Chilling damage in a changing climate in coastal landscapes of the subtropical zone: a case study from south Florida

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Abstract

Freeze events significantly influence landscape structure and community composition along subtropical coastlines. This is particularly true in south Florida, where such disturbances have historically contributed to patch diversity within the mangrove forest, and have played a part in limiting its inland transgression. With projected increases in mean global temperatures, such instances are likely to become much less frequent in the region, contributing to a reduction in heterogeneity within the mangrove forest itself. To understand the process more clearly, we explored the dynamics of a Dwarf mangrove forest following two chilling events that produced freeze-like symptoms, i.e., leaf browning, desiccation, and mortality, and interpreted the resulting changes within the context of current winter temperatures and projected future scenarios. Structural effects from a 1996 chilling event were dramatic, with mortality and tissue damage concentrated among individuals comprising the Dwarf forest's low canopy. This disturbance promoted understory plant development and provided an opportunity for *Laguncularia racemosa* to share dominance with *Rhizophora mangle*. Mortality due to the less severe 2001 event was greatest in the understory, probably because recovery of the protective canopy following the earlier freeze was still incomplete. Stand dynamics were static over the same period in nearby unimpacted sites. The probability of reaching temperatures as low as those recorded at a nearby meteorological station ($\leq 3\,^\circ$C) under several warming scenarios was simulated by applying 1° incremental temperature increases to a model developed from a 42-year temperature record. According to the model, the frequency of similar chilling events decreased from once every 1.9 years at present to once every 3.4 and 32.5 years with 1 and $4\,^\circ$C warming, respectively. The large decrease in the frequency of these events would eliminate an important mechanism that maintains Dwarf forest structure, and promotes compositional diversity.

Keywords: chilling events, climate change, community structure, disturbance, freeze tolerance, mangrove forests, mortality, recruitment, stand dynamics, subtropical coastal wetlands

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Introduction

Biotic responses to projected changes in global climate (Meehl *et al.*, 2007) seem certain to go beyond gradual shifts in modal conditions, extending also to changes in the intensity or periodicity of extreme events (Easterling *et al.*, 2000b; Fischlin *et al.*, 2007; Jentsch *et al.*, 2007). Much attention has been directed at climatic feedbacks

that could increase the severity or frequency of disturbances like hurricanes (Emanuel, 2005), droughts (Meehl *et al.*, 2007), or wildfires (Balling *et al.*, 2004). In contrast, disturbances likely to be reduced or eliminated in a warmer world have attracted less scrutiny, yet also would have important ecosystem consequences. In south Florida, which straddles tropical and temperate bioregions, examples include periodic cold temperature events that appear to control the northern distribution of species of tropical affinity (Stevens *et al.*, 2006; Stuart *et al.*, 2006). Easterling *et al.* (2000a) reported that

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the number of days with minimum temperatures below freezing has decreased in most regions of the world during the 20th century, in parallel with a 0.5 °C increase in average global temperature. Because disturbance events can play a critical role in maintaining biological diversity (Connell, 1978; Sousa, 1984; Tilman, 1996; Jentsch *et al.*, 2002), further attenuation in the freeze regime may induce changes in patterns of plant diversity and dominance. For instance, a region-wide reduction in the frequency, duration, or severity of cold temperature events may increase the likelihood that freeze-sensitive dominant species will increase in density and displace subcanopy vegetation, thereby reducing landscape heterogeneity. This important within-landscape process may coincide with more easily observed cross-landscape dynamics, such as the encroachment of coastally restricted species into interior wetlands, driven by changes in temperature, salinity, and/or fire regimes (e.g., Kangas & Lugo, 1990; Ross *et al.*, 2000).The regime of cold temperature events is one of many climate-related variables with the potential to affect vegetation pattern along subtropical coastlines in the future. Hurricanes are important organizing forces in the mangrove forest (Lugo, 2008), and changes in their intensity, frequency, or timing would elicit strong feedbacks (Ellison, 1994). In his seminal analysis of coastal zonation in mainland south Florida, Egler (1952) attributed much to the resident fire regime, which is expected to change in a warming world (Running, 2006). Ross *et al.* (2000) later demonstrated that sea level rise was responsible for a dramatic shift in the area's coastal vegetation in the half-century following Egler's study, both within the borders of the mangrove forest and where it interfaced with and supplanted inland marshes. These effects were greatly magnified by the interruption of freshwater sheetflow by roads, canals and levees, and by a substantial reduction in the ground water table (Parker, 1974). Both sea level rise and reduced freshwater input remain paramount drivers of mangrove forest ecology in the region today.

Behind the current invasion front, south Florida coastal vegetation is still in a state of transition. Here, monospecific stands of red mangrove (*Rhizophora mangle* L.) or, less often, black or white mangrove [*Avicennia germinans* (L.) Stearn. and *Laguncularia racemosa* (L.) C.F. Gaertn., respectively], in addition to buttonwood (*Conocarpus erectus* L.) and a small group of seaside herbs, have formed into distinct, physiographically determined assemblages (Lugo & Snedaker, 1974; Twilley, 1998). The upper plant canopy in these forests and shrublands plays an important structural role, reducing the likelihood of fire and perhaps buffering the understory from the impact of periodic freezes (Duever *et al.*, 1994). In this paper, we explore commu-

nity and population responses to two cold temperature events impacting mangroves along a coastal gradient. We focus on chilling-induced changes in stand structure in a Dwarf mangrove forest, and feedbacks between canopy structure and damage patterns during subsequent disturbance. We combine these observations with analysis of the winter temperature record from a nearby meteorological station, thereby providing a basis to project the influence of possible future reductions in chilling frequency or intensity.

Materials and methods

Study area

The study was conducted in mangrove communities in the Biscayne Coastal Wetlands (BCW) portion of Biscayne National Park, on the south Florida mainland (Fig. 1). Bounded on the east by Biscayne Bay and on the other sides by canals, the study area comprised five blocks of 25–30 ha, separated by east–west oriented drainage ditches. We report here on data collected in Blocks 1 and 4 from the south. These two units served as Treatment and Control, respectively, for an experimental rediversion of fresh water into the mangrove swamp from the L-31E canal, which borders the area on the west. Initiated in August 1997, the treatment elicited significant effects on the physical environment and Dwarf mangrove communities within about 200 m of the delivery structure, but impacts outside of that zone were negligible (Ross *et al.*, 2003). In this paper, we focus on stand dynamics in untreated Block 4, and beyond the extent of hydrologic treatment influence in Block 1 (Fig. 1).

