Knocking back invasions: variable resistance and resilience to multiple cold spells in native vs. nonnative fishes

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Abstract. Extreme climate events can interact synergistically with invasions to dramatically alter ecosystem structure, function, and services. Yet, the effects of extreme climate events on species invasions remain unresolved. Extreme climate events may increase resources and decrease biotic resistance by causing physiological stress and/or mortality of native taxa, resulting in invasion opportunities for nonnative species. Alternatively, extreme climate events may regulate nonnative populations, preventing them from achieving dominance. We examined whether a sequence of three cold spells had a negative or positive effect on fish invasions in the coastal Everglades. We compared resistance (initial effects) and resilience (rate of recovery) to the cold spells between native fishes and the dominant nonnative invader, the Mayan cichlid, across eight populations expanding two mangroves drainages in the southern Everglades. We tracked native fish and nonnative Mayan cichlid populations for 10 yr including 3 yr pre- and 4 yr post-cold spells. In both drainages, native fishes were more resistant to the cold spells than the nonnative species. While native fishes experienced declines at only one site, nonnative Mayan numbers were reduced by 90–100% across six sites where they were abundant pre-disturbances. Four years after the last cold spell, we saw limited resilience in the affected nonnative populations. Only one of the six affected sites fully recovered, whereas the other five sites showed no recovery in Mayan cichlid numbers. The recovered site was closest to a canal, known to act as thermal refuges for nonnative fishes. In summary, cold spells can reduce nonnative abundances, but whether cold spells can effectively knock back invasions (and range expansions) by tropical/subtropical nonnative species will depend on how the frequency and severity of cold spells are affected by climate change. We propose that these mortality-causing extreme events could provide rare management opportunities late in an invasion.

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INTRODUCTION

An expected consequence of climate change is an intensification of extreme climate events, such as droughts, hurricanes, and severe cold spells (Easterling et al. 2000, Karl et al. 2008, IPCC 2012).

Of particular interest are changes in the frequency and timing of these extreme events, which may result in a higher likelihood of multiple climate disturbances co-occurring at ecologically relevant time scales. This may include a sequence of severe events (100 yr), combined with less severe

episodic disturbance events (decadal events), whose effects on ecological communities can be profound and not easily disentangled (Boucek and Rehage 2014). The stressors imposed by these multiple disturbances can act synergistically to alter communities in ways that cannot be predicted by tracking responses to any extreme event independently (Peters et al. 2014). To this end, it is important that we develop an improved understanding of how communities respond to sequential extreme climate events, and thus better predict the future dynamics of ecosystem structure, function, and services.

One important effect of climate change are changes to the invasibility of ecosystems, whereby climate change may either promote or limit species invasions (Dukes and Mooney 1999, Hellmann et al. 2008, Rahel and Olden 2008, Diez et al. 2012, Bellard et al. 2013). Climate change may alter the pathways of invasion, the climatic constrains or filters experienced by nonnative taxa, their distributional patterns and impacts on native taxa, and the effectiveness of management actions (Hellmann et al. 2008). A recent meta-analysis on gradual climate change (higher temperatures, higher CO_2 levels, and altered precipitation) showed that climate change can favor nonnative species, particularly in aquatic systems (Sorte et al. 2012). No such comprehensive assessment has been conducted for the effects of extreme climate events on nonnatives, but a recent review by Diez et al. (2012) points to the fact that extreme climate events can either benefit or hamper invasions, highlighting the need for further research.

On one hand, extreme climate events may result in abrupt mortality and stressful conditions for native species that reduce biotic resistance, creating an "invasion window" for opportunistic and broadly tolerant nonnative species (Diez et al. 2012). This invasion window may result from resource opportunities that arise directly from greater resource availability related to the disturbance event (e.g., nutrients, light, space), or indirectly through reductions in the resource use of affected native taxa (i.e., relaxed competition and/or predation). The "size" of this invasion window will be directly proportional to the resilience of the native community; delays in native recovery may promote nonnative proliferation (Diez et al. 2012). For example, hurricanes can result in mass losses of both terrestrial and

marine vegetation that allow for the expansion of previously rare nonnative species (Horvitz et al. 1998, Steiner et al. 2010). Similarly, heatwaves have been documented to cause higher mortality and stress in native species and thus benefit nonnatives (Petes et al. 2007, Sorte et al. 2010).

Alternatively, extreme events may cause stress to nonnative species and regulate their populations, preventing nonnative dominance. Native species may be better adapted to stressors associated with extreme climate events since these are unlikely to be novel (Diez et al. 2012). For instance, droughts may reduce the invasibility of temperate grasslands (Kreyling et al. 2008), because native species are often competitively superior under resource limitation (e.g., lower water demands, Cavaleri and Sack 2010, and lower sensitivity to burning, Havill et al. 2015).

