruviana*	Primrose-willow	-13.0***	-14.3 to -11.7	0.3
NORTH	*Nephrolepis cordifolia*	Narrow swordfern	-12.6***	-13.2 to -12.0	0.2
NORTH	*Ruellia simplex*	Britton's wild petunia	-12.2***	-13.2 to -11.1	0.27
NORTH	*Melinis repens*	Natalgrass	-12.1***	- 13.3 to -10.9	0.21
NORTH	*Asparagus aethiopicus*	Sprenger's asparagus fern	-12.0***	-12.4 to -11.6	0.27
NORTH	*Urena lobata*	Caesarweed	-11.9***	-12.7 to -11.0	0.24
NORTH	*Syngonium podophyllum*	American evergreen	-11.2***	-12.0 to -10.5	0.25
MID	*Schinus terebinthifolius*	Brazilian peppertree	-10.7***	-12.3 to -9.0	0.18
MID	*Abrus precatorius*	Rosarypea	-9.7***	-10.2 to -9.2	0.24
MID	*Urochloa mutica*	Para grass	-9.6***	-10.2 to -9.1	0.25
MID	*Psidium guajava*	Guava	-8.8***	-9.6 to -8.0	0.23
MID	*Melaleuca quinquenervia*	Melaleuca	-8.1***	-9.2 to -7.0	0.11
MID	*Senna pendula var. glabrata*	Valamuerto	-7.3***	-9.1 to -5.4	0.21
MID	*Pennisetum purpureum*	Elephant grass	- 6.9***	-9.0 to -4.8	0.31
MID	*Nephrolepis brownii*	Asian swordfern	- 6.7***	-8.9 to -4.4	0.26
MID	*Sporobolus indicus*	West Indian dropseed	-6.5***	-9.1 to -4.0	0.19
MID	*Casuarina equisetifolia*	Australian-pine	-6.4***	-9.6 to -3.3	0.23
MID	*Eugenia uniflora*	Surinam cherry	-6.4***	-8.9 to -3.9	0.3
SOUTH	*Syzygium cumini*	Java plum	-5.8***	-6.4 to -5.3	0.19
SOUTH	*Bischofia javanica*	Javanese bishopwood	-5.5***	-6.0 to -5.1	0.18
SOUTH	*Acacia auriculiformis*	Earleaf acacia	-5.2***	-5.8 to -4.5	0.18
SOUTH	*Ardisia elliptica*	Shoebutton ardisia	-5.1***	-5.8 to -4.4	0.18
SOUTH	*Neyraudia reynaudiana*	Burma reed	-4.8***	-5.3 to -4.3	0.28
SOUTH	*Ficus microcarpa*	Chinese banyan	-4.1***	-5.5 to -2.8	0.22
SOUTH	*Albizia lebbeck*	Woman's tongue tree	-3.8***	-7.8 to 0.2	0.23
SOUTH	*Casuarina glauca*	Suckering Australian-pine	-3.5***	-5.5 to -1.5	0.18
SOUTH	*Schefflera actinophylla*	Octopus tree	-3.0***	-6.0 to 0.0	0.19
SOUTH	*Thespesia populnea*	Portia tree	-2.4***	-4.6 to -0.2	0.16
SOUTH	*Bauhinia variegata*	Mountain ebony	-2.3*	-5.2 to 0.5	0.18
SOUTH	*Scaevola taccada*	Beach naupaka	-2.1***	-4.4 to 0.1	0.16
SOUTH	*Colubrina asiatica*	Asian nakedwood	-1.8***	-3.9 to 0.3	0.36
SOUTH	*Manilkara zapota*	Sapodilla	-1.0***	-2.4 to 0.4	0.29

