

THE ROLE OF FIRE DISTURBANCE IN THE INVASION OF SOUTH FLORIDA  
PINE SAVANNAS BY BRAZILIAN PEPPER (SCHINUS TEREBINTHIFOLIUS)

A Thesis Presented

by

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to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements  
for the Degree of Master of Science  
Specializing in Plant Biology

October, 2008

## Abstract

Exotic plant species may facilitate their invasion into native communities through the modification of ecosystem disturbances such as fire regimes. Where frequent fires are common, invasive plants that suppress fire may induce a positive feedback which further suppresses fire and promotes their continued invasion. In the pine rockland savanna ecosystem of south Florida, the frequent understory fire regime may be altered by the fire-resistant invasive shrub Brazilian pepper (*Schinus terebinthifolius*). In this thesis, I document the interaction of Brazilian pepper and fire in these savannas. I show that fire causes significant (30%-50%) mortality among low-density populations of Brazilian pepper. However, Brazilian pepper exhibits rapid growth and reproduces quickly following fire, and in the absence of fire it has a low mortality rate. Furthermore, Brazilian pepper can cause a reduction in fire temperature from 47° C at low densities, to almost 200° C at high densities, where it can completely impede fire spread. This creates the potential for Brazilian pepper to initiate a fire-suppressing feedback if it can reach a density threshold during extended fire-free intervals. At a landscape scale, I analyzed digital aerial photographs to show that fire frequency correlates with the extent of Brazilian pepper invasion into pine savanna fragments in southern Florida. In savannas where fire is frequent, Brazilian pepper does not heavily invade, but savannas that are heavily invaded tend to be unburned for more than 20 years. This supports both the regulation of low-density Brazilian pepper populations by fire, and the potential for high-density Brazilian pepper populations to suppress fire and facilitate further invasion.

## **Acknowledgements**

I would like to thank my advisor, Brian Beckage, for invaluable advice and support during my time at UVM. I have learned much with respect to analyzing data, writing for publication, and asking insightful ecological questions, and for that I owe Brian a great deal of gratitude. I would also like to thank my committee members, Jane Molofsky and Alison Brody, for providing a critical ecological and evolutionary perspective on my research, and for excellent feedback and advice.

I had an enormous amount of assistance in support of this research. For hours of help in the field and the lab, I thank Charles Bartlett, Ben Palmer, Ben Blumberg, Sonali Saha, and especially Brian Warshay, without whose car the second chapter of this thesis would not exist. Thanks also to the staff and researchers of Everglades National Park, especially Hillary Cooley, Maya Vaidya, Rick Anderson, Bob Panko, Steve Newland, Robert Trincado, Pat Edwards and Lauren Serra, for facilitating an often challenging and always rewarding set of four field seasons, and for collaborating on the prescribed burn schedule. Sonya Thompson and Dallas Hazelton of the Miami-Dade County Department of Parks and Recreation helped with the study of pine savanna fragments detailed in Chapter 2.

My lab-mates, Kimmie Beal and Carrie Pucko, have been tremendous colleagues and even better friends- I could not have asked for a better lab experience.

Thanks also to the wonderful community of graduate students at UVM- being surrounded by a group of intelligent and fun people has been a highlight of my time here. To Ted Hart, Craig Brodersen, Robin Collins, Erin Sigel, Matt Kaproth, Manisha Patel, Andrew Dunn, Ken Bagstad, Scott Wagner, Chris Massa, Erin Quigley, Samir Doshi, Jared Nunery, Will Dixon, Ashley Lidman, Angus Beal, Jamie Parr, James Barnes, Ryan Salmon, Mary Ackley, Samantha Foster, Annette LaBauve, Sarah Wittman, Jill Hoffman, Dan Barkhuff, Langley Scherer, Jameson Bell, Luke Purvis, Tom Howland, and countless others, thank you for your friendship.

Most importantly, thank you to my parents, Don and Candyce, and my brother Jules, for the kind of unconditional support which is so consistent that it often goes underappreciated.