While the effects of warming and drought events have been subject to greater study (e.g., Kreyling et al. 2008, Sorte et al. 2010), attention to the effects of extreme cold events and to multiple extreme events remains limited, particularly in subtropical and tropical latitudes (Firth et al. 2011, Boucek and Rehage 2014). Kreyling et al. (2015) postulated that the thermal tolerance of nonnative species should match the temperature regime of their native range. Thus, it follows that tropical nonnatives introduced into higher latitudes should be less resistant to extreme cold than native species. Yet, this prediction has not been rigorously tested. Between 2008 and 2010, three episodic cold spells affected the coastal Everglades, providing an opportunity to examine differential effects and recoveries in native and nonnative taxa. These disturbances included a mild cold spell in January 2008, an extreme 100-yr cold spell in January 2010, and a moderate cold spell in December 2010—all of which reached stressful to lethal temperatures for many tropical native and nonnative fishes (Boucek and Rehage 2014). The January 2008 cold spell lasted 1 d with minimum air temperatures reaching −1.7° C. The January 2010 cold spell was the most severe cold spell recorded over the past 87 yr, with temperatures below 5.4° C for 12 d, and a minimum air temperature of −3.3° C. And, the December 2010 cold spell lasted 3 d with minimum temperatures of −0.6° C.

Our study asks, does this sequence of cold spells have a differential effect on native vs. nonnative fishes inhabiting coastal mangrove

regions of the Florida Everglades? Our previous work documented major effects on fish community structure due to the January 2010 cold spell (Boucek and Rehage 2014), but our objective here was to examine differential resistance and resilience to the sequence of cold events for native vs. nonnative fishes. We examined fish dynamics in two coastal drainages over 10 yr (2005–2014), including 3 yr pre- and 4 yr post-cold events. We tracked the response of the most widespread nonnative fish in South Florida (Mayan cichlid, *Cichlasoma urophthalmus*; Kline et al. 2013) relative to that of native fishes.

In agreement with Kreyling et al. (2015), we hypothesized that nonnative species would be more susceptible to the stresses associated with extreme cold events relative to native taxa and thus would exhibit lower resistance (Fig. 1). We predicted resilience or the rate of post-disturbance recovery (Fritz and Dodds 2004) to also be lower for the nonnative taxa. Since nonnative fish populations are smaller and more patchy relative to native fish populations (Trexler et al. 2000, Kline et al. 2013), recolonization of affected populations may rely on a limited number of source or refuge populations, which may slow recovery. Finally, we hypothesized greater spatial variability in resilience for nonnative relative to native fishes (Fig. 1b). While some nonnative populations may fail to recover, others could experience the "invasion window" described by Diez et al. (2012) and may become even more successful than pre-extreme events.

METHODS

To compare resistance and resilience, we sampled fishes in the two major drainages of Everglades National Park (ENP): the Taylor Slough (TS) and the Shark River (SR, Fig. 2a). SR is one of the largest coastal rivers in the southwestern Everglades connecting Shark River Slough, the main freshwater drainage in the southern Everglades, to the Gulf of Mexico (McVoy et al. 2011, Fig. 2b). The TS basin is the major freshwater drainage of the southeastern Everglades, which empties into Florida Bay (Fig. 2c). Both systems are focal areas of study for long-term ecological research (Florida Coastal Everglades Long Term Ecological Research or FCE LTER, http://fce.fiu.edu) and
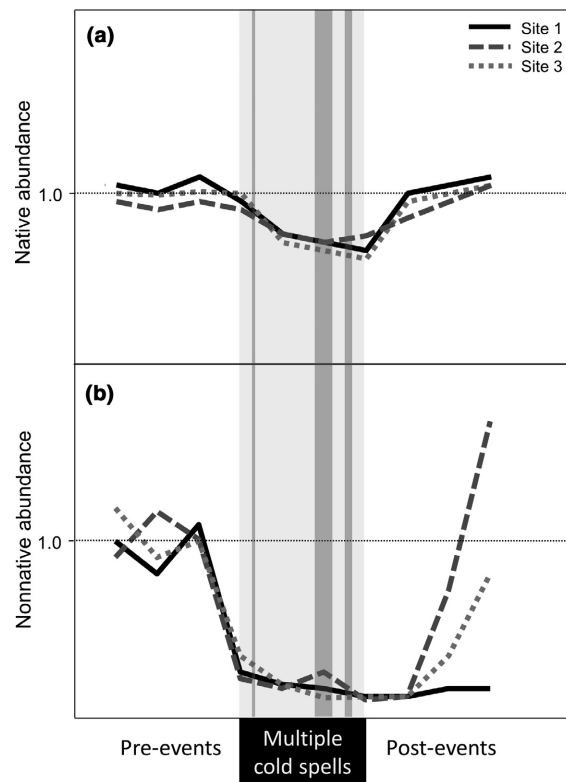

Fig. 1. Conceptualization of the responses of (a) native and (b) nonnative populations to a sequence of extreme temperature events, illustrating hypotheses tested and highlighting variation in resistance and resilience across multiple native and nonnative populations. Three cold spells of varying severity (dark gray lines of varying thickness) are shown in the disturbance period (light shading) per our study. The horizontal dashed line represents average pre-disturbance abundances across populations of each species type (native vs. nonnative). We hypothesize a stronger effect of sequential cold events and lower resilience for nonnatives, and for recovery to increase interpopulation variation in invasion success.

key focal areas for the Comprehensive Everglades Restoration Plan (NRC 2014).

