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SPECIAL FEATURE: EXTREME COLD SPELLS

A review of subtropical community resistance and resilience to extreme cold spells

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Abstract. Forecasted changes in global climate predict not only shifts in average conditions but also changes in the frequency and intensity of climate extremes. In the subtropics, the passage of extreme cold spells functions as a major structuring force for ecological communities, and can incur substantial losses to biodiversity, agriculture, and infrastructure. If these events persist in the future, it is likely that their effects on subtropical communities and ecosystems will become more pronounced, as tropical species migrate poleward. Recent extreme cold spells in subtropical China (2008) and United States (2010) occurred in ecosystems that are the subject of long-term ecological study, enabling key questions about cold spell affects to be addressed. In this study, we (1) discuss the meteorological drivers that resulted in these two extreme cold spells, and (2) use findings from case studies published in the *Ecosphere* Special Feature on effects of extreme cold spells on the dynamics of subtropical communities, and on poleward expansion of tropical species and other previously published works to identify consistencies of subtropical community resilience and resistance to extreme cold spells. In this review, we highlight three consistent findings related to this particularly type of extreme climate event: (1) cold spells drive predictable community change in the subtropics by altering ratios of coexisting tropical and temperate species; (2) certain landscape features consistently affect subtropical resistance and resilience to extreme cold spells; and (3) native tropical species are more resistant and resilient to extreme cold spells than tropical nonnative taxa. Our review should improve forecasts of the response of subtropical community dynamics in scenarios where extreme cold spells either increase or decrease in frequency and intensity.

Key words: climate change; community ecology; extreme climate event; Special Feature: Extreme Cold Spells; subtropics.

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Introduction

Forecasted changes in global climate include not only shifts in average conditions, but also changes in the frequency and intensity of climatic extremes (Easterling et al. 2000, Karl et al. 2008). Climate extremes can be defined as discrete weather events that fall within the statistical tails of some climate parameter, and create conditions exceeding the acclimation capacity of species occurring within the affected region, often causing large-scale mortality events (Gutschick and BassiriRad 2003, Smith 2011). One climate extreme predicted to change in frequency, intensity, and duration in the future is extreme cold spells (Kodra et al. 2011, Field 2012, Gao et al. 2015). Changes in the future dynamics of extreme cold spells will play a very important role in shaping the future distribution of species, community organization, and ecosystem function, especially in environments where species groups occur at their poleward or highest altitudinal distribution (Precht and Aronson 2004, Beck and Goetz 2011).

The subtropical zone (25–40° latitude) is thermally characterized by regions where long-term average minimum monthly temperatures are greater than 13°C, and the frequency of sub-0°C minimum temperature days ranges from once a year to less than annual (Holdrige's life zones; Neilson 1995). Despite being a warm environment, the occurrence of cold spells is common in the subtropics, with ecologically impactful events being reported in the United States (Boucek and Rehage 2014), China (Liu et al. 2014*a*, *b*), Taiwan (Hsieh et al. 2008), Australia (Gilman et al. 2008), Brazil (Gallucci and Netto 2004), and the northwest Mediterranean (Coles and Fadlallah 1991). Similar to other climate extremes, extreme cold spells affecting the subtropics are capable of driving whole-scale changes to ecosystem structure and function (Stone 2008, Boucek and Rehage 2014, Kemp et al. 2016, Santos et al. 2016). For instance, an extreme cold spell that affected the southeastern United States in 2010 drove a potential stable state shift in coral communities occurring in shallow waters off Florida's Middle and Upper Keys archipelago. The 2010 extreme climate event caused almost complete mortality of some key foundational stony coral reef building species, while having less of an effect on soft octocoral species. Since the spell, affected stony corals have shown little recovery, resulting in a stable, postcold event community with an increased dominance of soft octocoral species (Colella et al. 2012, Kemp et al. 2016).