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## Chapter 1: Introduction

### *Plant invasions*

The study of plant invasions has offered novel insights into important ecological processes (Sakai et al. 2001, Shea and Chesson 2002, Callaway and Maron 2006). Specifically, studies in invasion ecology have informed our understanding of life history attributes that are important to the colonization, establishment and range expansion of new plant species into existing communities (Arii and Parrott 2006). Invasion studies have also led to greater knowledge of community-level properties (Tilman 2004) and landscape patterns (With 2002) that dictate the susceptibility of plant communities to invasion. Furthermore, the impacts of invaders on native communities indicate mechanisms by which individual species can significantly alter the evolutionary trajectories (Callaway and Ridenour 2004), species abundances (MacDougall and Turkington 2005), ecosystem functioning (Vitousek 1990) and disturbance regimes (Mack and D'Antonio 1998) of their associated communities.

Much early work on invasion ecology focused on investigating shared life-history attributes of invasive species (Baker 1974, Sakai et al. 2001). Life-history characteristics of plant invaders differ considerably between species, but several attributes are fairly consistent, and suggest that the successful invasion, i.e. colonization, establishment and range expansion, of new species may be particularly sensitive to specific ecological processes (Kolar and Lodge 2001). The importance of propagule pressure to invasion success suggests that species with high fecundity may be more likely to colonize new communities (Lockwood *et al.* 2005) and that invasion

resistance in communities may be in part attributable to propagule limitation of novel species (Tilman 1997, Neubert and Caswell 2000). The frequency of multiple introductions of successful invaders suggests that genetic diversity and hybridization play an important role in species establishment in new environments (Ellstrand and Schierenbeck 2000). Range expansion of established exotic plants is particularly effective among plants with clonal reproduction (Brewer and Cralle 2003, Liu et al. 2006), high relative growth rates (Garcia-Serrano *et al.* 2005), and phenotypic plasticity (Richards *et al.* 2006). These attributes all play important roles in the invasion of novel species into new habitats, and may in fact be subject to strong selection and rapid evolution during the invasion process (Lavergne and Molofsky 2007).

In addition to life history attributes of invasive plants, properties of the invaded communities themselves are important to the invasion process (Higgins and Richardson 1998). Interspecific interactions between the invader and the native plant community may facilitate invasion, i.e. through soil microbe mutualisms (Callaway et al. 2004, Reinhart and Callaway 2004) or lack of resistance to allelopathic effects of the invader (Hierro and Callaway 2003, Vivanco et al. 2004). Invaded communities often lack natural enemies to control invader populations (Blumenthal 2006), offering evidence of the importance of top-down control within plant communities (Callaway and Maron 2006). Invasion ecology has additionally provided insight into the role of niche dynamics in community assembly. Evidence of established species reducing invasion success of species from the same functional guild suggests that successfully invaded communities may contain unoccupied niche space (Fargione et al. 2003, Tilman 2004),

and that successful invaders of these communities will be adapted to fill that niche space (Thuiller *et al.* 2006).

Research on invasions has led to a greater understanding of the importance of landscape patterns in the structure of plant communities (Hobbs 2001, Murphy and Lovett-Doust 2004). Increased habitat fragmentation may increase invasion by species with long-distance dispersal, but habitat connectivity can lead to greater landscape-scale invasion by invaders with poor dispersal (With 2004). Invasion of fragmented communities is further enhanced when the inter-fragment matrix habitat is suitable for establishment and dispersal of the invasive (With 2002, Jules and Shahani 2003). In addition to increasing the risk of invasion from the matrix, fragmentation may also lead to habitat sinks for native species, where their ability to resist invasion and evolve within the sink is inhibited by mortality and by immigration from un-fragmented source populations (Holt *et al.* 2004).

Finally, the response of a plant community to invasion indicates the susceptibility of entire communities to the pressures imposed by a single new species (Mack *et al.* 2000, Lockwood *et al.* 2007). At the evolutionary level, invasion can cause hybridization between natives and invasives, and subsequent loss of native genetic diversity (Lockwood *et al.* 2007). However, invasion might also increase selective pressure and the rate of evolution among native species (Lambrinos 2004, Callaway and Maron 2006). At the community level, established species are often negatively impacted by direct competition from new species, which may lead to a decline in their relative abundance (Mack *et al.* 2000, MacDougall and Turkington 2005). At the

ecosystem level, invaders can significantly alter hydrological patterns (Di Tomaso 1998), nutrient cycling patterns (Ehrenfeld 2003), and disturbance regimes (Mack and D'Antonio 1998), all of which can promote dynamic shifts in native plant communities (Vitousek 1986).