Across coastal drainages, nonnative fishes are known to account for 5–12% of fish abundance, with Mayan cichlids being the dominant invader in mangrove areas, and the most widespread fish invader ecosystem wide (Harrison et al. 2013, Kline et al. 2013). This invasive Central American cichlid provides a good nonnative model for examining resilience and resistance to extreme
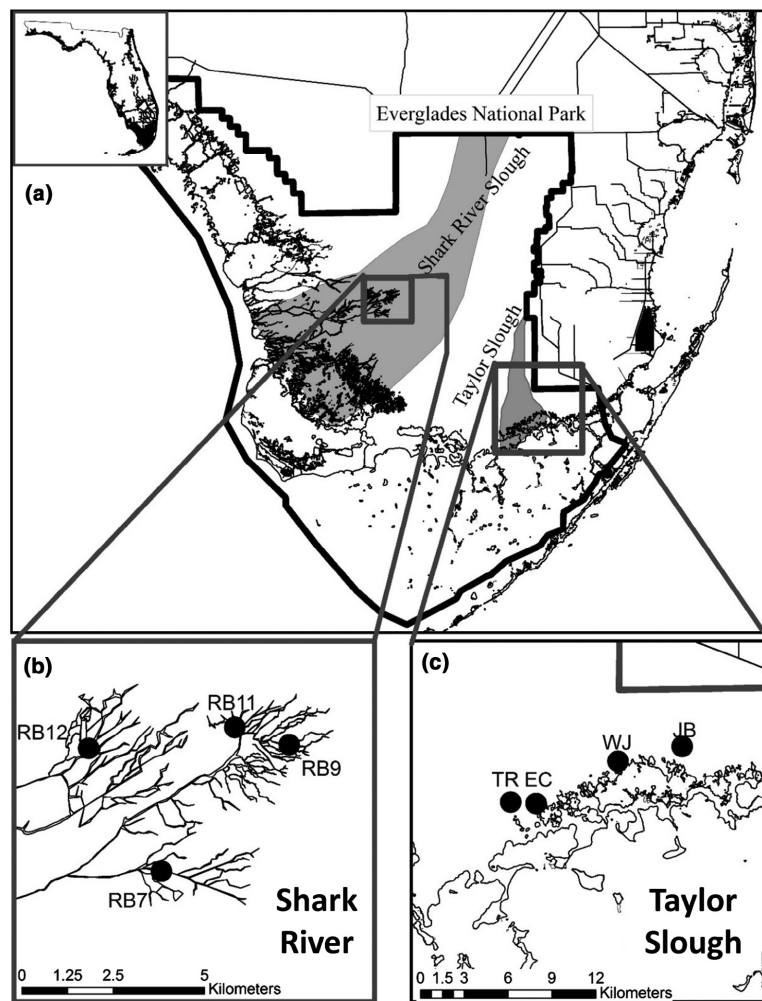
Fig. 2. Map of (a) the two study drainages in ENP, and detail of the location of the four sites sampled in the (b) Shark River (SR) and (c) Taylor Slough (TS) drainages, respectively.

climate events, having many of the traits of successful invasive fishes (Kolar and Lodge 2002, Moyle and Marchetti 2006). Mayan cichlids are a generalist predator (Bergmann and Motta 2005) with a broad range of physiological tolerances (Schofield et al. 2010), including salinity (up to 37 PSU, Stauffer and Boltz 1994), and a high reproductive rate (Faunce and Lorenz 2000). Additionally, this is the only nonnative fish species for which there is evidence of a negative effect on native species (Harrison et al. 2013), and thus of relevance to understanding the impact by nonnative species in the Everglades, and how impact may be mediated by climate variation.

Sampling was conducted in tidal mangrove creeks (dominated by red mangroves, *Rhizophora*

mangle) in both drainages. In the SR system, four sites located at the headwaters region of Rookery Branch were sampled (RB7, RB9, RB11, and RB12 in Fig. 2b; see Boucek and Rehage 2014 for additional details on this drainage). Sites averaged 1.2 m in depth, with mean salinity of 1.3 PSU (range = 0.2–14 PSU). In TS, sampling focused on four sites located at the downstream end of TS: Taylor River (TR), East Creek (EC), Joe Bay (JB), and West Joe Bay (WJ) (Fig. 2c, see Harrison et al. 2013 and Lorenz 2014*a* for additional details on this drainage). At TS, creeks were smaller, shallower (mean depth = 18.4 cm), and characterized by higher salinity (mean salinity = 7.5 PSU, range = 0–46.0 PSU). Sites were selected because Mayan cichlids are present and most abundant,

and thus, these sites are best poised to detect an effect from low temperature events.

