**RESEARCH REVIEW**

# Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures

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## Abstract

Tropicalization is a term used to describe the transformation of temperate ecosystems by poleward-moving tropical organisms in response to warming temperatures. In North America, decreases in the frequency and intensity of extreme winter cold events are expected to allow the poleward range expansion of many cold-sensitive tropical organisms, sometimes at the expense of temperate organisms. Although ecologists have long noted the critical ecological role of winter cold temperature extremes in tropical–temperate transition zones, the ecological effects of extreme cold events have been understudied, and the influence of warming winter temperatures has too often been left out of climate change vulnerability assessments. Here, we examine the influence of extreme cold events on the northward range limits of a diverse group of tropical organisms, including terrestrial plants, coastal wetland plants, coastal fishes, sea turtles, terrestrial reptiles, amphibians, manatees, and insects. For these organisms, extreme cold events can lead to major physiological damage or landscape-scale mass mortality.

Conversely, the absence of extreme cold events can foster population growth, range expansion, and ecological regime shifts. We discuss the effects of warming winters on species and ecosystems in tropical–temperate transition zones. In the 21st century, climate change-induced decreases in the frequency and intensity of extreme cold events are expected to facilitate the poleward range expansion of many tropical species. Our review highlights critical knowledge gaps for advancing understanding of the ecological implications of the tropicalization of temperate ecosystems in North America.

**KEYWORDS**

climate change, climate extreme, extreme cold events, poleward migration, range expansion, tropicalization, warming, winter climate change

## 1 | INTRODUCTION

In the face of accelerating climate change, ecologists are increasingly challenged to better understand the ecological impacts of changes in the frequency and intensity of extreme climatic events (Parmesan et al., 2000; Smith, 2011; USGCRP, 2018). Near tropical–temperate transition zones in North America, decreases in the frequency and intensity of extreme cold events are expected to enable the poleward range expansion of cold-sensitive tropical organisms (Figure 1; Tables 1 and S1), sometimes at the expense of temperate organisms (Carter et al., 2018; Cavanaugh et al., 2019; Weiss & Overpeck, 2005). Although astute scientists and naturalists have long recognized the critical influence of winter temperature extremes on tropical species' range limits (e.g., Davis, 1940; Lonard & Judd, 1991; Shreve, 1911), the ecological effects of extreme cold events have been understudied (Boucek et al., 2016).

In this communication, our aim is to highlight, within the context of climate change, the critical ecological role that extreme cold events play within tropical–temperate transition zones in North America. We begin with sections that consider the frequency and return interval of ecologically relevant extreme cold events, recent winter warming trends, and the general physiological effects of winter cold temperature extremes. Next, in taxa-specific sections focused on terrestrial plants, coastal wetland plants, coastal fish, sea turtles, terrestrial reptiles, amphibians, manatee, and insects, we examine cold sensitivity and assess the influence of extreme cold events on northern range limits and ecosystem properties. These taxa-specific sections also examine climate change effects and gauge the potential for ecological tropicalization, which is a term used to describe the transformation of temperate ecosystems by poleward-moving tropical organisms in response to warming temperatures (Vergés et al., 2014). Following the taxa-specific sections, we include sections focused on the critical role of range expansion pathways, microclimates, and thermal refugia. Then, we finish with a section that highlights knowledge gaps for advancing understanding of climate change impacts.
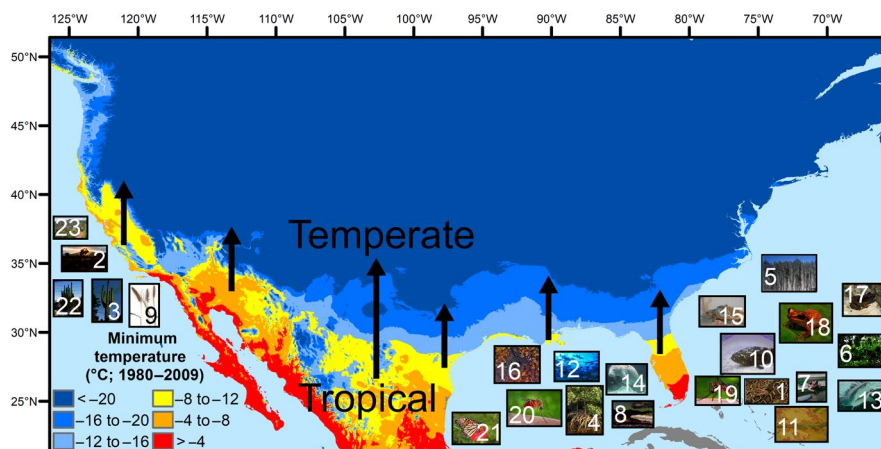


**FIGURE 1** A map illustrating tropical-temperate climate and ecological transition zones in North America. While the more temperate zones are depicted with blues, the more tropical zones are depicted with warm colors (i.e., red, orange, and yellow). In response to warming winters, cold-sensitive tropical organisms are expected to move northward, sometimes at the expense of cold-tolerant temperate organisms. The photos provide examples of tropical cold-sensitive organisms whose northern range limits are governed by winter cold temperature extremes (photo numbers correspond to the species in Table 1; see Table S1 for sources). Temperatures represent the absolute coldest temperature recorded for the period extending from 1980 to 2009, obtained from Daymet data (https://daymet.ornl.gov)

| Number | Common name | Scientific name (s) |
|--------|-------------|---------------------|
| 1 | Burmese python | *Python molurus bivittatus* |
| 2 | Joshua tree | *Yucca brevifolia* |
| 3 | Saguaro | *Carnegiea gigantea* |
| 4 | Red mangrove | *Rhizophora mangle* |
| 5 | Melaleuca | *Melaleuca quinquenervia* |
| 6 | Brazilian pepper | *Schinus terebinthifolius* |
| 7 | Cuban treefrog | *Osteopilus septentrionalis* |
| 8 | American crocodile | *Crocodylus acutus* |
| 9 | Buffelgrass | *Pennisetum ciliare* |
| 10 | Goliath grouper | *Epinephelus itajara* |
| 11 | Sawfish | *Pristis pectinata* |
| 12 | Cobia | *Rachycentron canadum* |
| 13 | Bull shark | *Carcharhinus leucas* |
| 14 | Manatee | *Trichechus manatus* |
| 15 | Loggerhead sea turtle | *Caretta caretta* |
| 16 | Kemp's ridley sea turtle | *Lepidochelys kempii* |
| 17 | Greenhouse frog | *Eleutherodactylus planirostris* |
| 18 | Coqui frog | *Eleutherodactylus coqui* |
| 19 | *Aedes aegypti* | *Aedes aegypti* |
| 20 | *Culex quinquefasciatus* | *Culex quinquefasciatus* |
| 21 | Monarch butterfly | *Danaus plexippus* |
| 22 | Organ pipe cactus | *Stenocereus thurberi* |
| 23 | Chapparal plants | *Ceanothus megacarpus, Malosma laurina* |

## 2 | EXTREME COLD EVENTS ARE INFREQUENT BUT ECOLOGICALLY IMPORTANT

Across the globe, there is much variation in the frequency, intensity, and ecological significance of extreme cold events within tropical–temperate transition zones. In some transition zones—especially those in the Southern Hemisphere (e.g., South America, Africa, and Australia, where cold Antarctic air is modulated by large stretches of ocean before reaching other continents)—winter temperature means, rather than extremes, appear to govern the poleward range limits of tropical organisms (Osland, Feher, et al., 2017). However, tropical–temperate transition zones in the Northern Hemisphere

(e.g., North America and Asia, where cold Arctic air can rapidly descend across large, high latitude land masses) are more strongly controlled by extreme cold events rather than mean winter temperatures (Osland, Feher, et al., 2017; Stuart et al., 2007). Cold air outbreaks from the poles into tropical–temperate transition zones are more frequent and intense in the Northern Hemisphere compared to the Southern Hemisphere (Smith & Sheridan, 2020).

Tropical–temperate transition zones in North America occur primarily in the southern United States and northern Mexico (see warm-to-cold color transitions in Figure 1). Across these zones, extreme cold events act in a similar manner as other ecologically important but infrequent disturbances such as hurricanes, fires, or floods, which can cause mass mortality, lead to large losses of aboveground biomass, reset successional dynamics, and, in the most severe cases, produce ecological regime shifts (Peters et al., 2011; Pickett & White, 2013; Turner, 2010). For example, extreme cold events can lead to ecological regime shifts in coastal wetlands, where cold-induced mangrove forest mortality events are followed by landscape-scale mangrove-to-marsh transitions, and conversely, the absence of cold events can lead to marsh-to-mangrove transitions (Cavanaugh et al., 2019; Osland, Day, et al., 2017).

Within the United States, Florida, Alabama, Mississippi, Louisiana, Texas, New Mexico, Arizona, and California are states that possess tropical–temperate transition zones (Figure 1). In northern Mexico, Tamaulipas, Nuevo Leon, Coahuila, Chihuahua, Sonora, and Baja California are states with tropical species whose northern range limits are governed by cold temperature extremes. In northern Mexico and the southwestern and south-central United States, extreme cold temperature controls on tropical species' distributional limits are also apparent at higher elevations along altitudinal gradients (Bojórquez et al., 2019; Brusca et al., 2013; Niering et al., 1963).

The Florida peninsula and the Sonoran Desert have been two notable hotspots for research on the effects of extreme cold events on tropical species' range limits in North America. The Florida peninsula spans a comparatively conspicuous tropical–temperate transition zone, with more cold-sensitive tropical species in south Florida and more cold-tolerant temperate species in north Florida. Ecologists working in Florida have long studied the critical ecological role of extreme cold events (Boucek et al., 2016; Davis, 1940; Olmsted et al., 1993). The Sonoran Desert region is the most tropical of North America's four great deserts (Shreve & Wiggins, 1964; Turner et al., 1995). The structurally diverse vegetation of the Sonoran Desert is unique in that it includes many species of columnar cacti and leguminous trees, both of which are rare or nonexistent in the other three shrub-dominated North American deserts (i.e., the Great Basin, Mojave, and Chihuahuan Deserts). Occasional catastrophic cold events (i.e., cold-induced mass mortality events) have historically been common and comparatively well studied in the northern Sonoran Desert along the Arizona-Sonora border (e.g., Bowers, 1981; Shreve, 1911; Steenbergh & Lowe, 1983).

Most winters in North-America's tropical–temperate transition zones are comparatively mild, without major frequent cold events that lead to landscape-scale mortality or physiological damage.

Major ecologically relevant cold events may occur just once every 20–30 years. To illustrate this point, we present 100 years of air temperature data from a location within the tropical–temperate transition in central Florida (Figure 2). In this example, the return time for ecologically relevant cold events is several decades (see red line within grey box), and most winters are comparatively warm, ecologically benign, and disturbance free (see blue peak outside of grey box). Due to accelerating climate change, the number of years with ecologically relevant cold events is expected to decrease (Carter et al., 2018; USGCRP, 2017, 2018). In other words, the red and blue lines in Figure 2 are expected to shift to the right, which would be above the threshold for cold damage or mortality. Although the temperatures along the y-axis and the position of the ecological threshold are species and location-dependent, the general relationships describing the return time and frequency of ecologically relevant extreme cold events apply to many other tropical–temperate transition zones across North America (i.e., all areas with warm-to-cold color transitions in Figure 1). Tropical–temperate ecotones in North America are highly sensitive to small changes in winter temperature regimes, and the northern limits of climatic zones that support tropical cold-sensitive species are expected to move northward under 2°C, 4°C, and 6°C increases in winter temperature extremes (Figure 3b,c,d, respectively).

Across North America, scientists use different terms to describe extreme cold winter temperature events, and these terms are often taxa- or region-specific. Some of these terms are introduced in the taxa-specific sections of this review. For example, sea turtle ecologists use the term "cold stunning event" (Griffin
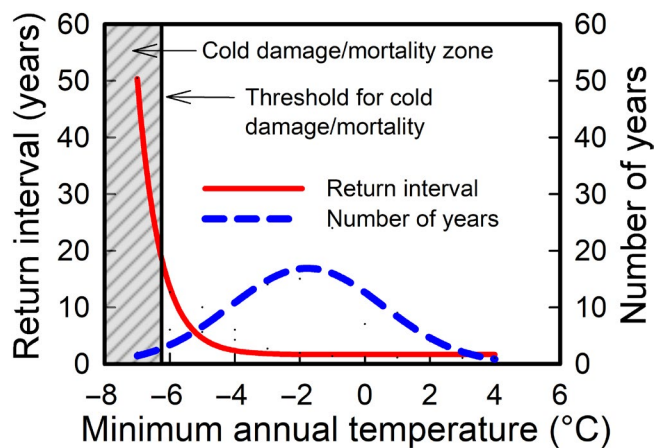
**FIGURE 2** Near tropical-temperate transition zones in North America, winter cold temperature extremes play a critical ecological role. Data from 1900–1999 were used to create this generalized depiction of the return time and frequency of ecologically relevant cold events for a location in central Florida. The vertical line represents a generalized threshold for cold damage or mortality, and the grey box represents the zone where cold damage or mortality would occur in this scenario. The return time for ecologically relevant cold events in this depiction is ~20 years (see red line in grey box). This generalized scenario was developed using knowledge of cold temperature thresholds for two plant species in this region (Osland, Day, Hall, et al., 2020; Osland & Feher, 2020)
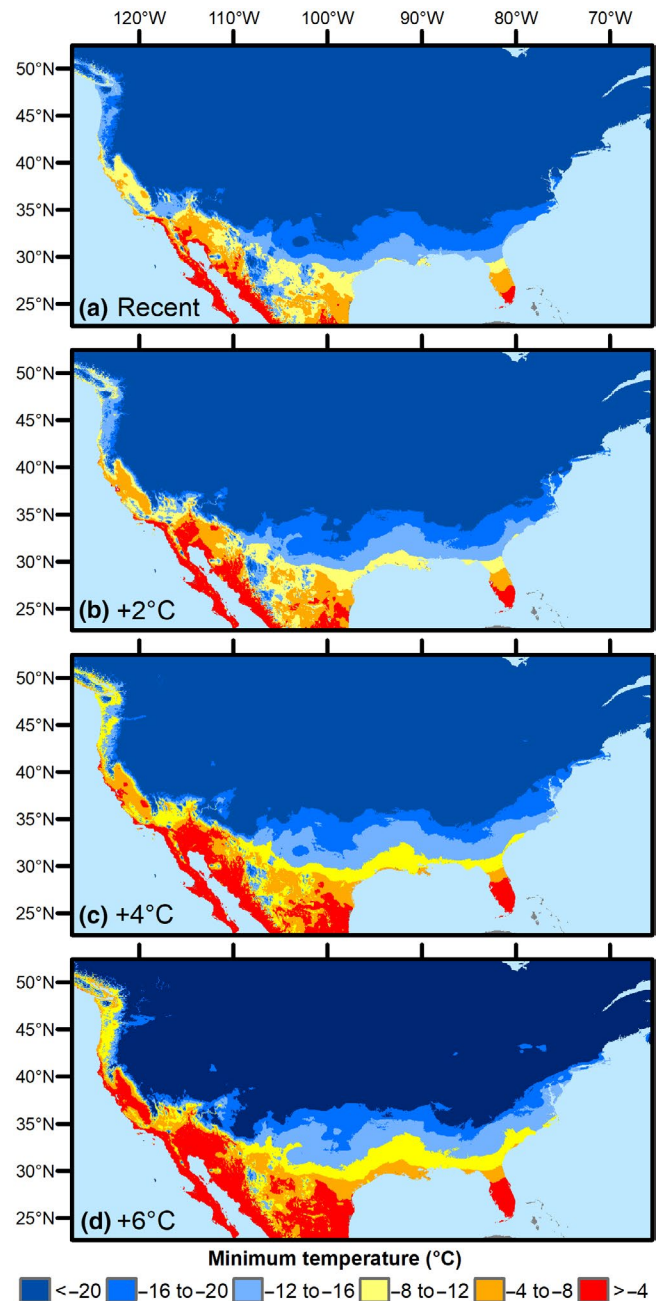
**FIGURE 3** Maps comparing the northward position of North American climatic zones supporting tropical cold sensitive species (i.e., red, orange, and yellow areas) under (a) recent climatic conditions (1980–2009) and three alternative future climate scenarios—a 2°C, 4°C, and 6°C increase in winter temperature extremes (b, c, d, respectively). For (a), temperatures represent the absolute coldest temperature recorded during the 30-year period, obtained from Daymet data (https://daymet.ornl.gov)

et al., 2019) and desert ecologists have used the term "catastrophic freeze" (Bowers, 1981). In Florida, citrus physiologists have used the terms "hard freeze" and "impact freeze" (Attaway, 1997). Other synonomous terms for winter cold temperature extreme events include "severe cold event" (Stevens et al., 2016), "cold snap" (Mazzotti et al., 2011), and "extreme cold spell" (Boucek et al., 2016). In the taxa-specific sections, we often use the term

appropriate to the particular taxon we are describing to remain consistent with that literature.

# 3 | RECENT DECADES HAVE WARMER WINTERS WITH FEWER EXTREME COLD EVENTS

To evaluate winter trends over recent decades, temperature data were analyzed from four representative sites in North America's tropical–temperate transition zone. From west to east, these sites included San Francisco (California, on the Pacific Ocean), Tuscon (Arizona, in the Sonoran Desert), New Orleans (Louisiana, along the northern Gulf of Mexico coast), and Tampa (Florida, on the east coast of the Gulf of Mexico). These sites were selected to span the regions discussed in this review, but also based on the length and quality of climate records. All four sites had a common period of record going back to at least 1948.

At each of the sites, three different winter parameters were investigated to determine how winters have been changing as the climate warms (USGCRP, 2017). These parameters include the following: (1) mean winter temperature, (2) the single coldest temperature recorded each winter, and (3) the number of days each winter with temperatures of 0°C or less (i.e., the number of subzero days). The clear tendencies in the time series (Figure 4; Table S2) show that (1) average winter temperatures are increasing, (2) the extreme minimum temperatures recorded each winter season are becoming milder, and (3) the number of annual subzero days is declining.

The decline in the number of subzero days is especially apparent in San Francisco (Figure 4a). Prior to 1980, most winters in San

Francisco had subzero events, with the winter of 1949 having a total of 17 days with subzero temperatures. However, for the latter 40 years of the time series (1981–2020), only 14 days in San Francisco had subzero temperatures. There has only been one subzero event since 1999 in San Francisco and no subzero events since 2008. For Tucson, there was a warming trend for all three winter parameters (Figure 4b; see also: Weiss & Overpeck, 2005). For New Orleans, the time series shows a relatively low number of subzero events in the late 1940s and 1950s, followed by a very high number of subzero events in the 1960s–1980s, and fewer subzero events over the past three decades (Figure 4c). Examination of the last 30 years (1991–2020) in New Orleans shows a total of 165 days with subzero temperatures, while the previous 30-year period (1961–1990) had 480 subzero days. Data from Tampa show a similar temporal pattern to New Orleans with 23 subzero days over the past 30 years (1991–2020) compared to 107 subzero days in the 30 years prior (1961–1990; Figure 4d).

# 4 | PHYSIOLOGICAL EFFECTS OF COLD TEMPERATURE EXTREMES: WHY ARE WARMING WINTERS RELEVANT?

Warmer winters with fewer extreme cold events can lead to the range expansion of tropical cold-sensitive species due to the decreases in the frequency of events that lead to cold-induced physiological damage and mortality. In the taxa-focused sections, we provide specific examples of the damage and mortality caused by extreme cold events. This section covers some of the more general (i.e., cross taxa) physiological effects of extreme cold temperatures,
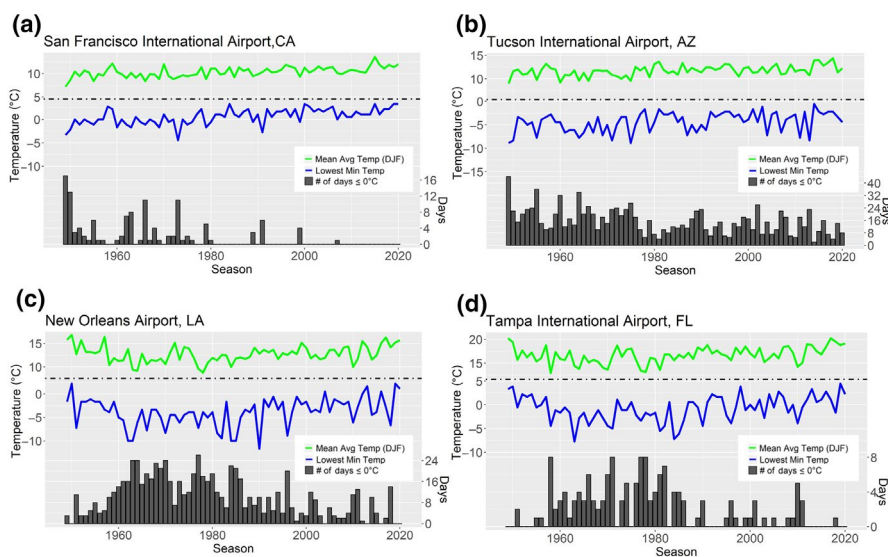


**FIGURE 4** Recent decades have had warmer winters with fewer extreme cold events. Winter temperature metrics from four representative locations in North America's tropical-temperate transition zones: (a) San Francisco, California; (b) Tucson, Arizona; (c) New Orleans, Louisiana; and (d) Tampa, Florida. The upper green lines show mean winter temperatures [Mean Avg Temp (DJF)]. The middle blue lines show the absolute coldest annual winter minimum temperature [Lowest Min Temp]. The lower grey bars show the number of subzero days each winter [# of days <= 0°C]. See Table S2 for trend test results. Temperature data were obtained from the Applied Climate Information System (http://scacis.rcc-acis.org)

which, even at temperatures above 0°C, can have significant effects on organismal function due to both direct damage to macromolecules as well as the indirect effects of reductions in enzyme activity. Low temperatures can lead to protein denaturation (Todgham et al., 2007), induction of the damaging gel phase of membranes (Wilson et al., 2003), and breakage of double- and single-stranded DNA (Yao & Somero, 2012). In addition, low temperatures can reduce the activity of the sodium–potassium ATPase enzyme, which is essential for the maintenance of ion balance in all organisms, and can induce chill coma in animals—a reversible loss of neuromuscular function that can lead to chilling injury (MacMillan & Sinclair, 2011; Overgaard & MacMillan, 2017). The vast majority of species are sensitive to chilling and die or are severely damaged long before the risk of ice formation in their body fluids (Lyons, 1973).