The alteration of disturbance regimes by invasive plants may have particularly strong consequences for plant community structure, because the scale of an altered disturbance regime is much larger than the scale of individual plant interactions (Mack and D'Antonio 1998). A disturbance regime altered by an invasive plant may persist in its altered state for longer than the lifetime of an individual invader, thus expanding the scale of invasion impacts temporally as well as spatially (Hastings *et al.* 2007).

Depending on the pre-invasion regime, invasive plants may act as either disturbance enhancers or disturbance suppressors. Thus, modification of the disturbance regime requires that the probability of disturbance of invader-occupied sites be greater than that of unoccupied sites, for disturbance enhancers, or less than that of unoccupied sites for disturbance suppressors (Buckley *et al.* 2007). Invasive plants may modify a wide range of disturbance regimes, including riparian erosion, flood potential, sand dune stability, and herbivore grazing intensity (Lockwood *et al.* 2007), yet fire regimes are perhaps the most frequently and dramatically affected (Vitousek 1986, D'Antonio 2000).

#### *Fire ecology*

Along with climate and soil features, fire is perhaps one of the most important natural forces that drives the evolution, composition and change of plant communities

(Bond and Keeley 2005). The fire regime experienced by a plant community is defined as the frequency, intensity, seasonality and type of fire (Brooks *et al.* 2004). Fire frequency generally refers to the time interval between fire events (Agee 1998). Intensity is a measure of the heat released by a fire, and generally correlates positively with mortality of plants (Bond and van Wilgen 1996). Seasonality of fire is usually dictated by annual patterns of rainfall which determine when fuel moisture is low and ignition probability is high (Bond and Keeley 2005). The type of fire refers to the pattern of fuel consumption and spatial spread. For example, canopy fires may burn into tree crowns, surface fires generally burn ground-level vegetation but do not spread to the canopy, and ground fires may burn organically rich soils, while the spread of all these fire types may be continuous or patchy (Bond and Keeley 2005). An established fire regime exerts a great deal of control over the life history strategies, colonization patterns and evolutionary processes within plant communities (Bond and Midgley 1995, Peterson and Reich 2001, Schwilk and Ackerly 2001, Drewa *et al.* 2002). Therefore, a change in fire regime will have wide repercussions among established community members.

Specific components of fire regimes are determined primarily by fuel characteristics (Brooks *et al.* 2004). The spatial arrangement of fuels can dictate fire type, for example, an intense crown fire regime requires sufficient understory fuel height to carry fire to the crown, and sufficient vegetative biomass in the crown to create a high intensity fire (Cruz *et al.* 2006). Fire intensity is generally determined by fine fuel biomass (Thaxton and Platt 2006) and fuel moisture content (Brooks *et al.*

2004), such that communities with high fine fuel loads (particularly perennial grasses) and periods of low fuel moisture are most susceptible to intense fires. Fire frequency is determined in large part by the recovery rate of fine fuel biomass following initial disturbance, and by the spatial continuity of fuels (Lippincott 2000, Brooks et al. 2004).

Given the importance of vegetation composition to fire regime properties, invasive plants that are able to successfully alter existing vegetation structure should have profound effects on fire regimes, which should then lead to a much larger-scale alteration of the plant community (Mack *et al.* 2000). If the new fire regime introduced by the invader causes the invader to have a higher relative population growth rate compared to the native species which it displaces, the invader may initiate a positive feedback on the fire regime, effectively fixing the new regime in place and thereby strengthening its establishment and facilitating its spread (Brooks et al. 2004, Eppstein and Molofsky 2007). While this process is fairly well documented among herbaceous invaders that promote increased fire frequency and intensity, such feedbacks may also be induced by relatively fire resistant woody species invading fire-prone systems such as savannas (D'Antonio 2000).

Savannas are forests with herbaceous understories and widely spaced canopies, in which fire dynamics play an important role in structuring plant communities (Beckage *et al.* 2006). For example, fire might dictate the wide spacing of trees in savannas by causing periodic mortality of young trees but not old trees (Bond and Keeley 2005). Savannas are generally characterized by relatively frequent surface fires, which do not spread to the canopy because of fire-resistant features of the canopy trees (Peterson and

Reich 2001). Fire intensity in savannas is spatially variable, but generally enough to reduce woody biomass and allow for the competitive release of graminoids (Fuhlendorf and Smeins 1997, Scholes and Archer 1997, Thaxton and Platt 2006). In the absence of fire, woody species can encroach into the herbaceous understory and transform the system to a closed forest state (Peterson and Reich 2001, Beckage et al. 2006).