Apart from affecting ecosystem structure and function, extreme cold spells incur substantial losses to agriculture and fisheries in the subtropics (Downton and Miller 1993, Zhou et al. 2011, Khounsy et al. 2012). For instance, a 2008 extreme cold spell that affected subtropical China resulted in losses of 40% of winter time crops, 30% of bee colonies, 75 million livestock, and 0.45 million tons of aquacultured fish (Zhou et al. 2011). Similar catastrophic losses to other natural resources have been observed in subtropical Florida's citrus industry (Sheridan 2003), where the passage of a series of extreme cold spells in 1980s killed approximately one-third of Florida's commercial citrus trees (Downton and Miller 1993). Thus, extreme cold spells, like many climate extremes, can elicit extreme ecosystem responses and incur substantial economic losses.

If these events persist in the future, extreme cold spells will continue to be one of the dominant structuring forces of ecological communities in the subtropics. Further, as tropical species continue to advance poleward into the subtropics due to climate warming, it is likely that the effects of these cold events on subtropical communities and ecosystems will become more pronounced. Thus, in order for us to forecast ecosystem dynamics in the subtropics, it is crucial for us to understand how and what factors dictate subtropical community responses to these extreme disturbances.

Recent extreme cold spells in subtropical China (2008) and United States (2010) occurred in ecosystems that are the subject of long-term ecological study, enabling key questions about cold event effects to be addressed. The once in 50-year cold spell in China (Chen et al. 2010, Liu et al. 2012) and once in 80-year event in the United States (Boucek and Rehage 2014) represented extreme events that caused a cascade of ecological changes that are documented in the multiple case studies of this special issue. In this introductory paper, we discuss the meteorological drivers that resulted in these two extreme cold spells, and highlight consistent findings in subtropical community resistance and resiliency to these extremes inform the papers featured and previously published works. Overall, we expect that the passage of extreme cold spells functions as a major force shaping subtropical community dynamics, changing structuring processes to those dictated by species tolerance to low temperatures, and the external features in the landscape that buffer communities from cold temperatures.

Climate Factors that Drive Extreme Cold Spells

In the subtropics, cold spells result from polar air moving into lower latitudes. Equatorial movement of polar air is often correlated with winter shifts in upper airflow from predominantly zonal (west–east) flow to meridional (north–south) flow, via changes in ocean–atmospheric teleconnections (Sheridan 2003, Chen et al. 2008, Wang et al. 2010, Na et al. 2012). For instance in the subtropical United States, upper airflows during the positive phase of the Pacific North American anomaly (PNA) coincide with 80% of the region's ecologically impactful cold spells (Downton and Miller 1993, Sheridan 2003). At the onset of extreme cold spells, minimum daily air temperatures decrease to extreme low values almost overnight. These extreme low temperatures persist for usually days before minimum daily air temperature returns to normal variability (Zhou et al. 2011, Boucek and Rehage 2014).

In China, the 2008 cold spell brought on not only extreme low temperatures that persisted for approximately a month, but also unseasonally high precipitation (Hong and Li 2009, Zhou et al. 2011). These extreme low temperatures in subtropical China and South-East Asia were a product of interactions between Siberian high (SH), intraseasonal oscillation (ISO), and El Nino–Southern Oscillation (ENSO) climate anomalies. Across Asia, this 2008 extreme event started in mid-January, when the Siberian high anomaly moved into an enhanced phase, coinciding with the movement of multiple cold air outbreaks into lower latitudes in central China. These cold air outbreaks were initially blocked from the subtropics by suppressed convention over Sumatra (associated with the dry phase of the ISO). However, in February, the ISO shifted from a dry phase to a wet phase, increasing convection and pushing cold air outbreaks as far south as the South China Sea. On average, ISO wet phases and cold air advection to subtropical China persist for 10 d, but in 2008, the transition out of this wet phase was stalled by a La Nina episode, causing the ISO wet phase to persist for 30 d, resulting in continuous cold air outbreaks in subtropical China for the entire month of February (see Hong and Li 2009 for additional details). On top of these cold air outbreaks, an anomalous and persistent summer monsoon-like flow pattern moved high-moisture tropical maritime air masses from the Bay of Bengal northward. The convergence of the tropical and polar air masses resulted in both extreme low minimum air temperatures in subtropical China for 24 d, and unseasonal precipitation (Zhou et al. 2011). As a result, the 2008 cold spell broke 50-year records for the maximum number of consecutive low temperature days throughout many regions of subtropical and temperate China (Chen et al. 2008). This extreme disturbance not only affected natural systems and resources, but also caused $22.3 billion dollars in damages to infrastructure, resulted in 129 human fatalities, and displaced 1.7 million people (Zhou et al. 2011).

