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Will extreme climatic events facilitate biological invasions?

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Extreme climatic events (ECEs) – such as unusual heat waves, hurricanes, floods, and droughts – can dramatically affect ecological and evolutionary processes, and these events are projected to become more frequent and more intense with ongoing climate change. However, the implications of ECEs for biological invasions remain poorly understood. Using concepts and empirical evidence from invasion ecology, we identify mechanisms by which ECEs may influence the invasion process, from initial introduction through establishment and spread. We summarize how ECEs can enhance invasions by promoting the transport of propagules into new regions, by decreasing the resistance of native communities to establishment, and also sometimes by putting existing non-native species at a competitive disadvantage. Finally, we outline priority research areas and management approaches for anticipating future risks of unwanted invasions following ECEs. Given predicted increases in both ECE occurrence and rates of species introductions around the globe during the coming decades, there is an urgent need to understand how these two processes interact to affect ecosystem composition and functioning.

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Ecosystems are experiencing not only gradual shifts in mean climate conditions but also dramatic changes in climate variability and prevalence of extreme climatic events (ECEs). ECEs such as droughts, floods, severe storms, and heat waves are changing in frequency, magnitude, timing, and duration, depending on the region and the specific climate event (WebPanel 1; Easterling *et al.* 2000; Karl *et al.* 2008). These extreme events can strongly influence terrestrial and aquatic ecosystems (Parmesan *et al.* 2000; Thibault and Brown 2008) and may combine synergistically with other agents of environmental change, such as species invasions, to dramatically change ecosystems.

Previous studies have shown that changes in broad climatic conditions may influence the probability of species invasions, while highlighting that the effects of changing climate are likely to be diverse and context-dependent (Rahel and Olden 2008; Walther *et al.* 2009; Bradley *et al.* 2010). However, the potential for ECEs in particular to promote species invasions has not been systematically assessed. Here, we use theory from community ecology and invasion biology to identify mechanisms and pathways by which ECEs may affect the establishment and spread of introduced species in recipient ecosystems. We then review current evidence for ECE impacts on invasions and assess the potential for changes in the frequency and magnitude of ECEs to affect species introductions in the future. By focusing on mechanisms of invasion following an ECE, we assess whether generalizations about invasion risk are possible across species, ecosystems, and ECE type. Finally, we highlight critical areas of research necessary for a better understanding of these processes, and suggest strategies for anticipating and subsequently managing invasions associated with ECEs.

In a nutshell:

- Extreme climatic events, such as intense heat waves, hurricanes, floods, and droughts, may facilitate biological invasions, leading to new science, management, and policy challenges
- These events often influence invasions through increased movements of non-native species and decreased biotic resistance of native communities to invader establishment, but specific outcomes depend on the ecosystem and type of event
- Efforts to minimize impacts of invasive species in a changing climate must include preparation for extreme events

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What is an extreme climatic event?

Climatic events can be defined as "extreme" according to two broad perspectives. First, extreme events are episodes that fall within the statistical tails of a climate parameter's historical range; a commonly used threshold is the most extreme 1% of annual values, equivalent to an annual event happening once per 100 years (eg a "100-year flood"). The frequency of such events will shift as the mean or variance of a climate variable changes (Meehl *et al.* 2000). Second, an extreme event can be defined by organism-based criteria, such as the conditions

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substantially exceeding the acclimation capacity of an organism (Gutschick and BassiriRad 2003). According to this definition, extreme events are specific to particular organisms or ecosystems because of differing physiological tolerances and evolutionary histories. This definition can also account for the relative "abruptness" of events (the magnitude of change per unit time), which will depend on the length of species life cycles and the successional stages of ecosystems (Jentsch *et al.* 2007). Here, we follow Smith (2011), who integrated these perspectives by defining an ECE as "an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability". This characterization allows us to draw from a diverse body of literature, while recognizing that the definition of an ECE has both statistical and ecological dimensions.