Because freezing requires nucleation, it typically does not occur at 0°C. Instead, freezing points in organisms are set by a combination of factors including body water content, solute content, and the presence of ice nucleators and ice binding proteins and may or may not be relevant for any given species (Wilson et al., 2003). For example, the tropical fruit fly *Drosophila melanogaster* has a freezing point of around −20°C, but dies of chilling injury at around −5°C (Strachan et al., 2011). Tissue ice formation induces a separate series of stresses than chilling. Extracellular ice formation is frequently lethal to most organisms because it can induce osmotic damage as solutes are excluded from the growing ice lattice, cause mechanical damage to cell membranes and walls, and potentially cause ischemia–reperfusion damage (Khan & Vincent, 1996; Krivoruchko & Storey, 2010; Toxopeus & Sinclair, 2018). However, extracellular ice formation can be common in plants, where ice nucleation occurs in the saturated extracellular air spaces of leaves or other tissues. Upon extracellular ice formation, water is distilled from the relatively high water content of plant cells (~70 to 80%), resulting in their freeze dehydration. This is because the water potential of ice is −1.16 × Temperature (°C) and is thus always lower than the water potential of adjacent liquid water within cells (Nobel, 2005). Taken together, these differences in the physiological effects of cold temperature extremes show that it is essential to consider cold tolerance as individual-, life stage-, and species-specific phenomena when conducting comparative studies or evaluating climate change responses.

## 5 | TERRESTRIAL PLANTS

Agronomists, botanists, foresters, and naturalists have long observed the importance of cold and freezing air temperatures for the survival, fitness, and productivity of a wide range of plant types.

There are many terrestrial tropical and subtropical plant species in North America whose northern or altitudinal range limits are governed by extreme freezing air temperature events (Holdridge, 1967; Sakai & Larcher, 1987; Woodward, 1987). Many tropical plants undergo chilling stress when temperatures fall below about 10°C (Levitt, 1980). However, there are some subtropical plant species that can tolerate temperatures a few degrees below 0°C but are then severely damaged or killed by temperatures between approximately −5°C and −15°C (Lonard & Judd, 1991; Osland, Day, Hall, et al., 2020; Osland & Feher, 2020).

In the desert ecosystems of the arid southwestern United States and northwestern Mexico, extreme freeze events control the northern and altitudinal distribution of foundation plant species like the giant saguaro cactus (*Carnegiea gigantea*; Figure S1; Niering et al., 1963; Shreve, 1911; Steenbergh & Lowe, 1976), desert ironwood tree (*Olneya tesota*; Turnage & Hinckley, 1938), organ pipe cactus (*Stenocereus thurberi*; Bowers, 1981; Parker, 1988; Turnage & Hinckley, 1938), senita (*Pachycereus schottii*; Felger & Lowe, 1967; Nobel, 1980c; Turnage & Hinckley, 1938), creosote bush (*Larrea tridentata*; D'Odorico et al., 2010; Ladwig et al., 2019; Pockman & Sperry, 1997), Joshua tree (*Yucca brevifolia*; Dole et al., 2003; Loik et al., 2000; Smith et al., 1983), little-leaf paloverde (*Parkinsonia microphylla*), and many others. Landscape-scale pulses of adult plant death in the Sonoran Desert are caused by catastrophic freezes (Bowers, 1981; McAuliffe, 1996; Steenbergh & Lowe, 1977). Low air temperatures affect small individuals of cactus species more than large individuals because stems of small diameters reach lower minimum apical temperatures than larger stems under the same environmental conditions (Nobel, 1980a, 1980b; Steenbergh & Lowe, 1969). On the other hand, the energy budgets of small-statured cacti can be coupled to microhabitat features, and warmed or insulated by objects such as rocks, other vegetation, litter, and snow (Geiger et al., 2012; Nobel et al., 1991). The distributional limits of many Sonoran Desert plants are regulated by winter freezes, and catastrophic freezes are known to cause large-scale die-offs of plants in this region (Bowers, 1981; Felger & Lowe, 1967; Shreve, 1914). For example, the northern limit of senita cactus (*P. schottii*), just north of the Arizona-Sonora border, is set by winter freeze-induced seedling mortality (Parker, 1989). The northern boundary of the Sonoran Desert itself is typically defined by the northern extent of such characteristic plants as saguaro (*C. gigantea*), triangle-leaf bur sage (*Ambrosia deltoidea*), canyon ragweed (*Ambrosia ambrosioides*), little-leaf palo verde (*P. microphylla*), and blue palo verde (*Parkinsonia florida*). This northern border coincides with the isotherm beyond which freezing temperatures have occurred lasting longer than 24 h (Bowers, 1981; Hastings, 1963). Notably, some lineages of southwestern origin have escaped constraints from freezing and have spread widely into the North American temperate zone. For example, the diminutive prickly pear cactus, *Opuntia fragilis*, has evolved substantial freeze tolerance that allows persistence in many locations in North America, including elevations up to 3048 m in Colorado and to 56°N latitude in British Columbia, Canada (Loik & Nobel, 1993b).

In the Sonoran Desert, freeze events that lead to mass plant mortality are rare. Bowers (1981) analyzed weather patterns for Tucson (Arizona) from 1894 to 1979, noting that there is much variation in plant-relevant winter cold events ranging from mild freezes with little effect on native plants, to severe freezes that inflict damage to frost-sensitive plants, to catastrophic freezes that kill or injure many species of plants over large areas. Catastrophic freezes usually occurred within 17 days of the winter solstice and are characterized

by the co-occurrence of low minimum temperatures and many consecutive hours of freezing. Between 1946 and 1979, there were four such catastrophic freezes that caused widespread frost damage to Sonoran Desert plants (Bowers, 1981). In Saguaro National Park, near Tucson, elevated adult mortality of saguaros since 2010 is probably related to a single event, a severe freeze in February 2011 that was the first major extended period of below-freezing temperatures in southern Arizona since the 1970s (Orum et al., 2016). The 2011 freeze event killed approximately 36% of older adult plants in Saguaro National Park and also killed substantial numbers of saguaros at Tonto and Organ Pipe Cactus National Monuments (Swann et al., 2018).

Along the southwestern coast of the United States, patterns of warmer winter temperatures are greatly influenced by elevation and proximity to the Pacific Ocean (Figure 1). Temperature gradients can be quite steep over short distances or elevations, resulting in an irregular mosaic of thermal stress environments across the region. This pattern is especially pronounced in comparison to the north–south temperature zonation of topographically uniform Florida (Figure 1). Although air temperatures rarely fall below 0°C along the Pacific coast, minimum temperatures can fall to –10°C just a few kilometers inland. Thus, plants in California can be exposed to simultaneous drought and high temperature stresses in summer while drought may persist into winter and be accompanied by rare freeze events (Davis et al., 2007). The restriction of some species in California to coastal habitats may be related to this spatial zonation. For example, the coastal barrel cactus (*Ferocactus viridescens*) is limited in occurrence to within ~15 km of the coast in San Diego County, California, which may be due to its limited ability to survive episodic freezing (Loik & Nobel, 1993a). Rare freezing events in southern California can also lead to zonation of plant communities along elevation gradients (Davis et al., 2007; Kelly & Goulden, 2008). The ability of southern California chaparral shrubs to persist in habitats visited by rare freezing events depends on the ability of xylem cells to tolerate or avoid embolism formation, in which air bubbles form within trachea or vessels of the xylem and block water flow (Davis et al., 1999). Such freeze-induced emboli can be fatal, and tradeoffs between xylem flow and resistance to cavitation are important for the survival of freezing and the geographic distribution of coastal species such as *Ceanothus megacarpus* (big pod ceanothus) and *Malosma laurina* (laurel sumac; Langan et al., 1997). The integrity of membranes and the photosynthetic apparatus within mesophyll leaf cells are also susceptible to freeze-induced damage, and patterns of damage are dependent on age, season, and location, yet consistent with observations of spatial and elevational distributions of the chaparral species *M. laurina*, *C. megacarpus*, *Rhus ovata* (sugar sumac), and *Ceanothus spinosus* (redheart; Boorse et al., 1998). Considering the low frequency and high impact of subzero air temperature events in coastal California, more information on the role of rare episodic freezing would help better understand how this region became a hotspot of biodiversity.

In semi-arid ecosystems of the south-central United States (e.g., south Texas) and northern Mexico, extreme freeze events dictate the northern distribution of many tropical plant species, including native woody plant species like great leadtree (*Leucaena pulverulenta*), anacahuita (*Cordia boissieri*), and coyotillo (*Karwinskia humboldtiana*; Bojórquez et al., 2019; Lonard & Judd, 1985, 1991). In the more humid and seasonal wet–dry ecosystems of south and central Florida, extreme freeze events govern the northern distribution of entire forest biomes (Greller, 1980) as well as the range limits of plant species such as poisonwood (*Metopium toxiferum*), gumbo limbo (*Bursera simaruba*), cocoplum (*Chrysobalanus icaco*), and pigeon plum (*Coccoloba diversifolia*; Box et al., 1993; Myers, 1986; Olmsted et al., 1993). In response to warming winter temperature extremes, many of these tropical freeze-sensitive native plant species are expected to move northward, within arid, semi-arid, and humid climates of western, central, and eastern parts of the continent, respectively (Box et al., 1999; Carter et al., 2018; Weiss & Overpeck, 2005; Figure 3). Species-specific rates of poleward range expansion are, however, highly variable and greatly influenced by the presence of plant traits that foster rapid movement into novel climates, and also interactions with other global change factors that may hinder or accelerate range expansion (Davis & Shaw, 2001; Parker, 1993; Zhu et al., 2012). Long-distance seed dispersal, high seed production and viability, rapid growth and establishment, and the ability to outcompete incumbent species are some of the traits useful for species to migrate in response to climatic shifts.

In North America, there are many invasive non-native plant species that are expected to also expand northward in response to winter climate change. Many of these species are currently abundant in tropical parts of Florida, which is a state that has become a prominent example of the negative ecological impacts of invasive non-native species. In the past century, many of Florida's native ecosystems have been affected, and in some cases transformed, by invasive non-native organisms (Rodgers et al., 2018; Simberloff et al., 1997; South Florida Ecosytem Restoration Task Force, 2015). In 2019, the Florida Exotic Pest Plant Council identified 84 invasive non-native plant species 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). Many of these plants are tropical freeze-sensitive species that are expected to expand northward into other parts of the southeastern United States in response to warming winters. Brazilian pepper (*Schinus terebinthifolius*) is one of Florida's most abundant and problematic invasive plant species and a prime example of the potential negative effects of invasive non-native range expansions (Osland & Feher, 2020). Millions of dollars are spent each year in Florida to mitigate the negative ecological impacts caused by Brazilian pepper invasions (Hiatt et al., 2019). In response to warming winters, this freeze-sensitive species is expected to migrate northward and transform ecosystems in north Florida and across much of the Gulf of Mexico and south Atlantic coasts of the United States (Osland & Feher, 2020). Melaleuca (*Melaleuca quinquenervia*; Turner et al., 1997), Old World climbing fern (*Lygodium microphyllum*; Hutchinson & Langeland, 2014), and Australian pine (*Casuarina equisetifolia*; Morton, 1980)

are other problematic freeze-sensitive non-native invasive species that could move northward from Florida into other parts of North America in response to warming winters.

Warming winters are also expected to facilitate the northward spread of invasive non-native plant species in the arid southwestern United States. Abatzoglou and Kolden (2011) analyzed a suite of climate projections for the mid-21st century and concluded that changes in the length of the freezeence-free season in this region will favor cold-intolerant, invasive, grasses (e.g., cheatgrass, *Bromus tectorum* [Griffith et al., 2014]; red brome, *Bromus rubens*; buffelgrass, *Pennisetum ciliare*). These grasses have been increasing in abundance and extent in the southwestern United States over the past three decades (Abatzoglou & Kolden, 2011; Esque & Schwalbe, 2002). Buffelgrass is an aggressive perennial grass species introduced from southern Africa that is transforming desert ecosystems in the Sonoran Desert by outcompeting native species, modifying ecohydrological processes, and altering fire regimes (Marshall et al., 2012; Williams & Baruch, 2000). Because buffelgrass is sensitive to freezing temperatures (Cox et al., 1988; Hussey & Bashaw, 1996; Stair et al., 1998), warming winter temperature extremes are expected to allow buffelgrass to continue expanding northward and affect desert ecosystems to the north of its current distribution (Jarnevich et al., 2018; Martin et al., 2015). Buffelgrass is also expanding its altitudinal distribution up mountain slopes, and in doing so carrying wildfires from the grass-invaded desert scrub to higher-elevation woodlands, and vice versa (Abatzoglou & Kolden, 2011; Esque & Schwalbe, 2002; Williams & Baruch, 2000).

## 6 | COASTAL WETLAND PLANTS

Coastal wetland ecosystems in the tropical–temperate transition zone are highly sensitive to changes in the frequency and intensity of extreme cold events, which can produce landscape-scale ecological transformations (Lugo & Patterson-Zucca, 1977; McKee et al., 2012; Sherrod & McMillan, 1985). Coastal wetlands are abundant in North America, especially along the low-lying and comparatively flat coasts of the Gulf of Mexico and Atlantic Ocean, where tropical mangrove forests and temperate salt marshes support critical habitat and provide many valuable ecosystem goods and services (Barbier et al., 2011). Both coasts span tropical–temperate transition zones that generate comparatively large gradients in coastal wetland ecosystem structure and function, and there are strong linear and nonlinear relationships between winter temperature regimes and coastal wetland plant community composition, vegetation height, aboveground biomass, and productivity (Feher et al., 2017; Gabler et al., 2017; Osland, Gabler, et al., 2018).

Extreme freeze events greatly influence whether a tidal saline wetland in eastern North America is dominated by woody trees or grass-like plants (i.e., mangrove forest or salt marsh graminoid plants, respectively; Cavanaugh et al., 2019; Osland, Grace, et al., 2019; Stevens et al., 2006). Salt marsh graminoid plants are freeze-tolerant and dominate coastal wetlands in climates with colder winters

(Pennings & Bertness, 2001). In contrast, extreme freeze events lead to mangrove physiological damage or mortality (Lovelock et al., 2016; Osland, Day, Hall, et al., 2020; Ross et al., 2009), which means that mangrove forests are most abundant in tropical and subtropical climates (e.g., south and central Florida, Mexico's Gulf of Mexico coast, and Mexico's Pacific coast; Duke et al., 1998; Saenger, 2002). The three most common mangrove species in North America are the black mangrove (*Avicennia germinans*), red mangrove (*Rhizophora mangle*; Figure S1), and white mangrove (*Laguncularia racemosa*; Felger et al., 2001; Osland, Feher, et al., 2018; Tomlinson, 2016). Two other species often considered as mangroves or mangrove associates are the buttonwood mangrove (*Conocarpus erectus*) and the sweet mangrove (*Maytenus phyllanthoides*), which can be sporadically common in tropical coastal wetlands, especially at higher intertidal elevations near landward transitional margins (Felger et al., 2001; Mendelssohn et al., 2017; Whitmore et al., 2005). The poleward range limits of mangroves along the Gulf of Mexico and Atlantic coasts are strongly governed by extreme freeze events. *Avicennia germinans* is the most freeze-tolerant species and its range extends furthest north—into salt marshes in north Florida, Louisiana, and Texas (Armitage et al., 2015; Cook-Patton et al., 2015; Osland et al., 2020). On the Pacific coast of Mexico, all five mangrove species are severely damaged due to frost during exceptional cold events in the Gulf of California (Felger, 2004; Felger et al., 2001).

In eastern North America, the adaptive capacity of mangroves to changing winter temperature regimes is very high. Long-distance dispersal mechanisms (Van der Stocken, Carroll, et al., 2019; Van der Stocken, Wee, et al., 2019) and rapid peat development (Krauss et al., 2014; McKee, 2011; Osland, Feher, et al., 2020) enable mangrove forests to adapt to climate change. Mangroves produce floating propagules that can be carried long distances by oceanic currents, especially when propagule release coincides with tropical storms that produce storm surges and rapidly moving northward surface currents (Kennedy et al., 2016, 2020; Van der Stocken, Wee, et al., 2019). Paleoecological records indicate that during the last glacial maximum (~19,000 years ago) mangrove range limits were much further south in Central America (Sherrod & McMillan, 1985). Due to a warming climate, the northern range limit of mangroves has moved poleward during the Holocene (Kennedy et al., 2016; Woodroffe & Grindrod, 1991), with local, decadal-scale range expansion and contraction phases occurring in the absence or presence of extreme freeze events, respectively (Cavanaugh et al., 2019; Osland, Day, et al., 2017). Mangroves have been expanding in the southeastern United States for approximately 30 years, since the last major freeze events occurred in the late 1980s (Cavanaugh et al., 2014, 2019; McClenachan et al., 2021; Osland, Day, et al., 2017). In response to accelerating anthropogenic climate change in the Anthropocene, warming winters are expected to accelerate the pace of poleward range expansion along the Gulf of Mexico and Atlantic coasts of North America, as mangrove forests move northward and replace grass-dominated salt marshes in much of Texas, Louisiana, and north Florida (Cavanaugh et al., 2019; Gabler et al., 2017; Osland et al., 2013). Many temperate salt marsh ecosystems in eastern North

America are expected to become tropicalized by poleward-moving mangrove forests. However, rising sea levels are expected to simultaneously lead to the landward migration of tidal saline wetlands at the expense of upslope and upriver ecosystems (Borchert et al., 2018; Doyle et al., 2010; Enwright et al., 2016); thus, mangroves forests could also be replacing inland terrestrial and freshwater forests as they expand northward.

In North America, mangrove range limits along the Gulf of Mexico and Atlantic coasts are highly responsive to changing winter temperature regimes. However, mangrove range limits along the Pacific coast of North America, in Mexico within Sonora and Baja California Sur, are governed by a different combination of macro-climatic drivers (Felger et al., 2001; Glenn et al., 2006; Whitmore et al., 2005). Near these Pacific coast range limits, extreme freeze events are rare and only occasionally affect mangroves and other coastal plants (Felger et al., 2001). Mangrove range limits in western North America have been understudied; however, the abundance and distribution of mangroves in those areas are thought to be most strongly influenced by aridity (Brusca et al., 2006; Glenn et al., 2006) and dispersal constraints (Bardou et al., 2020; Van der Stocken, Carroll, et al., 2019). Highly arid conditions (i.e., very low rainfall, high evapotranspiration, and minimal freshwater inputs) promote the development of hypersaline conditions that are inhospitable to mangroves and many other coastal wetland plants (Arreola-Lizárraga et al., 2004; Flores-Verdugo et al., 1992; Osland, Grace, et al., 2019). The northernmost mangrove forests in western Mexico occur in hypersaline coastal lagoons that entirely lack freshwater riverine input, and compared to more southerly, taller mangroves that occur in less saline estuarine habitats, the growth form of these northern mangroves is greatly stunted (Brusca et al., 2006; Felger, 2004; Glenn et al., 2006). Moreover, predominantly southward-moving oceanic currents (e.g., the coastal California Current) combined with large distances between suitable estuarine habitat are thought to hinder mangrove range expansion into climate-appropriate estuaries beyond current Pacific coast range limits (Bardou et al., 2020; Cavanaugh et al., 2018; Van der Stocken, Carroll, et al., 2019). For example, winter air temperature regimes indicate that mangroves may be able to survive in San Francisco Bay's coastal wetlands (Osland, Grace, et al., 2019), which are approximately 1500 km north of the current mangrove range limit in Baja California.

## 7 | COASTAL FISHES

One of the early uses of the term "tropicalization" was to describe the effects of range-expanding tropical fish species into temperate reef ecosystems (Vergés et al., 2014). Within tropical–temperate transition zones across the globe, warming winter ocean temperatures are expected to increasingly lead to the poleward range expansion of tropical fish species (Figueira & Booth, 2010; Nakamura et al., 2013). Along the Pacific coast of North America, the distributions of fishes are strongly affected by ocean currents and upwelling events (Carlisle et al., 2015; Páez-Osuna et al., 2016); however,

winter temperature effects on the distribution of some tropical species have been reported in shallow waters of the Gulf of California (Lehner, 1979; Thomson & Lehner, 1976). The warm-temperate ocean waters of southern California, and the subtropical waters of the Gulf of California (Mexico), show a warming trend during the past century (Lluch-Belda et al., 2009). As this trend is likely to continue, poleward expansion of tropical fish species is expected, and this phenomenon appears to already be taking place (Booth et al., 2018; Fernández-Rivera Melo et al., 2015; González-Cuéllar et al., 2013).

