Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*)

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Summary

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- Fire disturbance can mediate the invasion of ecological communities by nonnative species. Nonnative plants that modify existing fire regimes may initiate a positive feedback that can facilitate their continued invasion. Fire-sensitive plants may successfully invade pyrogenic landscapes if they can inhibit fire in the landscape.
- Here, we investigated whether the invasive shrub Brazilian pepper (*Schinus terebinthifolius*) can initiate a fire-suppression feedback in a fire-dependent pine savanna ecosystem in the southeastern USA.
- We found that prescribed burns caused significant (30–45%) mortality of Brazilian pepper at low densities and that savannas with more frequent fires contained less Brazilian pepper. However, high densities of Brazilian pepper reduced fire temperature by up to 200 C, and experienced as much as 80% lower mortality.
- A cellular automaton model was used to demonstrate that frequent fire may control low-density populations, but that Brazilian pepper may reach a sufficient density during fire-free periods to initiate a positive feedback that reduces the frequency of fire and converts the savanna to an invasive-dominated forest.

Introduction

Exotic plant species can facilitate their own invasion by establishing positive feedbacks within the native ecosystem (Sakai *et al.*, 2001; Eppstein & Molofsky, 2007). These feedbacks may include the alteration of soil biota to favor mutualists or suppress pathogens (Callaway *et al.*, 2004; Wolfe & Klironomos, 2005), the creation of nutrient-cycling patterns more favorable to the invader (Vitousek, 1986; Miki & Kondoh, 2002; Ashton *et al.*, 2005) and the modification of existing disturbance regimes (Mack & D'Antonio, 1998). Positive feedbacks may account for the observed lag-time in many exotic plant invasions, because they promote an accelerating rate of invasion from rarity (Von Holle *et al.*, 2003; Taylor & Hastings, 2005). Therefore, identifying invasions with the potential to initiate positive feedbacks is critical for effective management early in the invasion process (Sakai *et al.*, 2001; Brooks *et al.*, 2004; Wolfe & Klironomos, 2005).

Positive feedbacks may occur through the modification of the natural disturbance regime by the invader (Mack & D'Antonio, 1998; Brooks *et al.*, 2004). For a positive feedback between the invader and disturbance regime to occur, the probability of disturbance at invaded sites must be different

from the probability of disturbance at un-invaded sites (Buckley *et al.*, 2007). In cases where disturbance is required for invasion, exotic species that increase the probability of disturbance relative to native species should exhibit a threshold or Allee effect: above a minimum density threshold, the increased disturbance of invaded sites should favor recolonization through propagule pressure from the abundant exotic species (Buckley *et al.*, 2007). This is an example of a conditional invasion dynamic (Eppstein & Molofsky, 2007) under which an exotic population will successfully invade once it reaches a critical density threshold because of a positive environmental feedback, provided that the exotic population growth rate exceeds that of native competitors only when it is above the critical density threshold and not below it. There is ample empirical evidence to support this model (Fensham *et al.*, 1994; D'Antonio, 2000), particularly among exotic grasses that increase the frequency or intensity of disturbance by fire relative to native species (Lippincott, 2000; Platt & Gottschalk, 2001; Rossiter *et al.*, 2003).

In fire-prone ecosystems, however, the natural disturbance regime may inhibit invasion (Hester & Hobbs, 1992). In savannas, for example, frequent low-intensity fires can prevent invasion by woody shrubs (Peterson & Reich, 2001; Bond &

Keeley, 2005; Beckage *et al.*, 2006; Bowles *et al.*, 2007), and some exotic species have successfully invaded savannas following fire suppression (Loope & Dunevitz, 1981; Rose & Fairweather, 1997). We suggest the potential for a threshold effect via a disturbance-suppressing feedback mechanism. Under this disturbance-suppressing feedback, fire should cause mortality of low-density invasive populations, and frequent fires may be sufficient to prevent further invasion (Bowles *et al.*, 2007). However, at higher densities, the invasive plant may reduce the intensity or the extent of a fire event (Brooks *et al.*, 2004), which would reduce per-capita mortality from fire among high-density invasive populations relative to lower-density populations. If the growth rate of the invasive population exceeds its native counterparts in the absence of fire (Eppstein & Molofsky, 2007) then populations that reach densities where they reduce or suppress fires might further perpetuate their own invasion. Thus, the disturbance-suppressing feedback is an example of a conditional invasion dynamic (Eppstein & Molofsky, 2007) mediated by modification of the disturbance regime (Buckley *et al.*, 2007) under conditions where disturbance prevents invasion.

We examined the potential for a disturbance-suppressing feedback, initiated through the suppression of fire by the invasive shrub Brazilian pepper (*Schinus terebinthifolius*), to promote the invasion of a pine savanna ecosystem in south Florida. Pine savannas are fire-maintained ecosystems, with a graminoid-dominated ground cover that supports frequent understory fires (Snyder *et al.*, 1990). Brazilian pepper is present in many pine savanna remnants, where it can create a dense subcanopy and reduce native diversity (Loope & Dunevitz, 1981). Furthermore, on disturbed soils, Brazilian pepper may reach densities where it can reduce fine fuel biomass and create conditions unfavorable to fire (Doren & Whiteaker, 1990). For a disturbance-suppressing feedback to cause conditional invasion within pine savannas, we expect that (1) Brazilian pepper in low-density populations should have high mortality in response to fire, (2) Brazilian pepper should exhibit lower mortality in the absence of fire, (3) Brazilian pepper should, at high-densities, reduce the intensity and spread of fire, and (4) pine savannas that are burned frequently should have less Brazilian pepper invasion than unburned savannas. We integrate our empirical results with respect to these four conditions using a cellular automaton model to demonstrate that a coupled vegetation-fire feedback could facilitate the invasion of pyrogenic savannas by a fire-suppressing invasive shrub.