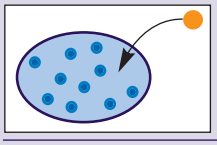
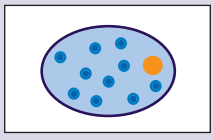
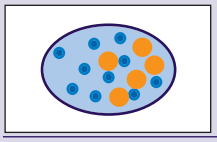
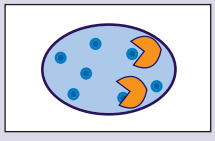
Mechanisms by which ECEs may influence biological invasions

The invasion process can be considered a progression of events in which individuals of a species are introduced to a novel location, establish a self-sustaining population, spread across the landscape, and reach levels of local and regional abundance that can eventually impact resident species and ecosystems (Theoharides and Dukes 2007). Therefore, for an ECE to have an effect on invasion, it must influence at least one of these stages (Table 1). Most research to date has focused on the establishment and population growth stages, but there is also evidence that ECEs may affect the transport of propagules into new regions and/or subsequent spread within a region. The manner in which ECEs influence the ecological impact of an invasion event is the least understood stage.

Previous empirical and theoretical work suggests that ECEs may act via different mechanisms across these stages. Identifying the mechanisms at the transport stage is relatively straightforward: ECEs such as storms (discussed below) can increase the chances of movement of non-native species propagules over long distances or across physical barriers. The effects of ECEs on establishment or population growth stages are more complex, but we suggest these will occur via two general pathways (Figure 1), both of which are based on the creation of an "invasion window". First, extreme events may cause abrupt and widespread mortality of resident species, thus acting as disturbances or "punctuated killing events" (Sousa 1984). Disturbances increase the availability of resources (eg nutrients, water, prey, space) to other species and may provide "resource opportunities" for introduced species (Shea and Chesson 2002). The duration of the invasion window is a function of the resilience of the native community as well as the magnitude, duration, frequency, and timing of the event(s) (Figure 1). Second, extreme events may stress (but not uniformly kill) resident individuals, decreasing their capacity to utilize resources and thereby limiting their growth and/or reproduction. Until the stressor ceases, conditions may be unsuitable for both native and non-native species (noted by the "abiotic resistance threshold" line in Figure 1). If residents do not immediately recover when the stressor ceases (eg when a severe drought ends), then resources become available that invaders could potentially access (Figure 1).

Mounting evidence suggests that non-native plant species may be favored following ECEs because they tend to have broader environmental tolerances than co-occurring native species (Dukes and Mooney 1999) as well as traits that favor rapid resource acquisition, growth, and colonization of disturbed areas (Pyšek and

Table 1. Extreme climatic events may influence different stages of invasion

Stage of invasion	*Mechanisms of ECE effects*	*Management actions*
Transport 	• Storm-driven large-scale movements, as from: o strong winds o storm surges	• Identify vulnerable habitats
Establishment 	• Reduced biotic resistance via: o disturbances o stressors	• Habitat restoration to increase resilience following ECEs and resistance to invaders
Spread 	• Overcoming dispersal barriers • Reduced biotic resistance (as for establishment)	• Early detection and eradication of non-native individuals • Bolster barriers between invaded and uninvaded areas
Impact 	• Changing per capita effects of invaders (eg drought leading to more concentrated density of non-native fish predators, or greater fuel build up due to drought-caused death of native woody plants leading to higher fire intensity)	• Increased awareness/effort post-ECE • Unique opportunities for eradication provided by some ECEs

Notes: Transport from an initial source population (orange circle) may initiate invasions in novel environments (large blue circle). Once introduced to a new area, additional ECEs may enhance progression through the stages of invasion, from establishment through population spread and ultimately impacts on native species (small blue circles). Targeted management actions can help limit the probabilities of advancement through each stage of invasion.

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Richardson 2007). Although no systematic reviews have assessed whether non-native species are favored by environmental extremes, disturbance theory and empirical data suggest that this is likely. Ultimately, the effects of changing ECEs on communities will depend on the combination of species-specific tolerances of non-native and native species (Figure 2).