The influence of winter temperatures on subtropical fishes is more apparent along coasts of the Gulf of Mexico and Atlantic Ocean, where extreme cold events periodically lead to mass mortality events (i.e., conspicuous fish kills that receive media and public attention). For example, an extreme cold event in 2010 resulted in fish kills across Florida's Gulf of Mexico and Atlantic coasts (Boucek & Rehage, 2014; Purtlebaugh et al., 2020; Stevens et al., 2016), which span ~6 degrees of latitude and ~2200 km of coastline. Another prime example stems from severe freeze events in 1983 and 1989, which produced fish kills across the region, from Texas to Florida. In Texas alone, the 1983 and 1989 events killed at least 31 million fish, comprised of 103 species (Martin & McEachron, 1996). Along these eastern North American coasts, the poleward distributions of subtropical fishes—for example, common snook (*Centropomus undecimalis*, Figure S2; Howells et al., 1990), smalltooth sawfish (*Pristis pectinate*; Poulakis et al., 2011), gray snapper (*Lutjanus griseus*; Hare et al., 2012), goliath grouper (*Epinephelus itajara*), and tarpon (*Megalops atlanticus*; Mace et al., 2017)—are ultimately limited by their cold tolerance. This is also the case for freshwater fishes introduced from the tropics, some of which can tolerate moderate salinity and occupy the upper reaches of estuaries (Greenwood, 2017; Idelberger et al., 2011).

The frequency at which the lower lethal water temperature (~10°C) of subtropical fishes is reached greatly influences whether a species occurs in a region, and if so, its population status. Recent population dynamics of a well-studied gamefish, common snook, highlight the critical ecological role of winter temperatures. In 2010, a severe cold event resulted in greater than 75% reductions of snook populations in some Florida estuaries (Stevens et al., 2016). These findings led to the temporary closure of the recreational snook fishery along the Gulf of Mexico coast, and recovery of the populations took up to 4 years. Since then, a decade of mild winters has allowed for expansion of the species approximately 200 km beyond its historic distribution (Anderson et al., 2020; Purtlebaugh et al., 2020). Adaptive behaviors (e.g., movement to thermal refugia during winter) have likely made this range expansion possible (Stevens et al., 2018) and illustrate some plasticity in the life-history traits of subtropical fish species.

Just as for other taxa, changes in the frequency, intensity, and duration of cold temperature extremes will greatly influence fish distributions and migrations. The frequency of extreme events is important because combined effects of consecutive events over short periods of time can elicit different responses by communities

(Boucek & Rehage, 2014; Stevens et al., 2006). The intensity of a cold event and the context of its onset determine the time available for fishes to respond. For example, in 2008, a rapid decrease in temperature that occurred in Florida during an otherwise mild winter resulted in mortality of subtropical species (Blewett & Stevens, 2014). If given more time, these species can respond to cold temperatures by moving to deep, wind-protected shorelines (Blewett & Stevens, 2014; Scharer et al., 2017). However, extended periods of cold weather allow near-surface water temperatures to equilibrate to air temperatures, and any thermal refuge provided by stratification at deeper sites may eventually be lost due to mixing. A well-studied cold event in 2010 had a large impact on fish due in part to its long duration, nearly a full week (Boucek et al., 2016). Although the event had only moderate effects on subtropical coastal vegetation such as mangroves, the effects on subtropical fish populations were extreme. The long duration of cold likely reduced the efficacy of deeper sites that would have otherwise provided thermal refugia during a shorter-term event (Blewett & Stevens, 2014; Boucek et al., 2017).

The ecological and economic implications associated with changes in winter temperatures and their effects on fisheries are complex and industry dependent (e.g., different for estuary vs. nearshore coastal fisheries). The ranges of tropical/subtropical estuarine fishes will likely expand poleward if winter temperatures continue to warm (Fodrie et al., 2010), and these species could support novel fisheries to the north of their current distribution. Some subtropical species already have adult ranges that extend to mid-Atlantic states—for example, gray snapper (Wuenschel et al., 2012), bull shark (*Carcharhinus leucas*; Matich & Heithaus, 2012), smalltooth sawfish (Norton et al., 2012), goliath grouper (O'Hop & Munyandorero, 2016), and tarpon (Mace et al., 2017), but their juvenile habitat is largely limited to subtropical estuaries. Poleward expansion of subtropical fish nurseries may prompt efforts to identify and protect these habitats if new fisheries targeting subtropical species are encouraged by managers. Warming winter temperatures are also likely to alter the migrations (or behavior) of nearshore coastal fishes. Winter movements of coastal migrants to the south (e.g., the winter run of sailfish, *Istiophorus platypterus*) and return trips back north (e.g., the spring run of cobia, *Rachycentron canadum*) have economic and cultural significance to coastal communities (Colburn et al., 2016). Large and collaborative passive acoustic telemetry networks established along the Atlantic (Young et al., 2020) and Gulf of Mexico (Lowerre-Barbieri et al., 2019) coasts are allowing the timing and geographic extent of coastal migrations to be better quantified for many managed sharks, rays, and sport fish. The migrations of a representative coastal migrant, lemon shark (*Negaprion brevirostris*), were found to vary by ~200 km depending on the severity of winter (Reyier et al., 2014). Fewer coastal fishes moving along the coasts in response to winter temperature drivers would have dramatic effects on recreational and commercial fisheries that depend on the migrations. Range expansions and altered migration patterns could eventually require greater management coordination (Pinsky et al. 2021) across U.S. states, especially for certain fishes that are managed at the state, not federal level. Mechanistic models can be used to proactively develop fisheries regulations and habitat protection efforts to support range-expanding species in novel areas.

## 8 | SEA TURTLES

As ectothermic (cold-blooded) reptiles, winter temperatures affect nearly all aspects of sea turtle ecology, and warming winter temperature regimes could affect their distribution and abundance in North America. Sea turtles have a complex life cycle, which includes several ontogenetic shifts in habitat use (Bolten, 2003; McClellan & Read, 2007; Seminoff, 2010). Near northern range limits, females usually deposit multiple clutches per season on nesting beaches during summer where incubation and hatching occur. In the tropics, they may have winter nesting seasons. Each clutch is separated by a period termed the internesting interval. After nesting is complete, the adults migrate to distant foraging areas where they spend several years before returning to mate and nest again, with the time between nesting migrations termed the remigration interval. Juveniles use shallow coastal habitats where they forage on benthic invertebrates, marine macroalgae, and seagrasses (Jones & Seminoff, 2013; Wallace et al., 2009; Williams et al., 2014). Cold temperature extremes in any of these habitats and life stages can have significant effects on sea turtle populations.

Cold temperatures affect reproduction in many ways including phenology, fecundity, and incubation (Davenport, 1997; Hamann et al., 2003; Hawkes et al., 2009). All follicles that will become eggs are developed at foraging areas; thus, cold temperature extremes at winter foraging sites can result in the development of fewer follicles and smaller clutch sizes (Hamann et al., 2003; Lamont & Fujisaki, 2014). Cold temperatures at foraging grounds can also affect remigration intervals by constricting the foraging season, which limits nutrient acquisition (Hays, 2000). During the nesting season, cold temperature extremes can increase internesting intervals and result in fewer clutches and lesser reproductive output (Schofield et al., 2009).

Perhaps the most significant and striking effect of extreme cold on sea turtles is direct mass mortality following stranding. While most freshwater and terrestrial turtle species that inhabit temperate environments hibernate to survive extreme cold (Claussen et al., 1991; Ultsch et al., 1999), sea turtles typically migrate to warmer waters to escape winter temperature extremes. Many sea turtle species utilize high latitude, resource-rich bays during summer and migrate to deeper or warmer waters in winter, especially along the U.S. Atlantic coast (Hawkes et al., 2011; Lamont & Iverson, 2018; Seney & Landry Jr, 2011). However, when extreme cold impacts an area suddenly and turtles have not already moved, they can suffer immobility, which can lead to stranding and eventually death. In the sea turtle literature, these mass stranding occurrences are called "cold stunning events" (Anderson et al., 2011; Foley et al., 2007; Still et al., 2005). During cold events in 2010 and 2018, for example, more than 2900 sea turtles stranded in St. Joseph Bay, a foraging

site in northwestern Florida (Lamont et al., 2018; Figure S3). The 2010 event resulted in the mortality of 434 individuals (Avens et al., 2012). Water temperatures below 8°C–10°C can significantly affect sea turtle physiology (Davenport, 1997). At these temperatures, blood chemistry can be altered (Anderson et al., 2011) and turtles can become lethargic and float at the water's surface (Avens et al., 2012; Milton & Lutz, 2003). Mortality rates increase significantly as temperatures drop below 5°C–6°C (Schwartz, 1978).

Some sea turtles along the Pacific coast of North America and in the Gulf of Mexico tend to winter in place (Lamont et al., 2018; Madrak et al., 2016), and green turtles have been observed active and foraging in water temperatures as low as 15.8°C (Hanna et al., unpublished data). The low temperatures elicit a languid response during which turtles spend extended periods inactive on the seafloor, which may result in increased risk of direct harvesting (Felger et al., 1976). For example, turtles impacted by extreme cold in the Gulf of California (Mexico) can fall prey to illegal harvesting by local artisanal dive fisheries for spiny lobster (*Panulirus interruptus*) and sea cucumber (*Apostichopus californicus*; Felger et al., 1976; Seminoff & Wallace, 2012).

In addition to affecting population abundance, cold-induced mortality can also affect population structure (Lamont et al., 2018). In two of the largest, recent cold stunning events in the Gulf of Mexico (2010 and 2018), a disproportionate number (>45%) of small turtles (<40 cm straight carapace length) stranded (Avens et al., 2012; Lamont et al., 2018). This disproportionate mortality can affect the structure of juvenile turtle populations at temperate foraging sites. A 20-cm turtle will be 30 cm in 3–4 years and 40 cm in 5–7 years; thus, removal of small turtles during extreme cold events will affect larger size classes for many years after the event. This appears to result in a variable size class structure with peaks in abundance of larger individuals (40–49.9 cm straight carapace length) in the years immediately following an event, followed by a shift to smaller size classes as new recruits enter the population (Lamont et al., 2018). In addition to size structure, this mortality most likely impacts other aspects of demography such as growth and survival. Finally, cold temperatures themselves can reduce somatic growth rates (Avens et al., 2012).

As sea turtles move farther northward in response to warming air and ocean temperatures, the potential for sea turtle mortality events in novel, northerly locations may also increase and affect range expansion dynamics. For incubating embryos, nesting farther north increases the risk of exposure to cold temperature extremes. For example, on the Atlantic coast of North America, green turtles have typically been considered a tropical/subtropical species with rare nesting occurring in Georgia and South Carolina. However in 2011, a green turtle nested as far north as Delaware (Shamblin et al., 2018). Although that nest successfully hatched, a late nest deposited on a temperate beach risks exposure to early winter temperature extremes. Similarly, warmer summer waters at northern foraging areas, such as Cape Cod Bay in Massachusetts, allows juvenile turtles to travel farther north to resource-rich habitats. However, these areas are also more susceptible to rapid decreases in temperature during fall, thereby exposing turtles to potential cold stun stranding. In Cape Cod Bay, higher cold-stunning years occurred when the Gulf of Maine had warmer sea surface temperatures in late October through early November (Griffin et al., 2019). Similarly, green turtles in the northeastern Pacific occasionally nest as far north as the Cape Region of the Baja California Peninsula, Mexico (Tiburcio-Pintos & Cariño-Olvera, 2017), but they forage throughout the Gulf of California and north as far as southern California (Seminoff & Wallace, 2012). Warming winters may allow this threatened turtle to extend its nesting sites northward into the Gulf of California.

As warming winters increasingly lead to the tropicalization of coastal and marine ecosystems in North America, sea turtles are expected to increasingly migrate northward of their current historical range limits. However, given the complexity and sensitivity of so many stages of the sea turtle life cycle to winter temperature extremes, we expect that future changes in the distribution and migration of sea turtles will be highly dynamic and heavily influenced by interactions with other aspects of global change. For example, sea turtles have temperature-driven sex determination such that the proportion of female embryos increases with incubation temperature (Yntema & Mrosovsky, 1982). Thus, many sea turtle populations are in danger of population feminization (i.e., production of females only) as global temperatures increase (Jensen et al., 2018). However, nesting range expansion onto more northerly, and thus cooler, beaches may help maintain population sex ratios.

## 9 | TERRESTRIAL AND FRESHWATER REPTILES

Like their marine counterparts (e.g., sea turtles and sea snakes), terrestrial reptiles are highly sensitive to freezing and chilling temperatures. The thermal physiology of reptiles affects their behavioral patterns, movements, and survival. Extreme cold events can impose strong natural selection on wild populations (Campbell-Staton et al., 2017). Near their northern range limits in North America, winter temperature regimes greatly influence the physiology, distribution, and abundance of tropical snake, lizard, turtle, and crocodilian species.

For terrestrial reptiles, the tropical–temperate transition zone in North America is especially striking in south Florida, where both temperate and tropical reptile species are present. For example, south Florida is the only part of North America where cold-tolerant American alligators (*Alligator mississippiensis*) can be found within the same watersheds as tropical, cold-sensitive American crocodiles (*Crocodylus acutus*). The northern distribution of American alligators extends much farther into higher latitudes than American crocodiles, in part due to differences in their behavioral responses to extreme cold events. While the American alligator seeks refuge during cold events, the American crocodile attempts to compensate for cold air temperatures by basking in the sun, which actually increases its exposure to lethal air temperatures (Mazzotti et al., 2016).

In addition to controlling the northern distribution of native tropical reptiles, extreme cold events also constrain the distribution of invasive non-native species. Prolonged periods of extremely cold winter temperatures in south Florida are uncommon, yet occasional cold "snaps" occur. Within the past century, the introduction of tropical non-native reptiles to Florida has had a tremendous impact on native ecosystems. Florida has had more non-native herpetofaunal species introductions than anywhere in the world (Engeman et al., 2011; Fujisaki et al., 2015; Krysko et al., 2011). Of the estimated 180 reptile and amphibian taxa that have been introduced to Florida, 63 species have become established, including 54 reptiles (48 lizards, 5 snakes, and 1 crocodile; Krysko et al., 2016). Most of these introductions (86%) have occurred due the pet trade (Krysko et al., 2016), and the northern distributions of many of these non-native species are governed by winter cold temperature extremes.

Burmese pythons (*Python bivittatus*) are an especially harmful and well-known example of the negative ecological impacts of pet trade-driven tropical reptile introductions (Figure S4). This large constrictor snake is an opportunistic apex predator, whose expansion within and around Everglades National Park has decimated mammal, bird, and other prey populations (Dorcas et al., 2012; McCleery et al., 2015; Sovie et al., 2016). Burmese pythons are sensitive to cold temperature extremes, and mortality can occur during exposure to several days of extremely cold, wet weather (Mazzotti et al., 2011, 2016). Pythons are projected to spread northward in response to warming winter temperature regimes (Jacobson et al., 2012). Two experiments tracking pythons through various freeze events in captive or laboratory settings revealed cold tolerance down to 0°C (Avery et al., 2010; Dorcas et al., 2011). Furthermore, recent evidence of directional selection in genomic regions enriched for genes associated with thermosensation, behavior, and physiology was detected in pythons sampled before and after a 2010 south Florida freeze event (Card et al., 2018). With this new evidence that cold adaptation genes are evolving measurably faster, it is likely that pythons can extend their range further north in response to warming winters. Furthermore, Card et al. (2018) reported that several of these genes are linked to regenerative organ growth, which is an adaptive response that controls organ size and function with feeding and fasting in pythons. Thus, there may be selective pressure that favors survivors with higher tolerance for cold and appropriate refuge-seeking behaviors. Green iguanas (*Iguana iguana*; Krysko et al., 2007), anole species (e.g., *Anolis sagrei*, *A. equestris*; Dalrymple, 1980; Kolbe et al., 2014), chameleon species (e.g., *Furcifer oustaleti*, *Chamaeleo calyptratus*), and Nile monitor lizards (*Varanus niloticus*) are other examples of problematic invasive non-native tropical reptiles that are cold sensitive and would have the potential to spread northward in warmer winters.

Beyond south Florida, extreme cold temperatures also play an important role in controlling the northern distribution of tropical reptile species in tropical–temperate transition zones along the Gulf of Mexico (i.e., Texas, Louisiana, Mississippi, and Alabama) and Atlantic (i.e., Georgia) coasts as well in arid and semi-arid parts of North America. For example, the freeze-sensitive brown anole is currently also established in Texas, Louisiana, Georgia, and California (EDDMapS, 2020). Green iguanas have expanded from their northern range limit in Mexico into south Texas (Hibbitts & Hibbitts, 2015). In the Sonoran Desert, the neotropical vine snake (*Oxybelis aeneus*) is just one example of a terrestrial native reptile whose distribution and habitat use are governed by winter temperatures (Van Devender et al., 1994).

Dispersal constraints may affect the potential for some reptile species to expand northward in response to climate change. However, due to the potential for long-distance dispersal via the pet trade, there are many reptile species in Florida that have the potential to rapidly move northward and westward in response to warming winters.

## 10 | AMPHIBIANS

As ectotherms, amphibians have evolved physiological and behavioral traits to allow them to survive in a range of environmental temperatures, but most are disabled or even killed by extreme cold (Lillywhite et al., 2017). Many amphibians have evolved traits to survive freezing through avoidance or freeze tolerance (Costanzo & Lee, 2013). Some species of amphibians (e.g., wood frogs, *Lithobates sylvaticus*) are so well adapted to cold temperatures that they can survive ice formation in tissues through physiological mechanisms (Costanzo et al., 2013). However, most amphibian species are much less immune to the detrimental effects of extreme cold temperatures. Tropical amphibians tend to have higher thermal minima than amphibian species from temperate climates (Brattstrom, 1968), and their only mechanism for survival in cold temperatures is to find a suitable refuge where they can endure until warmer temperatures return.

There are several North American examples of amphibians that appear to have recent northward range expansions in the tropical–temperate transition zone. In the southeastern United States, there are no native amphibian species that are exclusively found in subtropical regions (Means & Simberloff, 1987). However, there are several recently introduced invasive amphibian species that originated in tropical regions (Krysko et al., 2011; Meshaka, 2011). For example, greenhouse frogs (*Eleutherodactylus planirostris*) have spread widely throughout Florida and continue to expand their range (Meshaka et al., 2004), and Rio Grande chirping frogs (*Eleutherodactylus cystignathoides*) have been expanding in Texas and Louisiana (Battaglia et al., 2015). Cuban treefrogs (*Osteopilus septentrionalis*) have spread from the site of their original introduction in the Florida Keys in the early 1930s (Barbour, 1931) to occur in most of peninsular Florida (Dodd, 2013) and are increasingly being found in nearby states (Glorioso et al., 2018; Figure S5). There is a growing body of evidence that Cuban treefrogs can tolerate freezes through the use of microclimatic retreats (i.e., warmer shelter sites that provide protection from surrounding freezing temperatures) and are therefore likely to continue to expand their range (Haggerty & Crisman, 2015; Meshaka, 1996). Another species that has periodically established in

Florida and may be less freeze tolerant than Cuban treefrogs is the Puerto Rican common coquí (*Eleutherodactylus coqui*). Coquís have been documented in southern Florida from at least two separate establishment periods (Austin & Schwartz, 1975; Loftus & Hernon, 1984), but there is plausible evidence that this species was extirpated during a hard freeze in 1977 (Wilson & Porras, 1983). In response to winter warming, more of Florida is expected to become suitable for coquí, and this species would have a better chance of establishing there (Rödder, 2009).

Dispersal constraints may affect the ability of some amphibian species to move northward in response to warming winters. However, there are species (e.g., Cuban treefrogs and coquís) that have successfully established populations in new areas following long-distance transport (>100 km) with ornamental tropical plants. Some species have inadvertently traveled on horticultural shipments from Florida and other more tropical locations to nurseries across the United States (Glorioso et al., 2018; Kraus & Campbell, 2002; Morningstar & Daniel, 2020), which is a long-distance dispersal pathway that may enable more rapid poleward range expansion of some amphibian species in response to climate change.

The consequences of tropicalization of the amphibian fauna will vary depending on the species involved. Cuban treefrogs are a major threat to native amphibian communities because they can reduce the abundance (Rice et al., 2011) and occupancy (Waddle et al., 2010) of native treefrogs through competition and predation of native species (Meshaka, 2001). Cuban treefrogs produce a toxic secretion that can be noxious to humans and may be harmful to frog predators such as snakes (Goetz et al., 2018). In addition, Cuban treefrogs may have societal and economic impacts by causing power outages and other damages while seeking refuge from cold temperatures in buildings (Johnson et al., 2010). In Hawaii, invasive non-native coquí have become highly disruptive by altering the soundscape with loud choruses of vocalizations that have had an economic impact (i.e., decreasing property values and purchase interest; Kraus & Campbell, 2002; Rödder, 2009), and their potential ecological impacts include altering the native fauna and disrupting nutrient cycles in ways that could benefit invasive plant species (Beard & Pitt, 2005; Sin et al., 2008). The ecological impacts of other species like greenhouse and Rio Grande chirping frogs are currently unknown. Few studies have been conducted on these small, ground-dwelling amphibian species.

