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Non-linear shift from grassland to shrubland in temperate barrier islands

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Abstract. Woody plant encroachment into grasslands is a major land cover change taking place in many regions of the world, including arctic, alpine and desert ecosystems. This change in plant dominance is also affecting coastal ecosystems, including barrier islands, which are known for being vulnerable to the effects of climate change. In the last century, the woody plant species *Morella cerifera* L. (Myricaceae), has encroached into grass covered swales in many of the barrier islands of Virginia along the Atlantic seaboard. The abrupt shift to shrub cover in these islands could result from positive feedbacks with the physical environment, though the underlying mechanisms remain poorly understood. We use a combination of experimental and modeling approaches to investigate the role of climate warming and the ability of *M. cerifera* to mitigate its microclimate thereby leading to the emergence of alternative stable states in barrier island vegetation. Nighttime air temperatures were significantly higher in myrtle shrublands than grasslands, particularly in the winter season. The difference in the mean of the 5% and 10% lowest minimum temperatures between shrubland and grassland calculated from two independent datasets ranged from 1.3 to 2.4°C. The model results clearly show that a small increase in near-surface temperature can induce a non-linear shift in ecosystem state from a stable state with no shrubs to an alternative stable state dominated by *M. cerifera*. This modeling framework improves our understanding and prediction of barrier island vegetation stability and resilience under climate change, and highlights the existence of important nonlinearities and hystereses that limit the reversibility of this ongoing shift in vegetation dominance.

Key words: *alternative stable states; climate change; cold intolerance; ecosystem stability; Morella cerifera; regime shifts; resilience; shrub encroachment; vegetation-microclimate feedback.*

INTRODUCTION

Vegetation cover has important influences on the near-surface atmospheric conditions, including temperature, humidity, boundary layer stability, and rainfall formation (Geiger 1965, Pielke et al. 1998, Bonan 2008, Li et al. 2016). For example, deforestation and land use change disrupt the surface energy balance thereby altering the microclimate (Avisar et al. 2002, Bonan 2008, Lawrence and Vandecar 2014, Li et al. 2015, Runyan and D'Odorico 2016). A major change in land cover taking place in many regions of the world is associated with the encroachment of woody plants into grasslands, a phenomenon that has been observed in arctic, alpine, desert, and coastal ecosystems (Archer et al. 1995, Chapin et al. 2000, Maher et al. 2005, Bader et al. 2007, Knapp et al. 2008, McKee and Rooth 2008, Ravi et al. 2009). This abrupt replacement of grasses with woody plants has significant impacts on ecosystem structure, functioning, and the provision of ecosystem services such as livestock grazing, surface soil sheltering and carbon sequestration, and therefore has been viewed as an indicator of land degradation and desertification in dryland regions (Van Auken 2000).

Shrub encroachment has been ascribed to a variety of mechanisms including overgrazing, fire suppression, atmospheric CO₂ rise, and climate change, depending on the specific ecosystem considered (D'Odorico et al. 2012). Especially in cold regions where low temperature events limit the

growth of cold-sensitive woody plants, the ongoing climate warming provides opportunities for woody plants to be released from cold-induced damage, contributing to their expansion (Tape et al. 2006). Besides the gradual impact of regional climate warming, the vegetation-microclimate feedbacks may play a role in facilitating shrub encroachment in the shorter term by improving the environmental conditions for shrub species (D'Odorico et al. 2010, 2013). The increase in woody plant cover has been found to affect the microclimate by altering surface energy fluxes (Geiger 1965, Langvall and Örlander 2001, Beltrán-Przekurat et al. 2008, D'Odorico et al. 2010). Specifically, the nocturnal long-wave radiation emitted by the ground can be absorbed by the vegetation canopy and partially reflected and re-radiated back to the ground surface, consequently reducing the radiation loss to the atmosphere and creating warmer microclimate conditions in the shrubland (He et al. 2010, 2014). Because many of the encroaching woody plants are cold intolerant (Pockman and Sperry 1997, Körner 1998, Krauss et al. 2008), this local warming effect interacting with regional climate warming can in turn promote the survival and growth of cold-sensitive woody plants by reducing the exposure to extreme low temperature events. Thus, a positive feedback between vegetation and microclimate may exist in grassland-woodland ecotones (D'Odorico et al. 2013). In many cases woody plant encroachment has led to a relatively abrupt and potentially irreversible land cover change (Van Auken 2000, D'Odorico et al. 2012), suggesting the possible occurrence of a critical transition in a bistable system with alternative stable states of grassland and shrubland. Bistable ecosystem dynamics are often induced by the positive

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feedbacks between vegetation and the physical environment; thus, microclimate feedbacks and climate warming likely play a crucial role in the transition to shrub dominance in many landscapes worldwide (D'Odorico et al. 2013).

Freeze-induced damage limits the latitudinal distribution of many woody plants across the globe including mangroves in coastal ecosystems (Stuart et al. 2007), *Betula nana* (dwarf birch) and other shrub species in arctic regions (Wookey et al. 2009). The cold sensitivity of woody plants compared with grasses has been ascribed to many different physiological mechanisms, including cold-induced decrease in photosynthetic rates and primary productivity, reduced growth, limited regeneration capacity, and plant frost damage (Tranquillini 1979, Grace et al. 1989, Körner 1998). In cold environments, low temperatures and short growing seasons prevent plants from maintaining a balanced or positive carbon budget as a result of limited carbon assimilation. In addition, extreme temperature events can also cause freezing-induced xylem embolisms and a loss of hydraulic conductivity (Buchner and Neuner 2011, Medeiros and Pockman 2011). Furthermore, cold stress weakens the competitiveness of woody plants with respect to grasses by inhibiting seed production and germination and therefore the reproduction capacity (Körner 1998). The cold intolerance of woody plants often sets the latitudinal limits to their distribution; however, the decreased frequency of extreme cold events due to climate warming tends to reduce the chances that shrubs experience freezing damage in the cold months, and contributes to their expansion in transition zones (Cavanaugh et al. 2014), therefore highlighting the important role of warming effect in shrub encroachment in shrub-grass ecotones.