Underlying these proposed mechanisms for ECE effects on invasion is the assumption that biological interactions (with pathogens, predators, herbivores, and competitors) or abiotic conditions can provide resistance to invasions. However, the importance of biotic resistance in shaping species invasions continues to be debated in the ecological literature and can be complicated to tease apart from other factors, such as resource heterogeneity (Fridley *et al.* 2007; Melbourne *et al.* 2007). Moreover, evaluating biotic resistance clearly requires unambiguous specification of spatial scales. Native and non-native species richness are often positively correlated at large scales but negatively correlated at small scales, particularly those scales used in experimental studies (Fridley *et al.* 2007). ECEs may affect the invasion of communities both by reducing biotic resistance at local scales and also through effects on abiotic and biotic heterogeneity at landscape scales (Melbourne *et al.* 2007). Thus, even if communities do not exhibit strong biotic resistance, ECEs may influence invasions by changing resource heterogeneity and by resetting the pool of competing species through disturbance.

Below, we provide an overview of how ECEs can affect the abundance and impact of non-native species – through dispersal opportunities, disturbances, resource pulses, and physiological stress. As we highlight in the following sections, these are not mutually exclusive categories because ECEs often change conditions in a manner that spans multiple determinants of species invasions.

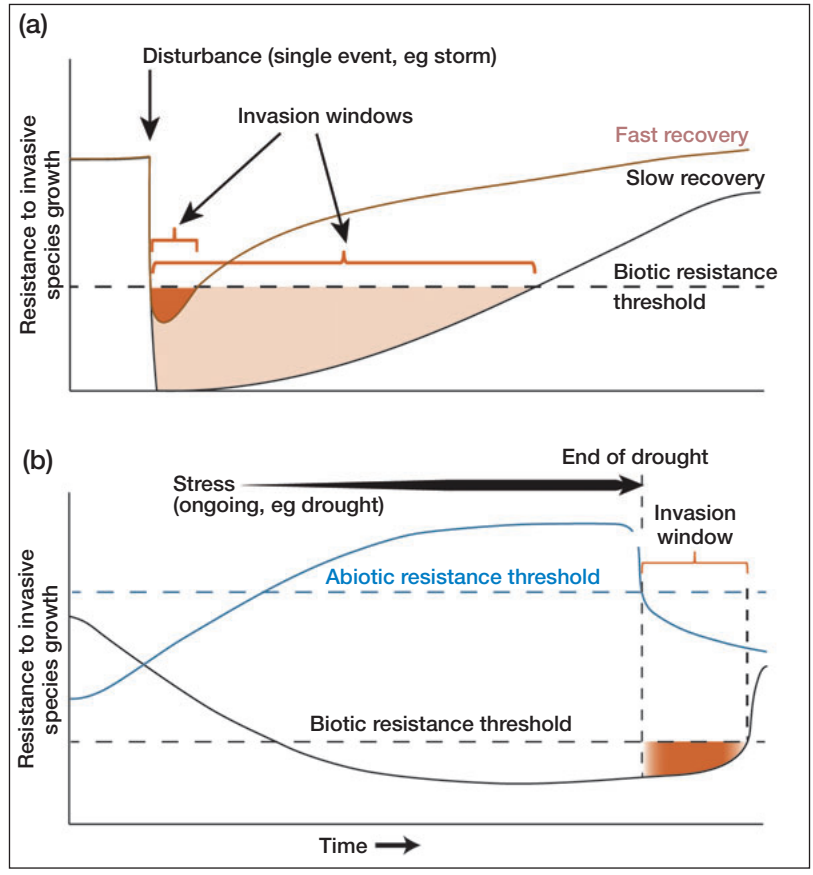

Figure 1. *Conceptual diagram of how extreme disturbance or stress events affect environmental conditions and resistance of an ecosystem to invasion. (a) Disturbance events immediately shift environmental conditions outside those where some or all of the species in the community can survive. As the resident community declines, biotic resistance due to competition and predation is relaxed. When biotic resistance declines past a threshold for a given invasive species, it creates an "invasion window" (shaded areas). The likelihood of increased invasive species dominance depends on the degree of reduction of biotic resistance and the rate at which the community recovers, restoring biotic resistance. Thus, the different sized invasion windows resulting from "fast" and "slow" recoveries are shown here. The frequency of disturbance (return time) and timing of the invasion window within a season (not pictured) can also be important for determining whether and which invasive species benefit. (b) Stress events can also lead to windows of opportunity for invasive species if there is a delay between when abiotic conditions become suitable for an invasive species and when native communities recover. Although the invasion window typically begins immediately following a