Mangroves in BCW exhibit a distinct zonation in structure and productivity that is likely driven by underlying hydrology and soils. Tall forests (mean aboveground production, 28.5 Mg ha^{-1} yr^{-1}; Ross *et al.*, 2001) prevail close to the coast and may exceed 20 m in height at maturity. Forest stature decreases inland, finally becoming a low scrub (mean aboveground production, 7.7 Mg ha^{-1} yr^{-1}; Ross *et al.*, 2001) <1.5 m tall that covers extensive areas several hundreds of meters or more from shore. The interior-ward decline in forest stature and productivity is associated with a transition from frequent and ephemeral to infrequent and persistent flooding regimes, organic to calcareous soils, and increased phosphorus limitation. The end members along this gradient represent Fringe and Dwarf forest, respectively, in the classification system of Lugo & Snedaker (1974). The distinction between Dwarf and Fringe forest trees is apparently not genetically based (Lin & Sternberg, 1992b), as the 'Dwarfed' architecture referenced in the former is determined primarily by
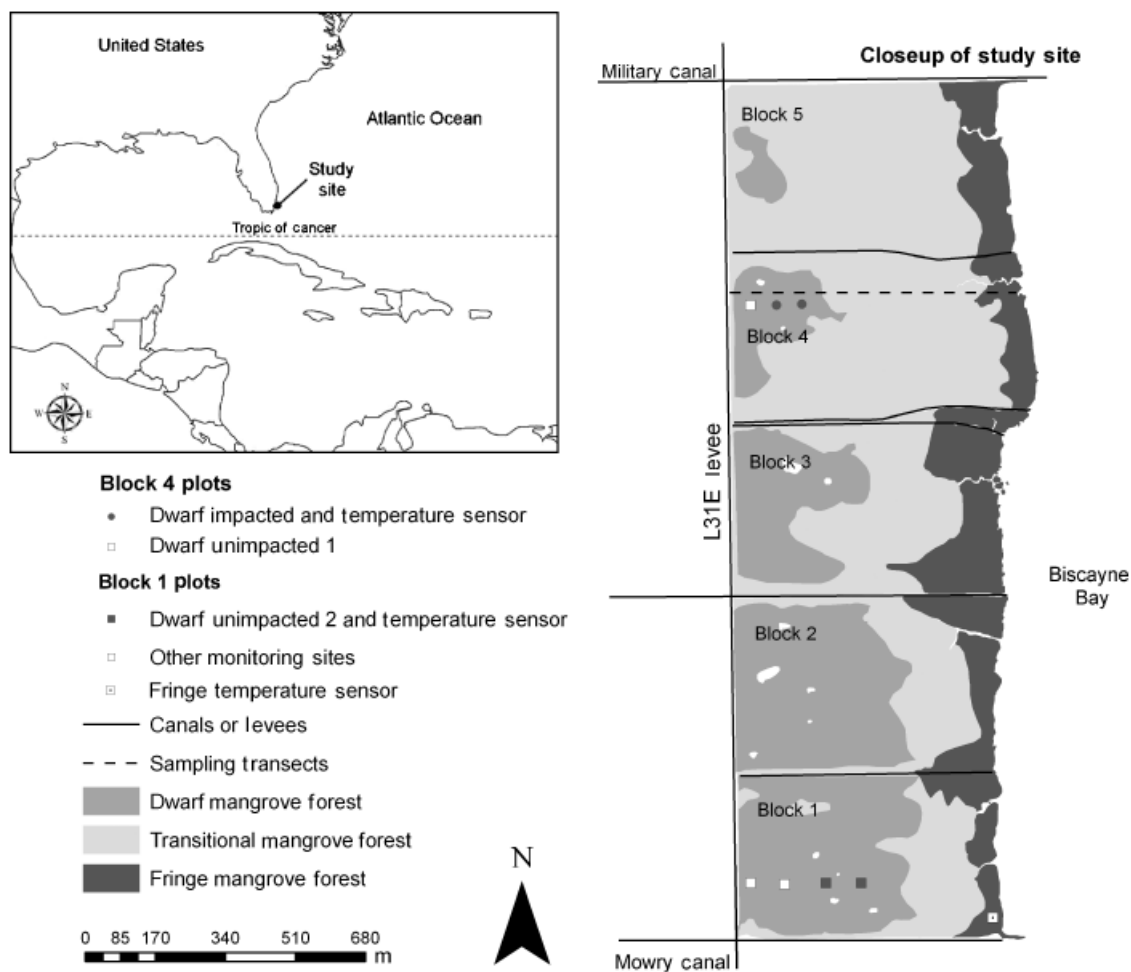
Fig. 1 Plot and transect layout within study area in southwestern Biscayne Bay, Florida, USA.

environmental factors such as those elaborated above (Koch & Snedaker, 1997; McKee *et al.*, 2002).

The coastal gradient in ecosystem characteristics in the study area coincides well with compositional variation in vegetation. Davis (1940) described a general sequence in which *R. mangle* was most abundant adjacent to the coast, while *A. germinans*, *L. racemosa*, and *C. erectus* became dominant at successively distant locations inland. However, species distributions within individual landscapes rarely fit this broad zonation pattern exactly. At BCW, *R. mangle* does form a nearly monospecific band within the first 20 m of the coast, but further inland a mixed species assemblage prevails through communities with canopy heights down to ~ 1 m. Beyond that point, *R. mangle* once again predominates in the center of the low Dwarf forest, where a moderately full canopy arches tens of centimeters above a dense seedling layer in which *L. racemosa* is often most abundant. *C. erectus* occurs mixed with the other three mangrove species in isolated tree islands within the

Dwarf forest, and along road and mosquito ditch embankments that frame the blocks. *C. erectus* and *L. racemosa* are codominant in mangrove forests west of the L-31E levee and canal.

Like other parts of south Florida, BCW is prone to a wide range of disturbances: lightning strikes (Smith *et al.*, 1994; Whelan, 2005; Zhang *et al.*, 2008); hurricanes or tropical storms (Craighead & Gilbert, 1962; Baldwin *et al.*, 2001; Ross *et al.*, 2006); and freeze events (Lugo & Patterson Zucca, 1977; Olmsted *et al.*, 1993). Lightning strikes are a regular source of small-scale (10–20 m diameter) patchiness in tall forests immediately adjacent to the coast, but similar impacts have not been observed in the Dwarf forest. Likewise, enormous hurricane impacts are usually restricted to the Fringe forest. The most recent major storm, Hurricane Andrew (1992), had minimal effect on the Dwarf forest, probably because even the largest stems were completely immersed during the period of highest winds. In contrast, cold temperature events are endemic to the Dwarf forest.

Prior to our study, the most recent took place on December 24–25, 1989, when temperatures reached $-4\,^{\circ}C$ at a National Weather Service station about 14 km west of the BCW study area (Degner *et al.*, 2002), but were $+1\,^{\circ}C$ at Homestead Air Reserve Base (HARB), the nearest meteorological station. Ecological impacts of the 'Christmas freeze' within the BCW study area are unknown, but extensive mortality was observed in Dwarf forests elsewhere in the region (Olmsted *et al.*, 1993).

Hereafter in this study, we apply the terms 'chilling event' or 'cold temperature event' generically to meteorological conditions that produce symptoms usually associated with freeze damage in plants, i.e., leaf browning and desiccation, regardless of whether or not true freezing temperatures are reached. Many tropical species, including mangroves, exhibit such symptoms at temperatures several degrees or more above $0\,^{\circ}C$ (Markley *et al.*, 1982). We reserve the term 'freeze event' for episodes in which temperatures are known to reach $0\,^{\circ}C$ or less.

Observations of chilling impact

We studied chilling events that took place on January 9, 1996 and January 5, 2001. Three to 4 weeks after each event, we documented direct, community-level effects through a general survey of leaf damage patterns throughout the study area, followed by detailed observations along three transects in Block 4 (Fig. 1). The transects were approximately 60 m apart, extending east from the base of the L-31E levee to a point beyond which no further chilling effects were observed. At 10 m intervals along each transect, we estimated the proportion of browned/fallen leaves in 20-cm height strata beginning at ground level. Estimation of damage was facilitated by viewing each stratum against the background of a rectangular ($20\,cm \times 30\,cm$) white board, held at $\sim 50\,cm$ distance from the eyes of the observer. A damage profile was created for each point by averaging separate observations facing north and south in each height stratum.

Survival, establishment, and stand development in census plots

In April–July 1995, seven plots were established in the BCW Dwarf forest in conjunction with the freshwater rediversion pilot project alluded to earlier. Four plots were in Block 1 and three in Block 4, whose Dwarf forest occupied a substantially smaller topographic basin. Plot locations were aligned along an E–W transect that bisected each block. Plots were rectangular in shape, with a width of 0.5 m and length that varied from 3 to 5 m, depending on initial stem density; we initiated monitoring with at least 100 individuals per plot. During the first census, and in subsequent annual surveys in November/December of the next 6 years, each newly encountered, lignified individual that had produced a minimum of two pairs of leaves was tagged and added to the database. Over the course of the study, we monitored the growth and survival of 1133 individuals within a total plot area of $10\,m^2$. The following information was recorded annually for each individual: status (live/dead), crown center and stem base coordinates within plot ($\pm 5\,cm$), height at crown base, total height, crown length and width, and basal diameter.