In the last century, the woody plant species *Morella cerifera* L. (Myricaceae) has encroached into grass swales composed of both graminoids and forbs in many of the barrier islands along the Virginia segment of the Atlantic seaboard of the USA (Young 1992, Young et al. 1995). *M. cerifera* is a nitrogen fixing shrub with relatively high growth rate and resource use efficiency which largely contributes to its expansion, and plays an important role in successional processes (Collins and Quinn 1982, Young et al. 1995). Conversion from grassland to shrubs to maritime forest is part of the typical successional pattern in coastal areas, however, recent studies have demonstrated that the majority of shrub expansion has occurred from previously established thickets compared to new colonization from a successional trajectory (Zinnert et al. 2011). Due to high shrub leaf area index, there has been little to no development of new maritime forest at the Virginia Coast Reserve (VCR), indicating a delay in succession (Brantley and Young 2007, Bissett et al. 2016). Patterns of *M. cerifera* expansion vary from island to island, with higher rates on some islands and loss of shrubs due to erosion on others. Even with these dynamics, the overall cover of *M. cerifera* has increased approximately 40% over the last 27 yr (Fig. 1) despite loss of island area across the VCR. This change in *M. cerifera* cover is associated with important effects on the surrounding environmental conditions such as temperature regime, water table depth, and soil nutrient levels. For example, recent research (Thompson et al. 2017) has documented an increase in soil moisture and nutrients as well as the occurrence of significantly higher winter minimum temperatures

inside shrub thickets, suggesting the existence of a warmer microclimate during winter resulting from the encroachment of *M. cerifera*. These islands lie at the northern limit of the latitudinal range of *M. cerifera* (Shao and Halpin 1995) and specifically, *M. cerifera* expansion has not been affected by direct human disturbances since 1930s (Thompson 2016), therefore the ongoing encroachment of *M. cerifera* and the possible warming effect through the surface energy balance may indicate that a positive feedback between vegetation cover and microclimate could exist due to the cold intolerance of *M. cerifera*. Processes related to land use (e.g., grazing and fire suppression) have also been invoked to explain woody plant encroachment in drylands (e.g., Van Auken 2000, D'Odorico et al. 2012, Yu and D'Odorico 2014). These processes do not seem to be relevant to the case of the VCR, where no recent history of grazing or fire management exists. Therefore, the VCR provides an ideal system for investigating how climate warming and microclimate feedback may interact to serve as a mechanism of shrub expansion, without confounding effect from other drivers.

In this study we (1) provide additional experimental evidence of the modified microclimate created by the establishment of *M. cerifera*; (2) present results from laboratory experiments demonstrating the cold sensitivity of this shrub species; and (3) develop a process-based modeling framework showing the potential emergence of bi-stable shrub-grass dynamics and a nonlinear shift from grassland to shrubland in Virginia barrier island vegetation as a result of positive feedbacks with microclimate conditions and *M. cerifera*'s cold sensitivity.

METHODS

Study site

This study focused on Hog Island (37°40' N, 75°40' W), a barrier island within the Virginia Coast Reserve Long-Term Ecological Research site (VCR LTER). The VCR includes a chain of barrier islands, and is the longest stretch of undeveloped coastline on the eastern United States. Hog Island is not affected by direct anthropogenic disturbance as it has been free of human occupation since the mid-1930s, though historic anthropogenic disturbances including grazing, lumbering and farming have been reported to occur earlier in the history of these barrier islands (Levy 1990). It is ~12 km in length and ~2 km across at the widest point. Hog Island consists of oceanfront strand and dunes, interior grass/forb dune/swale complexes with expanding shrub thickets, and tidal salt marshes on the lagoon side. The expanding species, *Morella cerifera*, forms dense monospecific patches of tall (4–7 m) thickets that exclude all other species (Thompson et al. 2017) (Fig. 1). Expansion of *M. cerifera* into grassland dominated by *Spartina patens* (Aiton) Muhl. and *Andropogon virginicus* L. has increased significantly on Hog Island since 1949 (Young et al. 1995, Zinnert et al. 2016) and currently covers more than 45% of the island. Because of its limited exposure to direct anthropogenic disturbances and its position at the northern latitudinal limit of cold sensitive *M. cerifera*, Hog Island is an ideal system for studying the impacts of climate warming and microclimate feedbacks on shrub encroachment.

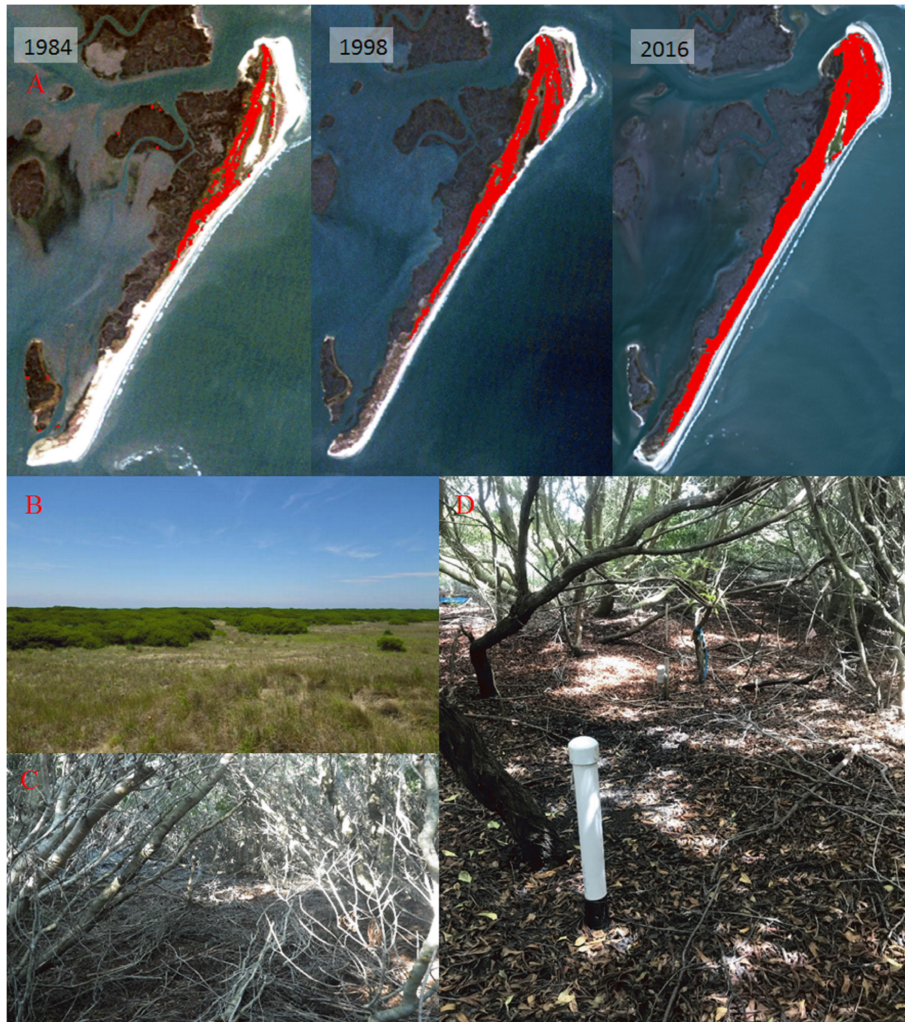


FIG. 1. Shrub encroachment on Hog Island, VA. (A) Expansion of *Morella cerifera* (red) on Hog Island, VA from 1984 (74 ha), to 1998 (184 ha) to 2016 (393 ha). (B) Shrubland-grassland ecotones on Hog Island. (C) Image inside a shrub thicket. (D) Temperature measurement inside the shrub thickets. Note the absence of other species.