disturbance event, it can occur at the end of a period of extreme stress. Stressful abiotic conditions (such as a prolonged drought) may increase resistance to invasion (light blue curve) but can also decrease the native community's ability to resist invasion (black curve). Thus, an invasion window may begin when the abiotic stress has improved to within suitable conditions for the invasive species (eg after rain ends a drought) but before the native community recovers.*

Dispersal opportunities

The unprecedented movements of species around the globe are largely driven by human activity, but emerging evidence suggests that ECEs may further promote the transport and introduction of non-native species (Table 1). For example, flooding events can facilitate dispersal of invasive species during unusually high periods of precipitation or rapid melting of snow and glaciers. Flooding events have been linked to numerous aquatic invasions, including the first known introduction of black carp (*Mylopharyngodon piceus*) into the Missouri River when floodwaters allowed fish to escape from hatchery ponds and subsequently spread downstream (Nico *et al.* 2005). Floods have also been implicated in the spread of other cultured fish species, such as tilapia (a group of species in the Cichlidae family) in Southeast

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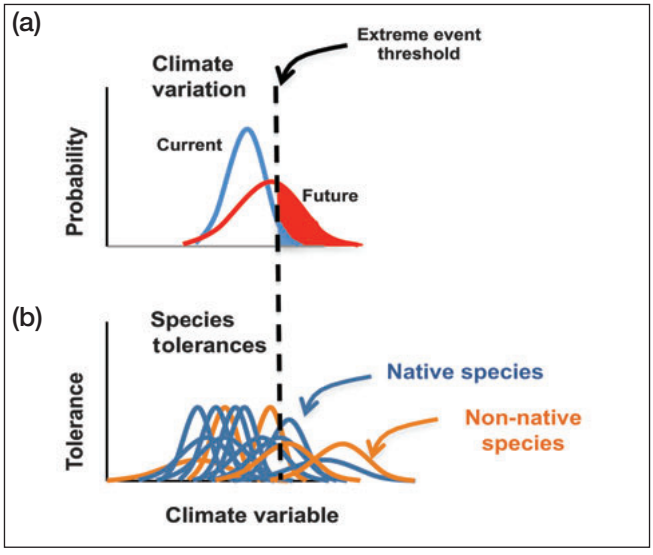

Figure 2. *Differences among species tolerance curves will determine community responses to disturbance or stress events. (a) Climate variables such as temperature and precipitation are expected to shift in both their mean and variance, and may create different frequencies of what are considered ECEs for a given community. Here, the threshold of what is extreme for this community is shown with a dashed vertical line and the differences in current and future frequencies of these events are shown with blue and red shading, respectively. (b) Communities contain both native and non-native species exhibiting a diversity of tolerances to particular climate factors. In this figure, curves represent how hypothetical native (blue) and non-native (orange) species respond to variation in a particular climate variable. When climate events fall outside of the tolerance curve of a species, it may be stressed or suffer high mortality. Ultimately, the ecological consequences of the shifting climate in (a) will depend on the specific combination of resident and introduced species response curves in (b).*

Asia (Canonico *et al.* 2005). In addition, severe flooding in 1993 resulted in extensive dispersal of zebra mussels (*Dreissena polymorpha*) to many new river drainages in the Mississippi River watershed (Tucker 1996). Non-native species have also increased after flooding in systems with upstream dams when fish are transported downstream over reservoir spillways (Schultz *et al.* 2003).