#### *South Florida pine savannas*

Pine savannas are an important component of the vegetation mosaic of Southern Florida. That mosaic is dominated by vast freshwater marsh systems, which historically flooded during the rainy season from May to October, and frequently burned during the dry season (Wade *et al.* 1980). Areas of higher elevation (greater than 1 meter above sea level) that avoid flooding may be dominated by hammocks, which are assemblages of temperate and tropical hardwood species, have closed canopies, and generally do not burn, even when fires burn surrounding vegetation (Wade *et al.* 1980). However, the historically dominant communities of higher elevations were pine rockland savannas, or pinelands, which were subject to a frequent fire regime (Taylor and Herndon 1981).

As with most savanna ecosystems, the pinelands of south Florida require periodic surface fires to reduce shrub densities in the under-story, to allow the recruitment of pine trees, and to maintain an herbaceous ground-story flora (Taylor and Herndon 1981, Snyder et al. 1990). The dominant canopy species in pinelands is the south Florida slash pine, *Pinus elliotti* var. *densa*, which is a self-pruning pine with fire-resistant bark typical of trees adapted to understory fires (Snyder et al. 1990, Schwilk

and Ackerly 2001). The pineland under-story is dominated by the fire-adapted palms *Serenoa repens* and *Sabal palmetto*, by the grasses *Andropogon cubanisii*, *Aristida* spp. and *Muhlenbergia filipes*, and by a suite of West-Indian hardwood shrubs at varying densities determined by fire history (Wade *et al.* 1980). The pinelands also host at least 9 endemic plant species, such as crenulate leadplant (*Amorpha crenulata*), many of which require fire to remove ground litter for germination or to reduce competition from hardwoods (Avery and Loope 1980, Fisher 2000).

The spatial extent of pine rockland savannas pre-European settlement followed the Miami Rock Ridge, an formation of oolitic limestone deposited as marine sediment (Wade *et al.* 1980). This limestone ridge stretches from northern Miami-Dade county south to Homestead, Florida, and eventually dissipates inside Everglades National Park. It ranges in elevation from 1-6 meters above sea level, making it among the highest and driest formations in southern Florida (Snyder *et al.* 1990). The Miami Rock Ridge has very shallow soil and very low nutrient levels, and the pineland plant community is adapted to these conditions (Doren and Whiteaker 1990a, Li and Norland 2001). What little organic material there is in the soil can dissolve the underlying limestone by to the leaching of aqueous acids (Wade *et al.* 1980). This creates a very heterogeneous microtopography of exposed limestone and deep depressions called solution holes.

The natural fire regime of pine savannas along the Miami Rock Ridge consists of frequent, low intensity surface fires (Glitzenstein *et al.* 1995, Beckage *et al.* 2003). These fires tend to follow annual rainfall cycles. The fuel moisture of the pineland vegetation is generally at its lowest at the end of the dry season, in May and June. This



corresponds to the onset of thunderstorms during the rainy season; the combination of lightning ignition sources and dry vegetation leads to an annual peak in fire frequency and extent at this transition from dry to wet season (Beckage et al. 2003, Slocum et al. 2007). However, anthropogenic influences of the 20<sup>th</sup> century have led to both accidental and prescribed fires occurring throughout the year, particularly in the dry season (Beckage et al. 2005, Slocum et al. 2007).

The fire regime of pine rockland savannas has been altered in more ways than its seasonality, however. Extensive urban and agricultural development has resulted in the loss of more than 90% of the original pinelands of southeastern Florida, and the remainder is highly fragmented (DeCoster *et al.* 1999). Most of the remaining fragments have been severely fire-suppressed over the past 50-100 years, with the exception of Long Pine Key, the largest remaining stand of pinelands, located within Everglades National Park and managed under a system of prescribed burns (Loope and Dunevitz 1981). Fire suppression in remnant pinelands has led to the loss of native plant diversity and the suppression of pine recruitment, both attributable to the development of a woody mid-story canopy of hardwood shrubs that had previously been fire-suppressed (Loope and Dunevitz 1981, Taylor and Herndon 1981). The threat that fire suppression poses to this ecosystem is particularly important because of the invasion potential of Brazilian pepper, an exotic shrub with the potential to further alter the fire regime of south Florida's pine rockland savannas (D'Antonio 2000, Brooks et al. 2004).