Dwarf forest census plot locations provided a framework for assessing chilling effects and monitoring post-chilling recovery. The two easternmost plots in Block 4 were directly affected by both the 1996 and 2001 chilling events, while the western plot in the same block was outside the affected area (Fig. 1). The former plots were grouped for analysis as Chilling-Impacted, and the latter plot was designated Chilling-Unimpacted 1. Because the vegetation represented by these plots differed somewhat in predisturbance structure, we also report on data from two plots from the eastern portion of the Dwarf forest in Block 1, outside the zone of influence of the hydrologic treatment, in an area that exhibited no visual effects from either event. These plots, which were grouped as Chilling-Unimpacted 2, closely resembled the Chilling-Impacted group in initial (1995) stand structure. Comparative patterns of mortality, recruitment, and stand development in these three plot-groups during 1995–2001 therefore provided a case study of population responses in nearby impacted and unimpacted areas.

Stand structure, seedling establishment, and mortality were examined by plot-group and species. We summarized species dynamics by calculating relative densities for the most common species, *R. mangle* and *L. racemosa*, in large and small size classes, based on an approximately equal division of the range of sizes present in 1995. To address immediate mortality from the two chilling events, we applied logistic regression to the survival of *R. mangle* and *L. racemosa* in the Chilling-Impacted group over the 1995–1996 and 2000–2001 periods, using species and initial height as independent predictors. These analyses bear the assumption that other sources of mortality were minimal in comparison to the chilling event during the years in question.

Meteorological records

During the 1996 chilling event, minimum temperatures in the BCW Dwarf forests were recorded at meteorological stations that had been temporarily established in

the centers of both Blocks 1 and 4. Temperature was measured with shielded copper-constantan thermocouples using a CR10 micrologger with a wiring panel temperature reference (Campbell Scientific Inc., Logan UT, USA). Values were recorded every minute and stored as half-hour averages. No on-site meteorological data were available during the 2001 chilling event, but temperature data for both events were available from HARB, 3 km distant. Several years after concluding the BCW monitoring program, we examined winter temperature patterns within the same landscape in more detail. In December 2003, we affixed two iButton® (Dallas Semiconductor Corp., Dallas, TX, USA) high resolution thermochrons (accuracy ± 1 °C; resolution of 0.125 °C) in weather shelters set 1.5 m above the soil surface in the Dwarf forest in Blocks 1 and 4, and in the Fringe forest of Block 1, about 30 m from the Biscayne Bay shoreline. We examined the diurnal temperature patterns at the three mangrove sites for 74 days of record (December 18, 2003–February 29, 2004), and used paired *t*-tests to compare daily minima at each field location with those recorded at HARB.

To put the 1996 and 2001 chilling events into historical context, we examined the HARB record, which extends from 1956 to present. First, we screened hourly data during winter months (December–February) for missing records, eliminating years in which gaps in the record precluded analysis (e.g., December 1971–February 1973, December 1992–February 1996). By applying the generalized linear modeling (GLM) procedure in STATISTICA (StatSoft Inc., Tulsa, OK, USA) to the remaining data, we tested whether the annual number of chilling events or chilling hours changed over the period 1956–2005. Since these two dependent variables were discrete (count) data, we assumed a Poisson's distribution of errors and applied the log-link option.

We also used the winter temperature record from HARB to project the future probability of chilling events in different BCW wetland settings. The first step was to model the historical distribution of daily minima. We analyzed data from 1956–2005 from December 10th to February 25th – a period that included all dates on which recorded temperatures fell to 3 °C or less at HARB. Because the frequency distribution of minimum temperatures was negatively skewed (Skewness = −0.606), we fit a β distribution curve (Yao, 1974) to it using the Capability function in SAS 9.1. We constrained the lower limit of the distribution at −8.0 °C, while using maximum likelihood estimates for the function's other three terms. For selected temperatures, we then calculated cumulative beta densities, which were equivalent to the probabilities of temperatures dropping to those levels or below under 1956–2005 climatic conditions. We also simulated the same probabilities under several warming scenarios, by adding 1–4 °C uniformly to the 1956–2005 temperatures and recalculating the beta distribution and cumulative densities. We chose 4 °C as upper limit for simulation, as it is the maximum projected global average surface warming by the end of 21st century (Meehl *et al.*, 2007).

Results

Patterns of chilling damage and mortality

The single weather station operating in the Dwarf forest during the 1996 freeze event was near the Chilling-Impacted plot-group, where −1 °C was recorded for several hours. Concurrent temperatures at HARB were 2.2 °C. Chilling effects in BCW were restricted to Dwarf forests in variable-sized patches enclosed by taller forest, which were prevalent within a short distance east of the L-31E Canal (Fig. 1). Block 4 was one of the smallest of these patches, and while the extent of damage there exceeded other blocks in the study area, its distribution within the patch paralleled that in other impacted areas (Fig. 2a). Chilling effects were not observed where the forest canopy exceeded 2.2 m in height. Effects were also minimal where canopy height and surface elevation were lowest, in the center of the basin; here, damage was nil or restricted to crowns emerging above the general canopy level of ca. 80 cm. Effects were most severe where average canopy height was 1–2 m, i.e., along the sides of the Dwarf forest basin. Within such areas, impacts usually decreased downward from the top of the plant canopy, with the level beneath which leaves were undamaged varying from about 20 cm to >1 m above the soil surface.

The logistic regression model for 1995–1996 survival identified a highly significant Species × Height interaction effect, so the effect of height was analyzed separately for the two species (Fig. 3a). Small *R. mangle* individuals had a much higher probability of survival than larger stems (χ^2 of 1-factor model = 63.40; $P < 0.001$), but height had no effect on *L. racemosa* survival. Based on the functions presented in Fig. 3a, small *R. mangle* stems had a higher likelihood of surviving the freeze than similar-sized *L. racemosa*, but the situation was the opposite for large individuals.

During the 2001 chilling event, no temperature data were directly available from the study area, but the low temperature at HARB was 2.7 °C. The damage profile associated with this event resembled that of the 1996 instance, in that symptoms were once again most severe along the sides of the basin and in the upper portions of the canopy (Fig. 2b). Though the record from HARB suggested that temperatures may have been slightly less severe than in 1996, leaf damage during the second
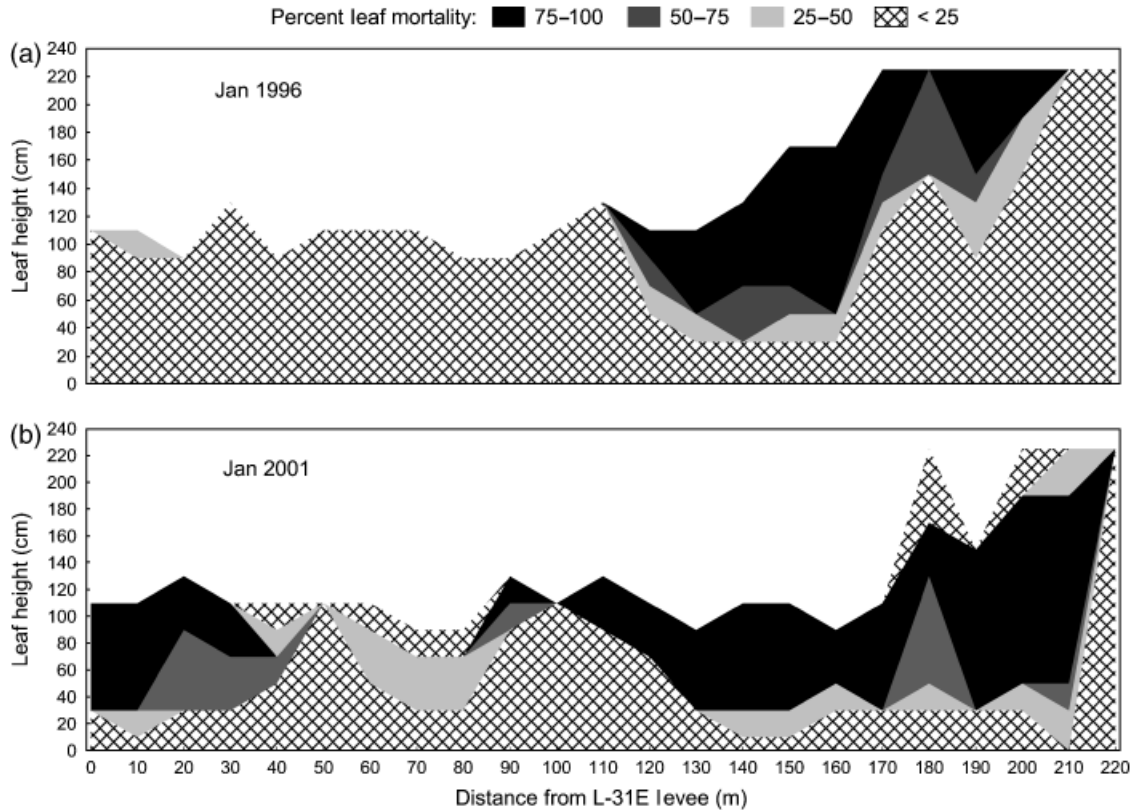
Fig. 2 Leaf mortality profiles along a Dwarf forest transect after two freezes. (a) A transect in Block 4 several weeks after the January 1996 freeze; (b) The same transect several weeks after the January 2001 freeze.