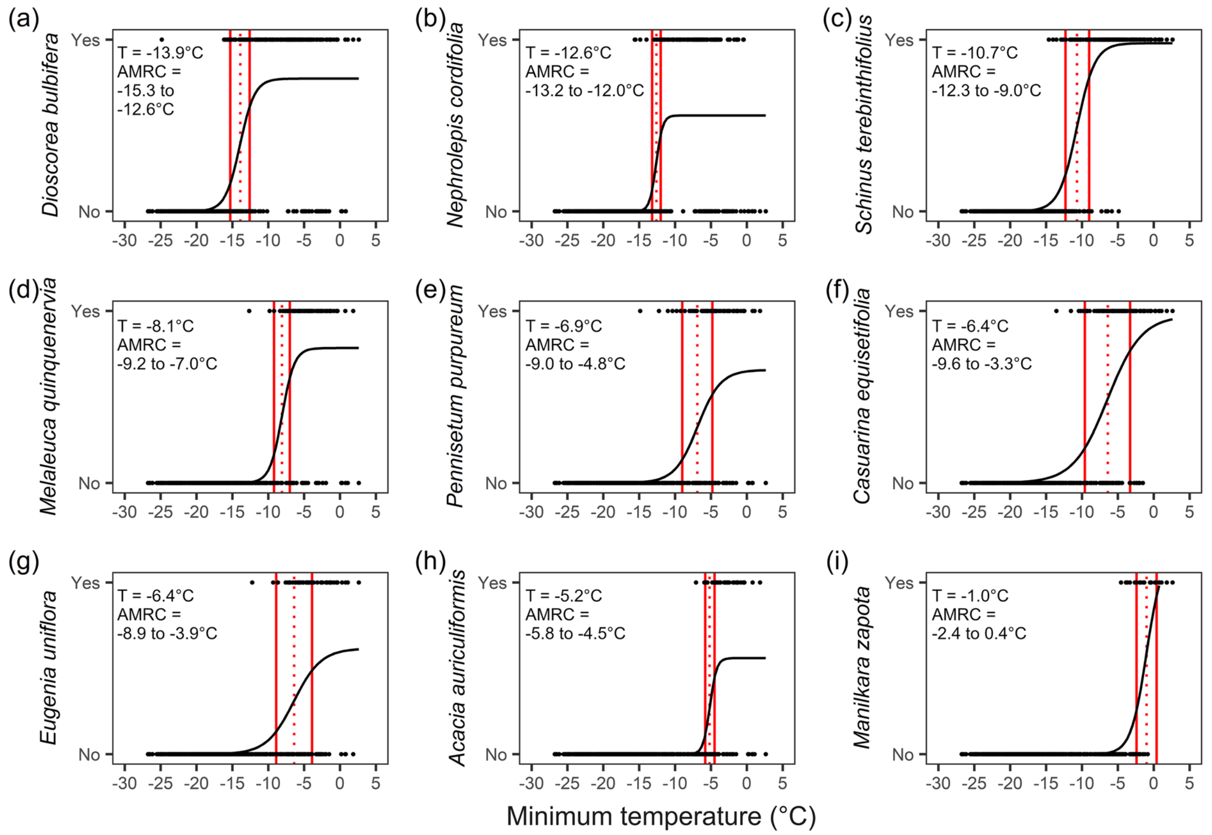

Fig. 3 The relationships between minimum temperature and the presence of nine tropical invasive non-native plants species: (**a**) *Dioscorea bulbifera* (air potato); (**b**) *Nephrolepis cordifolia* (narrow swordfern); (**c**) *Schinus terebinthifolius* (Brazilian pepper); (**d**) *Melaleuca quinquenervia* (Melaleuca); (**e**) *Pennisetum purpureum* (elephant grass); (**f**) *Casuarina equisetifolia* (Australian pine); (**g**) *Eugenia uniflora* (Surinam cherry); (**h**) *Acacia auriculiformis* (earleaf acacia); and (**i**) *Manilkara zapota* (sapodilla). We selected these nine species due their abundance and notoriety in the region and because they illustrate the variation in cold-tolerance in the region from more-to-less cold tolerant, respectively. Within each panel, the dotted vertical line represents the inflection point or discrete temperature threshold (T). The solid vertical lines depict the temperature threshold zone, which is defined by the lower and upper boundaries of the area of maximum rate of change (AMRC). Similar threshold results for the other 31 species are presented in Table 1

regions but classified in the caution or not considered a problem species categories in the IFAS North region because they are presently considered to be temperature limited in the North region [e.g., *Eugenia uniflora* (Surinam cherry), *Acacia auriculiformis* (earleaf acacia), and *Manilkara zapota* (sapodilla)] (Additional file 1: Table S3).