The transport of invasive species may also be promoted by the strong winds, large waves, and storm surges associated with high-magnitude storms. At large scales, the increasing frequency of extreme, large-scale storms that transport airborne dust particles between continents presents opportunities for the dispersal of non-native viruses, bacteria, and fungi (Kellogg and Griffin 2006); the deposition of this dust may also stress native communities. At more regional scales, storm events can facilitate the release of captive non-native species. Terrestrial organisms believed to have benefited from storm-assisted movements include the cactus moth (*Cactoblastis cactorum*; from the Caribbean to Mexico), the red palm mite (*Raoiella indica*; within the Caribbean), and the agricultural weed *Parthenium hysterophorus* across Swaziland (Burgiel and Muir 2010).

Disturbances and resource pulses

ECEs often create resource pulses (eg of light or space) that non-native species are able to utilize. These disturbances and resource pulses can facilitate both the establishment and spread phases of invasion (Figure 1). Storm events are among the most important of these disturbances, sometimes allowing non-native species to rapidly establish and spread (WebTable 1). For example, following Hurricane Andrew in Florida in 1992, non-native vines benefited from wind-driven tree canopy loss and spread widely across the state, despite the presence of native vines (Horvitz *et al.* 1998). Similar responses were observed following Hurricane Katrina in Louisiana in 2005 (Brown *et al.* 2011). In marine systems, storm surges and wave action can also leave communities susceptible to invasion (Denny *et al.* 2009). Pre- and post-hurricane surveys in Dominica recorded the burial of native seagrass beds by unusually large sediment loads as a result of storm surges associated with Hurricane Omar in 2008, which led to the establishment of invasive seagrasses (*Halophila* spp; Steiner *et al.* 2010).

Extreme floods may also act as disturbance agents with variable effects on invasions in aquatic systems. The physical changes to aquatic systems caused by floods can create opportunities for colonization, establishment, and spread by non-native species (Table 1), while suppression of flood regimes can also facilitate invasion. For example, Kercher and Zedler (2004) reported that the invasive reed canarygrass (*Phalaris arundinacea*) and broadleaf cattail (*Typha latifolia*) outgrew other native (and non-native) perennial species in experimentally manipulated cyclic and constant flooding and drought events. By contrast, in arid streams of the American Southwest, flooding has been shown to benefit native fishes. Floods allow many native species that evolved in areas where precipitation is often torrential – and where the onset of flooding can occur in seconds to minutes – to displace non-native fishes that evolved in mesic systems with more constant hydrology, where floods build over periods of hours to days (Meffe 1984).

Heat waves can cause persistent stress (discussed below) and also abrupt mortality of resident species. Both stress and mortality can facilitate the establishment and spread stages of invasion, when non-native species are able to either tolerate higher temperatures or more rapidly take up the resources made available by the deaths or reduced performance of native residents. In a marine coastal ecosystem in New Zealand, a heat wave caused the weekly high temperature to exceed the maximum from previous years by 7°C; this led to mortality that was an order of magnitude higher for a native mussel than for a non-native mussel species (Petes *et al.* 2007). In France's Rhône River, increases in non-native and eurytolerant (tolerant of a broad range of conditions)

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macroinvertebrates were temporally correlated with the 2003 European heat wave, as well as with severe flood events that may have contributed to increased resources (Daufresne *et al.* 2007).

Experimental manipulations corroborate the trends observed during and following heat waves. Sorte *et al.* (2010) simulated a heat wave in laboratory mesocosms of a marine epibenthic fouling community from California and found that the only species able to tolerate this disturbance were non-native in origin. Furthermore, the increased dominance of these non-natives persisted through 3 months of community development in the field, as a result of the non-natives' ability to rapidly capitalize on the increased resources (ie open space) both by growth and colonization of new recruits. Similarly, Song *et al.* (2010) showed that a heat wave led to a decrease in biomass of a native herbaceous *Wedelia* species (Asteraceae) but not its non-native congener, whereas White *et al.* (2001) found decreased native biomass and increased invasibility of a grassland system following extreme heat events. If indicative of responses to ECEs, these examples suggest that extreme disturbances have the potential to favor invaders because of differences in tolerances and non-native species abilities to preempt available resources (eg by growth and colonization) more quickly than native species.