## 11 | MANATEE

The West Indian manatee (*Trichechus manatus*) is a large marine mammal that lives at the freshwater–marine interface in low-energy estuaries, tidal creeks, and shallow nearshore waters where it feeds on seagrass and submerged aquatic vegetation. The Florida subspecies (*T. m. latirostris*) on the Atlantic and Gulf of Mexico coasts of the southeastern United States defines the northern limits for the species (Lefebvre et al., 2001). All extant manatee species and dugongs (order Sirenia) are tropical in distribution and share similar thermal tolerance to cold water temperature with physiological and

behavioral traits adapted to the tropics (Marsh et al., 2012; McNab, 2002). As obligate herbivores, their low-energy diet leads to low metabolic rates and low capacity for thermogenesis compared to other marine mammals of similar size (Irvine, 1983; O'shea, 1988). Additionally, high thermal conductance results in rapid heat transfer to and from the environment. Homeostasis of core body temperature for manatees can be controlled to some extent by a countercurrent exchange circulatory system that conserves heat under cold stress or radiates heat under heat stress (Rommel & Caplan, 2003).

For the Florida manatee at the tropical–temperate transition in North America, mortality events from winter freezes and continental cold fronts, which can extend down the entire Florida peninsula, have been a focus of research and a concern for federal and state managers charged with recovery of the protected West Indian manatee. Manatees are subject to acute hypothermia or chronic cold stress pathologies that can be debilitating or lethal (Bossart et al., 2003). When winter water temperatures begin to drop and stay below approximately 20°C, manatees have to move to warmer water (Hartman, 1979; Irvine, 1983). In summer, individuals are dispersed to a wide range of forage habitats, but in fall and winter, they converge and form large aggregations in areas near warm-water refugia (Deutsch et al., 2003). Three types of warm water refugia have been important to manatees (Laist et al., 2013): (1) natural artesian springs where warm geothermal groundwaters come to the surface (Hartman, 1979); (2) artificial warm-water discharges produced by thermoelectric power plants and other industrial plants (Moore, 1956; Figure S6); and (3) canals, boat basins, and drainage ditches with limited mixing of surface and bottom waters, which can maintain water temperatures passively by thermal inertia (Stith et al., 2011, 2012).

Cold winters have been less frequent in recent years and changes in manatee movements and habitat use are emerging. In cold winters, densities are higher at traditional warm water refugia where scientists monitor populations with photo-identification and aerial surveys. However, in warm winters, fewer numbers use these refugia because they can find adequate thermal protection at sites closer to prime foraging areas. However, expansion of the winter range beyond Florida due to winter warming may not be realized in the foreseeable future, given the magnitude of temperature changes required to reduce the need for refugia. The quality and quantity of natural artesian spring refugia are not found outside Florida, and current spring flows may be reduced with rising sea levels and increasing groundwater withdrawals. Furthermore, warm water discharges from power plants may decrease in the future as companies switch to more efficient technology and add alternative energy sources. Water conservation is an additional factor driving electricity production away from once-through cooling systems (Dieter et al., 2018). Nonetheless, further tropicalization of the climate would reduce morbidity and mortality probabilities from chronic cold stress within the current winter range.

Summer manatee sightings are increasing in numbers beyond historical range limits along the northern Gulf of Mexico (Fertl et al., 2005) and Atlantic coasts (Cummings et al., 2014; Rathbun et al., 1982).

However, the role of climate change has been understudied. Manatee population growth due to recovery efforts may play a larger role in these increases. Recently, the U.S. Fish and Wildlife Service reclassified the species from endangered to threatened status (U.S. Fish & Wildlife Service, 2017). Regardless, the large number of manatee individuals and now annual sightings of known individuals in Alabama and on coastlines in Georgia, South Carolina, and North Carolina suggest that these are expansions of the summer foraging range. Due to exploratory migrations, manatee sightings are also increasing farther north, including in the Chesapeake Bay (Reid, 1995), Delaware River, and Cape Cod.

## 12 | INSECTS

Across the globe, winter temperature regimes greatly influence the poleward distribution and abundance of insects (Robinet & Roques, 2010; Sinclair et al., 2003; Williams et al., 2015) and winter warming can facilitate poleward range shifts (Battisti et al., 2005; Crozier, 2003; Fält-Nardmann et al., 2018). Cold tolerance limits frequently parallel minimum temperature isotherms, supporting a widespread role for winter low temperatures in setting range limits (Lynch et al., 2014; Overgaard et al., 2014; Sinclair et al., 2012). Tropical insect species are typically sensitive to cold temperature extremes, which can lead to mortality at any life stage (Lee, 2010). Tropical species are less cold tolerant than their higher latitude relatives, which constrains the poleward distributions of tropical insect species (Halbritter et al., 2018; Overgaard et al., 2011). Thus, warming winter temperatures associated with climate change are expected to allow some tropical species to move northward into ecosystems that have typically supported temperate insect-dominated communities. Because insects often have disproportionate effects on the structure and functioning of ecosystems (Ayres & Lombardero, 2000; Weed et al., 2013), and many also are vectors of vertebrate (including human) pathogens, the ecological and societal consequences of tropical insect range expansions are large.

From a human health perspective, the northward movement of tropical mosquitoes in response to warming winters has the potential to facilitate the spread of harmful viruses (Monaghan et al., 2016; Morin et al., 2013). The tropical "southern house mosquito," *Culex quinquefasciatus*, a vector of many human and wild/domestic animal pathogens (e.g., St. Louis encephalitis, West Nile virus, Western equine encephalitis, possibly Zika virus) occurs from California to Florida but has been gradually expanding northward (Hahn et al., 2015; Turell et al., 2001). Although this mosquito species will occasionally feed on human blood, it prefers to feed on animals (Pruszynski et al., 2020). Over the past several decades, the two most important mosquito vectors for dengue, Zika, chikungunya, and yellow fever—*Aedes aegypti* and *Aedes albopictus*—have been expanding their ranges worldwide (Gubler, 2002; Lambrechts et al., 2010; Roth et al., 2014). In fact, the domesticated subspecies *Aedes aegypti aegypti* has become the most cosmopolitan species among all insect vectors (Christophers, 1960; Powell et al., 2018; Powell &

Tabachnick, 2013; Figure S7). Both *A. aegypti* and *A. albopictus* are tropical/subtropical species that are range-limited by winter low temperatures (Johnson et al., 2017; Joy et al., 2012). Both are established in Florida and Texas where local transmission of dengue, chikungunya, and Zika occurs (Johnson et al., 2017). Cold winter temperatures kill *A. aegypti* eggs, which currently constrains the species to southern tropical regions of the United States (e.g., southern Florida and Texas; Monaghan et al., 2016). However, the eggs of *A. albopictus* are able to diapause, increasing its ability to survive in colder winters and spread farther north than *A. aegypti* (Brady et al., 2014; Hawley et al., 1989; Johnson et al., 2017), and this species has now been reported from over 30 U.S. states. In response to warming winters, *A. aegypti* is now found in southern California and Arizona (Joy et al., 2012), and it is expected to increasingly move northward and become established in other parts of the southern United States (e.g., north Florida, Georgia, Alabama, Mississippi, Louisiana, north Texas, New Mexico), which means that Zika (Monaghan et al., 2016), dengue (Ebi & Nealon, 2016; Morin et al., 2013), and other mosquito-borne viruses (Iwamura et al., 2020) could potentially also expand northward and become locally transmitted in new areas. Numerous studies have produced global predictions of climatic suitability for *A. aegypti* and *A. albopictus* and all have concluded that warming winters are a primary factor driving mosquito range expansion poleward (Campbell et al., 2015; Khormi & Kumar, 2014; Monaghan et al., 2018). Rochlin et al. (2013) estimated that regions with suitable environmental conditions for the development of *A. albopictus* will increase by 50% by the end of the century, placing an additional 30 million people at risk.

For natural and managed forests, the northward movement of forest insect herbivores could have large ecological and economic implications (Ayres & Lombardero, 2000; Dale et al., 2001; Duehl et al., 2011). For example, the southern pine beetle (*Dendroctonus frontalis*) is the most destructive insect to pine forests in the southeastern United States. The southern pine beetle is sensitive to extreme cold winter temperatures, which control its northern range limit; thus, warming winters are expected to allow *D. frontalis* to expand into new areas and affect pine forests north of its current distribution (Lesk et al., 2017; Trân et al., 2007; Ungerer et al., 1999). Range limitation by winter cold is common in forest pest insects, so winter warming is leading to large-scale poleward range shifts in many insect species (Paradis et al., 2008; Sambaraju et al., 2019).

Many non-indigenous insect species that were initially constrained by cold temperatures are expanding their ranges poleward. The introduced sub-Saharan, arid-land African dung beetle (*Digitonthophagus gazelle*) has already expanded from the Gulf of Mexico coast to the southwestern United States, and it is expected to expand its range farther northward as winter climate warms (Harpootlian et al., 2001; Noriega et al., 2010). Similarly, the fire ant (*Solenopsis invicta*), which is native to the tropical regions of Argentina but has been introduced in the southern United States, Australia, and New Zealand, is moving poleward with climate warming. This species was estimated to be responsible for approximately US $600 million annually in damage to livestock, public health, and

wildlife in the United States alone (Pimentel et al., 2000). While initially thought to have low capacity for cold tolerance, recent work has demonstrated local adaptation in cold in this species, suggesting that further poleward expansion is possible (Lytle et al., 2020).

Continental-scale insect migrations can also be affected by changing winter temperature regimes. For example, most monarch butterflies (*Danaus plexippus*) in eastern North America migrate from temperate regions (Canada and the northern United States) to the tropics (Mexico) to avoid winter-time temperature extremes (Brower & Malcolm, 1991). However, warming winters have the potential to allow migratory monarchs to overwinter in areas north of their historical overwintering grounds (e.g., along the northern Gulf of Mexico coast, instead of Mexico; Howard et al., 2010).

## 13 | PATHWAYS TO RANGE EXPANSION

Since the last glacial maximum about 19,000 years ago, warming temperatures have allowed cold-sensitive tropical organisms to move northward to their current northern range limits in North America (Pielou, 1991; Woodroffe & Grindrod, 1991; Zink & Gardner, 2017). Many of these species have traveled large distances (~2000–3000 km) as they adjusted to a warming world. Despite this tremendous capacity for adaptive movement, the unprecedented pace of climate change in the coming centuries is expected to be much faster than the past, which will require even faster rates of range expansion. To complicate matters, there are many other aspects of global change that will interact with warming winters to affect species' northward movement. Thus, there is a need to more closely examine potential barriers to and opportunities for range expansion.

In the taxa-specific sections, we provide some examples of different range expansion pathways. For example, long-distance range extension is most likely for species that can fly or swim (e.g., birds, fish, manatee, sea turtles, insects), or those easily transported by humans. Some plants are capable of long-distance dispersal by water transport. For example, mangroves, whose water-dispersed propagules can be moved by tropical cyclones and oceanic currents (Van der Stocken, Wee, et al., 2019). Other plants can travel large distances when their seeds are carried by winds or animals. For example, the non-native Brazilian pepper tree can be widely dispersed by birds that have consumed its fruit (Ewel et al., 1982). Plants can also be dispersed by humans; for example, ornamental tropical plants sold at nurseries have often traveled long distances via truck transport on highways. In general, amphibian and reptile movements are slower than for birds or fish. However, there are many reptile and amphibian species that have moved large distances due to human transport; for example, Cuban treefrogs have crossed states while concealed in ornamental plant shipments (Glorioso et al., 2018), and Burmese pythons and other reptiles have traveled across oceans via the pet trade (Krysko et al., 2016). The massive introduction of invasive non-native tropical reptile (Engeman et al., 2011) and plant species (Simberloff et al., 1997) in Florida provides a cautionary example of the potential for transformative ecological change due to

human-assisted range extensions. Beyond just dispersal and movement capacity, habitat constraints can limit range expansion for some species (Corlett & Westcott, 2013; Zhu et al., 2012). For example, urban development or geological barriers northward of current range limits can reduce the habitat available for organisms to expand into. Collectively, these examples show that the pathways for range expansion are complex and warrant close consideration.

## 14 | MICROCLIMATES AND THERMAL REFUGIA

Thermal refugia play a critical role in the tropical–temperate transition zone by providing warmer microclimates, which enable tropical cold-sensitive species to survive extreme cold events. For example, during extreme cold events: manatees congregate near warmer waters (Laist et al., 2013); coastal fish (Stevens et al., 2018) and sea turtles (Lamont et al., 2018) move to warmer offshore, deeper, or spring-fed waters; reptiles (Mazzotti et al., 2016) and amphibians (Meshaka, 1996) seek shelter closer to warmer soil or water; and cold-sensitive plants are typically located in landscape positions that provide warmer microclimates (D'Odorico et al., 2013). Northern mangrove range limits along the northern Gulf of Mexico, for instance, are often located on barrier islands, which are far from the colder mainland and surrounded by comparatively warmer oceanic waters (Osland, Hartmann, et al., 2019). Human-built infrastructure can also provide thermal refuge to cold-sensitive species. For example, the Cuban treefrog seeks shelter in buildings (Johnson et al., 2010), manatees take advantage of the warmer water provided by thermoelectric plants (Moore, 1956), and the mangrove tree crab (*Aratus pisonii*) seeks warmer conditions provided by docks (Cannizzo et al., 2020). As tropical cold-sensitive species move beyond their current range limits, the warmer microclimates provided by thermal refugia will continue to shape range expansion dynamics.

## 15 | KNOWLEDGE GAPS TO BETTER UNDERSTAND CLIMATE CHANGE IMPACTS

In each of the taxa-specific sections, we provide examples of the critical influence of winter temperature extremes on tropical species' range limits. Most cold tolerance research has been focused on strongly cold-tolerant temperate species, leaving a large gap in our knowledge of the cold tolerance of tropical species. Many of the species that we highlight have been understudied, and to better assess the potential tropicalization of temperate ecosystems in response to climate change, there are many critical knowledge gaps to be filled. In this section, we identify a subset of these critical research areas within the context of the three key components of climate change vulnerability assessments: sensitivity, exposure, and adaptive capacity (Glick et al., 2011; Stein et al., 2014).

Knowledge gap #1: How sensitive are species, ecosystems, and biomes within tropical–temperate transition zones to extreme cold

temperatures? Much of our knowledge on this topic has developed from sporadic and opportunistic observations that quantify the damage or mortality caused by a specific extreme event to a species, ecosystem, or biome. These ad hoc observations are extremely valuable, but there is also a need for laboratory- and field-based manipulative experiments that elucidate physiological effects and better quantify temperature thresholds that lead to physiological damage or mortality. Moreover, opportunistic post-freeze observations from single locations could be made more strategic, organized, and valuable via their integration into regional coordinated networks of scientists that are collectively prepared to rapidly respond to and quantify the effects of extreme events along ecologically relevant abiotic gradients (e.g., Osland, Day, Hall, et al., 2020). For many species, historical patterns of range expansion and contraction have been understudied, and historical temperature data, in combination with temporal ecological data and knowledge of critical physiological temperature thresholds, can be used to better understand historical changes in ecological distribution, structure, and function due to cold sensitivity.

Knowledge gap #2: What is the expected exposure of species, ecosystems, and biomes to changes in the frequency and intensity of extreme cold temperatures? In prior decades, climate change vulnerability assessments focused primarily on changing means rather than changing extremes. However, given the demonstrated ecological importance of winter temperature extremes, future climate projections that better characterize changes in the frequency and intensity of winter temperature extremes could improve estimates of the biological effects of changing winters (Dillon et al., 2016). In addition to long-term projections (e.g., end of 21st century), vulnerability assessments could be improved by better understanding of the shorter-term potential for extreme winter events in the coming decades due to Arctic warming and jet stream dynamics that affect mid-latitude climates (Blackport & Screen, 2020; Cohen et al., 2019). To gauge exposure, future air temperature projections can be used for many cold-sensitive terrestrial organisms (e.g., plants); however, for marine and aquatic organisms (e.g., sea turtles, fishes, manatee), there is a need for customized models that quantify linkages between changing air temperatures and aquatic and coastal water temperatures. For coastal species (e.g., mangroves), models that incorporate ocean-driven microclimates (i.e., temperature variation across land-ocean gradients) are critical for assessing potential changes in species distribution and abundance (Osland, Day, & Michot, 2020; Osland, Hartmann, et al., 2019). Conversely, for montane species, models that incorporate mountain-driven microclimates (i.e., temperature variation due to landscape aspect, topographical variation, and elevation gradients) can improve estimates of upslope migration. Likewise, during drought years in arid and semi-arid regions, cloudless nights present greater risk of freezing exposure and have been understudied. For species that use refugia (e.g., frogs, pythons, fish, manatee), models that quantify the microclimatic protection offered by those refugia are critical.

Knowledge gap #3: What is the adaptive capacity of species, ecosystems, and biomes to changes in the frequency and intensity

of extreme cold temperatures? Adaptive capacity via range expansion depends on many factors including a species' potential for long-distance dispersal, growth, reproduction, abiotic stress tolerance, and biotic competition for resources in novel environments (e.g., Riley & Griffen, 2017). Figure 5 provides a generalized illustration of four alternative range expansion pathways for different species. Some of the species covered in this review (e.g., mangroves, Burmese pythons, Brazilian pepper, Cuban treefrogs, snook) have a tremendous capacity to adapt to climate change and clearly have the potential to expand their ranges northward in response to warming winters (Figure 5, lines a–c). In contrast, there are other species that lack the capacity to rapidly adapt or move from their current locations, often due to dispersal constraints or other biotic limits (Figure 5, line d). For foundation plant species, there is some indication that ecological regime shifts and northward range expansion could be accelerated by vegetation-microclimate positive feedbacks (D'Odorico et al., 2013) or from metabolic interactions with elevated $CO_2$ (Dole et al., 2003; Loik et al., 2000); however, these feedback mechanisms are understudied. Plastic responses to thermal extremes (including beneficial acclimatization or cumulative damage) will strongly influence adaptive capacity and are key priorities for future study (Williams et al., 2016). The effects of changing return intervals on range expansion rates are also poorly understood. As species move northward, how will changing return intervals—specifically, larger time periods between extreme cold events (i.e., longer return intervals)—affect physiological processes, population
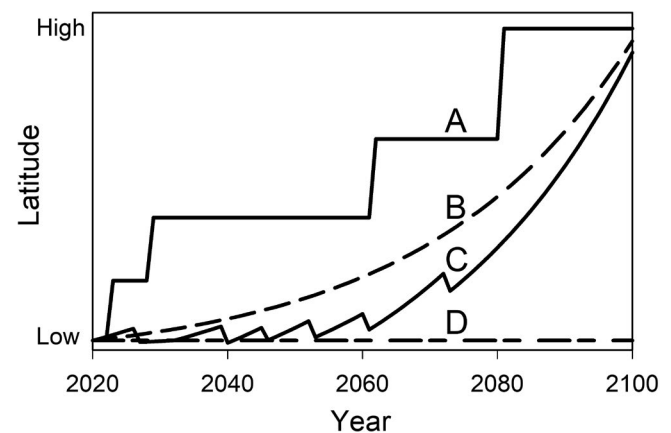


**FIGURE 5** Four generalized depictions of alternative poleward range expansion pathways for tropical organisms in response to warming winters. (A) depicts a species that moves north in a step-like fashion by long-distance transport in horticultural or pet trade shipments. (B) depicts a species with continuous, exponential poleward range expansion, while (C) depicts a species whose poleward range expansion is discontinuous and punctuated by extreme cold events that result in short-term range contractions, but these extreme cold events eventually dissipate, producing a smoother, continuous range expansion. In contrast, (D) depicts a species that is not able to expand poleward, perhaps due to dispersal constraints or other biotic limits. The y axis represents the latitude of the species' poleward range limit, where High represents a higher latitude north of the species' current range limit and Low represent a lower latitude near the species' current range limit

growth, and ecosystem development near moving range limits? For example, in Figure 5, line C depicts an expansion pathway that is initially dampened by recurring extreme cold events near northward moving range limits (see expansion and contraction cycles) but then unaffected by cold events as extreme cold events disappear (see line smoothening and the absence of contractions).

## 16 | CONCLUSIONS

In recent decades, ecologists have increasingly shown that ecological transformations due to climate change are often driven by climate extremes and extreme climatic events, rather than just changes in climatic means (Jentsch et al., 2007; Pecl et al., 2017; Smith, 2011). In this review, we have used a diverse assemblage of examples to highlight the critical role that extreme cold temperatures play in controlling the distribution, abundance, and structure of species, ecosystems, and biomes near tropical–temperature transition zones in North America. We have also examined the potential for tropicalization as tropical species move poleward in response to warming winters. Climate change-induced decreases in the frequency and intensity of extreme cold events are expected to facilitate the poleward range expansion of many tropical species. Assessing the ecological implications of the tropicalization of temperate ecosystems in North America would provide critical knowledge to inform natural resource managers.