Range expansion under alternative future winter warming scenarios

Our analyses of the impacts of future winter warming scenarios indicate that the 40 species identified in the temperature threshold analyses (Table 1) have the potential for range expansion across the southeastern United States (Figs. 4 and 5). The potential for range expansion is lowest under the +2 °C scenario, intermediate under the +4 °C scenario, and greatest under the +6 °C scenario. There is a gradient in the number of species capable of range expansion, with more species capable of range expansion in the warmer south and fewer species capable of range expansion in the colder north (Fig. 5; see south-north gradient in number of species).

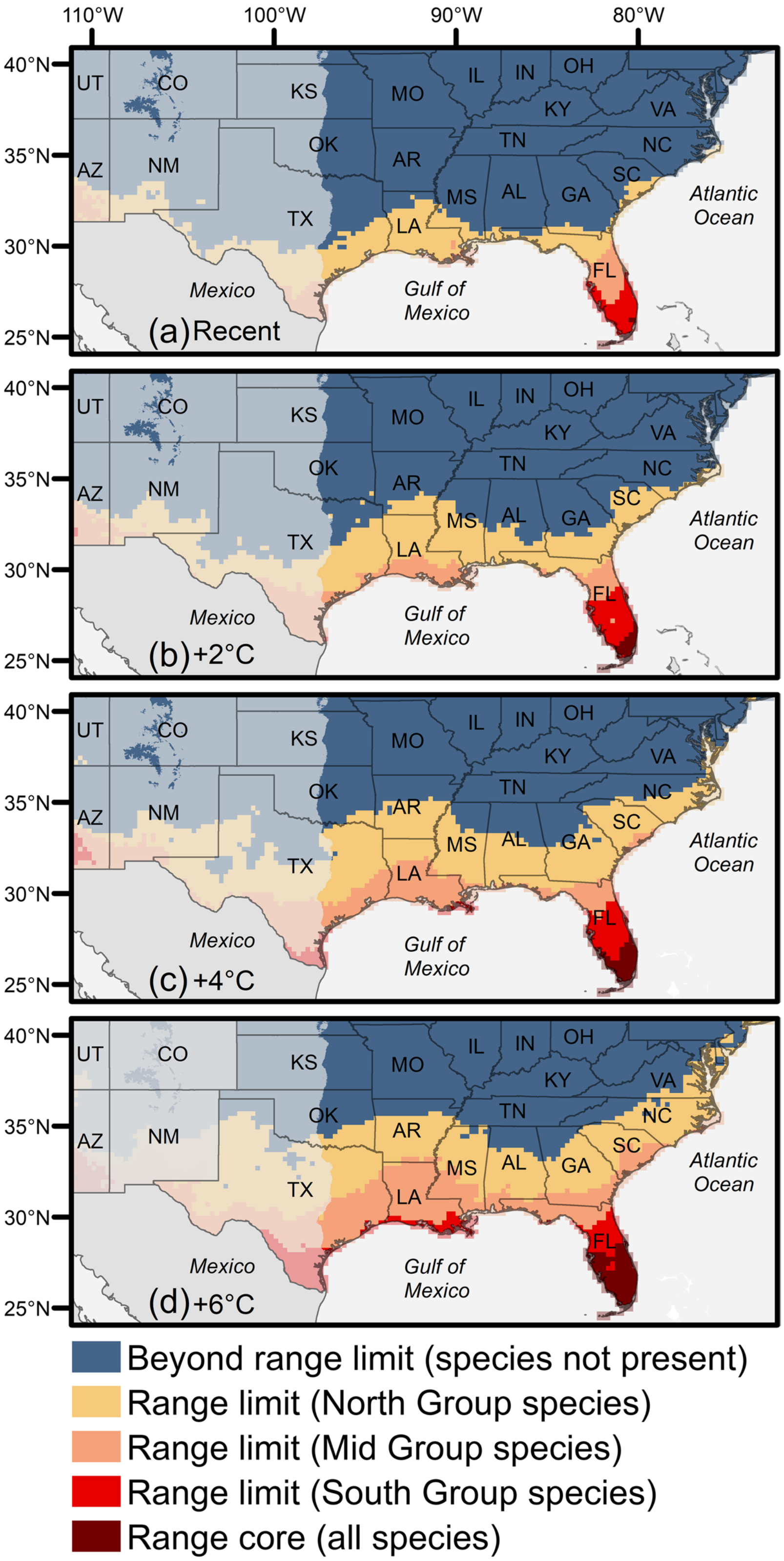

Fig. 4 Maps of the predicted range expansion of tropical invasive non-native plant species groups under **a** recent climatic conditions (1981–2010) and three alternative future climate scenarios with warmer winter temperature extremes—a + 2 °C, + 4 °C, and + 6 °C increase in winter cold temperature extremes (**b**–**d**, respectively). These maps show range limits for three different groups of species (North, Mid, and South). The plant species within these groups are identified in Table 1. The range core category indicates areas where temperature extremes are warm enough that freeze-induced mortality does not affect any of the species' distributions. The 40 temperature-sensitive species included in these analyses are identified in Table 1. Due to water availability constraints, we expect that the potential for range expansion of these tropical invasive species is most likely within Humid and Dry sub-humid climates (i.e., those areas not covered by the mask within the maps). The left side of these maps contains a transparent grey mask to denote Hyper Arid, Arid, or Semi-Arid areas determined from the Global Aridity Index (Zomer et al. 2022)