*Brazilian pepper*

Brazilian pepper (*Schinus terebinthifolius* Raddi., Anacardeaceae) is a woody shrub native to southeastern South America, including the countries of Brazil, Paraguay and Argentina (Barkley 1944). This plant has been widely distributed not just in Florida but also globally, and currently forms a nearly circum-global ring at subtropical latitudes, having also invaded Cuba, Hawaii, Fiji, Australia, and even Mediterranean Europe (Morton 1978, Panetta and McKee 1997, Cuda et al. 2006, Thuiller et al. 2006). Brazilian pepper was most likely introduced to Florida in the 1890's by plant collectors in the horticulture trade (Austin 1978, Morton 1978). The plant was not considered invasive until the 1950's, however, by the 1970's it had spread well beyond areas of human impact and into habitats as diverse as hammocks, pinelands, mangroves and coastal marsh edges (Schmalzer 1995, Lass and Prather 2004, Donnelly and Walters 2005).

In southern Florida, where soils tend to be nutrient-poor, Brazilian pepper performed particularly well on nitrogen- and phosphorous-enriched soils of former agricultural land (Li and Norland 2001, Dalrymple et al. 2003). A particularly good example of this is the 10,000 acre Hole-In-The-Donut (HID) within Everglades National Park. This land originally consisted of mixed wet prairie and pineland, but in the early 1900's it was rock-plowed to raise the land elevation, and then fertilized for farming until the 1970's, when the National Park Service acquired the land (Ewel *et al.* 1982). Brazilian pepper rapidly colonized the abandoned HID, such that by 1982 it formed a near-monoculture of dense canopy cover and nearly impenetrable under-story

(Ewel *et al.* 1982). This rapid invasion occurred in many locations throughout the region during this time, and continues today (Cuda *et al.* 2006).

The invasion of Brazilian pepper into southern Florida is consistent with many generalities of invasion ecology discussed earlier in this chapter. Brazilian pepper appears to have undergone a lag phase of approximately 50 years, which has been attributed to the continued degradation of the landscape causing steady propagule pressure increase and subsequent rapid invasion out of these disturbed “staging areas” (Ewel 1986). The lag time has also been attributed to hybridization events from multiple introductions, on Florida’s east and west coasts, leading to populations with increased fitness (Williams *et al.* 2005, Williams *et al.* 2007). Such hybridization may have important consequences to the success of biological control, as hybrid Brazilian pepper may be more resistant to previously host-specific natural enemies from its native range (Williams *et al.* 2005).

Certain physiological traits of Brazilian pepper may have facilitated its invasion as well. It exhibits a high degree of phenotypic plasticity, and is able to grow as a single-stemmed small tree, multi-stemmed shrub or woody vine, depending on the substrate and the density of the surrounding community into which it is invading (Spector and Putz 2006). Brazilian pepper may also have a slight advantage over some native species in gas exchange efficiency (Ewe and Sternberg 2003, Ewe and Sternberg 2005). However, it appears to have a distinct advantage over native species in terms of water use. Relative to many native competitors, Brazilian pepper has a deeper root

system, which reduces its sensitivity to seasonal variation in water table and salinity levels (Ewe and Sternberg 2002).

Brazilian pepper life-history attributes appear to be particularly important to its invasion success (Ewel et al. 1982, Randall 2000). Several of its life-history traits are relatively uncommon in invasive plants, including insect pollination, synchronous flowering, and dioecy (Ewel et al. 1982, Cuda et al. 2006). However, these uncommonalities may be offset by the fact that Brazilian pepper is pollinated by generalist insects, is capable of producing flowers year round, and can reach reproductive maturity quite rapidly, often within three years of germination (Ewel *et al.* 1982). Yet perhaps the most important aspect of Brazilian pepper reproductive biology is its incredible fecundity potential: mature females are capable of producing tens of thousands of single-seeded fruits each year. Avian seed dispersers such as robins are capable of dispersing massive amounts of seed over long distances to uninvaded habitats, and also increase germination potential (Ewel et al. 1982, Panetta and McKee 1997).