Shifting to the 2010 extreme cold spell in subtropical United States. Across the eastern United States, the 2009–2010 winter was the worst winter in terms of snow fall and low temperatures since 1950 (Wang et al. 2010). The severity of the 2009–2010 winter inspired the media to report that the next "mini ice age starts here," increasing public skepticism of climate warming (Wang et al. 2010, New York Times February 10, 2010; Wall Street Journal February 16, 2010). Like the 2008 China event, this extreme cold spell resulted from the interaction of multiple climate anomalies, namely the North Atlantic Oscillation (NAO) and the PNA. Starting on 28 December 2009, the NAO shifted into an extreme negative phase, indicating a weakening of the Icelandic Low and the Azores High, and the PNA shifted into the positive phase. These phase shifts coincided with a northerly directional change in surface wind anomalies across the United States, causing cold air outbreaks to sweep into lower latitudes and down into Florida. Extreme negative phases of the NAO usually occur during decades of longer term durations of lower phases of the NAO; therefore, it is likely that the longer the NAO remains in a negative phase, the more likely an extreme negative phase event will occur, and as a consequence, there is an increased probability that the United States will be affected by an extreme cold spell (Wang et al. 2010).

In Florida, cold air outbreaks are relatively common each winter, usually lasting one or two days, and without incurring meaningful ecological change. Once every 20 years, episodic cold spells affect subtropical Florida, whereby temperatures decrease to extreme low values (>3 SD from long-term temperature average) and remain at these low values for extended periods (up to seven days, Boucek and Rehage 2014). These episodic cold spells have occurred in the months of December or January in the years 1940, 1977, 1981, and 1985, all of which resulted in major ecological effects. Unlike these less severe episodic spells, the 2010 spell both drove minimum temperatures to extreme low levels (−4.16 SD from the 80-year winter time mean), but more damaging, this event kept temperatures at extreme lows for 14 d, 7 d longer the next longest cold spell (January 1940; Boucek and Rehage 2014). Effects of the 2010 cold event were severe or extreme for many taxonomic groups (e.g., corals, primary producers, and top predators; Kemp et al. 2011, Mazzotti et al. 2011, Adams et al. 2012, Matich and Heithaus 2012, Barr et al. 2013), and the Florida citrus industry and coastal fisheries incurred substantial losses (Fantz 2010, Barbour et al. 2014, Blewett and Stevens 2014).

Subtropical Extreme Cold Spells Relative to Other Extreme Climate Events

Despite the accepted gravity of climate extremes in shaping natural systems, there are few generalizations to address the population, community, and ecosystem responses to such events (Jentsch et al. 2007, Smith 2011). First, few generalizations exist because climate extremes are rare, and relatively few field studies have captured ecosystem responses to such events. Second, few experimental systems are in place that can simulate extreme climate conditions over relevant spatiotemporal scales (Smith 2011). Third, ecological responses to climate extremes cannot be predicted with less severe and more frequent disturbances because climate extremes can create stressors of sufficient amplitude and duration to elicit unexpected threshold responses (Jentsch et al. 2007, Smith 2011, Peters et al. 2012). Finally, climate extremes often create many stressors that can interact with other local drivers to change ecosystems in complex and often context-dependent ways, limiting our ability to develop overarching generalizations of ecological responses we may expect to climate extremes (Kreyling et al. 2011, Peters et al. 2012).

The effects of extreme cold spells on subtropical ecosystems may be less complicated than that of other climate extremes, and thus potentially easier to predict. First, subtropical cold spells are thermal events, unlike other climate disturbances such as tropical cyclones and drought that can incorporate multiple dimensions of stress (e.g., wind, fire, and precipitation in addition to temperature). Even extreme heatwaves co-occur with other extreme climate drivers, including droughts, stressful UV intensity, and increased fire risk, all of which may increase context specificity in ecological responses. For instance, during the 2011 heatwave in Australia, extreme temperatures were the dominant driver of change in coastal marine systems (Smale and Wernberg 2013). In contrast, in the 2003 European heatwave in northern Italy, Bertani et al. (2015) found that extreme drought conditions drove a state shift in primary producer communities in Mediterranean lakes. And a combination of extreme heat, extreme low precipitation, and high UV intensity drove changes in grassland communities following the same extreme 2003 European heatwave (Kreyling et al. 2011). In contrast, unlike heatwaves and other extremes, the impact of cold events may be easier to link to a single driver, fostering easier comparisons across place and time, and allowing for greater predictability in their effects.