### DATA AVAILABILITY STATEMENT
Data sharing not applicable – no new data generated, or the article describes entirely theoretical research.

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### REFERENCES

Abatzoglou, J. T., & Kolden, C. A. (2011). Climate change in western US deserts: Potential for increased wildfire and invasive annual grasses. *Rangeland Ecology & Management*, 64, 471–478.

Anderson, E. T., Harms, C. A., Stringer, E. M., & Cluse, W. M. (2011). Evaluation of hematology and serum biochemistry of cold-stunned green sea turtles (*Chelonia mydas*) in North Carolina, USA. *Journal of Zoo Wildlife Medicine*, 42, 247–255.

Anderson, J., Williford, D., González-Barnes, A., Chapa, C., Martinez-Andrade, F., & Overath, R. D. (2020). Demographic, taxonomic and genetic characterization of the snook species complex (*Centropomus* sp.) along the leading edge of its range in the northwestern Gulf of Mexico. *North American Journal of Fisheries Management*, 40, 190–208.

Armitage, A. R., Highfield, W. E., Brody, S. D., & Louchouarn, P. (2015). The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. *PLoS One*, 10, e0125404.

Arreola-Lizárraga, J. A., Flores-Verdugo, F. J., & Ortega-Rubio, A. (2004). Structure and litterfall of an arid mangrove stand on the Gulf of California, Mexico. *Aquatic Botany*, 79, 137–143.

Attaway, J. A. (1997). *A history of Florida citrus freezes*. Florida Science Source.

Austin, D. F., & Schwartz, A. (1975). Another exotic amphibian in Florida, Eleutherodactylus coqui. *Copeia*, 1975, 188.

Avens, L., Goshe, L. R., Harms, C. A., Anderson, E. T., Goodman Hall, A., Cluse, W. M., Godfrey, M. H., Braun-McNeill, J., Stacy, B., Bailey, R., & Lamont, M. M. (2012). Population characteristics, age structure, and growth dynamics of neritic juvenile green turtles in the northeastern Gulf of Mexico. *Marine Ecology Progress Series*, 458, 213–229.

Avery, M. L., Engeman, R. M., Keacher, K. L., Humphrey, J. S., Bruce, W. E., Mathies, T. C., & Mauldin, R. E. (2010). Cold weather and the potential range of invasive Burmese pythons. *Biological Invasions*, 12, 3649–3652.

Ayres, M. P., & Lombardero, M. J. (2000). Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment*, 262, 263–286.

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81, 169–193.

Barbour, T. (1931). Another introduced frog in North America. *Copeia*, 1931, 140.

Bardou, R., Parker, J. D., Feller, I. C., & Cavanaugh, K. C. (2020). Variability in the fundamental versus realized niches of North American mangroves. *Journal of Biogeography*, 48, 160–175.

Battaglia, C. D., Faidley, C. R., Hudson, A. N., Brown, M. D., Pardue, T. M., Reid, M. L., Bass, A. A., Townsend, C. L., & Carr, J. L. (2015). Distribution records for Louisiana amphibians and reptiles. *Herpetological Review*, 46, 579–581.

Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A., & Larsson, S. (2005). Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecological Applications*, 15, 2084–2096.

Beard, K. H., & Pitt, W. C. (2005). Potential consequences of the coqui frog invasion in Hawaii. *Diversity and Distributions*, 11, 427–433.

Blackport, R., & Screen, J. A. (2020). Weakened evidence for mid-latitude impacts of Arctic warming. *Nature Climate Change*, 10, 1065–1066.

Blewett, D. A., & Stevens, P. W. (2014). Temperature variability in a subtropical estuary and implications for common snook *Centropomus undecimalis*, a cold-sensitive fish. *Gulf of Mexico Science*, 32, 4.

Bojórquez, A., Álvarez-Yépiz, J. C., Búrquez, A., & Martínez-Yrízar, A. (2019). Understanding and predicting frost-induced tropical tree mortality patterns. *Global Change Biology*, 25, 3817–3828.

Bolten, A. B. (2003). Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In P. L. Lutz, J. Musick, & J. Wyneken (Eds.), *The biology of sea turtles* (Vol. II, pp. 243–257). CRC Press.

Boorse, G. C., Ewers, F. W., & Davis, S. D. (1998). Response of chaparral shrubs to below-freezing temperatures: acclimation, ecotypes, seedlings vs. adults. *American Journal of Botany*, 85, 1224–1230.

Booth, D. J., Beretta, G. A., Brown, L., & Figueira, W. F. (2018). Predicting success of range-expanding coral reef fish in temperate habitats using temperature-abundance relationships. *Frontiers in Marine Science*, 5, 31.

Borchert, S. M., Osland, M. J., Enwright, N. M., & Griffith, K. T. (2018). Coastal wetland adaptation to sea-level rise: Quantifying the potential for landward migration and coastal squeeze in northern Gulf of Mexico estuaries. *Journal of Applied Ecology*, 55, 2876–2887.

Bossart, G. D., Meisner, R. A., Rommel, S., Ghim, S., & Jenson, A. B. (2003). Pathological features of the Florida manatee cold stress syndrome. *Aquatic Mammals*, 29, 9–17.

Boucek, R. E., Gaiser, E. E., Liu, H., & Rehage, J. S. (2016). A review of subtropical community resistance and resilience to extreme cold spells. *Ecosphere*, 7, e01455.

Boucek, R. E., Heithaus, M. R., Santos, R., Stevens, P., & Rehage, J. S. (2017). Can animal habitat use patterns influence their vulnerability to extreme climate events? An estuarine sportfish case study. *Global Change Biology*, 23, 4045–4057.

Boucek, R. E., & Rehage, J. S. (2014). Climate extremes drive changes in functional community structure. *Global Change Biology*, 20, 1821–1831.

Bowers, J. E. (1981). Catastrophic freezes in the Sonoran Desert. *Desert Plants*, 232–236.

Box, E. O., Crumpacker, D. W., & Hardin, E. D. (1993). A climatic model for location of plant species in Florida, USA. *Journal of Biogeography*, 20, 629–644.

Box, E. O., Crumpacker, D. W., & Hardin, E. D. (1999). Predicted effects of climatic change on distribution of ecologically important native tree and shrub species in Florida. *Climatic Change*, 41, 213–248.

Brady, O. J., Golding, N., Pigott, D. M., Kraemer, M. U., Messina, J. P., Reiner, Jr., R. C., Scott, T. W., Smith, D. L., Gething, P. W., & Hay, S. I. (2014). Global temperature constraints on *Aedes aegypti* and *Ae. albopictus* persistence and competence for dengue virus transmission. *Parasites & Vectors*, 7, 338.

Brattstrom, B. H. (1968). Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comparative Biochemistry and Physiology*, 24, 93–111.

Brower, L. P., & Malcolm, S. B. (1991). Animal migrations: endangered phenomena. *American Zoologist*, 31, 265–276.

Brusca, R. C., Cudney-Bueno, R., & Moreno-Báez, M. (2006). *Gulf of California esteros and estuaries: analysis, state of knowledge and conservation priority recommendations*. Arizona Sonora Desert Museum.

Brusca, R. C., Wiens, J. F., Meyer, W. M., Eble, J., Franklin, K., Overpeck, J. T., & Moore, W. (2013). Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. *Ecology and Evolution*, 3, 3307–3319.

Campbell, L. P., Luther, C., Moo-Llanes, D., Ramsey, J. M., Danis-Lozano, R., & Peterson, A. T. (2015). Climate change influences on global distributions of dengue and chikungunya virus vectors. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140135.

Campbell-Staton, S. C., Cheviron, Z. A., Rochette, N., Catchen, J., Losos, J. B., & Edwards, S. V. (2017). Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole lizard. *Science*, 357, 495–498.

Cannizzo, Z. J., Lang, S. Q., Benitez-Nelson, B., & Griffen, B. D. (2020). An artificial habitat increases the reproductive fitness of a range-shifting species within a newly colonized ecosystem. *Scientific Reports*, 10, 554.

Card, D. C., Perry, B. W., Adams, R. H., Schield, D. R., Young, A. S., Andrew, A. L., Jezkova, T., Pasquesi, G. I. M., Hales, N. R., Walsh, M. R., Rochford, M. R., Mazzotti, F. J., Hart, K. M., Hunter, M. E., & Castoe, T. A. (2018). Novel ecological and climatic conditions drive rapid adaptation in invasive Florida Burmese pythons. *Molecular Ecology*, 27, 4744–4757.

Carlisle, A. B., Litvin, S. Y., Hazen, E. L., Madigan, D. J., Goldman, K. J., Lea, R. N., & Block, B. A. (2015). Reconstructing habitat use by juvenile salmon sharks links upwelling to strandings in the California Current. *Marine Ecology Progress Series*, 525, 217–228.

Carter, L., Terando, A., Dow, K., Hiers, K., Kunkel, K. E., Lascurain, A., & Schramm, P. (2018). Southeast. In D. R. Reidmiller, C. W. Avery, D. R. Easterling, K. E. Kunkel, K. L. M. Lewis, T. K. Maycock, & B. C. Stewart (Eds.), *Impacts, risks, and adaptation in the United States: Fourth national climate assessment* (Vol. II, pp. 743–808). U.S. Global Change Research Program.

Cavanaugh, K. C., Dangremond, E. M., Doughty, C. L., Williams, A. P., Parker, J. D., Hayes, M. A., Rodriguez, W., & Feller, I. C. (2019). Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 21602–21608.

Cavanaugh, K. C., Kellner, J. R., Forde, A. J., Gruner, D. S., Parker, J. D., Rodriguez, W., & Feller, I. C. (2014). Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 723–727.

Cavanaugh, K. C., Osland, M. J., Bardou, R., Hinijosa-Arango, G., López-Vivas, J. M., Parker, J. D., & Rovai, A. S. (2018). Sensitivity of mangrove range limits to climate variability. *Global Ecology and Biogeography*, 27, 925–935.

Christophers, S. R. (1960). *Aedes aegypti (L.): The yellow fever mosquito*. Cambridge University Press.

Claussen, D. L., Daniel, P. M., Jiang, S., & Adams, N. A. (1991). Hibernation in the eastern box turtle, *Terrapene c. carolina*. *Journal of Herpetology*, 25, 334–341.

Cohen, J., Zhang, X., Francis, J., Jung, T., Kwok, R., Overland, J., Ballinger, T. J., Bhatt, U. S., Chen, H. W., Coumou, D., Feldstein, S., Gu, H., Handorf, D., Henderson, G., Ionita, M., Kretschmer, M., Laliberte, F., Lee, S., Linderholm, H. W., … Yoon, J. (2019). Divergent consensuses on Arctic amplification influence on midlatitude severe winter weather. *Nature Climate Change*, 10, 20–29.

Colburn, L. L., Jepson, M., Weng, C., Seara, T., Weiss, J., & Hare, J. A. (2016). Indicators of climate change and social vulnerability in fishing dependent communities along the Eastern and Gulf Coasts of the United States. *Marine Policy*, 74, 323–333.

Cook-Patton, S. C., Lehmann, M., & Parker, J. D. (2015). Convergence of three mangrove species towards freeze-tolerant phenotypes at an expanding range edge. *Functional Ecology*, 29, 1332–1340.

Corlett, R. T., & Westcott, D. A. (2013). Will plant movements keep up with climate change? *Trends in Ecology & Evolution*, 28, 482–488.

Costanzo, J. P., do Amaral, M. C. F., Rosendale, A. J., & Lee, R. E. (2013). Hibernation physiology, freezing adaptation and extreme freeze tolerance in a northern population of the wood frog. *Journal of Experimental Biology*, 216, 3461–3473.

Costanzo, J. P., & Lee, R. E. (2013). Avoidance and tolerance of freezing in ectothermic vertebrates. *Journal of Experimental Biology*, 216, 1961–1967.

Cox, J. R., Martin-r, M. H., Ibarra-f, F. A., Fourie, J. H., Rethman, N. F. G., & Wilcox, D. G. (1988). The influence of climate and soils on the

distribution of four African grasses. *Journal of Range Management*, *41*, 127–139.

Crozier, L. (2003). Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia*, *135*, 648–656.

Cummings, E. W., Pabst, D. A., Blum, J. E., Barco, S. G., Davis, S. J., Thayer, V. G., & McLellan, W. A. (2014). Spatial and temporal patterns of habitat use and mortality of the Florida manatee (*Trichechus manatus latirostris*) in the mid-Atlantic states of North Carolina and Virginia from 1991 to 2012. *Aquatic Mammals*, *40*, 126–138.

Dale, V. H., Joyce, L. A., Mcnulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., & Michael wotton, B. (2001). Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience*, *51*, 723–734.

Dalrymple, G. H. (1980). Comments on the density and diet of a giant anole *Anolis equestris*. *Journal of Herpetology*, *14*, 412–415.

Davenport, J. (1997). Temperature and the life-history strategies of sea turtles. *Journal of Thermal Biology*, *22*, 479–488.

Davis, J. H. (1940). *The ecology and geologic role of mangroves in Florida.* Carnegie Institute of Washington Publications. Papers from Tortugas Laboratory, *32*, 303–412.

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, *292*, 673–679.

Davis, S. D., Pratt, R. B., Ewers, F. W., & Jacobsen, A. L. (2007). Freezing tolerance impacts chaparral species distribution in the Santa Monica Mountains. In D. A. Knapp (Ed.), *Flora and ecology of the Santa Monica mountains* (pp. 159–172). Southern California Botanists.

Davis, S. D., Sperry, J. S., & Hacke, U. G. (1999). The relationship between xylem conduit diameter and cavitation caused by freezing. *American Journal of Botany*, *86*, 1367–1372.

Deutsch, C. J., Reid, J. P., Bonde, R. K., Easton, D. E., Kochman, H. I., & O'Shea, T. J. (2003). Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic coast of the United States. *Wildlife Monographs*, *67*, 1–77.

Dieter, C. A., Maupin, M. A., Caldwell, R. R., Harris, M. A., Ivahnenko, T. I., Lovelace, J. K., Barber, N. L., & Linsey, K. S. (2018). *Estimated use of water in the United States in 2015: U.S. Geological Survey Circular. 1441*, 65 p., https://doi.org/10.3133/cir1441

Dillon, M. E., Woods, H. A., Wang, G., Fey, S. B., Vasseur, D. A., Telemeco, R. S., Marshall, K., & Pincebourde, S. (2016). Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. *Integrative and Comparative Biology*, *56*, 14–30.

Dodd, C. K. (2013). *Frogs of the United States and Canada.* John Hopkins University Press.

D'Odorico, P., Fuentes, J. D., Pockman, W. T., Collins, S. L., He, Y., Medeiros, J. S., DeWekker, S., & Litvak, M. E. (2010). Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. *Ecosphere*, *1*, 1–11.

D'Odorico, P., He, Y., Collins, S., De Wekker, S. F. J., Engel, V., & Fuentes, J. D. (2013). Vegetation–microclimate feedbacks in woodland–grassland ecotones. *Global Ecology and Biogeography*, *22*, 364–379.

Dole, K. P., Loik, M. E., & Sloan, L. C. (2003). The relative importance of climate change and the physiological effects of $CO_2$ on freezing tolerance for the future distribution of *Yucca brevifolia*. *Global and Planetary Change*, *36*, 137–146.

Dorcas, M. E., Willson, J. D., & Gibbons, J. W. (2011). Can invasive Burmese pythons inhabit temperate regions of the southeastern United States? *Biological Invasions*, *13*, 793–802.

Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., Meshaka, W. E., Andreadis, P. T., Mazzotti, F. J.,

Romagosa, C. M., & Hart, K. M. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 2418–2422.

Doyle, T. W., Krauss, K. W., Conner, W. H., & From, A. S. (2010). Predicting the retreat and migration of tidal forests along the northern Gulf of Mexico under sea-level rise. *Forest Ecology and Management*, *259*, 770–777.

Duehl, A. J., Koch, F. H., & Hain, F. P. (2011). Southern pine beetle regional outbreaks modeled on landscape, climate and infestation history. *Forest Ecology and Management*, *261*, 473–479.

Duke, N. C., Ball, M. C., & Ellison, J. C. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, *7*, 27–47.

Ebi, K. L., & Nealon, J. (2016). Dengue in a changing climate. *Environmental Research*, *151*, 115–123.

EDDMapS. (2020). *Early detection and distribution mapping system. The University of Georgia - Center for Invasive Species and Ecosystem Health.* http://www.eddmaps.org

Engeman, R., Jacobson, E., Avery, M. L., & Meshaka, Jr., W. E. (2011). The aggressive invasion of exotic reptiles in Florida with a focus on prominent species: A review. *Current Zoology*, *57*, 599–612.

Enwright, N. M., Griffith, K. T., & Osland, M. J. (2016). Barriers to and opportunities for landward migration of coastal wetlands with sea-level rise. *Frontiers in Ecology and the Environment*, *14*, 307–316.

Esque, T. C., & Schwalbe, C. R. (2002). Alien annual grasses and their relationships to fire and biotic change in Sonoran desertscrub. In B. Tellman (Ed.), *Invasive exotic species in the Sonoran region* (pp. 165–194). University of Arizona Press.

Ewel, J. J., Ojima, D. S., Karl, D. A., & DeBusk, W. F. (1982). *Schinus in successional ecosystems of Everglades National Park. South Florida Research Center Report T-676*. National Park Service.

Fält-Nardmann, J. J. J., Tikkanen, O.-P., Ruohomäki, K., Otto, L.-F., Leinonen, R., Pöyry, J., Saikkonen, K., & Neuvonen, S. (2018). The recent northward expansion of *Lymantria monacha* in relation to realised changes in temperatures of different seasons. *Forest Ecology and Management*, *427*, 96–105.

Feher, L. C., Osland, M. J., Griffith, K. T., Grace, J. B., Howard, R. J., Stagg, C. L., Enwright, N. M., Krauss, K. W., Gabler, C. A., Day, R. H., & Rogers, K. (2017). Linear and nonlinear effects of temperature and precipitation on ecosystem properties in tidal saline wetlands. *Ecosphere*, *8*, e01956.

Felger, R. S. (2004). Seed plants. In R. C. Brusca, E. Kimrey, & W. Moore (Eds.), *A seashore guide to the Northern Gulf of California* (pp. 147–163). Arizona-Sonora Desert Museum.

Felger, R. S., Cliffton, K., & Regal, P. J. (1976). Winter dormancy in sea turtles: independent discovery and exploitation in the Gulf of California by two local cultures. *Science*, *191*, 283–285.

Felger, R. S., Johnson, M. B., & Wilson, M. F. (2001). *The trees of Sonora, Mexico*. Oxford University Press.

Felger, R. S., & Lowe, C. H. (1967). Clinal variation in the surface-volume relationships of the columnar cactus *Lophocereus schottii* in northwestern Mexico. *Ecology*, *48*, 530–536.

Fernández-Rivera Melo, F. J., Reyes-Bonilla, H., Campos-Dávila, L., & Balart, E. F. (2015). Range extension of *Lutjanus inermis* (Peters, 1896) (Perciformes: Lutjanidae) to the central region of the Gulf of California, Mexico. *Journal of Applied Ichthyology*, *31*, 541–543.

Fertl, D., Schiro, A. J., Regan, G. T., Beck, C. A., Adimey, N., Price-May, L., Amos, A., Worthy, G., & Crossland, R. (2005). Manatee occurrence in the northern Gulf of Mexico, west of Florida. *Gulf and Caribbean Research*, *17*, 69–94.

Figueira, W. F., & Booth, D. J. (2010). Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology*, *16*, 506–516.

FLEPPC. (2019). *2019 List of invasive plant species*. Florida Exotic Pest Plant Council. www.fleppc.org

Flores-Verdugo, F., González-Farías, F., Zamorano, D. S., & Ramírez-García, P. (1992). Mangrove ecosystems of the Pacific coast of Mexico: distribution, structure, litterfall, and detritus dynamics. In U. Seeliger (Ed.), *Coastal plant communities of Latin America* (pp. 269–288). Elsevier Academic Press.

Fodrie, F. J., Heck, Jr., K. L., Powers, S. P., Graham, W. M., & Robinson, K. L. (2010). Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. *Global Change Biology*, *16*, 48–59.

Foley, A. M., Singel, K. E., Dutton, P. H., Summers, T. M., Redlow, A. E., & Lessman, J. (2007). Characteristics of a green turtle (*Chelonia mydas*) assemblage in northwestern Florida determined during a hypothermic stunning event. *Gulf of Mexico Science*, *25*, 131–143.

Fujisaki, I., Mazzotti, F. J., Watling, J., Krysko, K. L., & Escribano, Y. (2015). Geographic risk assessment reveals spatial variation in invasion potential of exotic reptiles in an invasive species hotspot. *Herpetological Conservation and Biology*, *10*, 621–632.

Gabler, C. A., Osland, M. J., Grace, J. B., Stagg, C. L., Day, R. H., Hartley, S. B., Enwright, N. M., From, A. S., McCoy, M. L., & McLeod, J. L. (2017). Macroclimatic change expected to transform coastal wetland ecosystems this century. *Nature Climate Change*, *7*, 142–147.

Geiger, R., Aron, R. H., & Todhunter, P. (2012). *The climate near the ground*. Harvard University Press.

Glenn, E. P., Nagler, P. L., Brusca, R. C., & Hinojosa-Huerta, O. (2006). Coastal wetlands of the northern Gulf of California: Inventory and conservation status. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *16*, 5–28.