Materials and Methods

Study site and species

We conducted our study within a pine rockland savanna ecosystem in the Long Pine Key (LPK) area of Everglades National Park, FL, USA. Pine rockland savanna canopies are characterized by an open physiognomy of widely scattered *Pinus elliottii* Engelm. var. *densa* Little & Dor. (south Florida slash pine; Doren *et al.*, 1993). Historically, pine rocklands were maintained in a savanna state by understory fires recurring every 3–7 yr near the beginning of the wet season from May to July (Beckage *et al.*, 2003; Slocum *et al.*, 2007). These fires rarely kill overstory trees, but do cause mortality among hardwood shrubs, maintaining an open and diverse understory (DeCoster *et al.*, 1999; Snyder, 1999; Schmitz *et al.*, 2002). With > 90% of original pine rockland savanna lost to development, LPK is the largest remaining tract in southern Florida (Fig. 1), and has been managed under a system of prescribed burns since 1958 (DeCoster *et al.*, 1999; Snyder *et al.*, 1990). Adjacent to LPK is an area of former pine savanna that was cleared and farmed until 1975, and currently harbors a large population of Brazilian pepper (Ewel *et al.*, 1982; Ewe & Sternberg, 2002).

Brazilian pepper (*S. terebinthifolius* Raddi.) is an exotic hardwood shrub that has successfully invaded much of southern Florida (Ewel *et al.*, 1982). Introduced by plant collectors during the late 1890s, Brazilian pepper had extensively invaded the region by the late 1970s (Morton, 1978). A prolific seed producer, Brazilian pepper reaches sexual maturity early and produces tens of thousands of single-seeded fruits annually among larger individuals (Ewel *et al.*, 1982). It is also morphologically plastic, growing as a single-stemmed small tree, multi-stemmed shrub or woody vine depending on site conditions and density (Spector & Putz, 2006). Brazilian pepper has potential allelopathic effects (Morgan & Overholt, 2005), high growth rates and vigorous resprouting (Snyder, 1999) and tolerance of fluctuating groundwater levels, which makes it a particularly successful invader of the hydrologically dynamic Florida Everglades (Ewe & Sternberg, 2002).

Feedback dynamics of Brazilian pepper

We monitored low-density populations of Brazilian pepper in multiple fire management units of Long Pine Key, or 'burn units', with different schedules of prescribed fire (Slocum *et al.*, 2003). We established one transect 20 m wide in each of six burn units, three of which would be burned during our study (Fig. 1). Transect lengths varied between 1.5 km and 2.6 km among the burn units (Stevens & Beckage, in press). In each transect, we surveyed for Brazilian pepper individuals, stopping every 20 m to conduct a 5-min visual survey. When we located a Brazilian pepper individual (defined as a discrete stem or cluster of stems from the same base), we tagged the largest basal stem and took GPS coordinates (WGS 1984, UTM Zone 17). If the first transect did not yield 30 individuals, we established another transect, of equal length to the first transect in that burn unit, elsewhere in the burn unit and repeated the search procedure until we reached a total of 30 individuals. We did not establish a third transect if 30 stems were not identified by the end of the second transect.

Fig. 1 The locations of field (a) and remote-sensing (b) study sites, located in southeast Florida, USA (c). (a) Within Everglades National Park (ENP), low-density transects are the 11 thin lines running north to south in six burn blocks at Long Pine Key. High-density transects are the three thick lines at the southern edge of burn block B. Burn blocks with cross-hatching were burned in 2006; those with stippling were burned in 2007. The area in white represents the original extent of the pine rockland savanna community, while gray represents low-elevation wet prairie. (b) Outside ENP, numbers 1–26 indicate the locations of our remote-sensing study sites (listed in the Supporting Information, Table S1). Major roads and cities are also shown.

To examine the effects of fire on low-density populations of Brazilian pepper, we conducted a preburn census of each plant during the summer of two years (July 2006 and June 2007). Burn units were burned by Everglades Fire Management in late July of each year, and we recensused all previously tagged plants in December of 2006 and 2007, approx. 5 months after the fires. For each census, we measured basal diameter, mortality and resprouting. Resprouting individuals contained old charred stems and new stems generally < 0.5 m tall.

We used temperature-sensitive paints to investigate the potential for Brazilian pepper individuals in low-density populations to reduce local fire temperature. Ten different temperature-sensitive paints by Tempilaq (Tempilaq, Tempil Division, Air Liquide America Corporation, South Plainfield, NJ, USA) were painted on a stainless steel tag and the tag was suspended from an 8-inch (approx 20 cm) garden stake. Each of the 10 paints melted at a different temperature (C): 107,

149, 204, 253, 316, 399, 538, 649, 788 and 871. These paints encompassed the range of expected pine savanna fire temperatures (Drewa *et al.*, 2002). Each tag was covered with tinfoil to keep water out, and inserted one stake at the base of each Brazilian pepper individual in burn units I2 and B before their prescribed burns (Fig. 1). We put another tag 3 m to the north of each individual in these low-density populations as a control.

We also examined whether high-density populations of Brazilian pepper could reduce fire intensity and subsequent mortality. We established three additional transects across a density gradient at the southern end of burn unit B (Fig. 1). This area has some of the highest densities of Brazilian pepper in all of Long Pine Key, as it shares a border with disturbed former farmland infested with Brazilian pepper. Each transect began at the edge of burn unit B and continued to the north until no Brazilian pepper individuals were found for 40 m.