episode penetrated to 40 cm, which was slightly closer to the ground than during the earlier event. However, these structural patterns were not reflected at the population level. Censused *R. mangle* individuals experienced no mortality at any size during 2000–2001. During the same period, *L. racemosa* did exhibit a size-dependent survival function ($\chi^2 = 41.13$; $P < 0.001$), but in this case, mortality was restricted to small stems (Fig. 3b). Thus, community-level effects of the two events differed, in that dominant individuals were affected in 1996 and understory stems in 2001.

Seedling establishment

Seedling establishment and survival varied substantially among species, sites, and years during the study. *R. mangle* seedling establishment was $< 10 \, \text{stems} \, \text{m}^{-2} \, \text{yr}^{-1}$ throughout the 1996–2001 period at all sites (Fig. 4). The banner year for establishment that *L. racemosa* experienced in 1996 coincided with the first chilling event, but appeared to be unrelated to the level of impact, with $\sim 25 \, \text{stems} \, \text{m}^{-2}$ established in both Chilling-Impacted and Chilling-Unimpacted 1 plots, and $18 \, \text{stems} \, \text{m}^{-2}$ in Chilling-Unimpacted 2. However, many more individuals from the 1996 cohort remained alive throughout

the remainder of the study in the Chilling-Impacted group ($20 \, \text{stems} \, \text{m}^{-2}$) than in the other two groups (9 and $4 \, \text{stems} \, \text{m}^{-2}$ in Chilling-Unimpacted 1 and 2, respectively). In subsequent years, *L. racemosa* seedling densities ranged from 0 to $10 \, \text{stems} \, \text{m}^{-2}$, with lower rates of establishment in Chilling-Unimpacted 1 than in Chilling-Impacted or Chilling-Unimpacted 2. The 2001 chilling event elicited no discernible effect on that year's establishment in either species.

Stand development following chilling

Stand dynamics in chilling impacted and unimpacted sites are summarized in Fig. 5. In 1995, the upper strata of all three stands were dominated by *R. mangle*, with *L. racemosa* scattered in the canopy but dominant in the seedling layer. At that time, the canopy was highest in the Chilling-Impacted plots, the only group that included individuals $> 1 \, \text{m}$ tall. During the next 6 years, the two unimpacted groups exhibited steady canopy development and slow increase in the importance of *L. racemosa*, as indicated by its gradual increase in relative density in the $> 40 \, \text{cm}$ height class in both stands. Not surprisingly, stand structure and composition in the Chilling-Impacted group were not nearly as
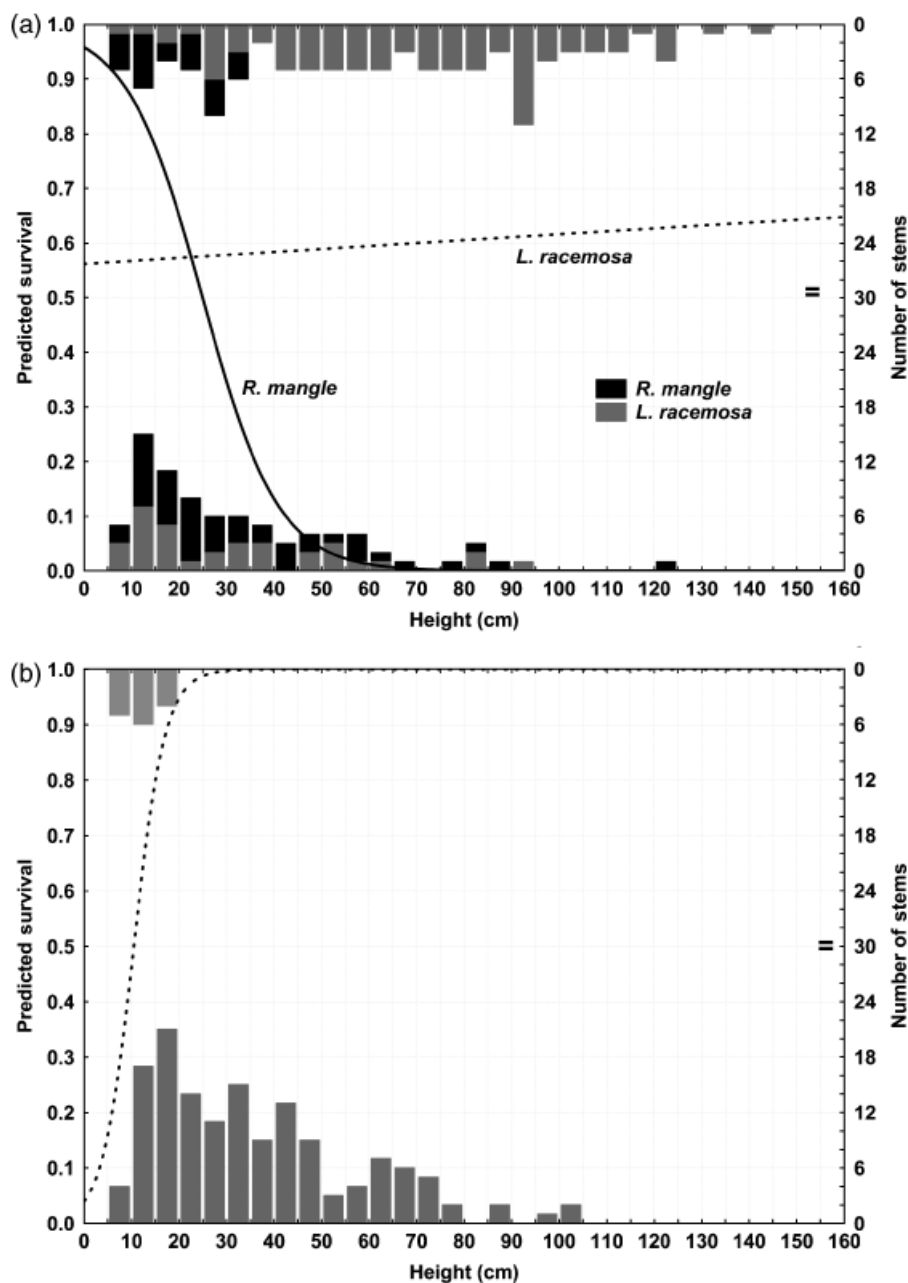
Fig. 3 Logistic regression functions of mangrove survival with respect to height in the Chilling-Impacted Dwarf plot, superimposed over histograms representing individuals that survived (bottom axis) and died (top axis) during the year following the event. (a) 1995–1996 survival of *Rhizophora mangle* and *Laguncularia racemosa*, i.e., in the wake of the January 1996 freeze; (b) 2000–2001 survival of *L. racemosa*, i.e., following the January 2001 freeze.