Germination and growth of Brazilian pepper confer further advantages over native competitors. Germination rates in undisturbed habitat range from 30-40%, a rate 10-35% higher than the native species *Ilex cassine* and *Myrica cerifera* (Ewel et al. 1982, Panetta and McKee 1997). In disturbed habitat, Brazilian pepper germination can be as high as 50% (Mytinger and Williamson 1987). Seedling growth of Brazilian pepper appears to be quite variable; seedlings are able to survive at very low growth rates in the dense shade cast by conspecific adults, until a gap increases light levels and

promotes a rapid growth response (Ewel et al. 1982, Cuda et al. 2006). Such plasticity among seedlings, together with the consistently high fecundity of mature individuals, may render inconsequential the relative lack of a long-lived seed bank for Brazilian pepper (Cuda *et al.* 2006). Among adults, Brazilian pepper maintains a growth rate up to twice as high as many of its native competitors, both under normal growing conditions (Pattison *et al.* 1998) and following fire (Snyder 1999). While not capable of vegetative propagation per-se, Brazilian pepper is able to re-sprout both following disturbance (Loope and Dunevitz 1981, Snyder 1999) and in the absence of disturbance (Woodall 1978).

Just as the attributes of Brazilian pepper which facilitate its invasion are generally consistent with invasion theory, so too are the ecological consequences of its invasion. As is often the case with invaded communities (*sensu* Mack *et al.* 2000), diversity appears to be reduced in areas with Brazilian pepper infestations. These effects are not limited to plants; for example, Brazilian pepper has been shown to cause a decline in native ant fauna relative to exotic ant fauna (Clouse 1999). Among native plant communities, Loope & Dunevitz (1981) found diversity in invaded pinelands to be 55% lower than in uninvaded pinelands. It appears that native endemic taxa are included in this decrease: at least two endemic species, *Galactia pinetorum* and *Chamaesyce deltoidea*, are negatively correlated with Brazilian pepper densities in remnant pineland fragments (O'Brien 1998). Causes of this negative effect of Brazilian pepper on native diversity may include direct competition for light, water or nutrients

(Ewel et al. 1982, Ewe and Sternberg 2002), allelopathy (Morgan and Overholt 2005) or disruption of the disturbance regime.

The alteration of pineland fire regimes by Brazilian pepper is perhaps the most dramatic potential consequence of its invasion. This is especially true in light of 1) the consequences of invasion-altered disturbance regimes on plant communities (Mack and D'Antonio 1998), 2) the primary importance of fire among all disturbance regimes to the evolutionary and ecological dynamics of plant communities (Bond and Keeley 2005), and 3) the apparent link between Brazilian pepper invasion and fire suppression (Loope and Dunevitz 1981). The relationship between Brazilian pepper and fire is complex: at low densities, fire may be an effective control of population spread (Doren and Whiteaker 1990b). However, at high densities, Brazilian pepper may be capable of complete fire suppression (Koepp 1978, Doren et al. 1991).

In this thesis, I examine the reciprocal relationship of fire and Brazilian pepper. I show that Brazilian pepper is capable of altering the frequent fire-regime of Florida pine savannas, thereby modifying the composition of these plant communities (D'Antonio 2000, Brooks et al. 2004). Brazilian pepper individuals can substantially reduce the temperature of savanna fires, even on a small scale. Importantly, this effect is very strong among high-density populations, which can completely impede fire spread. However, fire also negatively affects Brazilian pepper at low densities, by causing substantial mortality and reducing fecundity, thereby limiting the establishment and range-expansion potential of colonizing populations (Kolar and Lodge 2001, Buckley et al. 2007). The fact that Brazilian pepper is negatively affected by fire at low

densities but can suppress fire at high densities suggests a density threshold for invasion (Eppstein and Molofsky 2007), below which Brazilian pepper cannot invade, but above which Brazilian pepper should rapidly invade by suppressing future fires. We suggest that frequently burned pine savannas will be relatively un-invaded by Brazilian pepper, while unburned savannas will be more heavily invaded, and should remain fire-free as a consequence. Thus, the modification of an existing fire-disturbance regime by Brazilian pepper is an important mechanism to facilitate large-scale invasions.