Another aspect of extreme cold spells that make their effects tractable is their relatively short duration, usually measured in days to weeks, compared with other climate extremes that can last for years (e.g., droughts). The impact of such persistent extreme events can be complicated as it can be driven by secondary influences that occur after the initial restructuring effects related to physiological stress and physical damage caused by the climate extreme. Secondary drivers might include positive feedbacks that cause persistent state changes. For instance, in arid and semiarid grasslands, prolonged droughts combined with overgrazing can shift primary producer community dominance from perennial grasses to drought-resistant woody plants that sequester nutrients and form "islands of fertility," ultimately leading to an ecosystem state change (Peters et al. 2012).

Relative to other climate extremes, ecological responses to extreme cold spells should largely be governed by thermal constraints controlled by either internal (physiological optima) or external (landscape refuges) factors that dictate a species' ability to tolerate relatively short durations of cold temperatures. However, species can resist some negative deviations in temperature from less severe and more frequent cold spells; during extreme cold spells, temperatures often decrease below the physiological limits, particularly for many tropical species, resulting in abrupt, nonlinear decreases in species abundances.

In the next sections, we highlight three consistent findings stemming from the studies in the special issue, and discuss them in light of previous studies on subtropical community responses to extreme cold spells. Beyond bettering our understanding of ecological change mediated by extreme cold spells in the subtropics, identifying these consistencies may help guide interpretation of short-duration thermal disturbances occurring across the globe.

Changes in Community Structure Following Extreme Cold Spells in the Subtropics

In the subtropics, communities are composed of tropical species at the poleward extent of their range, temperate species at their equatorial range limit, and subtropical species within their core range. Tropical species evolved in warm, thermally aseasonal environments (i.e., thermal specialists; Tewksbury et al. 2008), while temperate and subtropical species have adapted to relatively wide seasonal fluctuations in temperature (thermal generalists; Sunday et al. 2014). Thus, tropical species are generally limited in their physiological acclimation to extreme cold and even exhibit maladaptive behaviors during extreme cold events (see Mazzotti et al. 2016). In comparison, temperate species have the physiological capacity to resist both relatively high and low temperature extremes (Sunday et al. 2014). Because tropical species are less resistant to extreme cold spells compared with temperate and subtropical species, cold events should shift community dominance in favor of more temperate species.

The studies in this issue, along with prior work, support this generalization. Starting with top predators in Florida, the 2010 event reduced abundances of tropical American Crocodile (*Crocodylus acutus*), while having little influence on broadly tolerant American Alligators (*Alligator mississippiensis*; Mazzotti et al. 2016). Moving down the food web, following the same event in Florida coastal rivers, an immediate decline in tropical fishes was observed, while temperate fish abundances remained unchanged or increased (Boucek and Rehage 2014, Santos et al. 2016). Switching over to the spell in China, similar decreases in tropical species dominance were observed following the 2008 event. For instance, Wang et al. (2016) showed that the 2008 cold spell caused disproportionate mortalities of tropical butterflies, resulting in an increased community dominance of temperate butterflies. In coral reef communities, a switch from tropical species to broadly temperature tolerant species was observed following both the 2008 China and the 2010 U.S. event (Chen et al. 2008, Kemp et al. 2011, 2016). Outside these two extreme cold spells, other research supports this generalization. In coastal subtropical zones across the globe, the passage of extreme cold spells has been shown to switch vegetation communities from tropical mangrove-dominated environments to temperate salt marsh-dominated habitats (Stevens et al. 2006, Osland et al. 2013, Cavanaugh et al. 2014). Subtropical cold spells, therefore, appear to lead to rapid shifts in community structure toward greater broadly tolerant species dominance.