The three transects had lengths of 80, 90 and 100 m and were each 2 m wide; every individual was tagged within the transect boundaries in June 2007. We calculated the Brazilian pepper density around each plant, at three different scales, by counting the number of conspecifics within a 2-m, 5-m and 10-m radius. We again used temperature-sensitive paints to examine the effects of high-density populations on fire temperature. Applying temperature-sensitive paints to stakes as already described, we put one stake every 10 m in the middle of the transect and inserted the last stake 10 m past the last Brazilian pepper individual. To calculate population density around each stake, we repeated the counting of Brazilian pepper at radii of three different distances, as described earlier.

To assess fire temperatures following the prescribed burns, we returned to all transects in August 2007, *c.* 2 wk after the fires. We recorded the highest temperature paint to melt in the fire, and assumed that the actual fire temperature was at the midpoint between this temperature and the temperature of the next highest paint. We also noted mortality of all plants in August, and confirmed mortality in December 2007.

The effect of fire on low-density Brazilian pepper individuals was analysed using a binomial model of plant mortality: $\vec{M} \sim Binomial(\vec{p})$ where $\vec{M}$ is the vector of observed mortality (1 = died, 0 = survived) and $\vec{p}$ is a vector of predicted mortality probabilities defined by $logit(\vec{p}) = \mathbf{X}\vec{\beta}$. The vector of estimated parameters is represented by $\vec{\beta}$ and $\mathbf{X}$ is the design matrix, which contains the diameter and burn status of each plant. The logit function is given by $logit(\vec{p}) = \log(\vec{p}/(1-\vec{p}))$. We fitted our model using maximum-likelihood in the R statistical software package (http://www.r-project.org) and distinguished between alternative models of plant mortality using the Akaike information criterion (AIC; Burnham & Anderson, 2002).

To assess the effects of Brazilian pepper on fire temperature in the low-density transects, we calculated the mean difference $\overline{\Delta T}$ in observed fire temperature between a tag at the base of each Brazilian pepper and the adjacent control tag 3 m from the stem. We calculated the likelihood of the observed temperature differences $\Delta \vec{T}$ given a predicted mean difference of $\overline{\Delta T}$ compared with 0, using the model $\Delta \vec{T} \sim Normal(\mu_t, \sigma^2)$, where μ_t is the predicted mean fire temperature difference and σ^2 describes the variance. The two models were compared using the likelihood ratio $L_{\overline{\Delta T}}/L_0$, where $L_{\overline{\Delta T}}$ is the likelihood of a temperature difference, and L_0 is the likelihood of no temperature difference.

For our high-density transects, we modeled the effect of Brazilian pepper density on fire temperature as $\vec{\mu} = \beta_0 + \beta_t * \vec{D}$, where $\vec{\mu}$ is the vector of predicted mean fire temperatures, β_0 is the intercept, and β_t is the parameter estimate for the effect of Brazilian pepper density $\vec{D}$ on temperature. The likelihood of the observed temperature values $\vec{T}$ in the high-density transects was calculated using the model $\vec{T} \sim Normal(\vec{\mu}, \sigma^2)$ to obtain parameter estimates. In addition to a null (intercept only) model, we tested the effects of Brazilian pepper density at three different radii (2, 5 and 10 m), and compared our four models using AIC to determine which density scale had the strongest effect on fire temperature.

We determined whether high densities of Brazilian pepper could decrease post-fire mortality of Brazilian pepper using a binomial model: $\vec{M} \sim Binomial(\vec{p})$, where $\vec{M}$ is the vector of observed mortalities from our high-density populations. We estimated $\vec{p}$, the predicted probabilities of mortality, as a function of density, using the logit link function $logit(\vec{p}) = \beta_0 + \beta_m \vec{D}$, where $\vec{D}$ is the conspecific density around each plant in the high-density transects, at one of three different radii (2, 5 and 10 m), and β_m is the parameter for the effect of density on mortality probability. The likelihoods of the three density models and a null model were compared using AIC.

Landscape invasion patterns

Digital aerial photographs were analysed to link landscape-scale patterns of Brazilian pepper invasion with fire history. We obtained digital orthorectified quarter quad (DOQQ) aerial photographs of southern Florida from the Florida Department of Environmental Protection's Land Boundary Information System (LABINS, http://www.labins.org). These images were taken in 2005, have 1 m^2 pixel resolution, and have color–infrared band information that is useful in classifying vegetation (Everitt *et al.*, 2002). We selected 26 remnant pine savanna fragments outside of Everglades National Park (Fig. 1), managed by the Miami-Dade County Parks and Recreation Department, to classify into vegetation types. Sites selected for our analysis (1) were known to be pinelands, (2) had known fire history dating back to at 1985 and (3) were not heavily managed for Brazilian pepper removal other than through prescribed burns (S. Thompson, Miami Dade Parks & Recreation Department, pers. comm.). We visited each site and took five ground control GPS points (GCPs) for each of three vegetation classes: pine stands, open grass and Brazilian pepper stands. We conducted a supervised classification of the DOQQ images in the ERDAS IMAGINE® remote sensing software package (ERDAS 2007), using the GCPs as training sites to identify a unique spectral signature for each vegetation class. Subsequently, we overlaid shapefiles of all fires since 1985, and subset the classified images into burn-units with different fire histories. There were a total of 80 burn units spread across the 26 savanna fragments (see the Supporting Information, Table S1).

To model the extent of Brazilian pepper invasion as a function of fire history, we first calculated the proportion of pixels in each burn unit that were classified as Brazilian pepper. We created two binary response variables of Brazilian pepper invasion extent, invaded and severely invaded, for all 80 burn units. Burn units in the invaded variable were coded as invaded if > 10% of pixels were classified as Brazilian pepper, and severely invaded if > 25% of pixels were classified as Brazilian pepper. Seven site-factors were defined to explain the probability of invasion and severe invasion by Brazilian

pepper using logistic regression. These included the variables: (1) occurrence of fire between 1985–2007; (2) number of fires during the same period; (3) distance (in km) to downtown Miami; (4) area of the burn unit (in km^2); (5) perimeter of the burn unit (in km); (6) area–edge ratio (km^2 km^{-1}); and (7) surrounding land cover type. Distance to Miami is a proxy for distance to a likely point of Brazilian pepper introduction (Morton, 1978), and for a gradual decrease in elevation with increasing distance to Miami (Snyder *et al.*, 1990). We defined the land cover surrounding each site as pine savanna, agricultural land, suburban/residential development or urban development.