The mean annual temperature ranges from 11.9° to 14.7°C, and mean annual precipitation typically varies between 1,065 to 1,167 mm/yr (Brantley and Young 2010). The long-term climate data from a nearby NOAA meteorological station in Painter, Virginia reveal that only 4 low temperature events ($<-15^{\circ}\text{C}$) have occurred since 1985, while 10 events were documented from the previous 30 yr. There is a general warming trend in mean winter temperature from 1955 to 2017, which we argue is contributing to *M. cerifera* expansion (Fig. 2).

Temperature data

The hourly air temperature measurements (hereafter referred to ‘dataset A’) were made 20 cm above the ground by temperature sensors located in 5 grassland and 5 shrubland sites (HOBO U23-003; Onset Inc., Bourne, Massachusetts, USA) on Hog Island, VA from July 2014 to June 2015. Additionally, we acquired bihourly air temperature records (‘dataset B’) on Hog Island from May 2015 to March 2016 from Thompson et al. (2017). As spatial extent of *M. cerifera*

thickets can be quite large, the temperatures were measured 10 m inside and outside the shrub thicket edge to identify the warming effect of *M. cerifera* shrubland. The daily minimum and maximum temperatures were extracted and used to determine the warming effect of shrubland and therefore the model parameter (see below). Thompson et al. (2017) found that temperatures inside of shrub thickets are similar to those of younger, free standing shrubs.

Freezing experiment

Experiments were focused on shrubs as grasses are dormant during low temperature events. We assessed the effect of freezing on hydraulic conductivity of adult *Morella cerifera* shrubs at -15° and -20°C ($n = 4$). These were compared to shrubs grown at 7° and 25°C to serve as reference conditions for hydraulic conductivity at lower temperatures (7°C) and under ideal growth conditions (25°C). Adult shrubs (~ 1.5 m height) of local stock were purchased from a nursery and transplanted into 12 L pots. Shrubs were randomly assigned into treatments. A subset of shrubs were

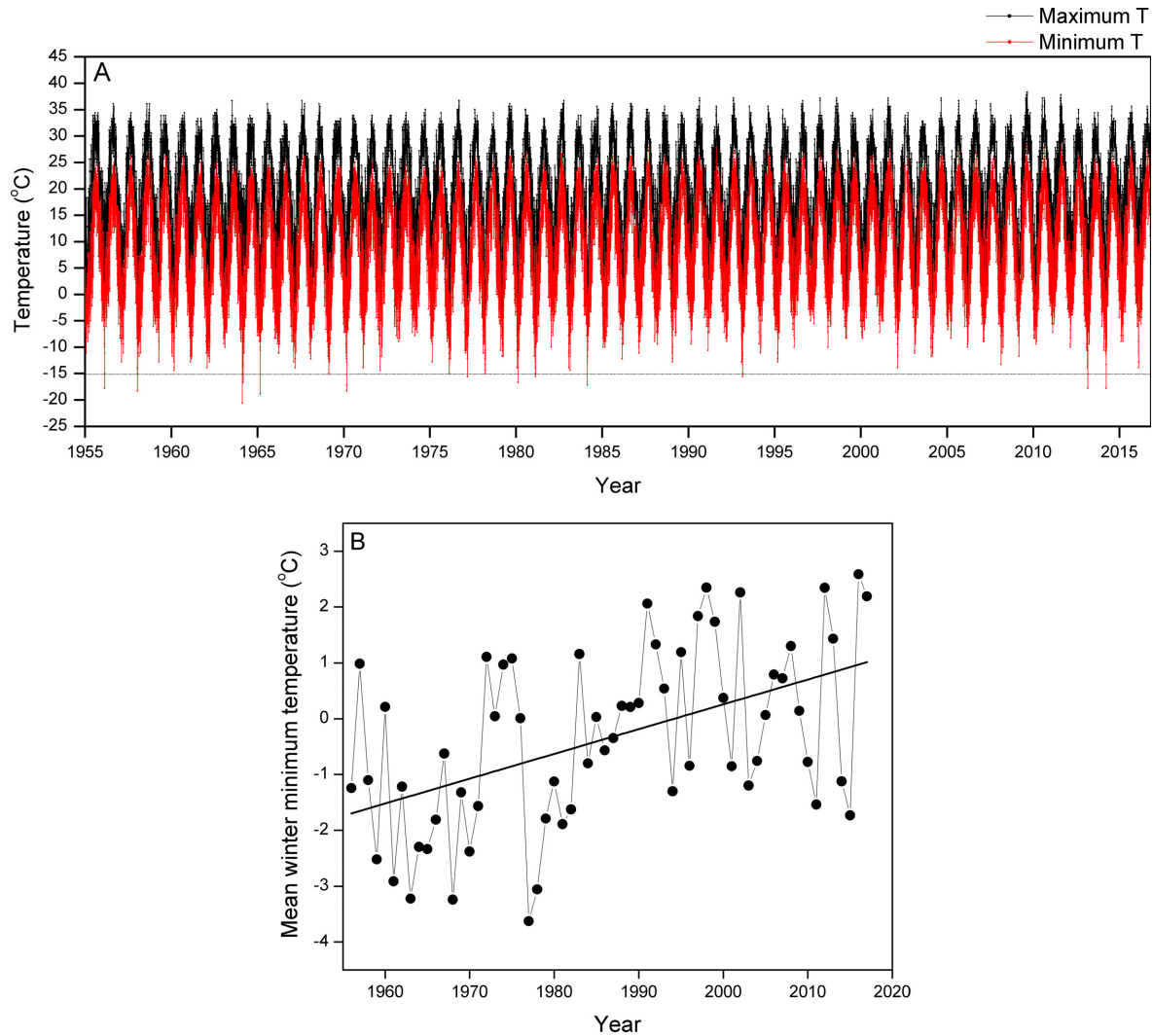


FIG. 2. Trends in daily maximum and minimum temperature (A) and annual mean winter minimum temperature (B) in Painter, VA between December 1955 and September 2017. Since 1985, only 4 low temperature events ($<-15^{\circ}\text{C}$) were observed. The annual mean winter minimum temperature also exhibited a significant increasing trend over time ($P < 0.001$) as shown by the OLS regression line.

grown in an environmental chamber (20°C night/ 25°C day, Model #E15; Conviron, Winnipeg, Manitoba, Canada) at $1,000\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR for 10-h photoperiod. The remaining shrubs were grown in low temperatures (4°C night/ 7°C day) in a cold room with $1,000\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic active radiation (PAR) and 10-h photoperiod to mimic natural conditions preceding low temperature events. Plants were given 21 d to acclimate to growing conditions. Freezing took place with intact plants placed in a chest freezer (Model FFFC09MIRW, Frigidaire, Charlotte, North Carolina, USA) at 0°C . Cooling/warming proceeded at $0.5^{\circ}\text{C}/\text{min}$ using the intrinsic rate of cooling of the freezer. Minimum temperature was maintained for 180 min at -15° , and -20°C before warming to 0°C . 0°C was used to reduce additional damage to tissues from rapid changes in temperature.