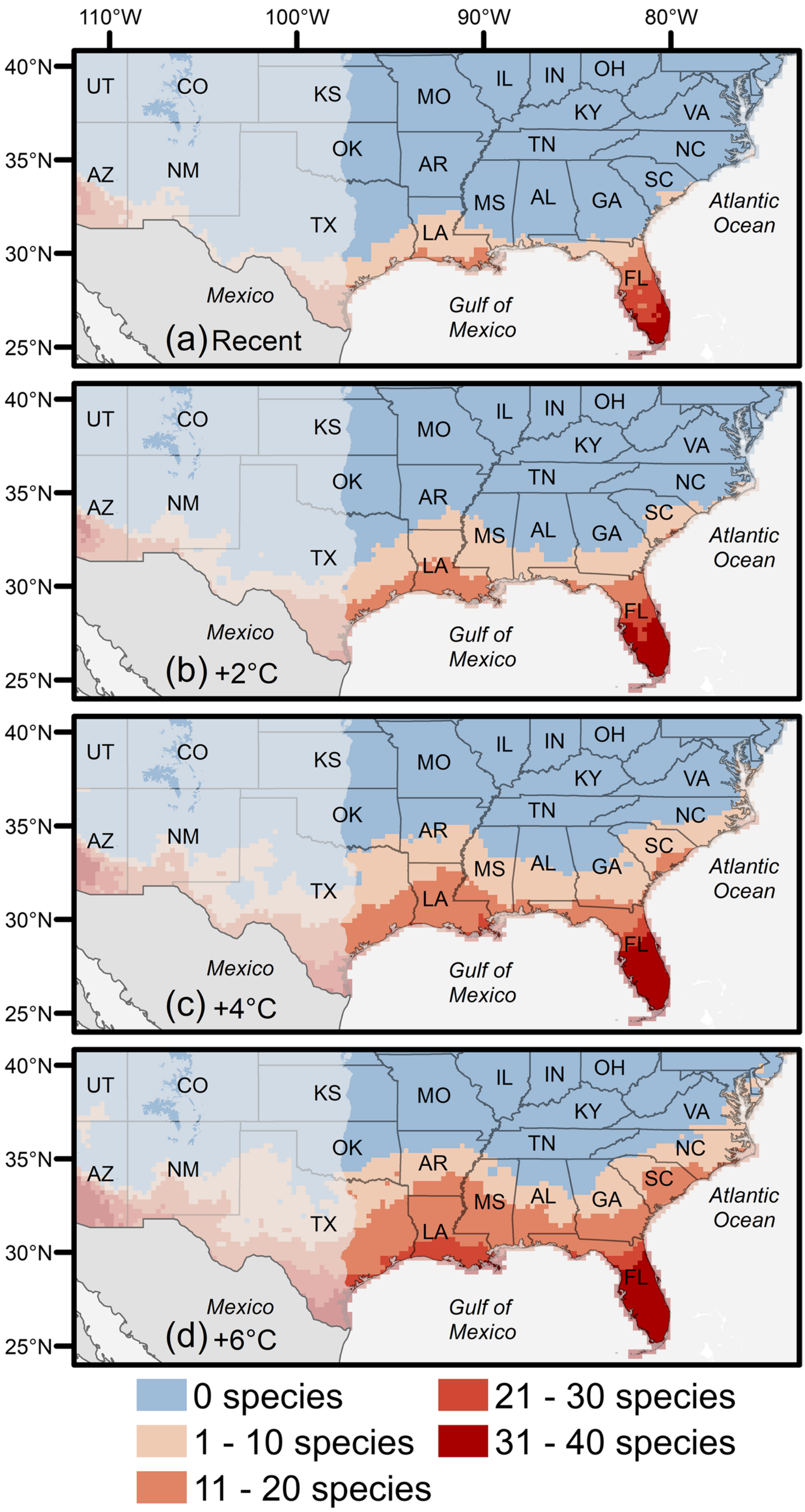

Fig. 5 Maps of the predicted range expansion of tropical invasive non-native plant species under (**a**) recent climatic conditions (1981–2010) and three alternative future climate scenarios with warmer winter temperature extremes—a + 2 °C, + 4 °C, and + 6 °C increase in winter cold temperature extremes (**b**–**d**, respectively). These maps show the predicted number of plant species present under each scenario. The 40 temperature-sensitive species included in these analyses are identified in Table 1. Due to water availability constraints, we expect that the potential for range expansion of these tropical invasive species is most likely within Humid and Dry sub-humid climates (i.e., those areas not covered by the mask within the maps). The left side of these maps contains a transparent grey mask to denote Hyper Arid, Arid, or Semi-Arid areas determined from the Global Aridity Index (Zomer et al. 2022)

Protected lands potentially vulnerable to range expansion

Our results quantify the area of protected lands that are potentially vulnerable to the range expansion of tropical invasive plant species due to warming winters (Fig. 6). The potentially vulnerable area is smallest under the +2 °C scenario, intermediate under the +4 °C scenario, and greatest under the +6 °C scenario (Fig. 6). The group-specific results indicate that the potentially vulnerable area is lowest for the South Group, intermediate for the Mid Group, and greatest for the North Group. For the North Group, the potentially vulnerable areas are 52,000, 105,000, and 145,000 km^2 for the +2 °C, +4 °C, and +6 °C scenarios, respectively. For comparison, an area of 150,000 km^2 is roughly equivalent to the states of Georgia or Illinois (USA). Please note that these areal estimates are based solely on climate and are likely greatly overestimated due to the influence of other biotic and abiotic factors.