Bayesian model averaging was used to select the site factors that best explained the probability of a site being invaded or severely invaded (Platt *et al.*, 2002). The probability p_i of each site being invaded above the given threshold was estimated as $\text{logit}(\vec{p}_i) = \mathbf{X}\vec{\beta}$, where $\vec{\beta}$ is a vector of parameters corresponding to the design matrix $\mathbf{X}$, containing the seven site-factors. For each combination of the site-factors, we estimated the posterior probability of that model, M_j, as

$$\Pr(M_j \,|\, \text{Data}) = \frac{\Pr(\text{Data} \,|\, M_j)\Pr(M_j)}{\sum \Pr(\text{Data} \,|\, M_j)\Pr(M_j)} \qquad \text{Eqn 1}$$

($\Pr(\text{Data} \,|\, M_j)$ is given by $\vec{i} \sim Binomial(p_i)$, that is, the probability of observed invasion extents $\vec{i}$ following the binomial distribution of predicted invasion extents p_i estimated by model j). We assumed that the previous probabilities $\Pr(M_j)$ for all models were the same, and so would not influence the posterior model probabilities. We fitted our models with the Bayesian model averaging approach using the function *bic.glm* in R (http://www.r-project.org). For both the invasion and severe invasion variables, we selected the three models with the highest posterior probabilities (Eqn 1) (Raftery, 1995).

Cellular automaton simulation

The invasion of pine savannas by Brazilian pepper was simulated using a cellular automata model that captures the main features of our pine savanna study system. Our model operated on a grid of 50×50 cells with each cell representing a discrete area (e.g. 10×10 m) that could be in one of five states: grass, juvenile pine, adult pine, juvenile hardwood or adult hardwood, juvenile invasive or adult invasive. In our simulations, we allowed the invasive to have a relatively higher probability of mortality in fire than pines (e.g. 0.9 for invasive juveniles and 0.8 for invasive adults compared with 0.7 for pine juveniles and 0.2 for pine adults). The probability of fire in a cell occupied by an invasive, by contrast, was lower than for grass or pine cells: 0.1 and 0.05 for a cell occupied by an invasive juvenile and adult, respectively, compared with 0.2 and 0.3 for a juvenile and adult pine and 0.4 for a grass cell. Burn probabilities and subsequent survival of vegetation types reflects qualitative observations of the fire ecology of pines

and other vegetation components as well as their sensitivity to fire (Platt *et al.*, 1988; Platt, 1999; Gilliam *et al.*, 2006). In the absence of fire, the invasive has a higher potential population growth rate than pines, gradually displacing both native hardwoods and pines through vegetative succession, as observed in some pinelands (Loope & Dunevitz, 1981). We did not explicitly include fecundity but only allowed a species to potentially establish in any cell within its dispersal distance. We permitted the invasive to have a longer dispersal distance than pines or hardwoods to reflect the importance of bird dispersal for Brazilian pepper (Ewel *et al.*, 1982).

Fires were initiated in randomly selected cells by lightning strikes and subsequently could spread to adjacent cells. Initiation of fire was dependent on the state of the cell struck: vegetation types have different degrees of flammability and therefore the likelihood of a fire starting in a given cell should be dependent upon the vegetation type occupying that cell (Bond & Midgley, 1995; Bond & Keeley, 2005). The number of lighting strikes in the landscape at each time step was modeled as a Poisson process with the mean or λ parameter equal to lightning strike intensity multiplied by the number of cells in the landscape. Lightning strike intensity was 0.001, 0.004 and 0.016 expected strikes per cell across our simulations, which corresponded to an expectation of 2.5, 10 and 40 lightning strikes in a 50×50 cell landscape. After a successful start, fire could potentially spread across the landscape in a probabilistic manner dependent on the state of surrounding cells.

We explored the process of invasion into a pine savanna by comparing the initial and final abundance of the invasive in the savanna landscape. The initial landscape fraction of the invasive was varied between approx. 0.01 and 0.9 across simulations with the remaining noninvasive portion of the landscape reflecting a typical pine savanna, predominantly consisting of grass cells followed by pines but also containing some hardwoods. The landscape was updated on an annual time-step in response to two processes: vegetative succession and fire initiation and spread. A model run was completed when a maximum number of time steps (i.e. 500 yr) was reached or when the landscape reached a stable composition, which we defined as no more than 1% change in landscape composition over 10 yr.

The savanna model was implemented in the Java programming language for portability, developmental efficiency and computation speed, but the program was called from within Mathematica (http://www.wolfram.com) to take advantage of its graphical and analysis features. More details on the structure of the model can be found in Beckage & Ellingwood (2008).