TS sites were sampled using 9 m² drop nets (three replicate nets per site) placed surrounding dwarf mangrove trees in ecotonal creeks (Lorenz et al. 1997, Harrison et al. 2013, Lorenz 2014a). Nets were set overnight, deployed the following day (within 3 h of sunrise), and dosed with a lethal concentration of rotenone (a biodegradable piscicide, Leary et al. 2013). Fishes were collected from the drop nets using dip nets, and drop nets were left a second night to recover any additional fishes. Caught fish were frozen and brought back to the laboratory to be identified and counted. Estimates of fish abundance for TS are reported as densities or fish/m².

In SR, fishes were sampled via boat-mounted electrofisher (Smith-Root® 9.0 unit; Rehage and Loftus 2007, Boucek and Rehage 2013, 2014). We conducted three replicate 5-min transects of boat electrofishing at each study site. We sampled by driving at idle speed along creek shorelines and applying standardized power per ambient temperature and conductivity conditions (Pope et al. 2009). Immobilized fishes were caught by two netters positioned at the bow of the boat, and fish were brought on board, identified, counted, and released where collected (except for nonnative fishes, which were euthanized with an overdose of MS-222, Leary et al. 2013). We report electrofishing catch per unit effort (CPUE) as follows: $\frac{(\text{Fish netted} + \text{fish shocked})}{\text{distance sampled}(m)} \times 100$ (Boucek and Rehage 2013). This is the sum of fish caught and shocked in a transect, adjusted for the length of shoreline sampled (measured with a GPS unit, mean length = 105.1 ± 1.4 m). Shocked fish consisted of fish that were not caught but were immobilized, accurately identified, and counted. Estimates of fish abundance for SR consist of CPUE or the number of fish/100 m of shoreline sampled.

At both drainages, fishes were sampled during the dry season. Previous research shows that during the dry season months (December to May), low water conditions concentrate fishes, thus increasing their catchability (Boucek and Rehage 2013, 2014, Harrison et al. 2013, Lorenz 2014b). During the wet season, fishes are dispersed throughout the landscape, including marshes surrounding creeks, and sampling is not representative of species richness nor abundance in ecotonal habitats. Creeks at both drainages

were sampled between 2005 and 2014, capturing fish dynamics for 3 yr prior (2005–2007) and 4 yr post-cold spells (2011–2014). For TS, drop netting was conducted monthly between December and April, making for a total sample size of 600 samples (3 replicate traps per site × 4 sites × 5 monthly samples × 10 yr = 600). For SR, electrofishing was conducted twice over the dry season (February–March and April–May), totaling 240 samples (3 electrofishing transects per site × 4 sites × 2 samples × 10 yr = 240).

Statistical analyses

In order to test our hypotheses about greater resistance and resilience for native relative to nonnative Everglades fishes, we compared yearly estimates of fish abundance pre and post the sequence of cold spells. We first extracted log-transformed yearly fish abundances (Ln $(x + 1)$) for all native fishes (sum of all species combined, and hereafter native abundance) and for the abundance of the dominant invader, Mayan cichlids (hereafter nonnative Mayan abundance) from the TS and SR datasets separately. We examined resistance of native fishes vs. nonnative Mayan cichlids by comparing fish abundances between the pre-cold spell period (2005–2007) and the first year post-cold spells (2011). We conducted these analyses separately by drainage, and we compared pre and post abundances across the four individual sites sampled in each drainage. Since data were not normally distributed, we determined statistical differences by calculating 95% confidence intervals (CIs) for pre- and post-cold spell means from a bootstrapped distribution with 1000 iterations. If the 95% CIs of pre- and post-cold spells abundance overlapped, fish populations were considered resistant to the extreme events.

We tested for variation in resilience among populations that exhibited declines in abundance, and therefore were not resistant to the cold spells. For these affected populations, we quantified resilience by fitting linear regressions to fish abundances in the post-disturbance years (2011–2014) and examining whether slopes were significantly different from zero. To assess inter-site variation in resilience, we compared the 95% CI of the slopes and deemed sites to have varying recovery rates if these did not overlap. Finally, we assessed if a site was fully recovered

by comparing fish abundances pre-cold spell (2005–2007) to the 2014 abundances (the last year sampled). We calculated 95% CIs for the pre- and 2014 abundances from a bootstrapped distribution with 1000 iterations. As done with the resistance comparisons, all resilience comparisons were done separately for the native fish and the nonnative Mayan cichlid abundances. We used the mosaic package in Program R for calculating CIs, and Sigma Plot® 11.0 for obtaining the resilience slopes and associated statistics.