Stressors

A third important mechanism by which extreme events may affect establishment of invasive species is by creating stressful conditions that reduce the biotic resistance of a community over longer time periods (Table 1). These stressful conditions may sometimes be punctuated by a large die-off at the end of the period, resulting in conditions similar to disturbances. The distinction is that stress events may not always lead to death, and the intermediate period of reduced competition and predation may lower the biotic resistance of communities. As with disturbances, these periods of stress may facilitate establishment or spread of invasive species (Figure 1).

Extreme heat waves and droughts are among the clearest examples of stressful conditions imposed by ECEs. The severe droughts predicted to increase in frequency with climate change can exceed the tolerances of resident species, leading to reduced vigor and widespread mortality events (Allen *et al.* 2010). Extreme droughts may involve either exceptional duration of drought conditions or shifted timing of drought relative to critical life-history stages. There are currently few data on which plant species are favored by drought-driven tree die-offs within forests, but non-native species are poised to increase in some drought-stricken ecosystems. For example, invasive grasses (eg *Bromus* spp) that are widespread in western North America may be suppressed temporarily by drought but can recover rapidly, and could then invade areas of pinyon pine (*Pinus* spp) or juniper (*Juniperus* spp) die-off (Kane *et al.* 2011). Drought has also contributed to the increasing prevalence of the invasive tamarisk (*Tamarix ramosissima*) in riparian areas across western North America (Stromberg 1998), where declining water tables select against native species. Both climatically induced drought and water extraction and water-table reduction by humans decrease water access for riparian plants and increase accumulation of salt in surface soils; these conditions act in concert to promote the more drought- and salt-tolerant *Tamarix* (Vandersande *et al.* 2001).

Although invasive species may initially be better able to colonize areas where drought has reduced biotic resistance, native species in drought-prone ecosystems can be better adapted to prolonged drought conditions than non-native species. For example, experimental drought reduced water-use efficiency much more in invasive dandelions (*Taraxacum officinale*) than in a native congener (*Taraxacum ceratophorum*) (Brock and Galen 2005). In Hawaii, the native grass *Heteropogon contortus* is more tolerant of drought than the dominant invader, *Pennisetum setaceum*, with which it typically competes (Goergen and Daehler 2002). In Venezuela, native grasses are more tolerant of high vapor-pressure deficits and water-stressed conditions than two African grasses that invade native savannas (Baruch and Jackson 2005). The many invasive plant species with high growth rates, leaf areas, and water use (Cavaleri and Sack 2010) may be at a disadvantage if drought conditions recur or persist after an ECE.

Extreme drought events can also lead to unusually low stream flows, which have been shown to promote resistance to aquatic invasions. The introduced brown trout (*Salmo trutta*) in New Zealand is more susceptible than native galaxiid fish to stresses associated with low flows; such events may therefore prevent trout from eliminating galaxiid fish in low gradient streams (Leprieur *et al.* 2006). In this case, water diversions caused the low-flow events, but we would expect similar outcomes under climate-induced drought conditions. Likewise, during a recent extreme drought in Victoria, Australia, many streams were reduced to small, isolated pools with depleted oxygen levels and high water temperatures; invasive common carp (*Cyprinus carpio*) were unable to survive these conditions and local populations were extirpated, whereas the native galaxiids survived (Lake 2003). Thus, ECEs that increase environmental stress levels may at times favor either non-native or native species in a manner that is taxon- and system-specific.