Results

Fire caused 30–45% overall mortality among low-density populations of Brazilian pepper, compared with 0–4% in the absence of fire, for all size classes combined. Mortality rates following fire were size-dependent, varying from 63 to 100%
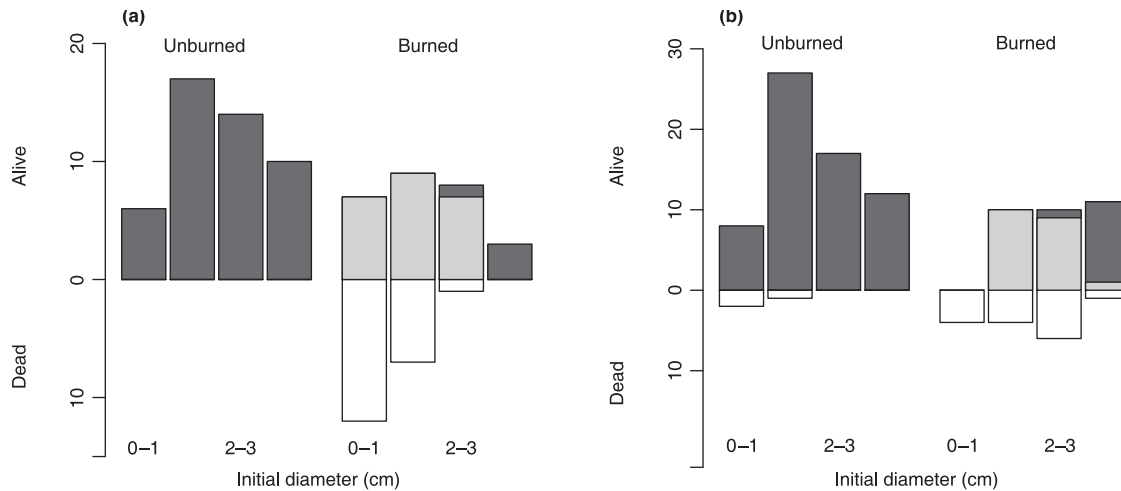
Fig. 2 Brazilian pepper (*Schinus terebinthifolius*) survivorship in (a) 2006 and (b) 2007. Total mortality was 45% in 2006 and 30% in 2007. Mortality was measured in the winter census of each year, when all plants were alive during the summer census of that year. Bars above 0 indicate the number of surviving plants for each size class, where tinted bars indicate the number of individuals that re-sprouted, and closed bars indicate the number of individuals that retained live foliage since the summer census. Open bars below 0 indicate the number of plants in each size class that died between censuses.

across the 2 yr for our smallest size class (< 1 cm at base) to 0–8% in our largest size class (> 3 cm at base; Fig. 2). Our best model of mortality, as judged by AIC, accounted for both fire and initial plant size (2007 AIC values: null = 23.8, fire = 5.5, fire + diameter = 0; see Table S2 for 2006 values). Mortality rates from fire for the 2 yr combined were 51% for small plants, with diameter < 2 cm, compared with 20% for larger plants with diameter > 2 cm, and all surviving small plants resprouted, while larger plants tended to retain some live foliage (Fig. 2). The high fire-related mortality of smaller individuals in low-density populations suggests that fire can limit establishment of low-density founding populations.

Isolated Brazilian pepper individuals caused a reduction of 48 C in fire temperature compared with that recorded at a paired control location just 3 m away. The mean temperature of the fire under Brazilian pepper individuals was 107 C, compared with 154 C at the control location. Our model allowing for a temperature difference caused by isolated Brazilian pepper had a greater likelihood than a null model (likelihood ratio = 343.2; 95% confidence interval for temperature difference = [15 C, 80 C]).

High densities of Brazilian pepper decreased fire temperature to a greater extent than did isolated individuals (Fig. 3a). Linear regression models of temperature on density at all three distances, 2, 5 and 10 m, were better fits to the data than a null model of no density effect, with the 2-m model the best fit (ΔAIC values: null = 21.5, 10 m = 8.4, 5 m = 6.7, 2 m = 0; parameter estimates are given in Table S2). When there was no Brazilian pepper within 2 m, average fire temperature ranged from 128 to 229 C, while at high densities of three plants within 2 m, the fire temperature never exceeded 68 C, and in some cases fire was apparently absent (Fig. 3a).

Brazilian pepper individuals in high-density populations also had lower probability of mortality in a fire (Fig. 3b). Density at all distances was again a better predictor of mortality than a null model, with the 5-m model the best fit (ΔAIC values: null = 24.3, 10 m = 5.7, 5 m = 0, 2 m = 9.2; parameter estimates are given in Table S2). Among individuals with fewer than two neighbors within 5 m, 88% (eight of nine plants) were killed by fire. Conversely, when individuals had more than two neighbors within 5 m, only 6% (2 of 31 plants) were killed by fire (Fig. 3b). Importantly, high-density populations also experienced reduced fire spread: 89% of surviving plants that had fewer than four neighbors per 5 m were burned, while 100% of plants with more than six neighbors per 5 m did not burn (Fig. 3b).

Fire was the strongest predictor variable of Brazilian pepper invasion extent into pine savanna fragments, as determined by our remote sensing analysis. The occurrence of fire was the best model to explain both the probability of invasion and the probability of severe invasion by Brazilian pepper (Table 1). The number of fires over a 20-yr period was the second best model, with reduced probability of invasion in sites experiencing more frequent fires (Table 1). We observed zero 'invaded' sites with greater than two fires (Fig. 4c), and zero 'severely invaded sites' with greater than one fire (Fig. 4e), although our sample size for sites with > 1 fire since 1980 was comparatively small (Fig. 4a). Other than fire occurrence and number, additional site-factors had little support in our models. No nonfire site-factor had > 10% posterior probability of being in the best model (Table 1).