Immediately post-freeze, 3–4 samples were excised per pot and prepared for hydraulic conductivity as described in Sperry et al. (1988). Stem segments were ~ 10 cm long and 5–10 mm in diameter. The hydraulic conductivity apparatus consisted of an IV-bag supplying a filtered ($0.2\ \mu\text{m}$) 20 mmol/L KCl

solution via low gravitational pressure (~ 5 kPa) to a stem segment. Removal of in situ embolisms was prevented by a low hydraulic head. Flow rate was determined by measuring the volume of water expelled over a known amount of time and hydraulic conductivity was calculated as the mass flow rate of the solution through the stem segment divided by the pressure gradient along the segment path length (k_h , $\text{kg}\cdot\text{m}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$). Stem specific conductance (k_s , $\text{kg}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}\cdot\text{m}^{-1}$) was calculated from k_h divided by sapwood area.

Modeling framework

We modeled the change rate in *M. cerifera*'s normalized density, S/S_c , as the result of a logistic growth and a mortality rate that is a temperature-dependent linear function of shrub biomass (D'Odorico et al. 2013),

$$\frac{d\left(\frac{S}{S_c}\right)}{dt} = \alpha \frac{S}{S_c} \left(1 - \frac{S}{S_c}\right) - \beta f(T_{\min}) \frac{S}{S_c}, \quad (1)$$

where S_c is the carrying capacity, which is assumed to be equal to 1, and α (year^{-1}) is the intrinsic growth rate of *M. cerifera*, and β (year^{-1}) is the maximum death rate caused by cold intolerance. The effect of temperature can be accounted for through the function, $f(T_{\min})$, of minimum temperature, T_{\min} as in D'Odorico et al. (2013),

$$f(T_{\min}) = \begin{cases} 1; & T_{\min} < T_1 \\ \frac{T_2 - T_{\min}}{T_2 - T_1}; & T_1 \leq T_{\min} \leq T_2 \\ 0; & T_{\min} > T_2, \end{cases} \quad (2)$$

where T_1 and T_2 are two critical temperatures defining the cold tolerance of *M. cerifera*. T_{\min} is defined as the local minimum temperature within shrub thickets where the vegetation-microclimate feedback creates a warming effect. For bare soil with no plant cover, near surface minimum temperature equals T_b (i.e. background temperature). The encroachment and establishment of *M. cerifera* results in a local increase, ΔT_{\max} , in minimum temperature (Hayden 1998, He et al. 2010). This warming feedback is assumed to be expressed by a linear function of shrub cover, S i.e.

$$T_{\min} = T_b + \Delta T_{\max} \frac{S}{S_c}, \quad (3)$$

where ΔT_{\max} represents the maximum warming effect with a full *M. cerifera* canopy.

The value of parameters α and β were determined empirically ($\alpha = 0.5 \text{ yr}^{-1}$ and $\beta = 10 \text{ yr}^{-1}$) in a way that shrub encroachment (i.e., an increase in S from 0 to $0.95 \times S_c$) occurs in about 20–30 yr, in agreement with studies documenting the rate of land cover change in these islands (Young et al. 2007); conversely, a full woody plant canopy can collapse into the state $S/S_c = 0$ within few years when temperature is consistently smaller than T_1 .

According to previous studies, temperatures below -15°C would start to cause cold stress injury in some *Morella* species (Larcher 1995). Based on the hydraulic conductivity experiment under temperature treatments, we used Eq. 2 with T_1 and T_2 estimated to be equal to -20° and -15°C , respectively. It should be noted that the overall modeling results are not sensitive to uncertainty in the determination of T_1 and T_2 . The maximum increase ΔT_{\max} in minimum temperature induced by the presence of a complete shrub cover was assumed to be equal to 2°C based on the results from two independent temperature datasets, which is also consistent with Thompson et al. (2017).

The stable states of these vegetation dynamics can be determined by inserting Eqs. 2 and 3 in Eq. 1, setting the left-hand side of Eq. 1 equal to zero with T_{\min} expressed as a function of S and ΔT_{\max} to account for the shrub-microclimate feedback. Equilibrium points were determined by setting $\frac{d(S/S_c)}{dt} = 0$. After solving for S/S_c , we find that the system has three possible equilibrium states i.e. $S_{e1} = 0$, $S_{e2} = 1$, and

$$S_{e3} = \frac{T_2 - \left(T_b + \frac{\alpha}{\beta}(T_2 - T_1)\right)}{\left(\tau - \frac{\alpha}{\beta}\right)(T_2 - T_1)} \quad (4)$$

where $\tau = \frac{\Delta T_{\max}}{T_2 - T_1}$. Since S_{e3} can only exist between 0 and 1, based on Eq. 4, bistability (i.e., a dynamic with two alternative stable states separated by an unstable state) exists only when

$$T_2 - \tau(T_2 - T_1) \leq T_b \leq T_2 - \frac{\alpha}{\beta}(T_2 - T_1) \quad (5)$$

$$\text{i.e. } -17^\circ\text{C} \leq T_b \leq -15.25^\circ\text{C}.$$

Statistical analyses

The difference in hourly (dataset A) and bihourly (dataset B) temperature between shrubland and grassland during nighttime and daytime was tested using Student's t -test ($\alpha = 0.05$). To focus on temperature differences on the coldest nights, we considered the days with the 10% and the 5% lowest minimum air temperatures and calculated their means to compare the minimum temperature difference between shrubland and grassland – and therefore estimate the parameter ΔT_{\max} in the modeling framework. The Student's t -test ($\alpha = 0.05$) was used to determine whether the minimum temperature difference is significant at 95% confidence interval. Differences in stem specific hydraulic conductance were determined with ANOVA with subsampling. Pairwise comparisons were made using Tukey's test ($\alpha = 0.05$).