Glick, P., Stein, B. A., & Edelson, N. A. (2011). *Scanning the conservation horizon: A guide to climate change vulnerability assessment*. National Wildlife Federation.

Glorioso, B. M., Waddle, J. H., Muse, L. J., Jennings, N. D., Litton, M., Hamilton, J., Gergen, S., & Heckard, D. (2018). Establishment of the exotic invasive Cuban treefrog (*Osteopilus septentrionalis*) in Louisiana. *Biological Invasions*, *20*, 2707–2713.

Goetz, S. M., Guyer, C., Boback, S. M., & Romagosa, C. M. (2018). Toxic, invasive treefrog creates evolutionary trap for native gartersnakes. *Biological Invasions*, *20*, 519–531.

González-Cuéllar, O. T., Reyes-Bonilla, H., Fourriére, M., Rojo, M., Hernández-Velasco, A., Sánchez-Alcántara, I., & Pfister, T. (2013). Range extensions of four species of parrotfishes (Scaridae) in the northern Gulf of California, Mexico. *Cybium*, *37*, 223–226.

Greenwood, M. F. D. (2017). Distribution, spread, and habitat predictability of a small, invasive, piscivorous fish in an important estuarine fish nursery. *Fishes*, *2*, 6.

Greller, A. M. (1980). Correlation of some climate statistics with distribution of broadleaved forest zones in Florida, USA. *Bulletin of the Torrey Botanical Club*, *107*, 189–219.

Griffin, L. P., Griffin, C. R., Finn, J. T., Prescott, R. L., Faherty, M., Still, B. M., & Danylchuk, A. J. (2019). Warming seas increase cold-stunning events for Kemp's ridley sea turtles in the northwest Atlantic. *PLoS One*, *14*, e0211503.

Griffith, A. B., Andonian, K., Weiss, C. P., & Loik, M. E. (2014). Variation in phenotypic plasticity for native and invasive populations of *Bromus tectorum*. *Biological Invasions*, *16*, 2627–2638.

Gubler, D. J. (2002). Epidemic dengue/dengue hemorrhagic fever as a public health, social and economic problem in the 21st century. *Trends in Microbiology*, *10*, 100–103.

Haggerty, C. J., & Crisman, T. L. (2015). Pulse disturbance impacts from a rare freeze event in Tampa, Florida on the exotic invasive Cuban treefrog, *Osteopilus septentrionalis*, and native treefrogs. *Biological Invasions*, *17*, 2103–2111.

Halbritter, D. A., Teets, N. M., Williams, C. M., & Daniels, J. C. (2018). Differences in winter cold hardiness reflect the geographic range disjunction of *Neophasia menapia* and *Neophasia terlooii* (Lepidoptera: Pieridae). *Journal of Insect Physiology*, *107*, 204–211.

Hamann, M., Limpus, C. J., & Owens, D. W. (2003). Reproductive cycles of males and females. In P. L. Lutz, J. Musick, & J. Wyneke (Eds.), *The biology of sea turtles* (Vol. *II*, pp. 135–161). CRC Press.

Hare, J. A., Wuenschel, M. J., & Kimball, M. E. (2012). Projecting range limits with coupled thermal tolerance-climate change models: an example based on gray snapper (*Lutjanus griseus*) along the US east coast. *PLoS One*, *7*, e52294.

Harpootlian, P. J., Morse, J. C., & Wheeler, A. G. (2001). *Scarab beetles (Coleoptera: Scarabaeidae) of South Carolina*. Clemson University Public Service Publishing.

Hartman, D. S. (1979). Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. *American Society of Mammalogists Special Publication*, *5*, 1–153.

Hastings, J. R. (1963). *Historical changes in the vegetation of a desert region*. Ph.D. Dissertation. Tucson, Arizona, USA: University of Arizona.

Hawkes, L. A., Broderick, A. C., Godfrey, M. H., & Godley, B. J. (2009). Climate change and marine turtles. *Endangered Species Research*, *7*, 137–154.

Hawkes, L. A., Witt, M. J., Broderick, A. C., Coker, J. W., Coyne, M. S., Dodd, M., Frick, M. G., Godfrey, M. H., Griffin, D. B. B., Murphy, S. R., Murphy, T. M., Williams, K. L., & Godley, B. J. (2011). Home on the range: Spatial ecology of loggerhead turtles in Atlantic waters of the USA. *Diversity and Distributions*, *17*, 624–640.

Hawley, W. A., Pumpuni, C. B., Brady, R. H., & Craig, Jr., G. B. (1989). Overwintering survival of *Aedes albopictus* (Diptera: Culicidae) eggs in Indiana. *Journal of Medical Entomology*, *26*, 122–129.

Hays, G. C. (2000). The implications of variable remigration intervals for the assessment of population size in marine turtles. *Journal of Theoretical Biology*, *206*, 221–227.

Hiatt, D., Serbesoff-King, K., Lieurance, D., Gordon, D. R., & Flory, S. L. (2019). Allocation of invasive plant management expenditures for conservation: Lessons from Florida, USA. *Conservation Science and Practice*, *1*(7). https://doi.org/10.1111/csp2.51

Hibbitts, T. D., & Hibbitts, T. J. (2015). *Texas lizards: A field guide*. University of Texas Press.

Holdridge, L. R. (1967). *Life zone ecology*. Tropical Science Center.

Howard, E., Aschen, H., & Davis, A. K. (2010). Citizen science observations of monarch butterfly overwintering in the southern United States. *Psyche*, *2010*, 689301.

Howells, R. G., Sonski, A. J., Shafland, P. L., & Hilton, B. D. (1990). Lower temperature tolerance of snook, *Centropomus undecimalis*. *Northeast Gulf Science*, *11*, 155–158.

Hussey, M. A., & Bashaw, E. C. (1996). Performance of buffelgrass germplasm with improved winter survival. *Agronomy Journal*, *88*, 944–946.

Hutchinson, J. T., & Langeland, K. A. (2014). Tolerance of *Lygodium microphyllum* and *L. japonicum* spores and gametophytes to freezing temperature. *Invasive Plant Science and Management*, *7*, 328–335.

Idelberger, C. F., Stafford, C. J., & Erickson, S. E. (2011). Distribution and abundance of introduced fishes in Florida's Charlotte Harbor estuary. *Gulf Caribbean Research*, *23*, 13–22.

Irvine, A. B. (1983). Manatee metabolism and its influence on distribution in Florida. *Biological Conservation*, *25*, 315–334.

Iwamura, T., Guzman-Holst, A., & Murray, K. A. (2020). Accelerating invasion potential of disease vector *Aedes aegypti* under climate change. *Nature Communications*, *11*, 1–10.

Jacobson, E. R., Barker, D. G., Barker, T. M., Mauldin, R., Avery, M. L., Engeman, R., & Secor, S. (2012). Environmental temperatures, physiology and behavior limit the range expansion of invasive Burmese pythons in southeastern USA. *Integrative Zoology*, *7*, 271–285.

Jarnevich, C. S., Young, N. E., Talbert, M., & Talbert, C. (2018). Forecasting an invasive species' distribution with global distribution data, local data, and physiological information. *Ecosphere*, *9*, e02279.

Jensen, M. P., Allen, C. D., Eguchi, T., Bell, I. P., LaCasella, E. L., Hilton, W. A., Hof, C. A. M., & Dutton, P. H. (2018). Environmental warming

and feminization of one of the largest sea turtle populations in the world. *Current Biology*, 28(1), 154–159.e4.

Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments: Events, not trends. *Frontiers in Ecology and the Environment*, 5, 365–374.

Johnson, S. A., McGarrity, M. E., & Staudhammer, C. L. (2010). An effective chemical deterrent for invasive Cuban treefrogs. *Human-Wildlife Interactions*, 4, 112–117.

Johnson, T. L., Haque, U., Monaghan, A. J., Eisen, L., Hahn, M. B., Hayden, M. H., Savage, H. M., McAllister, J., Mutebi, J.-P., & Eisen, R. J. (2017). Modeling the environmental suitability for *Aedes* (Stegomyia) *aegypti* and *Aedes* (Stegomyia) *albopictus* (Diptera: Culicidae) in the contiguous United States. *Journal of Medical Entomology*, 54, 1605–1614.

Jones, T. T., & Seminoff, J. A. (2013). Feeding biology: advances from field-based observations, physiological studies, and molecular techniques. In J. J. Musick, J. Wyneken, & K. Lohman (Eds.), *The biology of sea turtles* (Vol. III, pp. 211–248). CRC Press.

Joy, T. K., Gutierrez, E. H. J., Ernst, K., Walker, K. R., Carriere, Y., Torabi, M., & Riehle, M. A. (2012). Aging field collected *Aedes aegypti* to determine their capacity for dengue transmission in the southwestern United States. *PLoS One*, 7, e46946.

Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 11823–11826.

Kennedy, J. P., Pil, M. W., Proffitt, C. E., Boeger, W. A., Stanford, A. M., & Devlin, D. J. (2016). Postglacial expansion pathways of red mangrove, *Rhizophora mangle*, in the Caribbean Basin and Florida. *American Journal of Botany*, 103, 260–276.

Kennedy, J. P., Preziosi, R. F., Rowntree, J. K., & Feller, I. C. (2020). Is the central-marginal hypothesis a general rule? Evidence from three distributions of an expanding mangrove species, *Avicennia germinans* (L.) L. *Molecular Ecology*, 29, 704–719.

Khan, A. A., & Vincent, J. F. V. (1996). Mechanical damage induced by controlled freezing in apple and potato. *Journal of Texture Studies*, 27, 143–157.

Khormi, H. M., & Kumar, L. (2014). Climate change and the potential global distribution of *Aedes aegypti*: spatial modelling using geographical information system and CLIMEX. *Geospatial Health*, 8, 405–415.

Kolbe, J. J., Ehrenberger, J. C., Moniz, H. A., & Angilletta, Jr., M. J. (2014). Physiological variation among invasive populations of the brown anole (*Anolis sagrei*). *Physiological and Biochemical Zoology*, 87, 92–104.

Kraus, F., & Campbell, E. W. (2002). Human-mediated escalation of a formerly eradicable problem: the invasion of Caribbean frogs in the Hawaiian Islands. *Biological Invasions*, 4, 327–332.

Krauss, K. W., McKee, K. L., Lovelock, C. E., Cahoon, D. R., Saintilan, N., Reef, R., & Chen, L. (2014). How mangrove forests adjust to rising sea level. *New Phytologist*, 202, 19–34.

Krivoruchko, A., & Storey, K. B. (2010). Activation of antioxidant defenses in response to freezing in freeze-tolerant painted turtle hatchlings. *Biochimica Et Biophysica Acta (BBA) - General Subjects*, 1800(7), 662–668. https://doi.org/10.1016/j.bbagen.2010.03.015

Krysko, K. L., Burgess, J. P., Rochford, M. R., Gillette, C. R., Cueva, D., Enge, K. M., Somma, L. A., Stabile, J. L., Smith, D. C., Wasilewski, J. A., Kieckhefer iii, G. N., Granatosky, M. C., & Nielsen, S. V. (2011). Verified non-indigenous amphibians and reptiles in Florida from 1863 through 2010: Outlining the invasion process and identifying invasion pathways and stages. *Zootaxa*, 3028, 1–64.

Krysko, K. L., Enge, K. M., Donlan, E. M., Seitz, J. C., & Golden, E. A. (2007). Distribution, natural history, and impacts of the introduced green iguana (*Iguana iguana*) in Florida. *Iguana*, 3, 2–17.

Krysko, K. L., Somma, L. A., Smith, D. C., Gillette, C. R., Cueva, D., Wasilewski, J. A., Enge, K. M., Johnson, S. A., Campbell, T. S., Edwards, J. R., Rochford, M. R., Tompkins, R., Fobb, J. L., Mullin, S.,

Lechowicz, C., Hazelton, D. & Edwards, J. R. (2016). New verified nonindigenous amphibians and reptiles in Florida through 2015, with a summary of over 152 years of introductions. *IRCF Reptiles and Amphibians*, 23, 110–143.

Ladwig, L. M., Collins, S. L., Krofcheck, D. J., & Pockman, W. T. (2019). Minimal mortality and rapid recovery of the dominant shrub *Larrea tridentata* following an extreme cold event in the northern Chihuahuan Desert. *Journal of Vegetation Science*, 30, 963–972.

Laist, D. W., Taylor, C., & Reynolds, J. E. III (2013). Winter habitat preferences for Florida manatees and vulnerability to cold. *PLoS One*, 8, e58978.

Lambrechts, L., Scott, T. W., & Gubler, D. J. (2010). Consequences of the expanding global distribution of *Aedes albopictus* for dengue virus transmission. *PLOS Neglected Tropical Diseases*, 4, e646.

Lamont, M. M., & Fujisaki, I. (2014). Effects of ocean temperature on nesting phenology and fecundity of the loggerhead sea turtle (*Caretta caretta*). *Journal of Herpetology*, 48, 98–102.

Lamont, M. M., & Iverson, A. R. (2018). Shared habitat use by juveniles of three sea turtle species. *Marine Ecology Progress Series*, 606, 187–200.

Lamont, M. M., Seay, D. R., & Gault, K. (2018). Overwintering behavior of juvenile sea turtles at a temperate foraging ground. *Ecology*, 99, 2621–2624.

Langan, S. J., Ewers, F. W., & Davis, S. D. (1997). Xylem dysfunction caused by water stress and freezing in two species of co-occurring chaparral shrubs. *Plant, Cell & Environment*, 20, 425–437.

Lee, Jr., R. E. (2010). A primer on insect cold-tolerance. In D. L. Denlinger & R. E. Lee (Eds.), *Low temperature biology of insects* (pp. 3–34). Cambridge University Press.

Lefebvre, L. W., Marmontel, M., Reid, J. P., Rathbun, G. B., & Domning, D. P. (2001). Status and biogeography of the West Indian manatee. In C. A. Woods & F. E. Sergile (Eds.), *Biogeography of the West Indies: New patterns and perspectives* (pp. 425–474). CRC Press.

Lehner, C. E. (1979). A latitudinal gradient analysis of rocky shore fishes of the eastern Pacific. Ph.D. Dissertation. University of Arizona, Tuscon, Arizona, USA. In.

Lesk, C., Coffel, E., D'Amato, A. W., Dodds, K., & Horton, R. (2017). Threats to North American forests from southern pine beetle with warming winters. *Nature Climate Change*, 7, 713–717.

Levitt, J. (1980). *Responses of plants to environmental stress, Volume 1: Chilling, freezing, and high temperature stresses*. Academic Press.

Lillywhite, H. B., Shine, R., Jacobson, E., DeNardo, D. F., Gordon, M. S., Navas, C. A., Wang, T., Seymour, R. S., Storey, K. B., Heatwole, H., Heard, D., Brattstrom, B., & Burghardt, G. M. (2017). Anesthesia and euthanasia of amphibians and reptiles used in scientific research: Should hypothermia and freezing be prohibited? *BioScience*, 67, 53–61.

Lluch-Belda, D., Del Monte-Luna, P., & Lluch-Cota, S. E. (2009). 20th century variability in the Gulf of California SST. *CalCOFI Report*, 50, 147–154.

Loftus, W. F., & Hernon, R. (1984). Reestablishment of the cocqui, *Eleutherodactylus coqui* (Thomas) in southern Florida. *Herpetological Review*, 15, 23.

Loik, M. E., Huxman, T. E., Hamerlynck, E. P., & Smith, S. D. (2000). Low temperature tolerance and cold acclimation for seedlings of three Mojave Desert *Yucca* species exposed to elevated $CO_2$. *Journal of Arid Environments*, 46, 43–56.

Loik, M. E., & Nobel, P. S. (1993a). Exogenous abscisic acid mimics cold acclimation for cacti differing in freezing tolerance. *Plant Physiology*, 103, 871–876.

Loik, M. E., & Nobel, P. S. (1993b). Freezing tolerance and water relations of *Opuntia fragilis* from Canada and the United States. *Ecology*, 74, 1722–1732.

Lonard, R. I., & Judd, F. W. (1985). Effects of a severe freeze on native woody plants in the Lower Rio Grande Valley, Texas. *The Southwestern Naturalist*, 30, 397–403.

Lonard, R. I., & Judd, F. W. (1991). Comparison of the effects of the severe freezes of 1983 and 1989 on native woody plants in the Lower Rio Grande Valley, Texas. *The Southwestern Naturalist, 36*, 213–217.

Lovelock, C. E., Krauss, K. W., Osland, M. J., Reef, R., & Ball, M. C. (2016). The physiology of mangrove trees with changing climate. In G. Goldstein & L. S. Santiago (Eds.), *Tropical tree physiology: adaptations and responses in a changing environment* (pp. 149–179). Springer.

Lowerre-Barbieri, S. K., Kays, R., Thorson, J. T., & Wikelski, M. (2019). The ocean's movescape: fisheries management in the biologging decade (2018–2028). *ICES Journal of Marine Science, 76*, 477–488.

Lugo, A. E., & Patterson-Zucca, C. (1977). The impact of low temperature stress on mangrove structure and growth. *Tropical Ecology, 18*, 149–161.

Lynch, H. J., Rhainds, M., Calabrese, J. M., Cantrell, S., Cosner, C., & Fagan, W. F. (2014). How climate extremes—not means—define a species' geographic range boundary via a demographic tipping point. *Ecological Monographs, 84*, 131–149.

Lyons, J. M. (1973). Chilling injury in plants. *Annual Review of Plant Physiology, 24*, 445–466.

Lytle, A. J., Costa, J. T., & Warren, R. J. II (2020). Invasion and high-elevation acclimation of the red imported fire ant, *Solenopsis invicta*, in the southern Blue Ridge Escarpment region of North America. *PLoS One, 15*, e0232264.

Mace, M. M., Haffey, E. R., & Kimball, M. E. (2017). Low-temperature tolerance of juvenile tarpon *Megalops atlanticus*. *Environmental Biology of Fishes, 100*, 913–922.

MacMillan, H. A., & Sinclair, B. J. (2011). Mechanisms underlying insect chill-coma. *Journal of Insect Physiology, 57*, 12–20.

Madrak, S. V., Lewison, R. L., Seminoff, J. A., & Eguchi, T. (2016). Characterizing response of East Pacific green turtles to changing temperatures: using acoustic telemetry in a highly urbanized environment. *Animal Biotelemerty, 4*, 22.

Marsh, H., O'Shea, T. J., Reynolds, J. E., & Reynolds, J. E. III (2012). *Ecology and conservation of the Sirenia: Dugongs and manatees*. Cambridge University Press.

Marshall, V., Lewis, M., & Ostendorf, B. (2012). Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: A review. *Journal of Arid Environments, 78*, 1–12.

Martin, J. H., & McEachron, L. W. (1996). *Historical annotated review of winter kills of marine organisms in Texas bays. Management Data Series No. 118*. Texas Parks and Wildlife Department. Coastal Fisheries Division.

Martin, T. G., Murphy, H., Liedloff, A., Thomas, C., Chadès, I., Cook, G., Fensham, R., McIvor, J., & van Klinken, R. D. (2015). Buffel grass and climate change: a framework for projecting invasive species distributions when data are scarce. *Biological Invasions, 17*, 3197–3210.

Matich, P., & Heithaus, M. R. (2012). Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas*. *Marine Ecology Progress Series, 447*, 165–178.

Mazzotti, F. J., Cherkiss, M. S., Hart, K. M., Snow, R. W., Rochford, M. R., Dorcas, M. E., & Reed, R. N. (2011). Cold-induced mortality of invasive Burmese pythons in south Florida. *Biological Invasions, 13*, 143–151.

Mazzotti, F. J., Cherkiss, M. S., Parry, M., Beauchamp, J., Rochford, M., Smith, B., Hart, K., & Brandt, L. A. (2016). Large reptiles and cold temperatures: Do extreme cold spells set distributional limits for tropical reptiles in Florida? *Ecosphere, 7*, e01439.

McAuliffe, J. R. (1996). Saguaro cactus dynamics. In W. L. Halverson & G. E. Davis (Eds.), *Science and ecosystem management in the National Parks* (pp. 96–131). University of Arizona Press.

McCleery, R. A., Sovie, A., Reed, R. N., Cunningham, M. W., Hunter, M. E., & Hart, K. M. (2015). Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades. *Proceedings of the Royal Society B: Biological Sciences, 282*, 20150120.

McClellan, C. M., & Read, A. J. (2007). Complexity and variation in loggerhead sea turtle life history. *Biology Letters, 3*, 592–594.

McClenachan, G., Witt, M., & Walters, L. J. (2021). Replacement of oyster reefs by mangroves: Unexpected climate-driven ecosystem shifts. *Global Change Biology, 27*, 1226–1238.

McKee, K. L. (2011). Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine, Coastal and Shelf Science, 91*, 475–483.

McKee, K., Rogers, K., & Saintilan, N. (2012). Response of salt marsh and mangrove wetlands to changes in atmospheric $CO_2$, climate, and sea level. In B. A. Middleton (Ed.), *Global change and the function and distribution of wetlands: Global change ecology and wetlands* (pp. 63–96). Springer.

McNab, B. K. (2002). *The physiological ecology of vertebrates: A view from energetics*. Cornell University Press.

Means, D. B., & Simberloff, D. (1987). The peninsula effect: Habitat-correlated species decline in Florida's herpetofauna. *Journal of Biogeography, 14*, 551–568.