stable. The 1996 census, which was conducted about 10 months after that winter's chilling event, found *L. racemosa* the leading species in the the stand's reduced canopy layer. *L. racemosa*'s proportional representation also increased in the lower strata, due to that year's bumper crop of newly established seedlings. By 2000, both *R. mangle* and *L. racemosa* were well represented in a canopy that approached the density and size of the preimpact forest, while *L. racemosa* comprised an even larger majority than before within a dense seedling cohort (increase in relative density from 70.2% to 96.4%; Fig. 5). The effects of the 2001 chilling event were minor in comparison to those observed in 1996. The density of *R. mangle* and *L. racemosa* individuals in the larger size classes, i.e., >80 and >60 cm tall, respectively, was substantially reduced, perhaps by
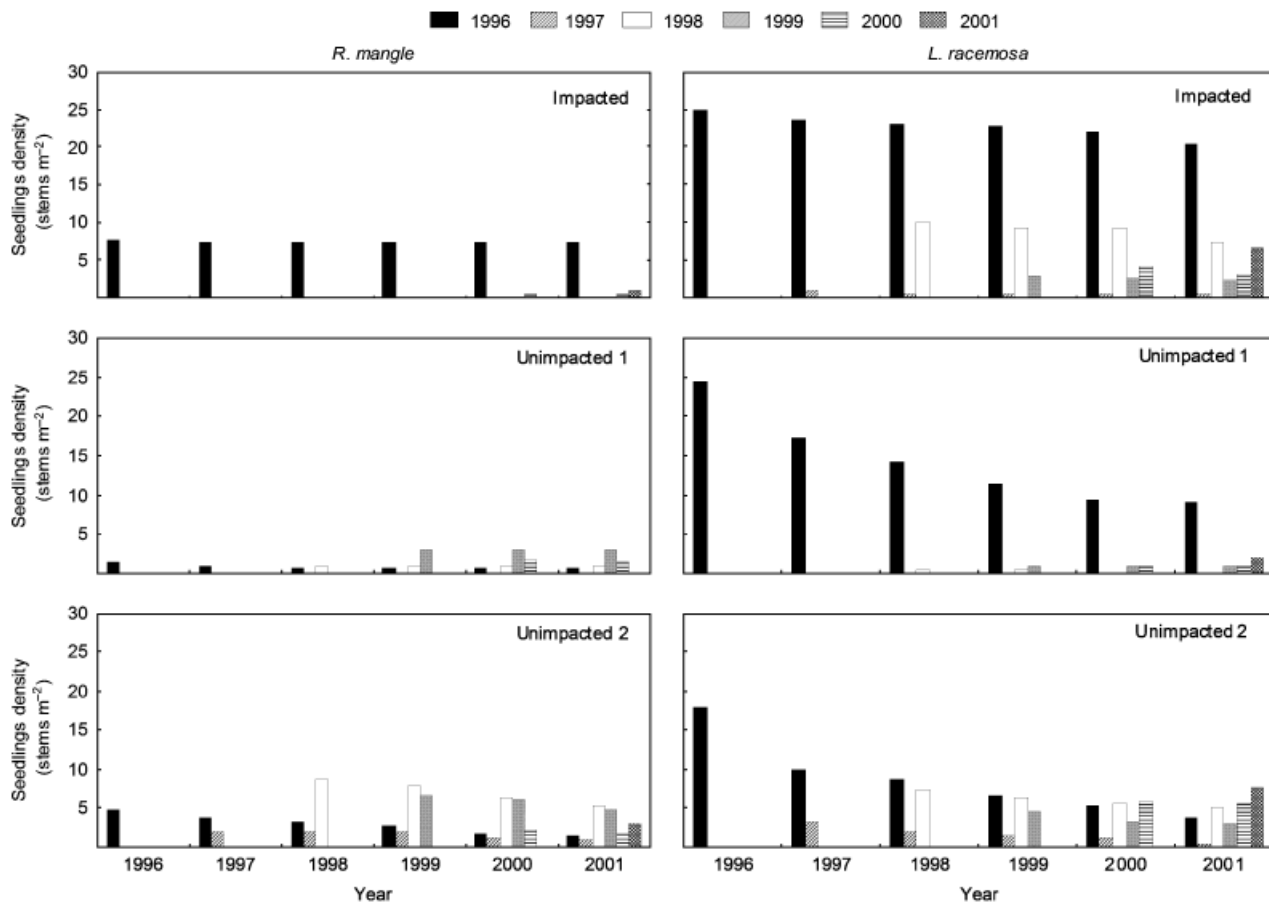
Fig. 4 Mean seedling densities of *Rhizophora mangle* and *Laguncularia racemosa* cohorts established in 1996–2000 in Chilling-Impacted and Chilling-Unimpacted (1 and 2) Dwarf forest sites.

pruning back of exposed branches, but overall density and species composition were not much affected.

Historical frequency of chilling events at BCW

The relationships between winter temperatures at HARB and at several microsites within the BCW study area were investigated by comparing daily minima from the NOAA meteorological station during the winter of 2003–2004 to coincident data from the network of recorders established in the study area. Because the nature of these relationships appeared to vary with temperature, we divided the data into two groups, i.e., those days with daily minima < 10 °C and those with minima ≥ 10 °C at HARB. Minimum temperatures at Chilling-Unimpacted 2 and in the adjacent Fringe forest were indistinguishable from HARB on cold days, while on warm days the effect of site was significant but minor, i.e., < 1 °C. In contrast, daily minima at the Chilling-Impacted plot were substantially lower than at HARB, especially on cold days. On the eleven days in which temperatures dipped below 10 °C at HARB, the

average minimum temperature at the Chilling-Impacted site was 3.7° cooler. These patterns are illustrated for the period December 19–21, when temperatures reached their seasonal minimum at all three field sites. Daytime temperatures were coolest in the Fringe forest, but daily lows were arranged in the order Chilling-Impacted < Chilling-Unimpacted < Fringe forest, with the Chilling-Impacted site appearing to represent a very distinct freeze pocket (Fig. 6).