■ Synergies among stressors

The consequences of ECEs for biological invasions will sometimes depend on other aspects of global change driven by anthropogenic stressors. For example, gradual climate change may force many organisms closer to their physiological tolerance limits, thereby reducing their competitive ability and resilience to extreme events. In the western US, the compounding effects of recurrent

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Figure 3. *(a) Mortality events due to hurricane damage, such as that in Mississippi due to Hurricane Katrina, can open up resources that will support the establishment of non-native species. (b) Prolonged drought in a high-elevation woodland on Mauna Kea, Hawaii, where invasive grasses are recovering more quickly than native species. (c) Palm oasis in the Nevada desert that burned as a result of the synergism of* Tamarix *invasion, increasing drought, and severe fire weather. (d) An old bridge normally hidden beneath the surface waters of Llwyn-on Reservoir, Wales, is clearly visible during the extreme drought of 2010. Droughts can create isolated pool habitats, such as those in the foreground, that intensify interactions between introduced and native species. Whether these changes favor native or introduced species may depend on the system and the specific tolerances and behavior of resident species.*

droughts and gradual climate change may induce higher tree mortality during an ECE (Adams *et al.* 2009). The resulting increase in resource availability (eg water, light, space) after a drought could provide a window of opportunity for introduced species better adapted to changing conditions. As discussed above, *T ramosissima* invasions of riparian zones in southwestern North America are facilitated by drought; however, native *Populus* spp can outcompete *T ramosissima* after flood events when soil moisture is high (Sher *et al.* 2000). Thus, the net outcomes of ECEs for these riparian ecosystems are likely to depend on interacting factors, such as alteration of groundwater and flow regimes by dams, in combination with ECEs and even fire occurrence.

The effects of ECEs are also likely to interact with ongoing changes in propagule pressure of non-native species. The expanding number and volume of commercial trade routes will continue to spread invasive species across the globe. This means that invasive species are more likely to be present in regional species pools, poised to take advantage of windows of opportunity created by ECEs (Olden *et al.* 2011). Additional synergistic interactions between ECEs and invasions could take place through positive feedbacks between non-native species and the physical environment, disturbance regimes, biogeochemical cycling, and biotic composition of invaded ecosystems (Crooks 2002). For example, in Hawaii, extreme drought causes mortality among some of the dominant native woody species (Figure 3; Lohse *et al.* 1995), thereby facilitating the dominance of non-native grasses. This increases the likelihood of fire and could potentially shift the ecosystem toward a grass-dominated state (CMD'A pers observation). Even previously fire-prone ecosystems may experience damaging fire frequencies and/or intensities through the interaction of ECEs and established invaders. The cogongrass (*Imperata cylin-*

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drica) invasion in Florida pine ecosystems has increased fire intensity, causing greater native species mortality and facilitating further invasion (Lippincott 2000). Although such interactions have rarely been studied, these examples highlight how positive feedbacks could allow invasive species to "transform" some ecosystems to new, possibly persistent states.

Similar effects may ripple across trophic levels. For example, changes in vegetation structure caused by hurricanes have been shown to precipitate shifts in bird communities resulting from new nesting opportunities in invasive vines (Brown *et al.* 2011). In the Bahamas, Schoener *et al.* (2001) found that predation by introduced lizards resulted in local extinction of the smaller native lizard species only after storm events reduced the natives' population sizes. The effects of ECEs on invasions at one trophic level may therefore depend on changes due to ECEs at other trophic levels.

Future research and management efforts

Research to date has shown that ECEs can affect the invasion process but that this relationship is complex and context-dependent. Although many studies suggest that ECEs can enhance dispersal and reduce biotic resistance to non-native species establishment (WebTable 1), few have examined how ECEs affect the magnitude of invader impacts on native systems. Also, ECEs do not uniformly favor non-native species, and many non-natives that benefit may have no substantial ecological effect. In some systems, events like extreme floods or persistent droughts may negatively affect established invaders, thereby providing opportunities for restoration of native species. Although this growing body of research allows us to identify some mechanisms by which ECEs influence invasions, we still lack sufficient information to make definitive predictions about how increasing ECEs will interact with the invasion process and with species impacts in most ecosystems.