Effects of Landscape Features on Subtropical Community Resistance and Resilience

Extreme cold spells affecting the subtropics can incur ecological change across entire regions. In both Florida and China, mortality of tropical species was observed from latitudes 19° N and 29° N, to latitudes of 24° N and 28° N, respectively (Stevens et al. 2016, Kemp et al. 2016). Despite the large footprint of the area affected by extreme cold spells, tropical species and subtropical community resistance and resilience vary across space.

Landscape features may either promote or reduce tropical species and subtropical community resistance to extreme cold events. Further, these landscape features may operate at every spatial scale. At the scale of a single forest patch, Ross et al. (2009), Chen et al. (2015), and Wang et al. (2016) found that larger trees that occupy the upper canopy are more severely damaged by extreme cold spells (by both physiological damage from cold shock and physical damage from icing) than smaller lower understory trees in Floridian and Chinese mangrove forests and in Chinese evergreen forests. In these forests, temperature and humidity both decrease moving up to the canopy, increasing stressful thermal conditions for taller trees (Ross et al. 2009). Similar differences between forest floor vs. canopy effects were also documented in small-bodied consumers habituating Chinese mangrove forests. Boreal mollusks suffered higher mortalities than their benthic counterparts in Chinese mangrove forests following the 2008 cold spell, likely due to similar temperature and humidity drivers (Liu et al. 2016).

Variation in cold spell resistance across patches also exists. Landscape features that may influence cross-patch resistance to extreme cold spells include (1) proximity to water bodies that can buffer patches from extreme cold temperature, (2) features that may block wind, and (3) elevation differences (e.g., valleys) that can trap cold air. Starting with examples from citrus groves in Florida, following a series of episodic cold spells in the 1980s, Downton and Miller (1993) showed that citrus grove resistance varied based on whether the grove was on a hill or in a valley, or whether the grove was close to a lake. Groves in valleys were more at risk to freeze damage due to the settling of denser cooler air in these valleys that create cold pockets. Similarly, groves on the windward north-facing sides of hills suffered more damage. In mangrove forest patches in subtropical China, Liu et al. (2012) came to a similar conclusion. Mangroves located on the leeward sides of hills suffered minimal damage following the 2008 cold spell relative to those on the windward side. In a similar fashion, subtle changes in elevation may trap cold air in addition to distance to oceans that can act as a heat source and alter mangrove cross-patch forest resistance in both subtropical China and the United States (Chen et al. 2010, 2015, Liu et al. 2014*a*, *b*, Zhang et al. 2016).

At the largest scales, ocean currents and ecosystem geomorphology can dictate cross-ecosystem resistance. For instance, Stevens et al. (2006) found nearly complete resistance for a tropical estuarine fish population in Florida at one estuary, and virtually no resistance in three others. These interestuary differences in tropical fish resistance were likely a result of multiple interacting factors, including availability and abundance of deepwater habitats (though mostly anthropogenic), abundance of freshwater springs, and proximity to warm tropical oceanic currents. Similarly, in the Florida Keys archipelago, following the 2010 cold event, shallow-water coral reefs in the middle to upper keys suffered community-wide change, while coral reefs in deeper water and closer proximity to the warm waters of the Gulfstream were less affected by the disturbance (Colella et al. 2012).

Like resistance, subtropical community resilience can vary across spatial scales. For instance, Rehage et al. (2016) showed that across eight nonnative fish populations affected by the 2010 disturbance, population resilience varied from within one year, to populations that have exhibited no recovery five years postdisturbance. Rehage et al. (2016) attribute this spatial variation in resilience to differences in distance to warm-water source populations. Likewise, Stevens et al. (2006) found that following the 2010 cold spell in Florida, resistance of a tropical estuarine piscivore was similar across three of four estuaries but resilience varied, possibly an effect related to interestuary differences in geophysical structuring that may influence reproduction, recruitment, and juvenile survival. Thus, landscape features are an important consideration as they can influence both resistance and resilience.