Mendelssohn, I. A., Byrnes, M. R., Kneib, R. T., & Vittor, B. A. (2017). Coastal habitats of the Gulf of Mexico. In C. Ward (Ed.), *Habitats and biota of the Gulf of Mexico: Before the deepwater horizon oil spill* (pp. 359–640). Springer.

Meshaka, W. E. (1996). Retreat use by the Cuban Treefrog (*Osteopilus septentrionalis*): Implications for successful colonization in Florida. *Journal of Herpetology, 30*, 443–445.

Meshaka, W. E. (2001). *The Cuban treefrog in Florida: Life history of a successful colonizing species*. University Press of Florida.

Meshaka, W. E. (2011). A runaway train in the making: The exotic amphibians, reptiles, turtles, and crocodilians of Florida. *Herpetological Conservation and Biology, 6*, 1–101.

Meshaka, W. E., Butterfield, B. P., & Hauge, J. B. (2004). *Exotic amphibians and reptiles of Florida*. Krieger Publishing.

Milton, S. L., & Lutz, P. L. (2003). Physiological and genetic responses to environmental stress. In P. L. Lutz, J. Musick, & J. Wyneken (Eds.), *Biology of sea turtles* (Vol. II, pp. 163–197). CRC Press.

Monaghan, A. J., Morin, C. W., Steinhoff, D. F., Wilhelmi, O., Hayden, M., Quattrochi, D. A., Reiskind, M., Lloyd, A. L., Smith, K., Schmidt, C. A., Scalf, P. E., & Ernst, K. (2016). On the seasonal occurrence and abundance of the Zika virus vector mosquito *Aedes aegypti* in the contiguous United States. *PLoS Currents Outbreaks, 8*. ecurrents.outbreaks.50dfc57f46798675fc46798663e46798677d-46798677da46798563da46798676.

Monaghan, A. J., Sampson, K. M., Steinhoff, D. F., Ernst, K. C., Ebi, K. L., Jones, B., & Hayden, M. H. (2018). The potential impacts of 21st century climatic and population changes on human exposure to the virus vector mosquito *Aedes aegypti*. *Climatic Change, 146*, 487–500.

Moore, J. C. (1956). Observations of manatees in aggregations. *1811*, 1–24.

Morin, C. W., Comrie, A. C., & Ernst, K. (2013). Climate and dengue transmission: Evidence and implications. *Environmental Health Perspectives, 121*, 1264.

Morningstar, C. R., & Daniel, W. M. (2020). *Osteopilus septentrionalis (Duméril and Bibron, 1841): U.S. Geological Survey, Nonindigenous Aquatic Species Database*. https://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=57

Morton, J. F. (1980). The Australian pine or beefwood (*Casuarina equisetifolia* L.), an invasive" weed" tree in Florida. *Proceedings of the Florida State Horticultural Society, 93*, 87–95.

Myers, R. L. (1986). Florida's freezes: An analog of short-duration nuclear winter events in the tropics. *Florida Scientist, 49*, 104–115.

Nakamura, Y., Feary, D. A., Kanda, M., & Yamaoka, K. (2013). Tropical fishes dominate temperate reef fish communities within western Japan. *PLoS One, 8*, e81107.

Nasci, R. S., Delorey, M. J., Eisen, R. J., Monaghan, A. J., Fischer, M., Hayden, M. H., Hahn, M. B., & Lindsey, N. P. (2015). Meteorological conditions associated with increased incidence of West Nile virus disease in the United States, 2004–2012. *American Journal of Tropical Medicine*, *92*, 1013–1022.

Niering, W. A., Whittaker, R. H., & Lowe, C. H. (1963). The saguaro: a population in relation to environment. *Science*, *142*, 15–23.

Nobel, P. S. (1980a). Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. *Botanical Gazette*, *141*, 188–191.

Nobel, P. S. (1980b). Influences of minimum stem temperatures on ranges of cacti in southwestern United States and central Chile. *Oecologia*, *47*, 10–15.

Nobel, P. S. (1980c). Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. *Ecology*, *61*, 1–7.

Nobel, P. S. (2005). *Physicochemical and environmental plant physiology* (3rd ed.). Elsevier.

Nobel, P. S., Loik, M. E., & Meyer, R. W. (1991). Microhabitat and diel tissue acidity changes for two sympatric cactus species differing in growth habit. *Journal of Ecology*, *79*, 167–182.

Noriega, J. A., Horgan, F. G., Larsen, T. H., & Valencia, G. (2010). Records of an invasive dung beetle species, *Digitonthophagus gazella* (Fabricius, 1787) (Coleoptera: Scarabaeidae), in Peru. *Acta Zoológica Mexicana*, *26*, 451–456.

Norton, S. L., Wiley, T. R., Carlson, J. K., Frick, A. L., Poulakis, G. R., & Simpfendorfer, C. A. (2012). Designating critical habitat for juvenile endangered smalltooth sawfish in the United States. *Marine Coastal Fisheries*, *4*, 473–480.

O'Hop, J., & Munyandorero, J. J. (2016). *SEDAR 47 stock assessment report for goliath grouper of the South Atlantic and Gulf of Mexico. FWC Report IHR2016-001*. Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute.

Olmsted, I., Dunevitz, H., & Platt, W. J. (1993). Effects of freezes on tropical trees in Everglades National Park Florida, USA. *Tropical Ecology*, *34*, 17–34.

Orum, T. V., Ferguson, N., & Mihail, J. D. (2016). Saguaro (*Carnegiea gigantea*) mortality and population regeneration in the cactus forest of Saguaro National Park: Seventy-five years and counting. *PLoS One*, *11*, e0160899.

O'shea, T. J. (1988). The past, present, and future of manatees in the southeastern United States: Realities, misunderstandings and enigmas. In R. R. Odom, K. A. Riddleberger, & J. C. Ozier (Eds.), *Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium* (pp. 184–204). Georgia Department of Natural Resources.

Osland, M. J., Day, R. H., Hall, C. T., Brumfield, M. D., Dugas, J. L., & Jones, W. R. (2017). Mangrove expansion and contraction at a poleward range limit: climate extremes and land-ocean temperature gradients. *Ecology*, *98*, 125–137.

Osland, M. J., Day, R. H., Hall, C. T., Feher, L. C., Armitage, A. R., Cebrian, J., Dunton, K. H., Randall Hughes, A., Kaplan, D. A., Langston, A. K., Macy, A., Weaver, C. A., Anderson, G. H., Cummins, K., Feller, I. C., & Snyder, C. M. (2020). Temperature thresholds for black mangrove (*Avicennia germinans*) freeze damage, mortality, and recovery in North America: Refining tipping points for range expansion in a warming climate. *Journal of Ecology*, *108*, 654–665.

Osland, M. J., Day, R. H., & Michot, T. C. (2020). Frequency of extreme freeze events controls the distribution and structure of black mangroves (*Avicennia germinans*) near their northern range limit in coastal Louisiana. *Diversity and Distributions*, *26*, 1366–1382.

Osland, M. J., Enwright, N., Day, R. H., & Doyle, T. W. (2013). Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. *Global Change Biology*, *19*, 1482–1494.

Osland, M. J., & Feher, L. C. (2020). Winter climate change and the poleward range expansion of a tropical invasive tree (Brazilian pepper - *Schinus terebinthifolius*). *Global Change Biology*, *26*, 607–615.

Osland, M. J., Feher, L. C., Griffith, K. T., Cavanaugh, K. C., Enwright, N. M., Day, R. H., Stagg, C. L., Krauss, K. W., Howard, R. J., Grace, J. B., & Rogers, K. (2017). Climatic controls on the global distribution, abundance, and species richness of mangrove forests. *Ecological Monographs*, *87*, 341–359.

Osland, M. J., Feher, L. C., López-Portillo, J., Day, R. H., Suman, D. O., Guzmán Menéndez, J. M., & Rivera-Monroy, V. H. (2018). Mangrove forests in a rapidly changing world: global change impacts and conservation opportunities along the Gulf of Mexico coast. *Estuarine, Coastal and Shelf Science*, *214*, 120–140.

Osland, M. J., Feher, L. C., Spivak, A. C., Nestlerode, J. A., Almario, A. E., Cormier, N., From, A. S., Krauss, K. W., Russell, M. J., Alvarez, F., Dantin, D. D., Harvey, J. E., & Stagg, C. L. (2020). Rapid peat development beneath created, maturing mangrove forests: Ecosystem changes across a 25-year chronosequence. *Ecological Applications*, *30*, e02085.

Osland, M. J., Gabler, C. A., Grace, J. B., Day, R. H., McCoy, M. L., McLeod, J. L., From, A. S., Enwright, N. M., Feher, L. C., Stagg, C. L., & Hartley, S. B. (2018). Climate and plant controls on soil organic matter in coastal wetlands. *Global Change Biology*, *24*, 5361–5379.

Osland, M. J., Grace, J. B., Guntenspergen, G. R., Thorne, K. M., Carr, J. A., & Feher, L. C. (2019). Climatic controls on the distribution of foundation plant species in coastal wetlands of the conterminous United States: knowledge gaps and emerging research needs. *Estuaries and Coasts*, *42*, 1991–2003.

Osland, M. J., Hartmann, A. M., Day, R. H., Ross, M. H., Hall, C. T., Feher, L. C., & Vervaeke, W. C. (2019). Microclimate influences mangrove freeze damage: Implications for range expansion in response to changing macroclimate. *Estuaries and Coasts*, *42*, 1084–1096.

Overgaard, J., Kearney, M. R., & Hoffmann, A. A. (2014). Sensitivity to thermal extremes in Australian *Drosophila* implies similar impacts of climate change on the distribution of widespread and tropical species. *Global Change Biology*, *20*, 1738–1750.

Overgaard, J., Kristensen, T. N., Mitchell, K. A., & Hoffmann, A. A. (2011). Thermal tolerance in widespread and tropical *Drosophila* species: does phenotypic plasticity increase with latitude? *The American Naturalist*, *178*, S80–S96.

Overgaard, J., & MacMillan, H. A. (2017). The integrative physiology of insect chill tolerance. *Annual Review of Physiology*, *79*, 187–208.

Páez-Osuna, F., Sanchez-Cabeza, J. A., Ruiz-Fernández, A. C., Alonso-Rodríguez, R., Piñón-Gimate, A., Cardoso-Mohedano, J. G., Flores-Verdugo, F. J., Carballo, J. L., Cisneros-Mata, M. A., & Álvarez-Borrego, S. (2016). Environmental status of the Gulf of California: A review of responses to climate change and climate variability. *Earth Science Reviews*, *162*, 253–268.

Paradis, A., Elkinton, J., Hayhoe, K., & Buonaccorsi, J. (2008). Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change*, *13*, 541–554.

Parker, K. C. (1988). Growth rates of *Stenocereus thurberi* and *Lophocereus schottii* in southern Arizona. *Botanical Gazette*, *149*, 335–346.

Parker, K. C. (1989). Height structure and reproductive characteristics of senita, *Lophocereus schottii* (Cactaceae), in southern Arizona. *Southwestern Naturalist*, *34*, 392–401.

Parker, K. C. (1993). Climatic effects on regeneration trends for two columnar cacti in the northern Sonoran Desert. *Annals of the Association of American Geographers*, *83*, 452–474.

Parmesan, C., Root, T. L., & Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society*, *81*, 443–450.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*, eaai9214.

Pennings, S. C., & Bertness, M. D. (2001). Salt marsh communities. In M. D. Bertness, S. D. Gaines, & M. Hay (Eds.), *Marine community ecology* (pp. 289–316). Sinauer Associates.

Peters, D. P. C., Lugo, A. E., Chapin, F. S., Pickett, S. T. A., Duniway, M., Rocha, A. V., Swanson, F. J., Laney, C., & Jones, J. (2011). Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere*, *2*, 1–26.

Pickett, S. T. A., & White, P. S. (2013). *The ecology of natural disturbance and patch dynamics*. Academic Press.

Pielou, E. C. (1991). *After the ice age: The return of life to glaciated North America*. University of Chicago Press.

Pimentel, D., Lach, L., Zuniga, R., & Morrison, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *BioScience*, *50*, 53–65.

Pinsky, M. L., Fenichel, E., Fogarty, M., Levin, S., McCay, B., St. Martin, K., Selden, R.L., Young, T. (2021). Fish and fisheries in hot water: What is happening and how do we adapt? *Population Ecology*, *63*, 17–26.

Pockman, W. T., & Sperry, J. S. (1997). Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia*, *109*, 19–27.

Poulakis, G. R., Stevens, P. W., Timmers, A. A., Wiley, T. R., & Simpfendorfer, C. A. (2011). Abiotic affinities and spatiotemporal distribution of the endangered smalltooth sawfish, *Pristis pectinata*, in a south-western Florida nursery. *Marine and Freshwater Research*, *62*, 1165–1177.

Powell, J. R., Gloria-Soria, A., & Kotsakiozi, P. (2018). Recent history of *Aedes aegypti*: Vector genomics and epidemiology records. *BioScience*, *68*, 854–860.

Powell, J. R., & Tabachnick, W. J. (2013). History of domestication and spread of *Aedes aegypti* – A review. *Memórias do Instituto Oswaldo Cruz*, *108*, 11–17.

Pruszynski, C. A., Stenn, T., Acevedo, C., Leal, A. L., & Burkett-Cadena, N. D. (2020). Human blood feeding by *Aedes aegypti* (Diptera: Culicidae) in the Florida Keys and a review of the literature. *Journal of Medical Entomology*, *57*, 1640–1647.

Purtlebaugh, C. H., Martin, C. W., & Allen, M. S. (2020). Poleward expansion of common snook *Centropomus undecimalis* in the northeastern Gulf of Mexico and future research needs. *PLoS One*, *15*, e0234083.

Rathbun, G. B., Bonde, R. K., & Clay, D. (1982). The status of the West Indian manatee on the Atlantic Coast north of Florida. In R. R. Odom, & J. W. Guthrie (Eds.), *Proceedings of the Symposium on Nongame and Endangered Wildlife. Technical Bulletin WL5* (pp. 152–165). Georgia Department of Natural Resources.

Reid, J. P. (1995). Chessie's most excellent adventure: The 1995 East Coast tour. *Sirenews*, *24*, 9–11.

Reyier, E. A., Franks, B. R., Chapman, D. D., Scheidt, D. M., Stolen, E. D., & Gruber, S. H. (2014). Regional-scale migrations and habitat use of juvenile lemon sharks (*Negaprion brevirostris*) in the US South Atlantic. *PLoS One*, *9*.

Rice, K. G., Waddle, J. H., Miller, M. W., Crockett, M. E., Mazzotti, F. J., & Percival, H. F. (2011). Recovery of native treefrogs after removal of nonindigenous Cuban treefrogs, *Osteopilus septentrionalis*. *Herpetologica*, *67*, 105–117.

Riley, M. E., & Griffen, B. D. (2017). Habitat-specific differences alter traditional biogeographic patterns of life history in a climate-change induced range expansion. *PLoS One*, *12*, e0176263.

Robinet, C., & Roques, A. (2010). Direct impacts of recent climate warming on insect populations. *Integrative Zoology*, *5*, 132–142.

Rochlin, I., Ninivaggi, D. V., Hutchinson, M. L., & Farajollahi, A. (2013). Climate change and range expansion of the Asian tiger mosquito (*Aedes albopictus*) in Northeastern USA: Implications for public health practitioners. *PLoS One*, *8*, e60874.

Rödder, D. (2009). 'Sleepless in Hawaii'-does anthropogenic climate change enhance ecological and socioeconomic impacts of the alien invasive *Eleutherodactylus coqui* Thomas 1966 (Anura: Eleutherodactylidae)? *North-Western Journal of Zoology*, *5*, 16–25.

Rodgers, L., Mason, C., Brown, R., Allen, E., Tipping, P., Rochford, M., Mazzotti, F., Kirkland, M., Miller, M., Peters, A., & Laroche, F. (2018). Status of nonindigenous species. In South Florida Water Management District (Ed.), *2018 South Florida Environmental Report – Volume I* (pp. 1–69). South Florida Water Management District.

Rommel, S. A., & Caplan, H. (2003). Vascular adaptations for heat conservation in the tail of Florida manatees (*Trichechus manatus latirostris*). *Journal of Anatomy*, *202*, 343–353.

Ross, M. S., Ruiz, P. L., Sah, J. P., & Hanan, E. J. (2009). Chilling damage in a changing climate in coastal landscapes of the subtropical zone: a case study from south Florida. *Global Change Biology*, *15*, 1817–1832.

Roth, A., Mercier, A., Lepers, C., Hoy, D., Duituturaga, S., Benyon, E., Guillaumot, L., & Souarès, Y. (2014). Concurrent outbreaks of dengue, chikungunya and Zika virus infections–an unprecedented epidemic wave of mosquito-borne viruses in the Pacific 2012–2014. *Euro Surveillance*, *19*, 20929.

Saenger, P. (2002). *Mangrove ecology, silviculture and conservation*. Springer.

Sakai, A., & Larcher, W. (1987). *Frost survival of plants: Responses and adaptation to freezing stress*. Springer-Verlag.

Sambaraju, K. R., Carroll, A. L., & Aukema, B. H. (2019). Multiyear weather anomalies associated with range shifts by the mountain pine beetle preceding large epidemics. *Forest Ecology and Management*, *438*, 86–95.

Scharer, R. M., Stevens, P. W., Shea, C. P., & Poulakis, G. R. (2017). All nurseries are not created equal: large-scale habitat use patterns in two smalltooth sawfish nurseries. *Endangered Species Research*, *34*, 473–492.

Schofield, G., Bishop, C. M., Katselidis, K. A., Dimopoulos, P., Pantis, J. D., & Hays, G. C. (2009). Microhabitat selection by sea turtles in a dynamic thermal marine environment. *Journal of Animal Ecology*, *78*, 14–21.

Schwartz, F. J. (1978). Behavioral and tolerance responses to cold water temperatures by three species of sea turtles (Reptilia, Cheloniidae) in North Carolina. *Florida Marine Research Publications*, *33*, 16–18.

Seminoff, J. A. (2010). Sea turtles in the Gulf of California. In R. C. Brusca (Ed.), *The Gulf of California: Biodiversity and conservation* (pp. 135–167). University of Arizona Press.

Seminoff, J. A., & Wallace, B. P. (2012). *Sea turtles of the eastern Pacific: Advances in research and conservation*. University of Arizona Press.

Seney, E. E., & Landry, Jr., A. M. (2011). Movement patterns of immature and adult female Kemp's ridley sea turtles in the northwestern Gulf of Mexico. *Marine Ecology Progress Series*, *440*, 241–254.

Shamblin, B. M., Godfrey, M. H., Pate, S. M., Thompson, W. P., Sutton, H., Altman, J., Fair, K., McClary, J., Wilson, A. M., Milligan, B., Stetzar, E. J., & Nairn, C. J. (2018). Green turtles nesting at their northern range limit in the United States represent a distinct subpopulation. *Chelonian Conservation and Biology*, *17*, 314–319.

Sherrod, C. L., & McMillan, C. (1985). The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contributions in Marine Science*, *28*, 129–140.

Shreve, F. (1911). The influence of low temperatures on the distribution of giant cactus. *The Plant World*, *14*, 136–146.

Shreve, F. (1914). The role of winter temperatures in determining the distribution of plants. *American Journal of Botany*, *1*, 194–202.

Shreve, F., & Wiggins, I. L. (1964). *Vegetation and flora of the Sonoran Desert* (Vol. I). Stanford University Press.

Simberloff, D., Schmitz, D. C., & Brown, T. C. (1997). *Strangers in paradise: Impact and management of nonindigenous species in Florida*. Island Press.

Sin, H., Beard, K. H., & Pitt, W. C. (2008). An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. *Biological Invasions*, 10, 335–345.

Sinclair, B. J., Vernon, P., Klok, C. J., & Chown, S. L. (2003). Insects at low temperatures: an ecological perspective. *Trends in Ecology & Evolution*, 18, 257–262.

Sinclair, B. J., Williams, C. M., & Terblanche, J. S. (2012). Variation in thermal performance among insect populations. *Physiological and Biochemical Zoology*, 85, 594–606.

Smith, E. T., & Sheridan, S. C. (2020). Where do cold air outbreaks occur and how have they changed over time? *Geophysical Research Letters*, 47. https://doi.org/10.1029/2020GL086983

Smith, M. D. (2011). The ecological role of climate extremes: Current understanding and future prospects. *Journal of Ecology*, 99, 651–655.

Smith, S. D., Hartsock, T. L., & Nobel, P. S. (1983). Ecophysiology of *Yucca brevifolia*, an arborescent monocot of the Mojave desert. *Oecologia*, 60, 10–17.

South Florida Ecosytem Restoration Task Force. (2015). *Invasive exotic species strategic action framework*. U.S. Department of Interior, Office of Everglades Restoration Initiatives.

Sovie, A. R., McCleery, R. A., Fletcher, R. J., & Hart, K. M. (2016). Invasive pythons, not anthropogenic stressors, explain the distribution of a keystone species. *Biological Invasions*, 18, 3309–3318.

Stair, D. W., Dahmer, M. L., Bashaw, E. C., & Hussey, M. A. (1998). Freezing tolerance of selected Pennisetum species. *International Journal of Plant Sciences*, 159, 599–605.