To estimate how often such events may have occurred in these settings in the past, we screened the HARB temperature record for periods in which temperatures dropped below 3 and 0 °C, which we surmised would coincide with chilling damage in vulnerable and less-susceptible Dwarf forest sites, respectively. We chose 3 °C for susceptible sites because (1) minima were slightly < 3 °C at HARB during both 1996 and 2001 chilling events, and (2) temperature minima recorded in our Chilling-Impacted site during cold nights in 2003–04 were slightly > 3° colder than those registered at HARB. We chose 0 °C because we found no evidence of chilling damage at our less-susceptible sites during the
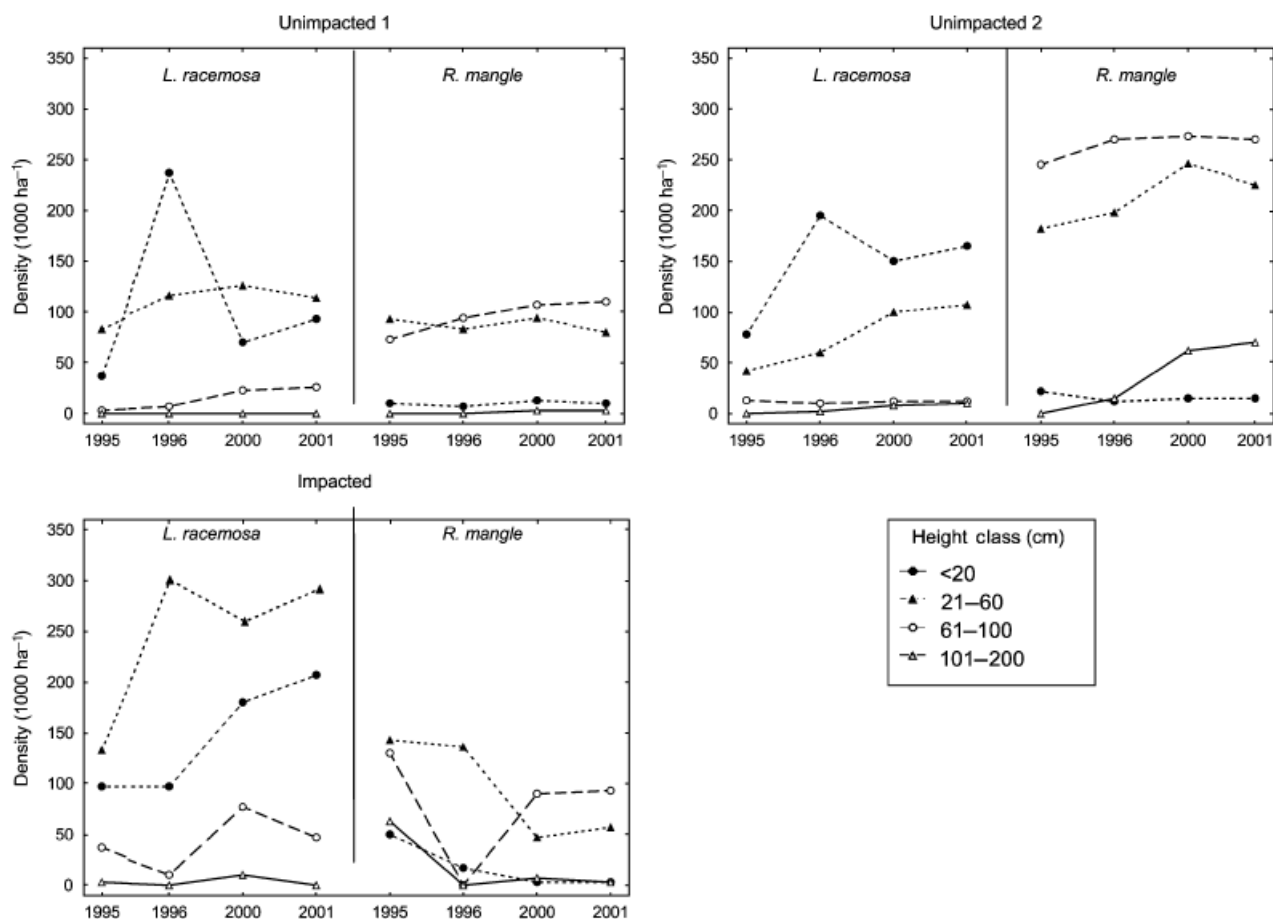
Fig. 5 Relative densities and height profiles of *Rhizophora mangle* and *Laguncularia racemosa* in freeze-impacted and nonimpacted sites in the Dwarf forest, 1995–2001. Densities in each size class are in thousands of individuals per hectare. Two other mangrove species, *Avicennia germinans* and *Commelina erecta*, were present in low numbers in several years, but are not included.

1996 and 2001 events, and because 2003–2004 minima at Chilling-Unimpacted 2 did not differ from those at HARB.

Over the 42 full years of record, temperatures at HARB fell below 0 °C only twice, in 1977 and 1985. Daily minima did reach 3 °C on 22 separate occasions, or about once every 2 years (Fig. 7). Over the period of record, there were a total of 107 h of such temperature. We used the GLM procedure to assess temporal trend in these data. Though there was a decreasing trend in both chilling events and the annual number of hours below 3 °C, their relationship with time was not significant (Wald statistic = 2.46, $P = 0.12$ and Wald statistic = 1.14, $P = 0.29$, respectively).

Projected occurrence of chilling events in a warmer climate

The frequency distribution of daily minima at HARB during December 10th-February 25th of 1956–2005 was

well fit by the beta function ($\chi^2 = 198.46$ for a bin size of 2 °C). According to the fitted function, the daily probability of reaching temperatures likely to cause chilling damage in vulnerable Dwarf mangrove sites under recent climatic conditions are 0.67%, which, based on 78-day season, equates to one event every 1.9 years. The corresponding values for less susceptible sites are 0.093%, or once every 14 years (Table 1). With 1° of warming, which is the low end of the IPCC projections for the next century, these return intervals become 3.4 and 32.5 years, respectively. With 4° of warming, which is considered an extreme climatic scenario, chilling events would recur every 32.5 years on vulnerable sites, and on less susceptible sites once every 1250 years.

Discussion

The relationship between climate and the distribution of terrestrial ecosystems forms the basis of most ecological classification systems (Emanuel *et al.*, 1985). The
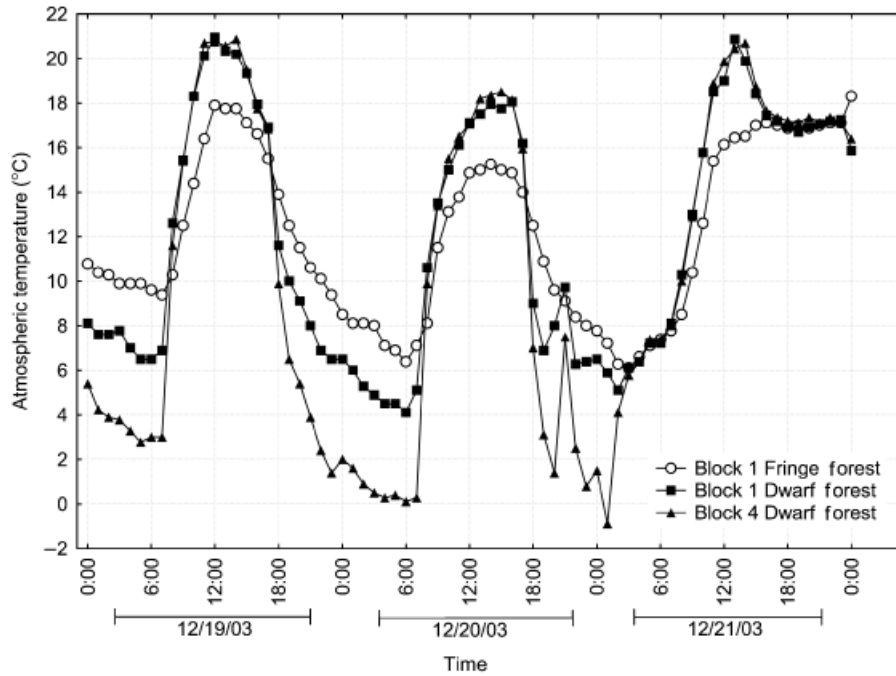
Fig. 6 Hourly variation in temperature (1 m above ground) at three BCW sites through the waxing and waning of a cold front in December 2003. Note the warmer nighttime temperatures in the Fringe site. Note also the difference in minimum temperatures between the two Dwarf forests, which varied markedly in the extent and degree of enclosure by taller vegetation (see Fig. 1).