Differences in Resistance and Resilience among Tropical Native and Nonnative Taxa

Native and nonnative species may differ in a variety of ways, including how they are affected by extreme events. Within the context of extreme cold events, nonnative tropical species appear to be less resistant and resilient than their tropical native counterparts. This finding agrees with hypotheses proposed by Kreyling et al. (2015), when measured the thermal tolerance of 27 North Hemisphere native and nonnative tree species. Kreyling et al. (2015) found that cold tolerance was related to the temperature conditions in the species' native range. The authors conclude that developing cold tolerance operates on relatively long timescales. Thus, it is possible that tropical species native to the subtropics may have developed limited tolerance to extreme cold spells, while tropical nonnative species with distributions in more core areas of the tropics have not yet acquired any physiological capacity or behaviors that may improve their resistance to extreme cold spells (Cook-Patton et al. 2015).

Findings from this Special Feature support this notion. Chen et al. (2015) found that mangroves introduced to subtropical China (*Sonneratia* *caseolaris, S. apetala*) suffered higher mortalities than native species. Similarly, bamboo fields planted with nonnative species suffered greater losses than fields seeded with native bamboo following the 2008 cold event (Junming et al. 2008, Zhou et al. 2011). In Florida, Boucek and Rehage (2014) and Rehage et al. (2016) found that tropical native fishes were both more resistant and resilient to extreme cold compared with their functionally similar nonnative counterparts. Similarly, Downing et al. (2015) found that nonnative bees in subtropical Florida were less resistant to the 2010 cold spell than native bees. Many nonnative species are introduced to the subtropics from lower latitudes, because of their high ornamental value (Schofield and Loftus 2015). Thus, as the dynamics of extreme cold spells change in the future, it is likely that invasion risk and the population stability of currently established nonnatives will track the changes in the frequency, intensity, and duration of extreme cold spells in the subtropics.

Conclusions: Subtropical Conservation in a Warming World with Extreme Cold Events

Although whether extreme cold spells will increase or decrease in frequency, intensity, or duration is uncertain and varies geographically (Vavrus et al. 2006, Kodra et al. 2011), the studies in this special issue show that any change in their dynamics may have consequences for subtropical ecosystems. If these events increase in frequency, we may expect nonnative population dynamics to become less stable, and the probabilities of new species invasions to be reduced. At the same time, we may see losses to many important natural resources in these latitudes, including coral reefs and mangrove forests, which provide key ecosystem services to the region, in addition to losses to agriculture and fisheries productivity. Further, increases in these events may function to slow the poleward migration of tropical species, as well as impair translocation success in conservation efforts, which could be particularly problematic as tropical species are at very high risk from climate warming (Sunday et al. 2014).

Under scenarios where extreme cold spells remain constant or increase in frequency, we could consider developing conservation and management strategies that account for variation in resistance to these events, considering both the component species within that community (nonnative, tropical, temperate), and the landscape features the community occupies. For habitats and communities that offer little resistance to these cold disturbances, we could implement strategies to provide extra protection for tropical species occurring in those areas that are at increased risk to cold spell effects (discussed in Stevens et al. 2006). This added protection may be particularly important for highly managed tropical fisheries that due to harvest are increasingly responsive to climate stressors (Stevens et al. 2006, Britten et al. 2014, Santos et al. 2016). On the other hand, habitats that have landscape features that offer high resistance to these disturbances could be identified and set aside as refuges for endangered and/or imperiled tropical species occurring in the subtropics such as American Crocodiles (Mazzotti et al. 2016). Similarly, these cold spell refuge habitats could serve as key introduction sites of the species being considered for assisted migration programs and translocation conservation strategies.

Last, decreases in the frequency of these events could provide long-term benefits to agriculture and aquaculture, like Florida citrus, and that could add facilities at higher latitudes (Sheridan 2003). Likewise, we may expect tropical fisheries to become more stable and potentially increase in productivity (Stevens et al. 2006, Santos et al. 2016). Decreases in the frequency of these events may also increase the population stability of threatened tropical species occurring within the subtropics (i.e., American Crocodile; Mazzotti et al. 2016), as well as increase habitat suitability in the subtropics for tropical species threatened by climate warming (Liu et al. 2012, Kemp et al. 2016). Regardless of the fate of extreme cold spells in the future, our special issue highlights key responses that we can expect subtropical systems to exhibit in light of these extreme events.

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