Results

Native vs. nonnative resistance

We documented a major decline in the abundance and contribution of nonnative Mayan cichlids to coastal Everglades fish communities as a result of the 2008–2010 cold spells. Pre-cold events, nonnative Mayan cichlids accounted for an average of 21.9% of fish abundance in TS and 5.2% in SR. Post-disturbance, nonnatives represented only 4.4% of the fish caught in TS and remained at zero in SR up to 2014, the last year sampled in the study. Contrary to these pronounced nonnative declines, native fish assemblages exhibited overall resistance to the sequence of cold spells. We documented no negative effect of the cold spells on native fish abundance at all TS sites and at three of the four SR sites (Fig. 3). The exception was RB 12 in SR, where native fish abundance decreased by 80% as a result of the cold events (Fig. 3a). At TS, native fish numbers were higher the year immediately following the cold events than prior to them (Fig. 3b).
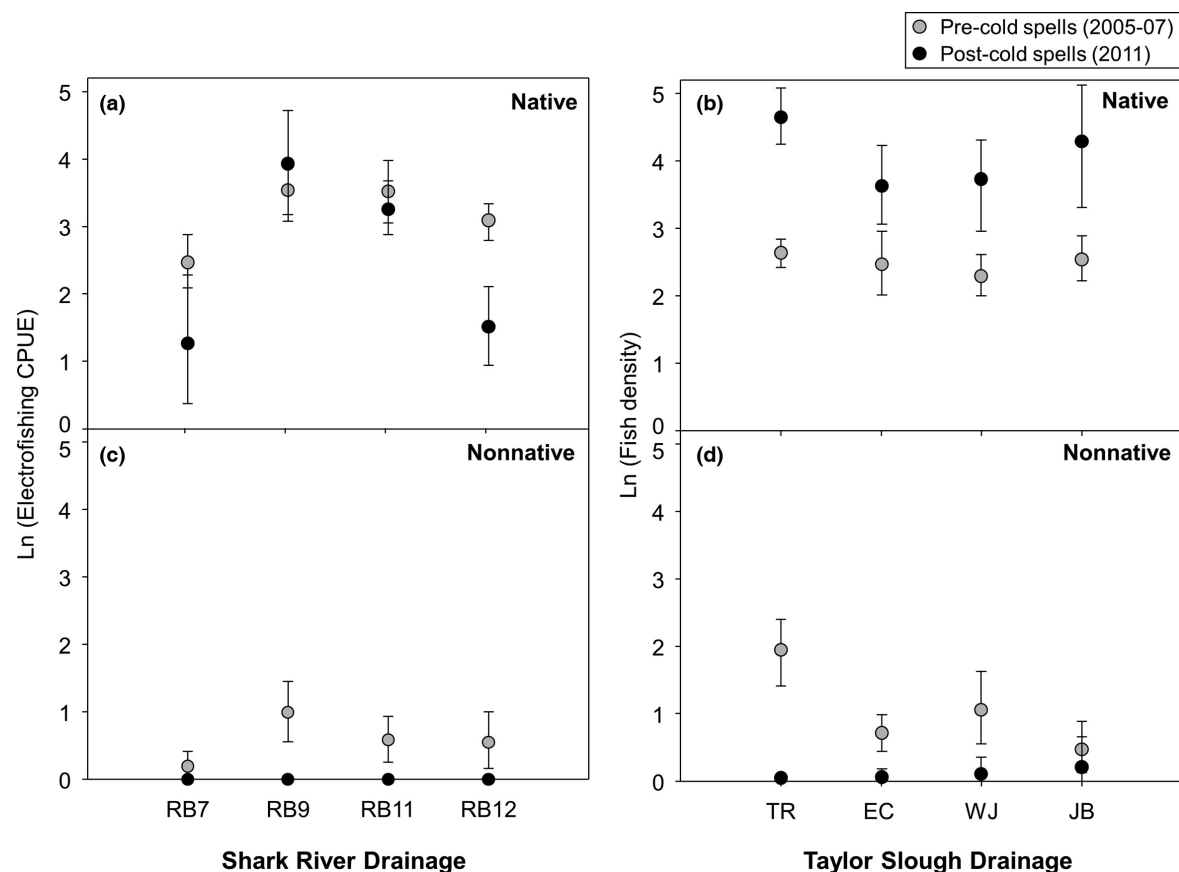

Fig. 3. Fish abundances (mean ± 95% CIs) pre- (2005–2007, gray symbols) and post-cold spells (2011, black symbols) for native fishes in the (a) SR and (b) TS drainages and for nonnative Mayan cichlids in (c) SR and (d) TS, respectively. The four sites sampled in each drainage are shown (see Fig. 2 for site locations).

For nonnative Mayan cichlids, we documented significant declines at all sites where their pre-cold spell abundance was relatively high. This included six out of the eight sites sampled: RB9, RB11, and RB12 in SR and TR, EC, and WJ in TS (Fig. 3c–d). The sites with no effects were those with the lowest nonnative Mayan cichlid abundance pre-cold spells (RB7 and JB). At the three affected SR sites, Mayan abundance dropped to zero in 2011, while at TS sites, Mayan numbers decreased by 90–98% relative to pre-disturbance.