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**Chapter 2: Fire effects on demography of the invasive shrub Brazilian pepper**

*(Schinus terebinthifolius)* in Florida pine savannas

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## Abstract

Fire is a common disturbance in savanna ecosystems that may either facilitate or impede exotic plant invasions. Although fire can create recruitment opportunities for exotic plants, it can also prevent their invasion if it exerts strong negative effects on their demographic processes. Savannas may, therefore, be able to resist invasion provided the natural, frequent-fire regime remains intact. We examined the effects of fire on the demography of the invasive shrub Brazilian pepper, which is invading fire-prone slash pine savannas of southern Florida. We studied survivorship, growth and reproduction of low-density populations of Brazilian pepper in a pine savanna within Everglades National Park to investigate whether fire might suppress the initial stages of invasion. We found a significant decrease in Brazilian pepper survivorship following fire, particularly among small individuals. We further found that fire reduced fecundity of surviving Brazilian pepper individuals for at least 2 years. However, re-sprouting individuals that survived fire had high relative growth rates the following year, which could facilitate population recovery during inter-fire periods. We use a simple population simulation to show that a cohort of Brazilian pepper colonizing pine savannas at low densities can be rapidly eliminated with fire-return intervals of 4 years or less, but individuals can persist for > 50 years with fire-return intervals of 8 years or more. Our study suggests the need to maintain the historical frequent-fire regime in order to prevent invasion of these pine savannas by fire-intolerant shrubs such as Brazilian pepper.

## Introduction

Fire is a common disturbance agent in many plant communities, and consequently is an important factor in the invasion of those communities by exotic plant species (Mack and D'Antonio 1998). Fire may create opportunities for colonization and subsequent invasion, by removing pre-existing vegetation, but may also cause mortality or otherwise suppress population growth of the exotic species (D'Antonio 2000). Therefore, demographic responses to fire by exotic plants are important in determining their invasion success under a specific fire regime (Jacquemyn et al. 2005, Lockwood et al. 2007). A species can invade a fire-prone community if its population growth is enhanced by fire relative to the native community (Buckley *et al.* 2007), for example, through higher survival in the fire (Bond and Midgley 1995, Rossiter et al. 2003), or by increasing fecundity after the fire (i.e. through serotiny, Richardson *et al.* 1990).

Conversely, fire may prevent invasion by an exotic plant species if it is frequent or intense enough to cause substantial mortality (Lonsdale and Miller 1993), or reduce reproductive rates (Emery and Gross 2005). While this response to fire is less well documented (D'Antonio 2000), it has been observed in pyrogenic savanna ecosystems, where frequent fires can exclude invasion by woody shrubs (D'Antonio 2000, Bowles et al. 2007). Fire may be an effective control strategy for such fire-intolerant exotic plant species, but some fire-intolerant species have the ability to suppress fire if they establish at high enough densities (Doren and Whiteaker 1990, Brooks et al. 2004).

Therefore, frequent fires are essential to keep these exotic plant populations at low densities and avoid future fire suppression.

In southern Florida, the exotic hardwood shrub Brazilian pepper (*Schinus terebinthifolius* Raddi.) is an invasive species that might be sensitive to fire at early stages of community invasion. Doren and Whiteaker (1990) showed that dense populations of Brazilian pepper growing on disturbed soils were negatively impacted by fire at small sizes, but not at large sizes, where they reduced fine fuel biomass. In addition to invading disturbed soils, Brazilian pepper is also invading pine rockland savannas of southeastern Florida, which naturally experience frequent understory fires (Wade et al. 1980, Loope and Dunevitz 1981). In particular, Brazilian pepper is present at low densities in Long Pine Key, a tract of pine savanna within Everglades National Park that is managed by prescribed burning (DeCoster *et al.* 1999). In pine savannas outside the National Park that have been fire suppressed, Brazilian pepper is present at much higher densities (Loope and Dunevitz 1981), suggesting that frequent fire may prevent invasion of these savannas.

We document the effects of prescribed understory fires on the demography of low-density populations of Brazilian pepper within pine rockland savannas. If fire is able to prevent invasion of pine savannas by Brazilian pepper, then Brazilian pepper should exhibit a negative demographic response to fire at one or more life history stages. We specifically examine the effects of fire on 1) mortality, 2) growth, 3) reproductive maturity, and 4) fecundity of Brazilian pepper. Given the potential for a fire-suppressive effect of high-density Brazilian pepper within pine rockland savannas

(Stevens and Beckage 2008), understanding the demography of low-density Brazilian pepper in these savannas is important to preventing its alteration of the fire regime and accompanying rapid invasion.