RESULTS

The analysis shows that shrubland has a lower frequency of freezing events (records with temperature below 0°C) than grassland for both dataset A (540 times vs. 622 times in total of 8,172 records) and dataset B (134 times vs. 159 times in total of 3,571 records). In the nighttime, the shrubland was (on average) consistently and significantly warmer than the grassland both during the whole year ($P = 0.012$ and 0.004 for dataset A and B, respectively) and during the winter season ($P < 0.01$ for both datasets) (Fig. 3); conversely, in the daytime, the grassland was consistently warmer than the shrubland, both during the whole year ($P < 0.0001$ for both datasets) and the winter season ($P < 0.01$ for both datasets) (Fig. 4). The warming effect due to the existence of shrub cover was further confirmed by the significant increase in minimum temperatures in shrubland (Fig. 5). The results from dataset A show that the mean of the 5% lowest minimum temperatures in shrubland and grassland were $-6.14 \pm 0.45^\circ$ and $-7.43 \pm 0.31^\circ\text{C}$, respectively; these two values were statistically different ($P = 0.024$). The mean of the 10% lowest minimum temperatures in shrubland and grassland were $-4.09 \pm 0.45^\circ$ and $-5.60 \pm 0.37^\circ\text{C}$, respectively; these values were also statistically different ($P = 0.012$). Similar results were found from dataset B. The mean of the 5% lowest minimum temperatures measured in the shrubland was $-3.74 \pm 0.60^\circ\text{C}$, statistically higher ($P = 0.003$) than the mean temperature of $-6.11 \pm 0.43^\circ\text{C}$ in the grassland. The mean of the 10% lowest minimum temperatures in shrubland and grassland are $-1.68 \pm 0.53^\circ$ and $-4.09 \pm 0.44^\circ\text{C}$, respectively; these values were statistically different ($P = 0.001$). These results are in agreement with Thompson et al. (2017) who analyzed a segment of dataset

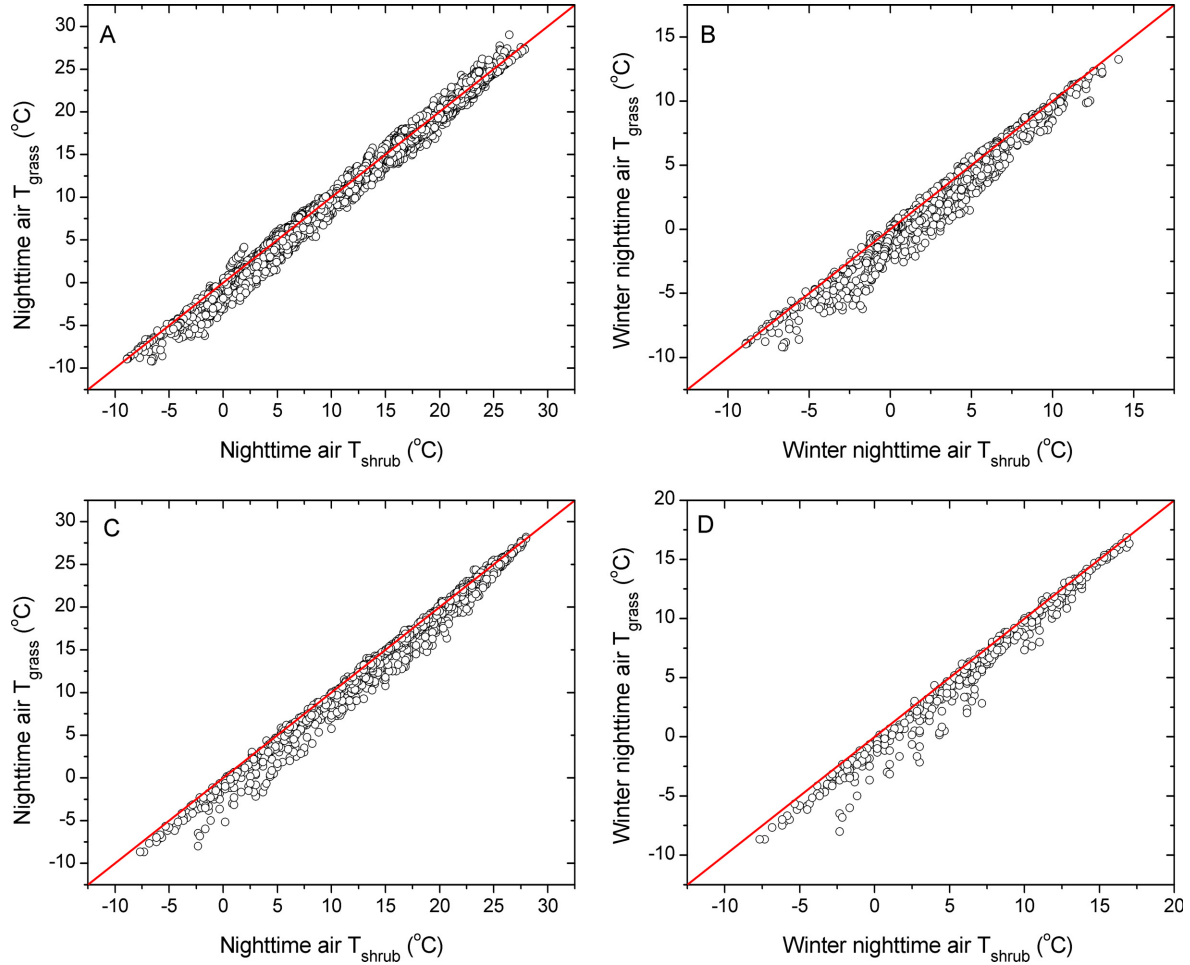


FIG. 3. Nighttime temperature comparison between shrubland and grassland in Hog Island during the whole year (A, C) and the winter season (B, D) based on dataset A (A, B) and B (C, D). Dataset A includes hourly temperature records from July 2014 to June 2015 and dataset B has bihourly temperature records from May 2015 to March 2016. In the nighttime, the shrubland is consistently warmer than the grassland, both during the whole year ($P = 0.012$ and 0.004 for dataset A and B, respectively) and the winter season ($P < 0.0001$ and $P = 0.009$ for dataset A and B, respectively).

B. The mean temperature difference between shrubland and grassland during the coldest nights was about 2°C . We also assume that the magnitude of this warming effect is $\Delta T_{\max} \approx 2^{\circ}\text{C}$, based on the results shown in Fig. 5.

In our experimental analysis, at reference temperatures of 7° or 25°C , stem-specific hydraulic conductance (k_s) was not statistically different, but freezing-induced cavitation significantly reduced stem hydraulic conductance at $T_2 = -15^{\circ}\text{C}$ ($P < 0.0001$). k_s was reduced to ~ 0 at $T_1 = -20^{\circ}\text{C}$ (Fig. 6).