Nonnative resilience

We found evidence of spatial variation in resilience when comparing recovery rates among affected sites (Table 1). At the SR drainage, there was no recovery; not a single Mayan was caught at the three affected sites in the 4 yr post-cold spells (Fig. 4a). In contrast, Mayans were not extirpated from the TS drainage, and one of the three TS sites showed a full recovery (WJ, Fig. 4b). The recovery rate at WJ was six times higher than that seen at TR and EC, for which we saw no positive slope (Table 1). By 2014, Mayan abundance at WJ was comparable to pre-cold spells numbers, whereas at the TR and EC sites, Mayan numbers remained at significantly lower levels than pre-disturbance (Fig. 5). At the one TS site where no effect from the cold spells was seen (JB), post-disturbances abundances were higher than prior to the events (Figs. 4 and 5). Last, for the one SR site where native fishes declined (RB12), its recovery rate was similar to that of the Mayan

cichlids in WJ, with a full recovery by 2014 (Table 1).

Discussion

Extreme climate events can alter dispersal opportunities, habitat suitability, and resource availability for nonnative species, as well as the strength of species interactions that govern biotic resistance, thus having the potential for major effects on invasion dynamics (Diez et al. 2012). These effects may be particularly strong as a result of a multiple, sequential extreme events. In this study, we documented the effects of a sequence of three cold spells on coastal Everglades fish communities. Rare cold events may strongly constrain range shifts, invasions, and assisted colonization events (Kreyling et al. 2015). As we predicted, native fishes were resistant to the cold spells, while the dominant nonnative invader, the Mayan cichlid, was not. Across two drainages, nonnative Mayan cichlids suffered 90–100% declines in abundance at six of eight sites sampled. In comparison, only one out of eight native fish assemblages was negatively affected.

Four years after the cold spells, recovery of nonnative Mayan cichlids was very limited. There was no recovery at the SR drainage and only one of the three affected sites fully recovered at TS. The recovered site was located closest to a canal-known to act as thermal refuges for nonnative fishes (Adams and Wolfe 2007, Schofield et al. 2010, Blewett and Stevens 2014). We expected extreme cold events to increase

Table 1. Recovery trajectories post-cold spells for the six affected sites in the two drainages. Shown are slopes fitted to post-events abundances, P-values, 95% confidence intervals and R^2 values.

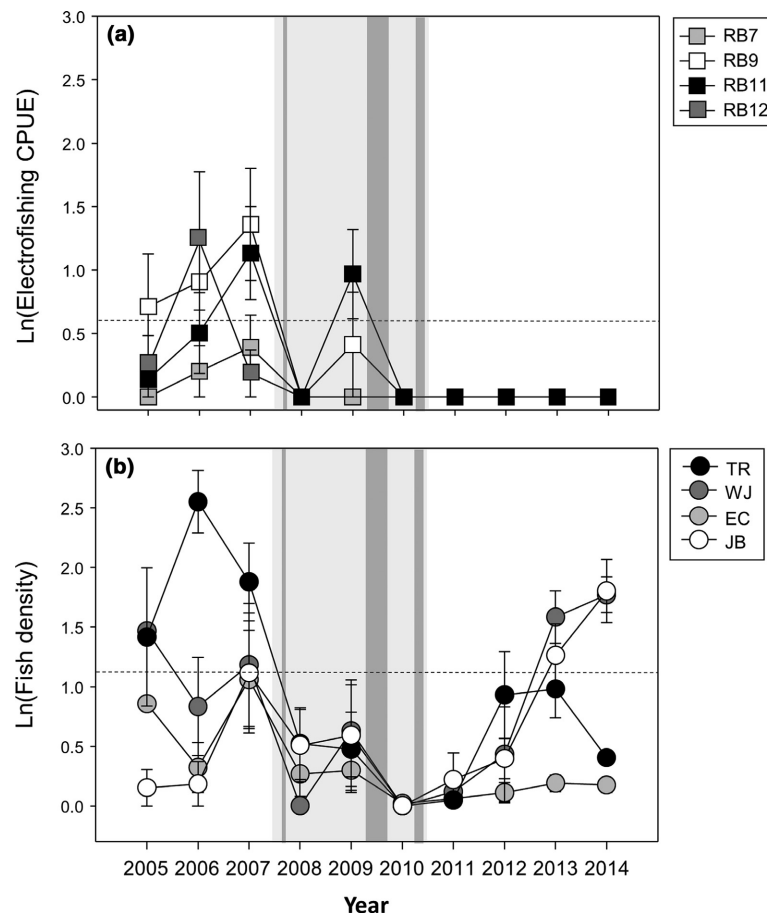| Site	Species	Slope	P-value	95% CI	R^2
Taylor Slough drainage					
EC	Nonnative	0.04	0.173	0.01, 0.2	0.06
TR	Nonnative	0.14	0.305	0.01, 0.1	0.09
WJ	Nonnative	0.62	<0.001	0.50, 0.7	0.59
All affected sites	Nonnative	0.27	0.001	0.11, 0.4	0.18
Shark River drainage					
RB12	Native	0.47	<0.001	0.09, 0.8	0.26
RB7	Nonnative	0			
RB9	Nonnative	0			
RB11	Nonnative	0			
All affected sites	Nonnative	0			