Our model simulations qualitatively support the potential for the observed patterns of Brazilian pepper mortality in fire together with the suppression of fire by Brazilian pepper to

Table 1 Bayesian logistic model selection of factors predicting Brazilian pepper (*Schinus terebinthifolius*) invasion extent. BIC is the Bayesian information criterion, and models with ΔBIC > 2 are unlikely to be the best candidate model

Site-factors	Mean($\bar{\beta}$)[b]	SD	Odds ratio[c]	Pr($\bar{\beta} \neq 0$)[d]	Model[e] 1	2	3
Probability of invasion (Brazilian pepper > 10%)							
Burned	−1.893	1.110	0.15	0.84	*		*
Number of fires	−0.193	0.474	0.82	0.16		*	
Distance[a]	−0.002	0.010	0.99	0.10			*
Area (km²)	0.000	0.000	1.00	0.00			
Edge (km)	0.000	0.000	1.00	0.00			
Area : edge	0.000	0.000	1.00	0.00			
Land cover type	0.000	0.000	1.00	0.00			
Model probability					0.74	0.14	0.12
ΔBIC					0	3	4
Probability of severe invasion (Brazilian pepper > 25%)							
Burned	−1.582	1.517	0.21	0.56	*		*
Number of fires	−1.106	1.403	0.33	0.44		*	
Distance[a]	0.000	0.000	1.00	0.00			
Area (km²)	0.000	0.000	1.00	0.00			
Edge (km)	0.000	0.000	1.00	0.00			
Area : edge	−0.001	0.003	1.00	0.06			*
Land cover type	0.000	0.000	1.00	0.00			
Model probability					0.51	0.44	0.05
ΔBIC					0	0	4

The probabilities of invasion and severe invasion were modeled on seven site-factors. The three models with the most support are shown for each invasion extent, in order of decreasing posterior probabilities.
[a]Distance to downtown Miami, measured in km.
[b]Average parameter value estimated across all models containing that parameter, weighted by model probability.
[c]Odds ratio is exp($\bar{\beta}$), the relative expected difference in probability of invasion caused by a unit increase in a given site factor.
[d]Probability of parameter being included in the best model.
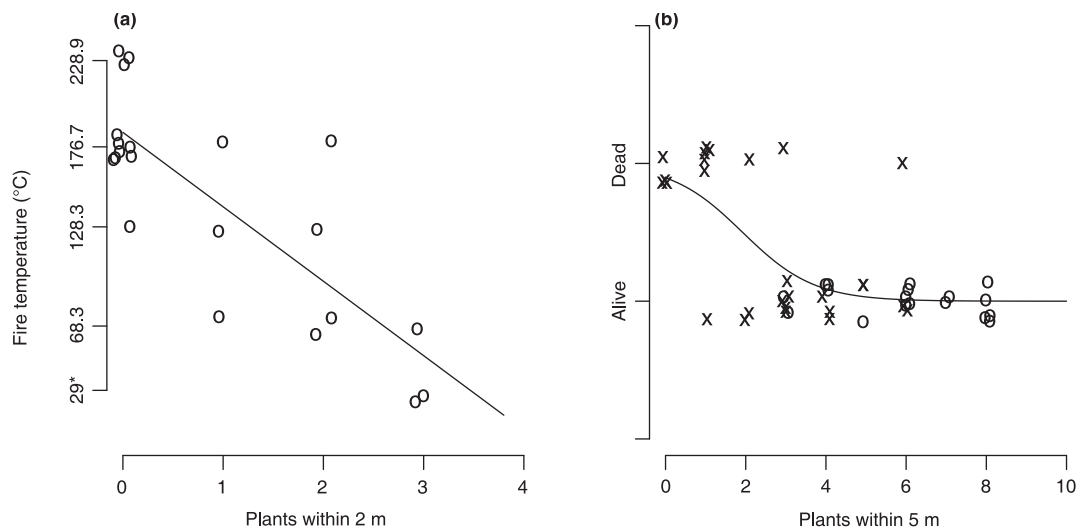[e]Variables with asterisks have high (> 0.05) probability of being in a given model.

Fig. 3 High densities of Brazilian pepper (*Schinus terebinthifolius*) reduce fire temperature (a) and probability of mortality (b). Intraspecific density at a 2-m radius was the best model to explain variation in fire temperature in (a). Density at a 5-m radius was selected using Akaike information criterion (AIC) as the best model to explain variation in Brazilian pepper mortality in (b) (crosses, burned; circles, did not burn; line, predicted probability of mortality). Plants surviving at low densities burned and re-sprouted; plants surviving at high densities resisted fire and did not burn. Points in both figures are jittered for clarity in both horizontal and vertical directions. *, 29 C is the average July temperature, and indicates areas that did not burn, or experienced temperatures too low to be recorded by the lowest fire paint.
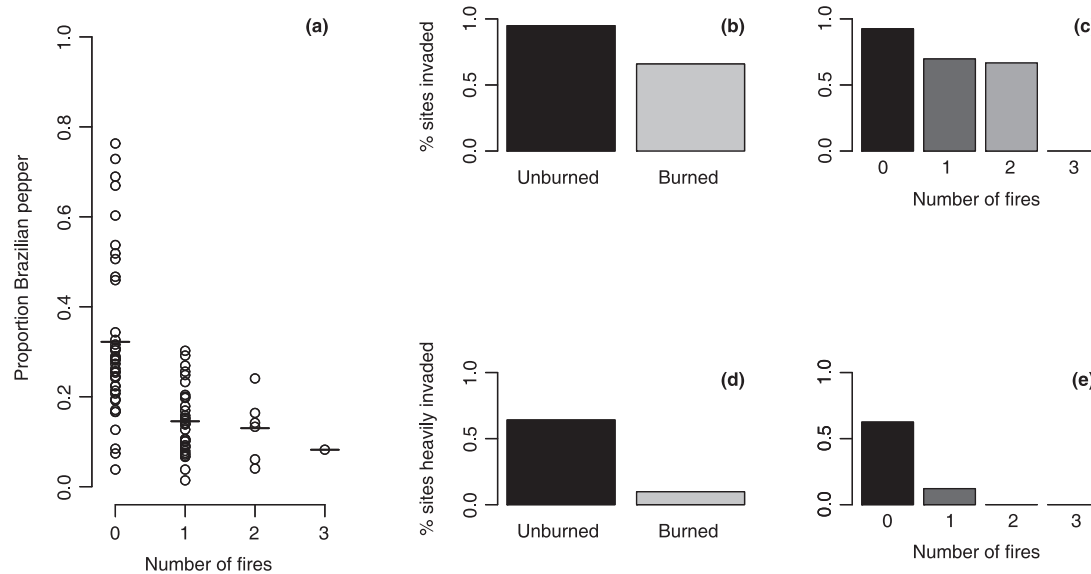
Fig. 4 The extent of invasion of Brazilian pepper (*Schinus terebinthifolius*) into pine savanna fragments as derived from remote sensing data. The proportion of pixels from each site that were classified as Brazilian pepper is shown in (a). The observed proportion of savanna fragments that were invaded (sites with > 10% Brazilian pepper) decreased with fire, where the best model of invasion extent was the occurrence of fire (b) and the second best model was the number of fires (c). The trend was similar in sites that were severely invaded (> 25% Brazilian pepper), where the two best models again were occurrence of fire (d) and number of fires (e).