Steenbergh, W. F., & Lowe, C. H. (1969). Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument, Arizona. *Ecology*, 50, 825–834.

Steenbergh, W. F., & Lowe, C. H. (1976). Ecology of the saguaro: I. The role of freezing weather on a warm-desert plant population. In *Research in the Parks. National Park Service Symposium Series No. 1* (pp. 49–92). U.S. National Park Service. https://www.nps.gov/parkhistory/online_books/symposia/1/contents.htm

Steenbergh, W. F., & Lowe, C. H. (1977). *Ecology of the saguaro: II. Reproduction, germination, establishment, growth, and survival of the young plant. National Park Service Scientific Monograph Number Eight*. U.S. National Park Service.

Steenbergh, W. F., & Lowe, C. H. (1983). *Ecology of the saguaro: III. Growth and demography. Scientific Monograph Series, Number 17*. U.S. Department of Interior National Park Service.

Stein, B. A., Glick, P., Edelson, N., & Staudt, A. (2014). *Climate-smart conservation: Putting adaptation principles into practice*. National Wildlife Federation.

Stevens, P. W., Blewett, D. A., Boucek, R. E., Rehage, J. S., Winner, B. L., Young, J. M., Whittington, J. A., & Paperno, R. (2016). Resilience of a tropical sport fish population to a severe cold event varies across five estuaries in southern Florida. *Ecosphere*, 7, Article e01400.

Stevens, P. W., Boucek, R. E., Trotter, A. A., Ritch, J. L., Johnson, E. R., Shea, C. P., Blewett, D. A., & Rehage, J. S. (2018). Illustrating the value of cross-site comparisons: Habitat use by a large, euryhaline fish differs along a latitudinal gradient. *Fisheries Research*, 208, 42–48.

Stevens, P. W., Fox, S. L., & Montague, C. L. (2006). The interplay between mangroves and saltmarshes at the transition between temperate and subtropical climate in Florida. *Wetlands Ecology and Management*, 14, 435–444.

Still, B., Griffin, C., & Prescott, R. (2005). Climatic and oceanographic factors affecting daily patterns of juvenile sea turtle cold-stunning in Cape Cod Bay, Massachusetts. *Chelonian Conservation and Biology*, 4, 870–877.

Stith, B. M., Reid, J. P., Langtimm, C. A., Swain, E. D., Doyle, T. J., Slone, D. H., Decker, J. D., & Soderqvist, L. E. (2011). Temperature inverted haloclines provide winter warm-water refugia for manatees in southwest Florida. *Estuaries and Coasts*, 34, 106–119.

Stith, B. M., Slone, D. H., De Wit, M., Edwards, H. H., Langtimm, C. A., Swain, E. D., Soderqvist, L. E., & Reid, J. P. (2012). Passive thermal refugia provided warm water for Florida manatees during the severe winter of 2009–2010. *Marine Ecology Progress Series*, 462, 287–301.

Strachan, L. A., Tarnowski-Garner, H. E., Marshall, K. E., & Sinclair, B. J. (2011). The evolution of cold tolerance in Drosophila larvae. *Physiological and Biochemical Zoology*, 84, 43–53.

Stuart, S. A., Choat, B., Martin, K. C., Holbrook, N. M., & Ball, M. C. (2007). The role of freezing in setting the latitudinal limits of mangrove forests. *New Phytologist*, 173, 576–583.

Swann, D., Conver, J., Winkler, D., & Harper, C. (2018). *Climate change and the saguaro cactus: Saguaro National Park. Natural Resource Report NPS/SAGU/NRR—2018/1583*. National Park Service.

Thomson, D. A., & Lehner, C. E. (1976). Resilience of a rocky intertidal fish community in a physically unstable environment. *Journal of Experimental Marine Biology and Ecology*, 22, 1–29.

Tiburcio-Pintos, G., & Cariño-Olvera, M. M. (2017). Collective efforts for the conservation of sea turtles in the Gulf of California. *Letras Verdes, Revista Latinoamericana de Estudios Socioambientales*, 22, 7–26.

Todgham, A. E., Hoaglund, E. A., & Hofmann, G. E. (2007). Is cold the new hot? Elevated ubiquitin-conjugated protein levels in tissues of Antarctic fish as evidence for cold-denaturation of proteins in vivo. *Journal of Comparative Physiology B*, 177, 857–866.

Tomlinson, P. B. (2016). *The botany of mangroves*. Cambridge University Press.

Toxopeus, J., & Sinclair, B. J. (2018). Mechanisms underlying insect freeze tolerance. *Biological Reviews*, 93, 1891–1914.

Trân, J. K., Ylioja, T., Billings, R. F., Régnière, J., & Ayres, M. P. (2007). Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecological Applications*, 17, 882–899.

Turell, M. J., O'Guinn, M. L., Dohm, D. J., & Jones, J. W. (2001). Vector competence of North American mosquitoes (diptera: culicidae) for West Nile virus. *Journal of Medical Entomology*, 38, 130–134.

Turnage, W. V., & Hinckley, A. L. (1938). Freezing weather in relation to plant distribution in the Sonoran Desert. *Ecological Monographs*, 8, 529–550.

Turner, C. E., Center, T. D., Burrows, D. W., & Buckingham, G. R. (1997). Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, USA. *Wetland Ecology and Management*, 5, 165–178.

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, 91, 2833–2849.

Turner, R. M., Bowers, J. E., & Burgess, T. L. (1995). *Sonoran Desert plants: An ecological atlas*. University of Arizona Press.

U.S. Fish and Wildlife Service. (2017). Endangered and threatened wildlife and plants; Reclassification of the West Indian Manatee from endangered to threatened. *Federal Register*, 82(64), 16668–16704.

Ultsch, G. R., Carwile, M. E., Crocker, C. E., & Jackson, D. C. (1999). The physiology of hibernation among painted turtles: the eastern painted turtle *Chrysemys picta picta*. *Physiological and Biochemical Zoology*, 72, 493–501.

Ungerer, M. J., Ayres, M. P., & Lombardero, M. J. (1999). Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography*, 26, 1133–1145.

USGCRP. (2017). *Climate science special report: Fourth national climate assessment* (Vol. I). U.S. Global Change Research Program.

USGCRP. (2018). *Impacts, risks, and adaptation in the United States: Fourth national climate assessment* (Vol. II). U.S. Global Change Research Program.

Van der Stocken, T., Carroll, D., Menemenlis, D., Simard, M., & Koedam, N. (2019). Global-scale dispersal and connectivity in mangroves. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 915–922.

Van der Stocken, T., Wee, A. K. S., De Ryck, D. J. R., Vanschoenwinkel, B., Friess, D. A., Dahdouh-Guebas, F., Simard, M., Koedam, N., & Webb, E. L. (2019). A general framework for propagule dispersal in mangroves. *Biological Reviews*, 94, 1547–1575.

Van Devender, T. R., Lowe, C. H., & Lawler, H. E. (1994). Factors influencing the distribution of the Neotropical vine snake *Oxybelis aeneu*s in Arizona and Sonora, Mexico. *Herpetological Natural History*, 2, 25–42.

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., Booth, D. J., Coleman, M. A., Feary, D. A., Figueira, W., Langlois, T., Marzinelli, E. M., Mizerek, T., Mumby, P. J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A. S., … Wilson, S. K. (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140846.

Waddle, J. H., Dorazio, R. M., Walls, S. C., Rice, K. G., Beauchamp, J., Schuman, M. J., & Mazzotti, F. J. (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, 20, 1467–1475.

Wallace, B. P., Avens, L., Braun-McNeill, J., & McClellan, C. M. (2009). The diet composition of immature loggerheads: insights on trophic niche, growth rates, and fisheries interactions. *Journal of Experimental Marine Biology and Ecology*, 373, 50–57.

Weed, A. S., Ayres, M. P., & Hicke, J. A. (2013). Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*, 83, 441–470.

Weiss, J. L., & Overpeck, J. T. (2005). Is the Sonoran Desert losing its cool? *Global Change Biology*, 11, 2065–2077.

Whitmore, R. C., Brusca, R. C., León de la Luz, J. L., González-Zamorano, P., Mendoza-Salgado, R., Amador-Silva, E. S., Holguin, G., Galván-Magaña, F., Hastings, P. A., Cartron, J.-L. E., Felger, R. S., Seminoff, J. A., & McIvor, C. C. (2005). The ecological importance of mangroves in Baja California Sur: Conservation implications for an endangered ecosystem. In J. E. Cartron, G. Ceballos, & R. S. Felger (Eds.), *Biodiversity, ecosystems, and conservation in northern Mexico* (pp. 298–333). Oxford University Press.

Williams, C. M., Buckley, L. B., Sheldon, K. S., Vickers, M., Pörtner, H.-O., Dowd, W. W., Gunderson, A. R., Marshall, K. E., & Stillman, J. H. (2016). Biological impacts of thermal extremes: Mechanisms and costs of functional responses matter. *Integrative and Comparative Biology*, 56, 73–84.

Williams, C. M., Henry, H. A., & Sinclair, B. J. (2015). Cold truths: How winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90, 214–235.

Williams, D. G., & Baruch, Z. (2000). African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. *Biological Invasions*, 2, 123–140.

Williams, N. C., Bjorndal, K. A., Lamont, M. M., & Carthy, R. R. (2014). Winter diets of immature green turtles (*Chelonia mydas*) on a northern feeding ground: integrating stomach contents and stable isotope analyses. *Estuaries and Coasts*, 37, 986–994.

Wilson, L. D., & Porras, L. (1983). *The ecological impact of man on the South Florida herpetofauna*. University of Kansas Museum of Natural History.

Wilson, P. W., Heneghan, A., & Haymet, A. (2003). Ice nucleation in nature: supercooling point (SCP) measurements and the role of heterogeneous nucleation. *Cryptobiology*, 46, 88–98.

Woodroffe, C. D., & Grindrod, J. (1991). Mangrove biogeography: The role of quaternary environmental and sea-level change. *Journal of Biogeography*, 18, 479–492.

Woodward, F. I. (1987). *Climate and plant distribution*. Cambridge University Press.

Wuenschel, M. J., Hare, J. A., Kimball, M. E., & Able, K. W. (2012). Evaluating juvenile thermal tolerance as a constraint on adult range of gray snapper (*Lutjanus griseus*): A combined laboratory, field and modeling approach. *Journal of Experimental Marine Biology and Ecology*, 436, 19–27.

Yao, C.-L., & Somero, G. N. (2012). The impact of acute temperature stress on hemocytes of invasive and native mussels (*Mytilus galloprovincialis* and *Mytilus californianus*): DNA damage, membrane integrity, apoptosis and signaling pathways. *Journal of Experimental Biology*, 215, 4267–4277.

Yntema, C. L., & Mrosovsky, N. (1982). Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. *Canadian Journal of Zoology*, 60, 1012–1016.

Young, J. M., Bowers, M. E., Reyier, E. A., Morley, D., Ault, E. R., Pye, J. D., Gallagher, R. M. & Ellis, R. D. (2020). The FACT Network: Philosophy, evolution, and management of a collaborative coastal tracking network. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 12, 258–271. https://doi.org/10.1002/mcf2.10100

Zhu, K., Woodall, C. W., & Clark, J. S. (2012). Failure to migrate: Lack of tree range expansion in response to climate change. *Global Change Biology*, 18, 1042–1052.

Zink, R. M., & Gardner, A. S. (2017). Glaciation as a migratory switch. *Science Advances*, 3, e1603133.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

1    **Supporting Information Document:**

2    This document contains two tables (Table S1 and Table S2) and seven figures (Figures S1-S7)

3    associated with the following manuscript:

4

5    **Title:** Tropicalization of temperate ecosystems in North America: The northward range

6    expansion of tropical organisms in response to warming winter temperatures

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19    and Atmospheric Administration, La Jolla, CA, USA

20 Table S1. Sources for the photos in Figure 1. The numbers correspond to the photo numbers in Figure 1. All but one of the photos are
21 from U.S. Government websites.

| Number | Common name | Scientific name(s) | Source | Credit | Website |
|---|---|---|---|---|---|
| 1 | Burmese python | *Python molurus bivittatus* | USGS | Bryan Falk | https://www.usgs.gov/media/images/a-burmese-python-coiled-grass-everglades |
| 2 | Joshua tree | *Yucca brevifolia* | NPS | Brad Sutton | https://www.nps.gov/jotr/learn/news/newspaper.htm |
| 3 | Saguaro | *Carnegiea giganteus* | USFS | Charlie McDonald | https://www.fs.fed.us/wildflowers/plant-of-the-week/carnegiea_gigantea.shtml |
| 4 | Red mangrove | *Rhizophora mangle* | USGS | Michael Osland | Not on a website |
| 5 | Melaleuca | *Melaleuca quinquenervia* | USDA | NA | https://www.ars.usda.gov/southeast-area/fort-lauderdale-fl/iprl/docs/melaleuca/ |
| 6 | Brazilian pepper | *Schinus terebinthifolius* | USDA | NA | https://www.ars.usda.gov/southeast-area/fort-lauderdale-fl/iprl/docs/schinus-terebinthifolius-brazilian-pepper-tree/ |
| 7 | Cuban treefrog | *Osteopilus septentrionalis* | USGS | Brad M. Glorioso | https://www.usgs.gov/media/images/invasive-cuban-treefrog-new-orleans-la |
| 8 | American crocodile | *Crocodylus acutus* | NPS | NA | https://www.nps.gov/ever/learn/news/joe-bay-is-open-to-non-motorized-boating.htm |
| 9 | Buffelgrass | *Pennisetum ciliare* | NPS | NA | https://www.nps.gov/orpi/learn/nature/invasive-plant-species.htm |
| 10 | Goliath grouper | *Epinephelus itajara* | NOAA | NA | https://www.fisheries.noaa.gov/southeast/endangered-species-conservation/goliath-grouper |
| 11 | Sawfish | *Pristis pectinata* | NOAA | NA | https://www.fisheries.noaa.gov/species/smalltooth-sawfish |
| 12 | Cobia | *Rachycentron canadum* | NOAA | NA | https://www.fisheries.noaa.gov/species/cobia |
| 13 | Bull shark | *Carcharhinus leucas* | NOAA | NA | https://graysreef.noaa.gov/science/research/fish_tagging/visitors.html |
| 14 | Manatee | *Trichechus manatus* | USGS | NA | https://www.usgs.gov/centers/wetland-and-aquatic-research-center-warc/science/manatee-health-assessment-and-biomedical?qt-science_center_objects=0#qt-science_center_objects |
| 15 | Loggerhead sea turtle | *Caretta caretta* | USGS | NA | https://www.usgs.gov/news/after-hurricane-devastation-sea-turtle-scientists-rebound-help-rebuild |
| 16 | Kemp's ridley sea turtle | *Lepidochelys kempii* | USGS | Margaret Lamont | https://archive.usgs.gov/archive/sites/soundwaves.usgs.gov/2018/02/staff.html |
| 17 | Greenhouse frog | *Eleutherodactylus planirostris* | USGS | Brad M. Glorioso | https://armi.usgs.gov/gallery/species.php?itis=173568 |
| 18 | Coqui frog | *Eleutherodactylus coqui* | USGS | Chris Brown | https://armi.usgs.gov/gallery/species.php?itis=173559 |
| 19 | *Aedes aegypti* | *Aedes aegypti* | CDC | NA | https://www.cdc.gov/features/stopmosquitoes/index.html |
| 20 | *Culex quinquefasciatus* | *Culex quinquefasciatus* | CDC | NA | https://www.niaid.nih.gov/diseases-conditions/west-nile-virus |
| 21 | Monarch butterfly | *Danaus plexippus* | USDA | Peggy Greb | https://www.ars.usda.gov/oc/images/photos/oct19/d3980-1/ |
| 22 | Organ pipe cactus | *Stenocereus thurberi* | NPS | NA | https://www.nps.gov/articles/nps-geodiversity-atlas-organ-pipe-cactus-national-monument-arizona.htm |
| 23 | Chapparal plants | *Ceanothus megacarpus, Malosma laurina* | NPS | NA | https://www.nps.gov/samo/learn/nature/chaparral.htm |

22

23 Table S2. Test for trends in winter temperature (Temp) data from four representative locations in

24 North America's tropical-temperate transition zones, reporting Spearman's correlation ($r_s$)

25 between year and: (1) mean winter temperature (Mean Avg Temp), (2) the absolute coldest

26 annual winter minimum temperature (Lowest Min Temp), and (3) the number of subzero days

27 each winter (# of days $\leq 0°C$). See trend depictions in Figure 4.

| | Mean Avg Temp | | Lowest Min Temp | | # of days $\leq 0°C$ | |
|---|---|---|---|---|---|---|
| | $r_s$ | $p$ | $r_s$ | $p$ | $r_s$ | $p$ |
| San Francisco (CA) | 0.55 | 0.000 | 0.62 | <0.001 | -0.66 | <0.001 |
| Tucson (AZ) | 0.39 | 0.000 | 0.41 | <0.001 | -0.46 | <0.001 |
| New Orleans (LA) | 0.19 | 0.104 | 0.23 | 0.047 | -0.39 | 0.001 |
| Tampa (FL) | 0.32 | 0.007 | 0.22 | 0.068 | -0.30 | 0.011 |

28

29    Figure S1. Within the tropical-temperate transition zone, extreme cold temperatures control the

30    northern distribution of foundation plant species like the saguaro cactus (*Carnegiea gigantea*;

31    left) and red mangrove (*Rhizophora mangle*; right). Photo credits: NPS (saguaro) and Michael

32    Osland (mangrove).
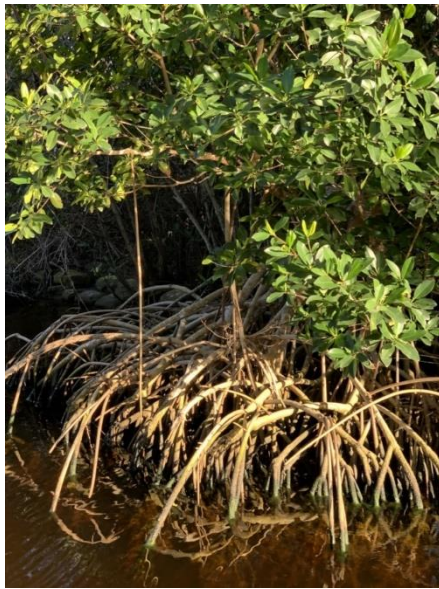


33

34

35    Figure S2. Winter temperature extremes control the distributions of subtropical fishes and drive

36    movements of coastal migrants. The photo on the left is of the common snook (*Centropomus*

37    *undecimalis*), aggregating at a spring head in northern Florida during winter. The photo on the

38    right shows a biologist tagging a coastal migrant, cobia (*Rachycentron canadum*), with an

39    acoustic transmitter during its run along the Florida panhandle. Photo credits: Florida FWC [Phil

40    Stevens (left) and Jessica Carroll (right)].



41

42     Figure S3. USGS scientists picking up cold-stunned sea turtles floating at the surface of St.

43     Joseph Bay in northwestern Florida (USA) during an extreme cold event in 2018. Note the cold-

44     stunned juvenile sea turtles in the boat. During cold stun events, mortality is often highest for

45     juvenile, smaller sea turtles (Lamont et al. 2018). St. Joseph Bay is located in the northeastern

46     Gulf of Mexico, approximately 50 km southeast of Panama City and 350 km northwest of Tampa

47     Bay. Photo credit: USGS.



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51    Figure S4. Extreme cold events constrain the distribution of many invasive non-native tropical

52    reptile species. Burmese pythons (*Python bivittatus*) are an especially harmful and well-known

53    example of the negative ecological impacts of pet trade-driven tropical reptile introductions. This

54    large constrictor snake is an opportunistic apex predator, whose expansion within and around

55    Everglades National Park (southwestern Florida, USA) has decimated mammal, bird, and other

56    prey populations. Burmese pythons are also sensitive to cold temperature extremes and expected

57    to expand northward in response to warming winters. Photo credit: USGS.



58

59

60    Figure S5. Dispersal constraints may affect the ability of some species to expand their range

61    northward in response to warming winters. However, there are species [e.g., the Cuban treefrog

62    (*Osteopilus septentrionalis*), as shown in this photo] that have successfully established

63    populations in new areas following long-distance transport (>100 km) in ornamental tropical

64    plants. These species have inadvertently traveled on horticultural shipments from Florida and

65    other more tropical locations, which is a long-distance dispersal pathway that may enable more

66    rapid poleward range expansion of certain amphibian species in response to climate change.

67    Photo credit: Brad M. Glorioso.

68



69

70

71    Figure S6. Near the northern limits of the distribution of the West Indian manatee (*Trichechus*

72    *manatus*), individuals of the southeastern United States forage on seagrass and submerged

73    aquatic vegetation. With advancing cold the population contracts toward Florida warm-water

74    refugia where they often form large aggregations. This photo shows an aggregation at an

75    artificial warm-water discharge produced by a thermoelectric power plant. Photo credit: USGS.



76

77    Figure S7. The northern range limits of most tropical insect species are governed by cold

78    temperature extremes, which can lead to mortality of eggs, larvae, pupae, or adults.This photo is

79    of *Aedes aegypti*, which is a cold-sensitive mosquito species. This species is expected to

80    increasingly move northward due to warming winters and become more established in other

81    parts of the southern United States. Photo credit: CDC.

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