Several areas of research could help improve both our basic understanding of invasive species responses to ECEs and our ability to anticipate and mitigate their effects in the future. First, it is important to determine whether there are specific characteristics of introduced species and recipient native communities that are likely to lead to invasion after ECEs. Are there traits and demographic characteristics of introduced species that would allow them to tolerate extremes better than native species? What makes some native communities more vulnerable to invasion post-ECE than others? Are communities that have evolved with higher natural climatic variability more resilient to ECEs? These are basic ecological questions with clear management implications. However, despite these remaining uncertainties about ECE effects on invasions, our review points to concrete actions that managers can take to prepare for and to mitigate the impacts of extreme events (WebPanel 2). Resource managers can begin to target their efforts toward species that appear more likely to invade after an ECE, such as introduced vines following hurricanes (Horvitz *et al.* 1998). Similarly, efforts can be made to increase resilience of communities that may be susceptible to ECEs and subsequent invasions. Riparian zones of riverine ecosystems that are prone to flooding are a clear example of where targeted restoration efforts may help increase community resilience to invasion after flooding events.

A second research area is to identify biological thresholds of responses to extreme events. It is currently unclear where the critical tolerance thresholds are, which, once crossed, will cause dramatic change in a community's trajectory. Part of this challenge is to understand how synergies among global change drivers affect system thresholds, especially because extreme conditions can arise as a result of the co-occurrence of unusual, though not extreme, values of two or more climate variables (Denny *et al.* 2009). A more mechanistic understanding of the conditions that lead to changes in a system is necessary if we are to anticipate the results of ECEs in different ecosystems.

Progress on these questions will require a range of approaches, including manipulative experiments, observational studies, and modeling. Controlled experiments are most useful for isolating mechanisms and are becoming more powerful as approaches are developed for manipulating extreme values for two climate variables concurrently (Smith 2011). Observational studies are critical for understanding dynamics over larger spatial and temporal scales and for systems not amenable to controlled manipulation. Successful observational studies of the impacts of ECEs will rely on long-term monitoring of areas prone to ECEs (eg hurricane corridors, drought-prone areas) and rapid mobilization of research efforts to take advantage of chance events. Managers have a critical role to play in this research by identifying susceptible and control areas for study. Coupling observational studies directly to management needs and actions will allow comparisons among events of varying magnitudes, durations, and frequencies at broad spatial and temporal scales. Finally, new modeling approaches are needed to integrate experimental and observational data with ecological theory in order to build risk assessments of future invasions in response to ECEs. Currently, most theoretical investigations of how biological systems shift among alternative states (eg between uninvaded and invaded states) have focused on gradual changes in drivers such as climate variables (Scheffer and Carpenter 2003) with the goal of identifying early-warning signals that critical thresholds are being approached (Scheffer *et al.* 2009). Only recently have modeling efforts focused on shifts among alternate states in response to stochastic climatic events (Schooler *et al.* 2011) and the modeling of transient dynamics over ecologically relevant timescales (Hastings 2010). Such modeling can also be extremely useful for managers by evaluating alternative management scenarios in the face of both gradual climate change and ECEs.

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In summary, the intersection between ECEs and biological invasions represents an important focus for understanding and predicting future changes in a wide range of ecosystems. We suggest that future studies of climate change and species invasions should not only consider future trends in mean values of climatic factors but instead should elucidate the mechanisms by which ECEs influence invasions across a broad range of taxa, trophic levels, ecosystems, and biogeographic regions. Management of natural areas will increasingly require planning for and mitigation of the effects of ECEs in an ever more invaded world.

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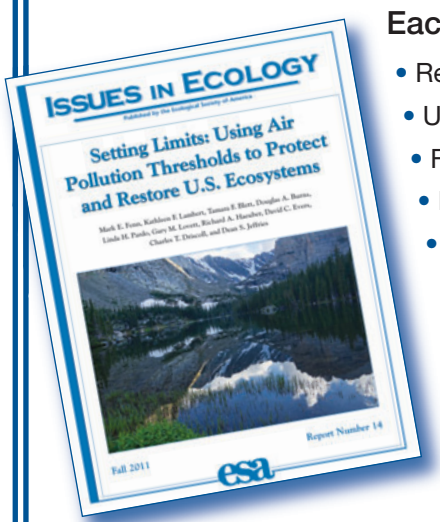

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