result in rapid transitions between uninvaded and invaded landscape states (Fig. 5). As the initial landscape fraction of the invasive increased in our model simulations, a threshold was approached where the community rapidly changed to a state dominated by the invasive. Below this threshold abundance of the invasive, the native community remained intact with the invasive limited to low densities. However, once the initial abundance of the invasive surpassed this threshold, the native community was displaced by the invasive. The abrupt change in state results from the nonlinear feedback between fire and vegetation, and creates sensitivity to the length of fire-free period, which allows for increased establishment of the invasive, and changes in lightning strike frequency, which can shift the location of the threshold (Fig. 5a vs b vs c).

Discussion

We found evidence suggesting that Brazilian pepper may invade pinelands through a fire-suppressing feedback. The intensity and spread of fire are reduced by the increasing density of Brazilian pepper: the suppression of fires by Brazilian pepper increased dramatically between two and six plants per 5 m radius, and Brazilian pepper appears capable of reducing fire intensity to the point of complete fire suppression (Fig. 3). In the pine savannas of Miami-Dade County, Brazilian pepper invaded more extensively in the absence of fire (Fig. 4), but at low densities it experienced significant mortality in response to fire (Fig. 2). These characteristics can lead to nonlinear feedbacks and ecological thresholds with rapid shifts from an uninvaded to invaded state when these thresholds are crossed

(Fig 5). Our results are further supported by a negative correlation between Brazilian pepper invasion and the occurrence of fire at the landscape level. Brazilian pepper is an apparent disturbance suppressor (D'Antonio, 2000; Brooks *et al.*, 2004; Buckley *et al.*, 2007) and it is this suppression of the fire regime that allows for the increase in Brazilian pepper's population growth above that of its native competitors in pine savannas, leading to conditional invasion (Eppstein & Molofsky, 2007). The scale of this fire-invasive feedback is important, as shown by Eppstein & Molofsky (2007), because a small population that exceeds this density can initiate the feedback process locally, and spread outward through continued disturbance suppression.

We found that variation in Brazilian pepper density affects fire temperatures at a small scale, but that mortality of Brazilian pepper is most strongly affected by a fire-invasive feedback at a slightly larger scale (Fig. 3). Brazilian pepper reduces understory fine fuel biomass, making it less likely that fire will spread to its canopy and burn the plant (Koepp, 1978; Doren & Whiteaker, 1990). Small-scale density of Brazilian pepper (at a 2-m radius) best explained variation in fire temperature, probably because fine-fuel biomass responds to small-scale differences in Brazilian pepper canopy cover (Doren & Whiteaker, 1990), with large effects on fire temperature (Lippincott, 2000; Thaxton & Platt, 2006). High density of Brazilian pepper at a larger scale represents a greater potential for the suppression of fire spread, owing to the low flammability of Brazilian pepper stands and resulting lack of fuel connectivity (Loope & Dunevitz, 1981). Thus, density at a 5-m radius best explained variation in Brazilian pepper mortality, because some dense stands did not burn at all.
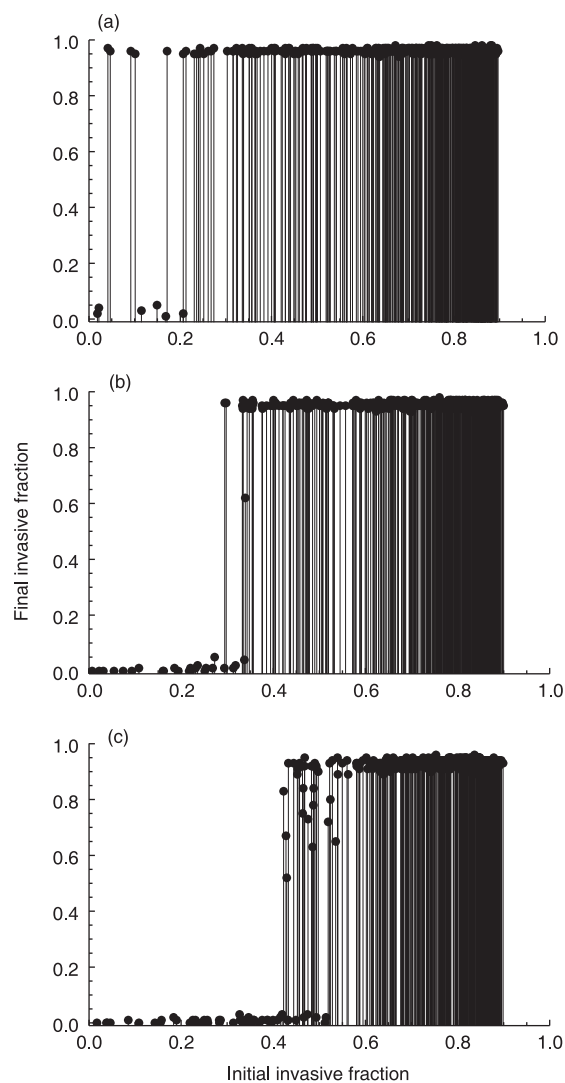
Fig. 5 Final state of the ecological community as a function of increasing initial abundance of the invasive. Increasing initial abundance of a fire-suppressing invasive leads to an ecological threshold with an abrupt transition between an uninvaded and invaded state. The transition to an invaded state requires higher initial abundance of the invasive as lightning intensity increases: Lightning intensity is 0.001, 0.004 and 0.016 expected strikes per cell in (a), (b) and (c), respectively. These simulations suggest that long fire-free intervals or increased propagule pressure can result in the conversion of the native community to an invaded state.