Ecosystem stability is here investigated using our modeling framework and looking at how the rate of change in S/S_c varies as a function of S/S_c (Fig. 7). This analysis shows how the stable states of the system vary with different background temperature ranges (Fig. 7). Specifically, we found that (1) when T_b is lower than -17°C , $f(T_{\min})$ equals either 1 or $\frac{T_2 - T_{\min}}{T_2 - T_1}$ (see Eq. 2) because T_{\min} cannot exceed -15°C even with the maximum warming effect (i.e. ΔT_{\max}). In these climate conditions the ecosystem is stable only with no woody plant cover ($S = 0$) because there are no other stable equilibrium points in the interval $(0, 1)$; (2) when T_b lies between -17° and -15.25°C , the rate of change of

normalized shrub density would follow $\frac{d(S/S_c)}{dt} = \alpha S(1 - S/S_c) - \beta(S/S_c)f(T_{\min})$, which becomes $\frac{d(S/S_c)}{dt} = \alpha S(1 - S/S_c)$ when T_{\min} exceeds -15°C as a result of the warming effect of shrub cover. For example, in the case of $T_b = -16^{\circ}\text{C}$, the rate of change of S/S_c will shift to the latter equation when S reaches 0.5, which is when the T_{\min} increases to -15°C (Fig. 7). Therefore, in this case the system has two stable equilibrium points $S_{e1} = 0$ and $S_{e2} = 1$, and an unstable equilibrium S_{e3} , which ranges between 0 and 1; (3) when T_b is larger than -15.25°C , $f(T_{\min})$ equals $\frac{T_2 - T_{\min}}{T_2 - T_1}$ (when $T_{\min} \leq -15^{\circ}\text{C}$) or 0 (when $T_{\min} > -15^{\circ}\text{C}$). In these conditions the system has only two equilibrium points in the interval $(0, 1)$, $S_{e1} = 0$ (unstable) and $S_{e2} = 1$ (stable), and the dynamics tends to a full shrub cover state, regardless of the initial shrub cover conditions. Therefore, because of the nonlinear response of vegetation to near surface temperature associated with this feedback, vegetation response to climate warming may exhibit a threshold behavior with an abrupt transition from the grassland stable state to full shrub cover ($S = S_c$) as T_b increases above about -15°C (Fig. 8).

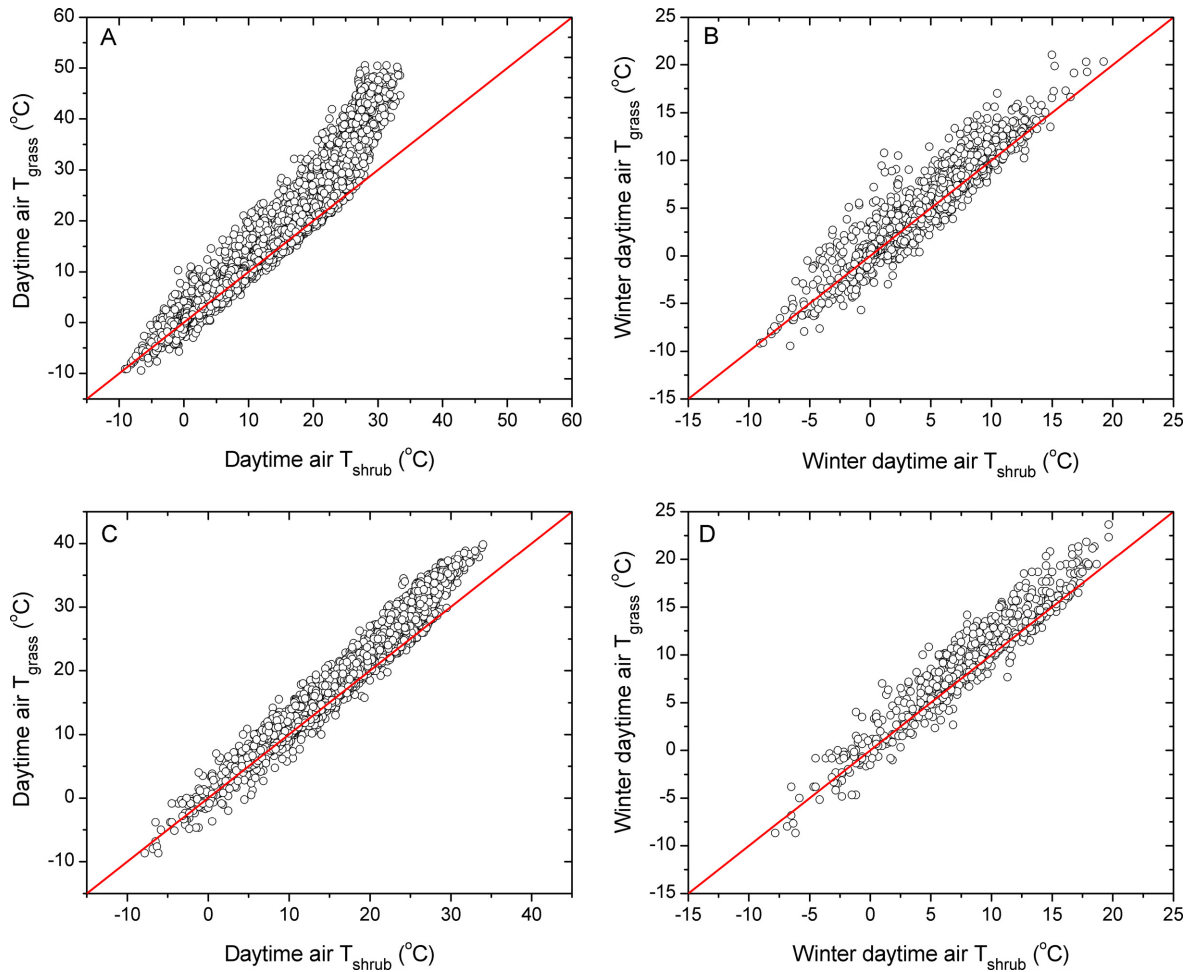


FIG. 4. Daytime temperature comparison between shrubland and grassland in Hog Island during the whole year (A, C) and the winter season (B, D) based on dataset A (A, B) and B (C, D). In the daytime, the grassland is consistently warmer than the shrubland, both during the whole year ($P < 0.0001$ for both dataset A and B) and the winter season ($P = 0.0003$ and $P = 0.0014$ for dataset A and B, respectively).

DISCUSSION

The modeling results clearly show that a small increase in the background minimum temperature, T_b , can cause a shift in the state of the system from one stable state with no shrub dominance to its alternative stable state with a full shrub canopy. The transition is expected to occur in a non-linear way through the positive feedback between vegetation and microclimate (Fig. 8). Based on the results shown in Fig. 6, we set $T_1 = -20^\circ\text{C}$, which is a conservative estimate because there is evidence that plant mortality from irreversible xylem damage occurs already when the stem conductance is reduced by 80% (Bartlett et al. 2016). When temperature is below -15°C , *M. cerifera* would suffer from cold induced injury and lose competitiveness with grasses, thereby leading to the stabilization of the ecosystem with full grass cover.