Fig. 4. Mean yearly abundances (±SEs) for nonnative Mayan cichlids across the pre- and post-cold events years in the (a) SR and (b) TS drainages. Light shading indicates the disturbance period, while the darker lines indicate the timing and severity of the three cold spells (thickness corresponds to severity). For reference, the average pre-disturbance abundance across all sites is indicated in both drainages by the horizontal dotted line.

spatial structuring across nonnative populations (Fig. 1; Boucek, R. E., E. E. Gaiser, H. Liu, and J. S. Rehage, *unpublished manuscript*), and we saw mixed support for this hypothesis. In SR, severe effects reduced abundances to zero across all sites, while at TS, spatial heterogeneity increased with two sites having relatively higher nonnative Mayan abundance (WJ and JB), one intermediate (TR) and one low (EC, Fig. 5). Last, we noted an increase in native abundance in TS post-cold event. Harrison et al. (2013) showed that the presence of Mayan cichlids had negative effects on some native species. The decline in Mayans following the cold spells may have released certain native species from competitive and/or predatory effects.

The dichotomy between native and nonnative resistance, or ability to persist in the face of disturbance (Fritz and Dodds 2004), stems for differences between the two fish faunas. While native coastal fish communities at both drainages are composed of a mix of temperate freshwater and tropical euryhaline species, nonnative species such as the Mayan cichlid are of tropical origin (Loftus 2000, Boucek and Rehage 2014). In fact, all 17 nonnative species presently established in ENP have a tropical/subtropical origin, and therefore are susceptible to thermal stress (Schofield et al. 2010, Kline et al. 2013). This inability to tolerate low temperatures is likely a major factor limiting the distribution of many of these nonnative fishes to South Florida (Shafland
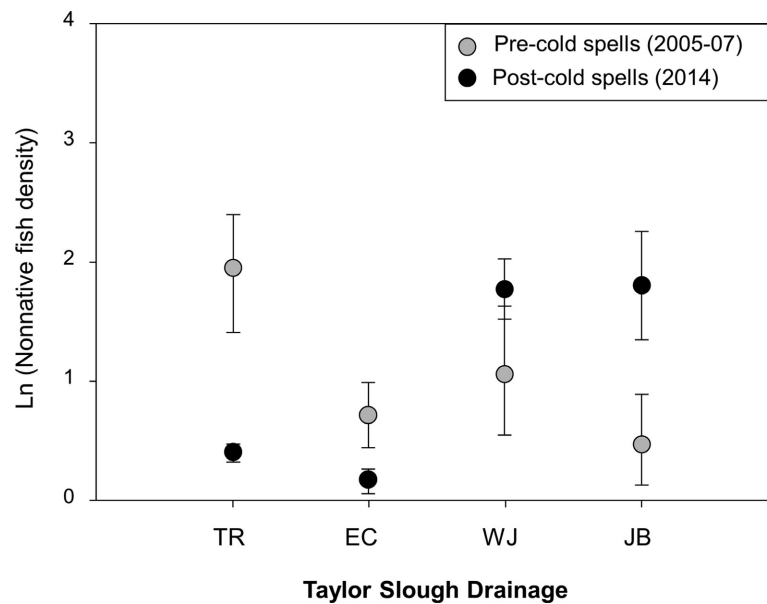
Fig. 5. Nonnative Mayan cichlid abundances (mean ± 95% CIs) for the pre-cold spell period (2005–2007, gray symbols) and 2014 (black symbols, the last year post-cold spell) for all sites in the Taylor Slough drainage. Sites are arranged from west to east (left to right, see Fig. 2 for site location)—sites to the east are closest to a canal.

and Pestrak 1982, Paperno et al. 2008, Shafland et al. 2008, Schofield et al. 2010, Idelberger et al. 2011), and generally preventing range expansion for many nonnative species (Lynch et al. 2013, Kreyling et al. 2015). During the cold spells, water temperatures dipped below the 9.5–11.1° C lethal limit of Mayan cichlids (Schofield et al. 2010). In the SR drainage, minimum water temperatures reached 8.1° C for the January 2008, 6.2° C for the January 2010, and 9.1° C for the December 2010 cold spells, respectively, likely resulting in the 100% declines in Mayan cichlid numbers observed. This finding agrees with previous studies showing that cold spells can cause mass mortality of nonnative species in the tropics/subtropics and drive abundances to very low numbers (Canning-Clode et al. 2011, Firth et al. 2011, Mazzotti et al. 2011).

Whether these large mortality events will "reset" invasions, and either permanently or temporarily cause the retreat of invasions, will depend on the resilience of affected populations. Two factors govern resilience or the rate of post-disturbance recovery (Fritz and Dodds 2004, Hershkovitz and Gasith 2013). First, resilience can be achieved by reproduction of surviving individuals to increase population densities. Nonnative species typically have life-history traits that promote rapid population growth, thus recovery is expected to be fast if surviving adults persist (Diez et al. 2012). South Florida's Mayan cichlids are no exception, achieving sexual maturity within their first year of life and reproducing in large spawning events directly preceding the wet season, when the most resources (food, space, etc.) are available, and with biparental care that enhances nest success (Faunce and Lorenz 2000). Second, resilience can result from immigration and recolonization from either local or regional refuges. In our nonnative fish populations, resilience was low, with only one site fully recovering in 4 yr. We hypothesize that this low resilience is directly related to the severity of the events, particularly the January 2010 cold spell, and the resulting high levels of mortality observed.