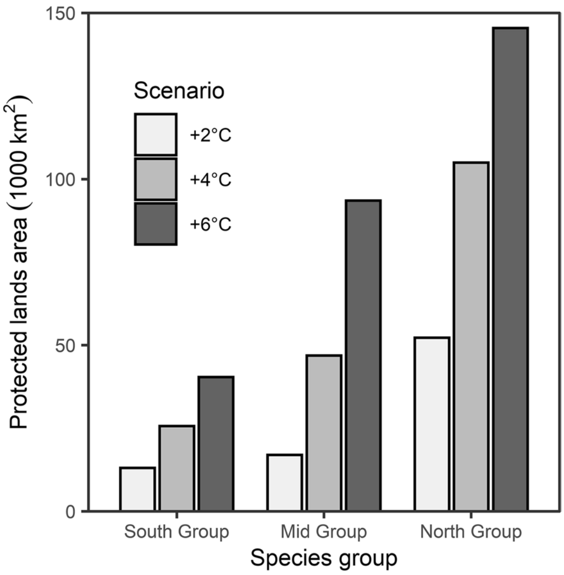

Fig. 6 The area of protected lands that could potentially be affected by the range expansion of tropical invasive non-native species under three alternative future climate scenarios with warmer winter temperature extremes—a+2 °C, +4 °C, and +6 °C increase in winter cold temperature extremes. Protected lands are areas that have been designated as having a protected status, meaning that they are owned by federal, state, local, or private institutions with the capacity for continued conservation. The results are presented for three different groups of species (North, Mid, and South). The plant species within these groups are identified in Table 1, and the group-specific areas that are vulnerable to range expansion are shown in Fig. 4

Discussion

Extreme winter temperature thresholds control tropical invasive plant range limits

Plant ecologists working in the tropical-temperate transition zone in North America have a rich history of investigating species-specific differences in plant sensitivity to freezing and chilling temperatures (e.g., Shreve 1914; Davis 1940; Holdridge 1967; Craighead 1971; Lugo and Patterson-Zucca 1977; Lonard and Judd 1991; Ross et al. 2009). In Florida, these species-specific differences greatly influence the distributions of tropical native plant species (Greller 1980; Myers 1986; Box et al. 1993). Based upon accounts of physiological damage and/or mortality to tropical invasive non-native plants following extreme freezing and/or chilling events (e.g., Snow 1964; Morton 1980; Simberloff 1996; Turner et al. 1997; Langeland and Burks 1998; Hutchinson and Langeland 2014), we expected that the northern range limits of tropical invasive non-native plants in this region would also be strongly governed by species-specific threshold responses to extreme cold winter temperatures (i.e., the generalized illustration in Fig. 1).

Our results show that species-specific differences in cold tolerance govern the northern distributional limits of tropical invasive plants. There are some species, such as *Scaevola taccada* (beach naupaka), *Colubrina asiatica* (Asian nakedwood) (McCormick 2007), and *Manilkara zapota* (sapodilla), whose northern distributions are constrained primarily to south Florida due to their higher sensitivity to cold temperatures (see Fig. 4 and species in South Group within Table 1). Our analyses indicate that species in this group have temperature thresholds between -6 °C and -1 °C. There are other species, such as *Schinus terebinthifolius* (Brazilian peppertree) (Osland and Feher 2020), *Melaleuca quinquenervia* (melaleuca), *Casuarina equisetifolia* (Australian-pine) (Morton 1980), and *Eugenia uniflora* (Surinam cherry) (Snow 1964), that are moderately cold sensitive with northern range limits currently constrained to central or north Florida (see Fig. 4 and species in the Mid Group within Table 1). Our analyses indicate that species in this group have temperature thresholds between -11 °C and -6 °C. Finally, there are more cold-tolerant species, such as *Tradescantia fluminensis* (small-leaf spiderwort) (Gorchov 2019), *Dioscorea bulbifera* (air potato), and *Nephrolepis cordifolia* (narrow swordfern), whose northern distributions extend into north Florida and in some cases beyond Florida into adjacent states (e.g., Georgia, Alabama, Mississippi, and/or Louisiana) (see Fig. 4 and species in North Group within Table 1). Our analyses indicate that species in this group have temperature thresholds between -16 °C and -11 °C.

Prior research in the southeastern United States has revealed strong agreement between field observations of freeze-induced plant mortality and species distribution-derived temperature thresholds (Osland et al. 2013, 2020a; Osland and Feher 2020). Our results provide a foundation for better understanding species-specific thresholds and differences in cold sensitivity that affect northern range limits. However, there is a need for complementary research that tests the winter temperature thresholds identified in this study using field observations (i.e., freeze-induced plant mortality or damage observations) and manipulative cold temperature experiments in greenhouses, common gardens, and field settings. Regional coordinated measurements of freeze damage, mortality, and recovery across freeze severity gradients and after extreme freeze events (e.g., Osland et al. 2020a) can be particularly valuable for refining temperature thresholds that affect range limits.