Life-Zone Classification proposed by Holdridge (1947) uses hierarchical climate indicators to analyze global and regional-scale biogeographic patterns. At the global scale, bioclimatic zones are first defined by mean annual temperature (MAT), and secondarily by the frequency of killing freezes, which comprises a predictable stress to which the biota has evolved. Local topography, the distribution of large bodies of water, and vegetation structure can affect the temperature regime at the regional scale, and numerous vegetation associations may be present, depending on soils, plant physiology, or lesser climatic variables (Lugo *et al.*, 1999). The three warmest bioclimates are: tropical (MAT $\geq 24\,°C$; freeze absent), subtropical (MAT $12–24\,°C$; freeze return interval >3 years), and warm temperate (MAT $12–24\,°C$; freeze return interval ≤ 3 years) (Holdridge *et al.*, 1971). South Florida qualifies as tropical on the basis of temperature (MAT $24.4\,°C$), but the occurrence of the chilling events that were the object of our investigation places the area between the three bioclimatic regions. For the most part, the region's ecologists have characterized its climate as subtropical (e.g., Craighead, 1971), while recognizing that the patterns in the intensity of winter cold temperature events represented an important source of regional-scale biotic heterogeneity. The assumption underlying our study is that with further climatic warming, cold temperature episodes will di-minish in coastal landscapes, likely resulting in cross-scale modification to the distribution of vegetation. The extent of warming and the sensitivies of various communities to it will determine how severe the ecological repercussions will be.

Chilling events and coastal landscape structure

Well before the establishment of a modern climatic monitoring network on the south Florida mainland, freezes were noteworthy and well documented, perhaps due to their impacts on agriculture. During the 25-year period 1894–1918, subzero temperatures were reached in at least 9 years in the area between Miami and Flamingo, near the end of the peninsula (W. Krome; described in Craighead, 1971). A weather station established at Homestead Experiment Station (HES) in 1931 showed temperatures $\leq 0\,°C$ in 29 of the next 58 years (NOAA, 2006). This rate of one subzero temperature episode every 2 years was not approached at HARB, the station closest to our site, where only two such events were recorded during the period 1956–2005. HARB and HES are 4 and 16 km from the coast, respectively, so the difference between the two climatic records may reflect a strong moderating effect of the waters of Biscayne Bay on cold temperatures.
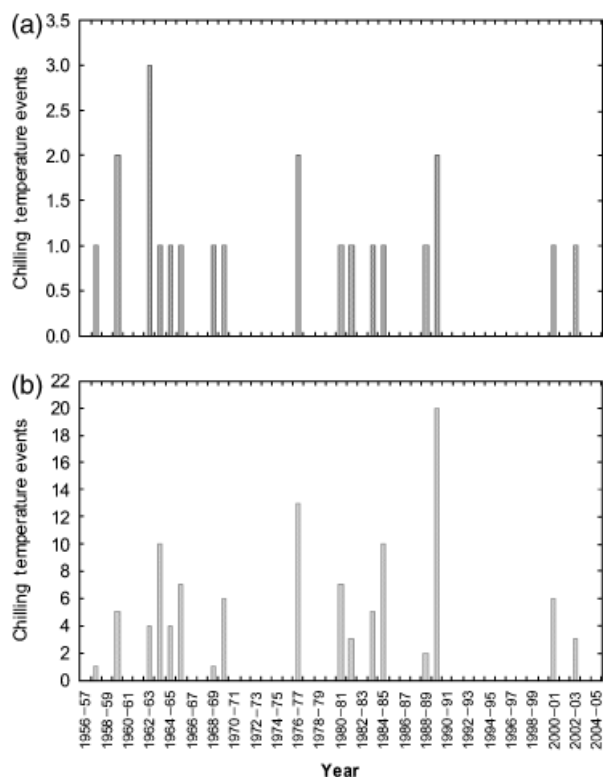
Fig. 7 Annual number of chilling events (a) and chilling hours (b) recorded at Homestead Air Reserve Base, 1957–2005. Chilling events are grouped into those likely to have affected susceptible sites ($\leq 3\,^\circ$C) and less susceptible sites ($\leq 0\,^\circ$C). Fragmentary data from 1972–73 and 1992–1995 are not included.

Table 1 Daily and annual probabilities of experiencing freeze damage in vulnerable and less susceptible Dwarf mangrove sites during the mid-winter period (December 10–February 25), under climatic conditions of 1956–2005, and under several likely 21st Century warming scenarios (IPCC)

Site vulnerability to freeze	Vulnerable sites		Susceptible sites	
Climatic conditions	Daily prob-ability (%)	Return interval (years)	Daily prob-ability (%)	Annual prob-ability (%)
Baseline (1956–2005) winter climate	0.68	1.90	0.09	13.8
Baseline + 1 $^\circ$C	0.38	3.41	0.04	32.5
Baseline + 2 $^\circ$C	0.20	6.58	0.02	87.8
Baseline + 3 $^\circ$C	0.09	13.84	0.004	288
Baseline + 4 $^\circ$C	0.04	32.48	0.001	1250

Return intervals were obtained from annual probability of freeze occurrence which was simply the product of daily probability and number of potential days (78) on could occur in a particular year.

The low frequency of subzero temperatures at HARB does not mean that chilling events have been unimportant in the nearby mangrove forests. Mangroves are sensitive to both cold air and water. The northern distribution limit of these communities coincides with the 20 $^\circ$C isotherm of sea temperature in much of the world (Duke *et al.*, 1998), and many species, including the BCW dominants *R. mangle* and *L. racemosa*, demonstrate some damage symptoms when air temperatures drop below 4 $^\circ$C (Markley *et al.*, 1982). Chilling events in south Florida are usually associated with low humidity, clear skies, and windless nights. Under these conditions, radiative cooling is accompanied by the collection of colder, denser air in topographic depressions (Winsberg *et al.*, 2003), where cold air sinks in more rapidly than it can drift out (Hough, 1945). Within the coastal wetland landscape, the effects of the subdued topography on temperature are mostly indirect, through its influence on vegetation structure. This is especially true in the Dwarf forest basins, where an increase in surface elevation of 10 cm typically results in an increase in mangrove canopy height of 1 m or more (Fig. 2). The resultant vegetation mosaic provides a template for frost pockets to form in small, vegetation-defined basins that limit air movement. Consequently, nighttime winter temperatures in these enclosed microsites may be substantially colder than in more open nearby locations. For instance, winter nightly minima in one of our Dwarf forest sites during 2003–2004 averaged >3 $^\circ$C lower than those recorded at HARB on the coldest nights of winter, while temperatures at an adjacent open site were similar to those at HARB (Fig. 6).

Spatial variation in mangrove forest temperature can also extend to the vertical dimension. While we did not measure this temperature profile directly, the results of our studies of community- and population-level responses of cold-sensitive vegetation are consistent with several longstanding assumptions. The first is that cold temperatures can be moderated by the proximity of water, even at local scales (Obeysekera *et al.*, 1999). Onsite stage recorders indicated that surface water was not present during either of the incidents we studied, but the organic soils in these sites are constantly saturated (Ross *et al.*, 2003). In combination with the relatively dense ground vegetation layer, these wet soils likely result in a saturated air layer close to the ground, and a strong humidity gradient across the first meter or so above it. One consequence of this gradient in humidity would be a temperature profile in which the warmest conditions were found near the ground surface. The upward-increasing damage pattern we observed in both chilling events (Fig. 2) was consistent with such a profile.

Physiological factors may also have contributed to the observed vertical stratification of leaf damage. For instance, Ball *et al.* (1997, 2002) found that *Eucalyptus pauciflora* leaf damage in wintertime arose primarily from the co-occurrence of low temperatures and high light intensities, which caused photosynthetic inhibition and subsequent oxidative damage due to free radicals. A similar interaction may occur on bright south Florida mornings that usually follow the coldest winter nights.

Another assumption implicit in the above discussion is the importance of plant canopies in buffering extremes in the subcanopy temperature regime (Hough, 1945; Myers, 1986). Our data on patterns of vegetation damage and population demographics in the wake of the two chilling events strongly support this assumption. Comparison of the damage profiles from the 1996 and 2001 events (Fig. 2) suggests that cold temperatures extended wider and penetrated deeper into the canopy in the second instance. We suspect that a contributing factor was the prior condition of the Dwarf forest canopy, intact at the time of the first event, but still in an incomplete stage of recovery in the second instance. A primary repercussion was a shift in the concentration of mortality from individuals of canopy stature in the 1996 event to small seedlings, which were more exposed in 2001. Imbert *et al.* (1996) described the phenomenon by which large trees protect smaller ones from disturbance as the 'shield effect.' The disturbance in their study was a hurricane, but the principle could apply equally to protection from cold temperatures provided to the understory by the Dwarf forest canopy in 1996. Reduced by the first disturbance, the shield effect of the mangrove canopy had not entirely recovered within the 5 years between chilling events.