We also expect that due to the compounding effects and severity of three cold spells over a short period of time, nonnative resilience may have been primarily reliant on regional immigration (e.g., "rescue effect"; Gotelli 1991). This hypothesis stems from the variation in resilience observed across space. Of the six sites affected, the site that recovered was located closest to a canal (8.5 km, WJ in Fig. 2c), a potential source for nonnative

migrants. The SR sites are at an average of 28 km from the nearest canal, while the EC and TR are at 13–15 km (Fig. 2). The 2500 km of canals currently bisecting Everglades and other South Florida habitats (McVoy et al. 2011) are known to provide permanent deep-water habitat for fishes, including high numbers of nonnatives (D. A. Gandy and J. S. Rehage, *unpublished manuscript)*, and act as thermal refuges (Adams and Wolfe 2007, Schofield et al. 2010, Blewett and Stevens 2014).

Canals are voluminous and cut deep in to the limestone bedrock (4–5 m in depth), receiving warm groundwater from the aquifer. For example, during the January 2008 cold event, minimum water temperatures in Everglades habitats (marshes and alligator ponds) reached 3.7–11.1° C, while in nearby canals, minimum temperatures were only 20.4° C (Schofield et al. 2010). Our hypothesis is further supported by the fact that the only site where nonnative fishes experienced resistance to the cold spells, and where nonnatives were more abundant post relative to pre-cold events, is the TS site located closest to a canal (7 km, JB in Fig. 2). Furthermore, recent telemetry data show that Mayan cichlids inhabiting canals disperse greater distances into surrounding marshes than native fishes (>20 km from a canal in a season, Parkos and Trexler 2014). Thus, recovery may be slow because of the reliance on regional immigration, but it is expected at all affected sites (including the SR sites), since source populations are plentiful in the ecosystem and mobility is high for this invader. Anecdotal records show that Mayan cichlids have recovered from previous cold spells within several years of these mortality events (Trexler et al. 2000).

We propose that extreme climate events such as this sequence of cold spells may provide a management opportunity for nonnative species. Eradication and control programs are known to be most effective early in the invasion sequence (Simberloff et al. 2013). Management is often too expensive, destructive, or implausible later in an invasion once species are well-established and spread throughout the landscape. For fishes in particular, we lack effective control methods that can be used over large spatial areas and that are selective and target nonnative species only (Britton et al. 2011). Although nonnative eradication is most often an unattainable goal (Simberloff et al. 2013), climate extremes that cause mass mortality events could provide a rare opportunity for suppression and/or containment of affected populations. Resource managers could capitalize on these events by preventing immigration from source or refuge habitats (e.g., through containment measures such as barriers, Bullen and Carlson 2003) or by preventing rapid population growth at affected sites (e.g., through removal programs, Mueller 2005) that could be most effective if timed after mortality events.

In our case, intervention following an extreme cold spell could be targeted at preventing non-native fishes from regaining their pre-extreme abundances in wetland habitats or at minimizing recolonization from canal refuges back into these wetland habitats. This type of management would represent an extension of efforts at managing or restoring natural disturbance regimes to benefit native taxa and negatively affect nonnatives (e.g., fire regimes, Huston 2004; hydrological regimes, Kiernan et al. 2012). There are not many applications of this approach, but a study by Havill et al. (2015) showed that a nonnative C_4 grass species was more sensitive to burning during a drought than its native counterpart, supporting the notion that nonnative management should be poised for opportunities arising from a combination of disturbances, including extreme events.

Ecological communities worldwide will experience important reorganizations owing to the shifting distributions of nonnative species in response to climate change (Diez et al. 2012, Bellard et al. 2013). In fact, a meta-analysis by Sorte et al. (2012) shows that nonnative taxa show stronger responses to both the beneficial and detrimental effects of climate change relative to native taxa. Our study agrees with this finding with respect to extreme climate events. We showed that extreme cold spells can negatively affect nonnative fishes, with effects being more severe than those seen on native fishes, lasting several years, and with recovery being spatially variable and possibly reliant on regional refugia. For tropical and subtropical nonnative species, such as Mayan cichlids, the potential for an extreme cold event to curb invasions and positively impact native ecosystems and economies will depend on the future occurrence of cold spells. Models show that despite warming trends, cold spells will persist in the future, but major uncertainties remain on changes in their

frequency, intensity, and duration (Vavrus et al. 2006, Kodra et al. 2011, IPCC 2012, Gao et al. 2015). Changes to these parameters will directly influence the frequency with which ecologically important thresholds are reached and have major implications for the dynamics of both current and future invasions; deserving continued attention as improved forecasting becomes available.

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