Poleward range expansion in a warming world

Our findings indicate that small changes in the severity of winter cold temperature extremes can trigger large changes in the distribution and abundance of tropical invasive species in the southeastern United States. We illustrate the potential for northward range expansion of groups and species in Figs. 4 and 5, respectively. These results indicate that north Florida, Georgia, South Carolina, Alabama, Mississippi, Louisiana, and Texas are areas that are particularly vulnerable to the range expansion of tropical invasive plant species. Due to water availability constraints, we expect that the potential for range expansion of our focal tropical invasive species is most likely within the Humid and Dry sub-humid climates shown in these figures.

Due to the influence of land-ocean temperature gradients and the thermal buffering effects of warmer ocean waters (Osland et al. 2017, 2019b), the potential for range expansion is greatest in coastal areas, which typically have warmer temperatures than inland counterparts (e.g., see warmer temperatures along the coast in Figs. 4 and 5). Thus, coastal regions are likely to serve as biological invasion hotspots from which invasive species expand into inland areas. For example, the southern coast of Georgia is expected to be a range expansion hotspot for tropical species due to warmer temperatures along the coast as well as the proximity to current range limits of many invasive species in north Florida near Jacksonville. Similarly, climatic conditions along the southern and central Texas coast are already suitable for many of the tropical invasive plants included in this study. Some of our focal species [e.g., *S. terebenthifolius* (Brazilian peppertree) and *D. bulbifera* (air potato)] are already established and expanding in Texas (EDDMapS 2020). However, not all of our focal species are capable of long-distance dispersal and range expansion to Texas and other areas that are not immediately adjacent to Florida. Thus, there is a need to examine the potential for natural and/or human-facilitated dispersal of these species across the region.

For the cold-sensitive species identified in our analyses, there is a need for research that examines the roles of microclimate, plant traits, and dispersal pathways that may facilitate or hinder northward range expansion in response to warming winters. Our results begin to elucidate the potential for range expansion in response to warming temperatures. However, there are many natural and anthropogenic processes that affect the ability of plants to successfully migrate in response to climate change (Zhu et al. 2012; Corlett and Westcott 2013). For example, long-distance dispersal, growth, stress tolerance, reproduction, and biotic competition are all processes that affect the ability of species to successfully migrate. While some species will not be able to migrate northward in response to warming winters, other species possess traits that lead to a higher potential for northward movement and range expansion.

Beyond just natural dispersal pathways, there is a need to investigate the role of human-facilitated dispersal. Some of the plant species identified in our analyses can be legally sold as ornamental plants; thus, horticultural practices (Reichard and White

2001) and human-facilitated transport could accelerate the pace of range expansion for some species as they are planted north of current range limits in areas that are increasingly becoming suitable for population growth due to warming winters. Long-distance transport of seeds and propagule via roads, construction equipment, or recreational equipment (Veldman and Putz 2010; Rew et al. 2018) can also facilitate range expansion. Long-distance dispersal during extreme events (e.g., hurricanes and floods) is another mechanism that could accelerate the pace of range expansion for some species (Van der Stocken et al. 2019; Kennedy et al. 2020).

The influence of microclimate on invasive plant range expansion has been understudied. For many tropical species in the southeastern United States, thermal refugia play a critical role to enable organisms to survive extreme cold winter temperatures (Osland et al. 2021). For example, coastal fishes (Stevens et al. 2018), sea turtles (Lamont et al. 2018), amphibians (Meshaka 1996), reptiles (Mazzotti et al. 2016), and manatees (Laist et al. 2013) seek thermal refugia to survive extreme cold events. Similarly, thermal refugia can reduce damage and mortality to mangroves during extreme freeze events (Ross et al. 2009; Osland et al. 2019b), which means that near northern range limits, mangroves are more abundant and taller near microclimates that provide a thermal buffer during extreme freeze events (Osland et al. 2020b). Similarly, we expect that microclimates will greatly influence the landscape position of range-expanding tropical invasive plants. For species that are capable of long-distance dispersal, we expect that landscape settings that provide thermal refugia will serve as range expansion hotspots.