R. mangle and *L. racemosa*, the two most abundant mangrove species in the BCW Dwarf forest, occupied different canopy strata at the outset of our study. Thus, differences in species response to the 1996 and 2001 chilling events, i.e., higher mortality in *R. mangle* in the first event and higher mortality in *L. racemosa* in the second, may be a function of the distinct stratification of structural damage discussed above. Species sensitivities appeared to play an additional role. For instance, large *R. mangle* stems were much more likely than similar-sized *L. racemosa* to succumb during the year following the 1996 chilling event (Fig. 3a). This response appeared to be a result of the different capacities of the two species to resprout from dormant basal buds, because initial observations a few weeks after the event suggested that *L. racemosa* had experienced *more* dieback (Ross *et al.*, 2003). Sprouting capacity is limited in *R. mangle*, because its dormant buds retain viability for only a year or so (Tomlinson, 1986). In contrast,

L. racemosa is known to resprout readily from long-lived buds (Baldwin *et al.*, 2001), but its seedlings may take several years to build up a population of dormant buds, or to accumulate the belowground resources needed to sustain sprout growth. The *L. racemosa* seedlings damaged in the 2001 incident may have been too young or small to have attained this capacity. The literature is not unanimous on the relative frost-tolerance of *L. racemosa* and *R. mangle*. Olmsted *et al.* (1993) reported that *R. mangle* was far more sensitive to freezes in 1977 and 1981 in Everglades National Park, but Lugo & Patterson Zucca (1977) found that *L. racemosa* suffered more immediate damage in the 1977 freeze at Cedar Key, FL, near the northern terminus of both species' ranges. Neither of these studies demonstrated the relatively persistent effect on community composition that we report in Fig. 5.

The pronounced increase in the relative abundance of *L. racemosa* in the impacted plots during 1995–2001 (Fig. 5) was largely attributable to the immediate effects of the chilling events, i.e., the concentration of temperature impacts on the tallest individuals, where *R. mangle*, the more sensitive species, was initially dominant. *L. racemosa* increased in abundance by establishing a large population of seedlings prior to the disturbance, mostly clustered on slightly elevated microsites among the prop roots of the larger *R. mangle* trees (Ross *et al.*, 2003). Seedling establishment during the study period appeared to be unaffected by the chilling events, as the density of newly established seedlings was similar on impacted and unimpacted sites (Fig. 4). Very likely, seedling establishment in intact stands is possible for this shade-intolerant species (Wadsworth, 1959; Ball, 1980; Roth, 1992) because of relatively high incident light at ground level in the unproductive Dwarf forest. Though outgrown by *R. mangle* during the early postdisturbance years (Ross *et al.*, 2003), many *L. racemosa* individuals succeeded in occupying openings in a more evenly mixed Dwarf forest canopy, while the unimpacted stands remained static and *R. mangle*-dominated.

Chilling impacts on coastal wetlands in a warming climate

In our analysis of historical temperature data and projection of future chilling events, we used 3 and 0 °C temperature minima at HARB as benchmarks of chilling damage in susceptible and less-susceptible sites, respectively. These values were selected on the basis of limited data: (1) one winter season of coincident temperature measurement at a long-term climatic monitoring station and at single examples of each site type, and (2) temperature records from the monitoring station

during two chilling events. Despite the uncertainty associated with these estimates, the quantification of relationships between field locations and long-term monitoring stations is an important and frequently ignored step in assessing the ecological impact of climate projections (Woodroffe & Grindrod, 1991). Our analysis, which suggests very substantial differences in historical chilling frequency among neighboring Dwarf forest sites, serves to highlight the spatial variation inherent in natural landscapes.

Days with minima $\leq 0\,°C$ at HARB were too infrequent to detect trend during 1956–2005, but incidences of minima $\leq 3\,°C$ exhibited a nonsignificant downward trend over the period. This result differs from those reported more generally for the southeastern US, where average minimum temperatures dropped during the second half of the 20th century (Karl et al., 1996), in sharp contrast to the warming reported in most of the US and worldwide (Easterling et al., 2000a). Easterling (2002) also reported a nominal but nonsignificant decrease in frost days for the southeastern region over the same period. HARB's location at the southern end of the Florida peninsula, within a few kilometers of the coast, causes it to be atypical among southeastern climate stations. However, its position at the periphery of a rapidly expanding urban area does make it vulnerable to heat island effects (Camilloni & Barros, 1997), and these may have had some influence.

Growth limitation in Dwarf mangrove communities has been attributed to a range of factors, including nutrient limitation, anaerobic soils, and episodes of high salinity (Davis, 1940; Egler, 1952; Craighead, 1971; Lugo & Snedaker, 1974; Lin & Sternberg, 1992b). At the same time, the repeated vegetation pruning associated with the chilling events that still frequently impact the most susceptible BCW sites (once in 2 years or less) also must play some role in constraining the stature of these shrublands. This constraint is likely to be relaxed considerably in coming decades, however. Various global climate scenarios project an increase in mean global temperatures of 0.6–4.0 °C (best estimates) during the next century (Meehl et al., 2007). Our own projections of the future probability of chilling events suggest that, with a 3 °C increase in temperature, the frequency of chilling events in susceptible sites would decrease by about an order of magnitude, and less susceptible sites would be virtually chill-free (Table 1). However, during the 20th century minimum temperatures increased about twice as much as mean daily temperatures worldwide (Easterling et al., 1997). If that trend continues, chilling events may cease to be a regular disturbance in the south Florida coastal zone even sooner, with substantial implications for vegetation pattern.

Conclusions

Concern over the effects of global warming on mangrove communities have largely focused on the capacity of mangrove soil development to keep pace with sea level rise (e.g., Ellison, 1994; Burkett et al., 2001). In south Florida, where recent sea level rise has been ~ 25 cm/100 year, encroachment of mangroves in both seaward and landward directions has been documented in different settings (Parkinson, 1989; Snedaker et al., 1994; Ross et al., 2000). A second issue recently addressed by Stevens et al. (2006) is the tendency of cold-sensitive mangroves to expand poleward into coastal marshes, aided by a relaxation in the freeze regime. The latter is a specific case of a worldwide phenomenon in which small changes in disturbance regime can affect the competitive balance between trees and herbaceous plants, and therefore forest–grassland dynamics at broad scales (Kangas & Lugo, 1990; Longman & Jenik, 1992; Bond et al., 2005). However, disturbance can also affect compositional diversity *within* communities, which may depend on localized disturbances to create a successionally diverse mosaic of habitat patches. Change in the periodicity or intensity of disturbance may alter the ability of species other than the successional dominants to persist in stable ratios at larger spatial scales (Heinselman, 1973; Jentsch et al., 2002).

In this study we examined the potential ecological effects of alterations in the winter temperature regime within the mangrove forest, in areas that decades earlier had transitioned from coastal marsh to mangrove swamp. We found that chilling events affected composition and structure dramatically, freeing understory plants to succeed into the suddenly reduced canopy, and providing a means by which *L. racemosa* could share dominance with *R. mangle*, at least in the short term. In nearby unimpacted sites, we found stand dynamics to be very static over the same period. Chilling events, which currently recur at 1–2 years intervals on susceptible sites and at 10–20 years intervals on less susceptible ones, are therefore an important organizing force within the mangrove forest, contributing to diversity within and among sites. The large decrease in the frequency of these events predicted by our analysis would remove one of several mechanisms that maintains structural variability within the Dwarf forest, and promotes a mixed-species composition.

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