The cold intolerance of *M. cerifera* has been widely documented in the literature (for example, Larcher 1995), is further supported by our freezing experiment (Fig. 6), and is evidenced by the fact that the barrier islands in which its encroachment has been documented (i.e., Hog Island, in Virginia) are at the northern limit of *M. cerifera*'s latitudinal range. It has also been documented that in these islands the

establishment of *M. cerifera* has modified the microclimate by increasing nocturnal temperatures and mitigating the exposure to extreme low temperature events and cold-induced stress, especially during extremely cold nights. Even though the mechanisms underlying this warming effect still have to be documented, studies developed in other grass-shrub transition zones have highlighted how the presence of shrub cover may alter the surface energy fluxes, for example, by reducing the nocturnal longwave radiation loss (D'Odorico et al. 2013) or the diurnal ground heat flow (He et al. 2010, 2015). Likewise, these effects could explain how the shrubland of *M. cerifera* may create warmer microclimatic conditions. Field measurements on Hog Island have documented significantly higher average minimum temperatures inside the shrub thickets than in grass swales (Figs. 3 and 5; Young et al. 1992, Thompson et al. 2017). The warming effect promotes further survival and growth of young seedlings especially in ecotone areas close to the "tree line" (Maher et al. 2005, Maher and Germino 2006). Moreover, warming could also indirectly benefit shrub growth by enhancing microbial activity and nutrient cycling (Thompson et al. 2017). Through this vegetation-microclimate feedback, *M. cerifera* shrubs act as 'ecosystem engineers', i.e., as

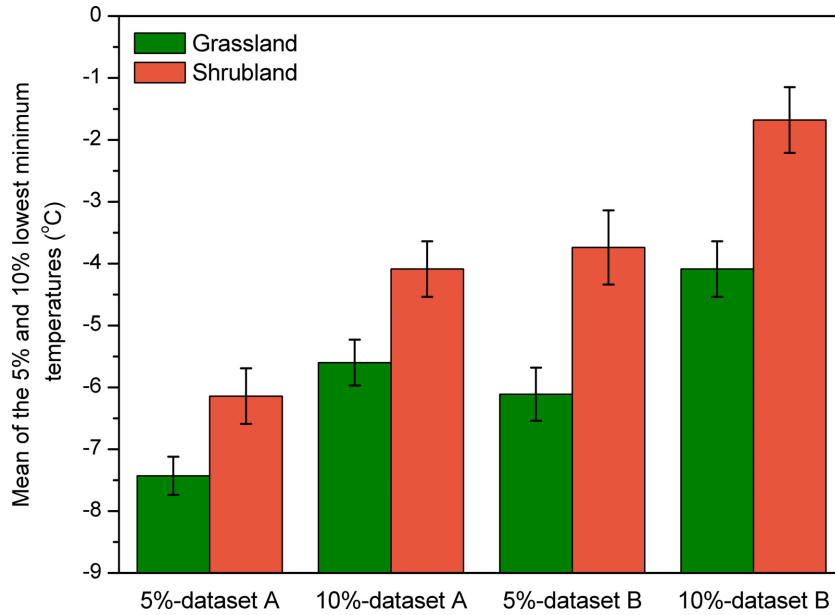


FIG. 5. Difference in mean daily minimum temperature between shrubland and grassland in Hog Island calculated from both dataset A and B. The mean of the 5% and 10% lowest minimum temperatures were calculated respectively to determine the warming effect of shrubland and therefore estimate the parameter ΔT_{\max} in our modeling framework. The Student's t test analysis ($\alpha = 0.05$) indicates a statistically significant warmer temperature in the shrubland than in the grassland ($P \leq 0.024$).

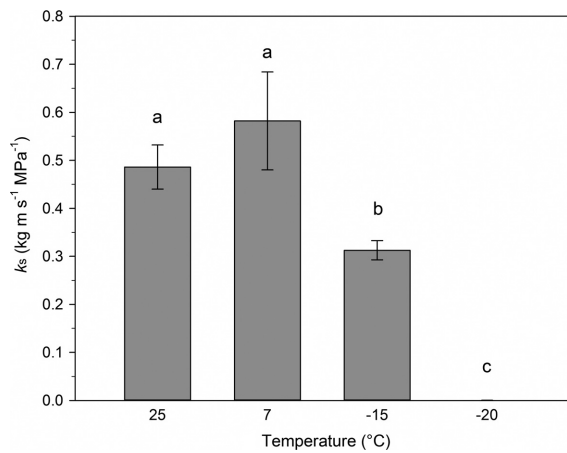


FIG. 6. Mean \pm 1 SE stem-specific hydraulic conductance (k_s) for *M. cerifera* shrubs after freezing. Letters indicate differences according to post-hoc Tukey's test ($\alpha = 0.05$).

organisms that create their own habitat (Jones et al. 1994), thereby promoting their own survival and growth. Due to the positive vegetation-microclimate feedback, the grassland could eventually experience an abrupt transition to another stable state with full woody plant when the minimum background temperature exceeds a threshold value as a result of climate warming.

The abrupt and discontinuous transition, both temporally and spatially, from grassland to shrubland has been observed in several ecosystems around the world (Archer et al. 1988, Chapin et al. 2000, Maher et al. 2005, Bader et al. 2007, Knapp et al. 2008, McKee and Rooth 2008, Ravi et al. 2009, D'Odorico et al. 2013). The positive feedback between vegetation and microclimate can substantially

release the pressure of *M. cerifera* from cold induced injury or mortality. When a combination of regional climate warming and microclimate feedback results in an increase in minimum temperature within shrub thickets that exceeds the threshold temperature for woody plant growth, an abrupt transition is expected to take place between the two stable states of the system, namely from grass to shrub dominance. It should be noted that at the study sites an increase in shrub cover was also observed from 1949 to 1989 even though this period experienced several extreme cold events. However the rate of expansion was greater between 1974 and 1989 (Young et al. 2007). This effect may be attributed to other mechanisms such as the feedback of bird dispersal of seeds or the lagging effects of previous anthropogenic disturbances (Young et al. 1995). Records from the 1970s document that shrub thickets of *M. cerifera* were not present on most islands (McCaffrey and Dueser 1990). Climate warming has been invoked as one of the major factors causing grass replacement by shrubs (Van Auken 2000, D'Odorico et al. 2012) and is projected to accelerate in the near future as a result of anthropogenic CO₂ emissions (Cox et al. 2000) thereby creating a more favorable environment for the encroachment of cold-sensitive shrubs into regions where the extreme cold events usually exclude their existence.