We found landscape-scale patterns in Brazilian pepper invasion that are consistent with the predictions of a local-scale disturbance-suppressing feedback. Given that fire results in high mortality of low-density Brazilian pepper populations, frequent fire should reduce the invasion of Brazilian pepper into pine savannas. Furthermore, because Brazilian pepper can suppress fire at high densities, severely invaded savannas should experience fewer fires. We found that the occurrence of fire was strongly related to Brazilian pepper abundance (Table 1). Frequent fire appeared to be important in preventing

severe (> 25%) invasions by Brazilian pepper, with no sites that were burned more than once categorized as severely invaded, while > 50% of unburned sites considered severely invaded (Fig. 4). The high preponderance of invasion at unburned sites shows that Brazilian pepper can successfully invade in the absence of disturbance (Loope & Dunevitz, 1981). Furthermore, there is evidence from our remote-sensing data that in some savannas with high abundance of Brazilian pepper, fire failed to penetrate these sites despite burning adjacent sites with less Brazilian pepper (J. T. Stevens & B. Beckage, unpublished). Therefore, the landscape-scale patterns of fire and Brazilian pepper invasion appear to support the predictions of our disturbance-suppressing feedback model.

Positive feedbacks can lead to nonlinearities and threshold responses in diverse natural processes from climate change to the desertification of arid lands (van de Koppel *et al.*, 1997; Higgins *et al.*, 2002; Walker & Meyers, 2004; Beckage *et al.*, in press). In our study system, the feedback between Brazilian pepper and fire has the potential to create ecological thresholds with abrupt transitions to alternative stable states (Suding *et al.*, 2004; Beckage & Ellingwood, 2008). A reduction in the frequency of fire or increased length of fire-free periods could provide the opportunity for the establishment of Brazilian pepper at a threshold density (Fig. 5) that initiates a fire-suppressing feedback and a concomitant rapid expansion of Brazilian pepper and other fire-sensitive woody species (Loope & Dunevitz, 1981; Rose & Fairweather, 1997). Brazilian pepper can then form a closed canopy that suppresses pine regeneration and reduces understory diversity, eventually resulting in the loss of the pine savanna community and the creation of a Brazilian pepper-dominated alternative stable state (Loope & Dunevitz, 1981; Platt *et al.*, 2002). The suppressant effect of Brazilian pepper on subsequent fire probability can result in a hysteresis: a return to the prethreshold levels of fire ignitions would be insufficient to restore the community to its pre-threshold pine savanna state, but rather a higher level of fire ignitions would be required to return to the system to a pine savanna alternative stable state (Fig. 5) (Scheffer *et al.*, 2001; Beckage & Ellingwood, 2008). The strong feedbacks between Brazilian pepper and fire can make restoration of pine savannas dominated by Brazilian pepper difficult (Suding *et al.*, 2004). We suggest that, without anthropogenic management, extraordinary climatic conditions would be required to reintroduce fire into the Brazilian pepper stands, so that the change in community state is essentially irreversible.

Community transitions between uninvaded (pine savanna) and invaded (Brazilian pepper stands) states in our system are expected to be sensitive to conditions affecting fire regimes, including climate change, landscape fragmentation and anthropogenic fire suppression (Knick & Rotenberry, 1997; D'Antonio, 2000; Beckage *et al.*, 2003; Beckage *et al.*, 2006). The location of the threshold for initiation of a strong fire-suppression feedback is determined by Brazilian pepper density (Fig. 5). The most effective management efforts would be those that focus

on maintaining a frequent fire regime that prevents Brazilian pepper from reaching the invasion threshold density that initiates a fire suppressing feedback in uninvaded pine savannas. Within pinelands in Everglades National Park, the maintenance of the historical 3–7 yr fire return interval largely appears to have been effective at keeping Brazilian pepper below the threshold density for the onset of positive feedback that results in an alternative invaded state (Beckage *et al.*, 2003; Slocum *et al.*, 2007; Stevens & Beckage, in press).

The study of plant invasions has increasingly focused attention on the issue of invasion through the alteration of disturbance regimes, particularly of fire regimes (Higgins & Richardson, 1998; Mack & D'Antonio, 1998; Brooks *et al.*, 2004; Callaway & Maron, 2006). However, to date, there are few empirical examples of invasion through fire suppression (D'Antonio, 2000). In this study, we have shown that the invasive shrub Brazilian pepper may invade by just such a mechanism. Small populations of Brazilian pepper are susceptible to fire, and frequent fire may keep Brazilian pepper at low densities. However, populations that establish during fire-free periods at a density sufficient to reduce fire temperature and spread can facilitate continued invasion and irreversibly convert pine savannas to Brazilian pepper thickets.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Study sites used in remote sensing analysis

Table S2 Parameter estimates and Akaike's information criterion (AIC) values for all models

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