The value of early detection and rapid response and preemptive regulation for managing range-expanding plants

Our analyses of land ownership indicate that there are many protected lands in the southeastern United States that are potentially vulnerable to the range expansion of tropical invasive plants. These are lands that are owned by federal, state, local, or private institutions with a complete or partial permanent protection from natural land cover conversion (USGS Gap Analysis Project 2022). One of the most effective approaches for managing invasive species on these protected lands is predicting future species responses to inform early detection and rapid response (EDRR), where invasive species presence is detected during the early stages of invasion and where management efforts are implemented fast enough to eradicate or contain invasive species populations while they are still localized (Westbrooks 2004; Reaser et al. 2020). Our results indicate that there are many tropical invasive plant species in Florida that are expected to expand northward in response to warming winters. Natural resource management near the front lines of range expansion (e.g., within and just north of current range limits) can be informed by: (1) knowledge regarding which species have the potential to expand into their management areas in response to warming winters, which is information that is needed for early detection; (2) awareness of the societal and ecological impacts of invasive species that are expected to expand into their regions (e.g., the information contained within the UF/IFAS risk assessment); and (3) management approaches that can be used to eradicate or contain range-expanding invasive species populations while they are still localized. This information can help managers prevent or at least slow the pace of plant invasions associated with northward range expansions.

Given the current lack of regulations governing the sale, transport, and planting of invasive plant species in much of the southeastern United States, we expect that interactive effects of human-facilitated dispersal, human-facilitated establishment, and winter climate change have the potential to accelerate the northward range expansions of some tropical invasive plants. Preemptive regulations could restrict dispersal by limiting the sale, transport, and planting of cold-sensitive invasive species in areas that are vulnerable to future range expansion. Projections of future range expansion could be used to guide the development of preemptive regulations. For example, 12 of our focal species are prohibited from use in Florida according to federal and/or state regulations (Additional file 1: Table S3) (Lieurance and Flory 2020). However, the planting of these twelve species is not prohibited in the surrounding states that are vulnerable to range expansion. Similarly, the UF/IFAS risk assessment for non-native plants is based upon species' risks within current distributions (Lieurance and Flory 2020). The potential for range expansion could be incorporated into assessments to enable managers to anticipate and prepare for future changes in distribution due to warming winters.

Conclusions

During the past century, the state of Florida has become a global hotspot for biological invasions (Dawson et al. 2017; Pyšek et al. 2017, 2020). Our results show that many of these invasive plant species are tropical, cold-sensitive species whose northern range limits are governed by extreme cold winter temperatures. In a rapidly warming world, these tropical, cold sensitive species have the potential to expand northward across the southeastern United States. Our analyses focus on the tropical-temperate transition zone in the southeastern United States where winter temperature extremes play a critical ecological role (Boucek et al. 2016; Osland et al. 2021). However, the range expansion of tropical species is a global phenomenon (e.g., Vergés et al. 2014), and there is a need for investigations in other regions and continents concerning the potential for poleward range expansion of tropical invasive species in response to warming winters.

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Data availability The data used in this study are publicly available from the following sources: (1) the plant species occurrence data are available from the Early Detection & Distribution Mapping System database (EDDMapS 2020); (2) the temperature data are available from the PRISM Climate Data produced by the PRISM Climate Group (Oregon State University; prism.oregonstate.edu); (3) the aridity data are available from the Global Aridity Index (Zomer et al. 2022); (4) the species risk assessment data are available from the University of Florida (UF) Institute of Food and Agricultural Sciences' (IFAS) Assessment of Nonnative Plants (Lieurance and Flory 2020); and (5) the protected lands data are available from the U.S. Geological Survey Protected Areas Database of the United States (USGS Gap Analysis Project 2022).

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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