Conditions for *M. cerifera* establishment must be favorable with respect to salinity (Sande and Young 1992), elevation, and distance from the shoreline (Young et al. 2011). Sediment flux is an important consideration in this dynamic landscape, with development of a freshwater lens necessary for establishment and growth. Once established, shrubs are able to survive under periods of high saline conditions that may occur during storm overwash (Tolliver et al. 1997, Naumann et al. 2008). Enhanced leaf area index of shrubs coupled with microclimate warming likely increases evapotranspiration

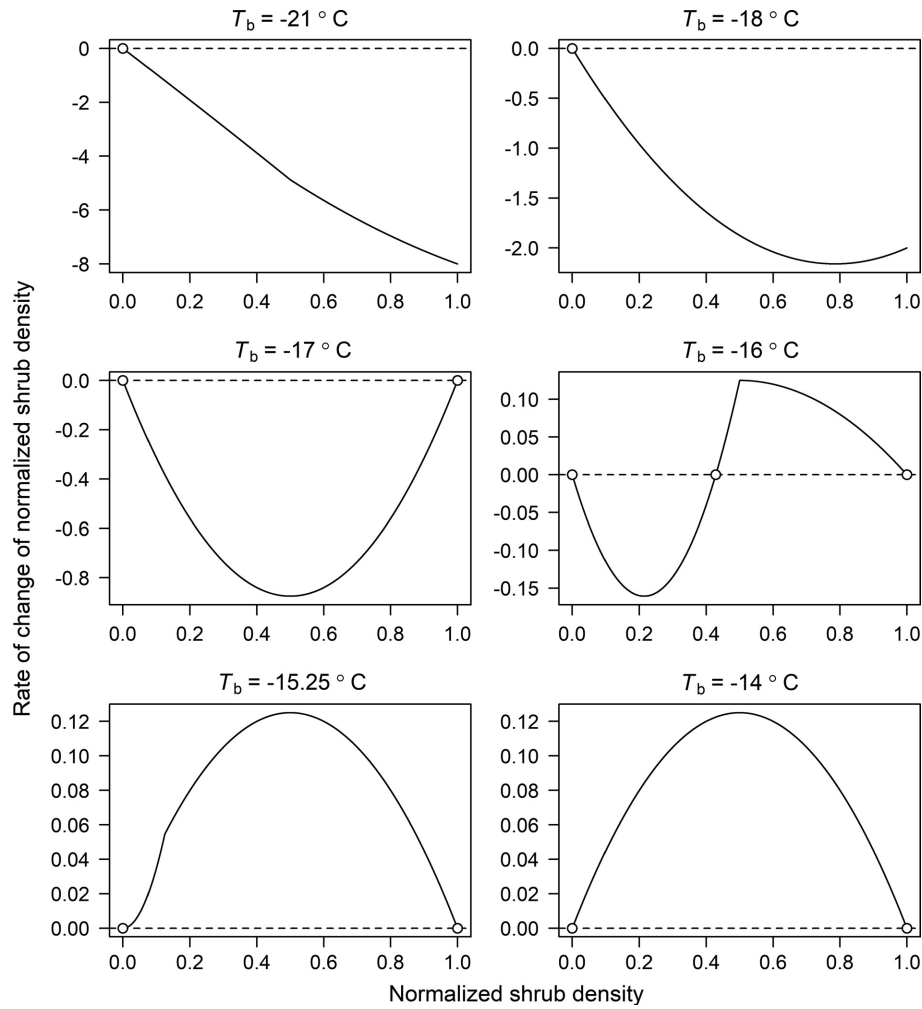


FIG. 7. The rate of change of normalized shrub density ($d(S/S_c)/dt$) vs. normalized shrub density (S/S_c) under different background temperature (T_b) conditions.

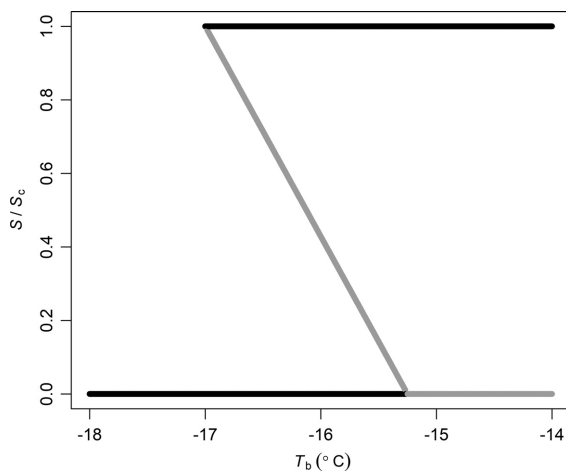


FIG. 8. Bi-stable states induced by vegetation-microclimate feedback in shrubland-grassland ecotones. Stable and unstable states are indicated by dark and grey lines respectively. S/S_c is the normalized density of *M. cerifera* ranging from 0 to 1, T_b is the temperature without the presence of *M. cerifera*. When T_b reaches a threshold value (approximately -15°C), the ecosystem would shift rapidly from grassland to shrubland which is highly hysteretic.

(Shao et al. 1995), creating a potential additional feedback with water availability in a system dependent on precipitation for recharging the freshwater lens (Aguilar et al. 2012). Despite the multiple environmental drivers that control shrub establishment, expansion across several islands has occurred at an unprecedented rate since the 1980s (Zinnert et al. 2016), even with accelerated sea-level rise (Sallenger et al. 2012) and reduction in island area.

The abrupt transition to shrubland can be highly hysteretic and potentially irreversible as evidenced by the ineffectiveness of many shrub-removal programmes (Rango et al. 2005, Bestelmeyer et al. 2009, D’Odorico et al. 2012) especially when self-sustained internal feedbacks act through their impact on ecosystem structure, functioning and resilience (Thompson et al. 2017). The ongoing shrub expansion in Hog Island (VA) would decrease plant species diversity and modify wildlife habitats (Zinnert et al. 2017). Increased carbon and nitrogen input into the system from shrub expansion (Brantley and Young 2010) alters biogeochemical cycling and may impact adjacent communities. In the short-term, shrubs provide resistance to storm events, by stabilizing sediments and reducing energy associated

with storms (Claudino-Sales et al. 2008, U.S. Army Corps of Engineers 2013). Over longer timeframes, this resistance may prevent natural island migration through increasing shoreline erosion and creating a barrier to sediment overwash, thereby increasing the vulnerability of barrier islands to sea level rise (Zinnert et al. 2016, Thompson et al. 2017). As barrier islands protect lagoons and marshes with many economically and ecologically important species, the transition from grassland to shrubland has far reaching consequences on multiple ecosystems. Our simplified modeling framework provides a general theoretical mechanism for the emergence of bi-stable vegetation dynamics in shrubland-grassland ecotones and facilitates our understanding and prediction of how the stability of these ecosystems may nonlinearly change under future climate change scenarios.

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