## Methods

### *Study site and species*

Pine rockland savannas of southeastern Florida are fire-dependent ecosystems (Wade *et al.* 1980). They are dominated by the canopy species *Pinus elliottii* var. *densa* Little & Dor. (south Florida slash pine), which is resistant to understory fires (Doren *et al.* 1993). The understory contains a diverse herbaceous flora, including at least 40 south Florida endemic species, a number of which depend on fire to reduce competition from hardwoods (Loope and Dunevitz 1981, Snyder *et al.* 1990, O'Brien 1998). The natural fire regime was one of understory fires every 3-7 years, which occurred at the beginning of the rainy season, when increased lightning strikes ignited dry fuels (Beckage *et al.* 2003, Slocum *et al.* 2007). These fires historically suppressed hardwood trees and opened gaps for pine recruitment (Doren *et al.* 1993, Beckage and Platt 2003). More recently, the fire regime has shifted towards the dry season due to anthropogenic influence (Slocum *et al.* 2007), and in savanna remnants outside Everglades National Park, fires have been largely suppressed and Brazilian pepper has extensively invaded (Loope and Dunevitz 1981).

Brazilian pepper is native to southeastern South America, and was introduced to Florida in the 1890's (Austin 1978, Morton 1978). A hardwood evergreen shrub, Brazilian pepper can produce multiple stems that create a dense shade canopy, and has numerous advantages over native hardwood species (Ewel *et al.* 1982). Germination rates in undisturbed habitat range from 30-40%, a rate 10-35% higher than the native species *Ilex cassine* and *Myrica cerifera* (Ewel *et al.* 1982). Among adults,

Brazilian pepper maintains a growth rate up to twice as high as many of its native competitors, both under normal growing conditions (Pattison *et al.* 1998) and following fire (Snyder 1999). Brazilian pepper is pollinated by generalist insects, is capable of producing flowers year round, and can reach reproductive maturity rapidly, often within three years of germination (Ewel *et al.* 1982). Brazilian pepper is dioecious, which is less common among invasive plants, but its invasiveness is facilitated by its high fecundity, with mature females capable of producing tens of thousands of single-seeded fruits annually (Ewel *et al.* 1982).

*Fire effects on Brazilian pepper: field methods*

We located populations of Brazilian pepper within six fire management units, or burn blocks, of pine savanna in the long Pine Key area of Everglades National Park. Brazilian pepper grows at low densities in Long Pine Key, where the pine savannas are managed under a system of prescribed burns (Loope and Dunevitz 1981, DeCoster *et al.* 1999). Three of the six burn blocks we sampled were burned during our study (Table 2.1). We established a 20-meter wide transect through each burn block, and tagged each Brazilian pepper within the transect with a stainless steel tag around the largest stem. Every 20 meters, we conducted a thorough visual search for 5 minutes. We extended each transect the length of the burn block; if the transect did not contain at least 30 individuals, we established a second transect through the burn block. If we did not find 30 individuals after two transects, we did not establish a third transect.

We conducted a summer census of each plant for two years (July 2006 and June 2007). Everglades Fire Management conducted prescribed burns in late July of each

year (Table 2.1). Approximately five months following the fires (in December of each year), we conducted a winter census. During each census, we noted mortality and resprouting (resprouting individuals contained old charred stems and new green stems generally less than 0.5 m in height). We also measured the basal diameter of the tagged stem on a north-south axis. Fecundity (fruit production) was counted during the winter censuses; we assumed the measured fruit count was near 100% (i.e. that no fruits had been dispersed), because the fruits were just beginning to ripen, and early December is the beginning of the fruiting season for Brazilian pepper (Ewel et al. 1982). Plants without fruits but with persistent pedicels indicating flowering were assumed to be mature males.

*Fire effects on Brazilian pepper: analysis*

We modeled the vector of observed mortalities for all Brazilian pepper plants,  $\bar{M}$ , as a binomial distribution conditional on predicted mortality probabilities  $\bar{p}$ :  $\bar{M} \sim \text{Binomial}(\bar{p})$ . We estimated the logit (log odds) of  $\bar{p}$  as  $\text{logit}(\bar{p}) = \mathbf{X}\bar{\beta}$ , where  $\bar{\beta}$  is a vector of estimated parameters corresponding to the occurrence of fire and to basal diameter, and  $\mathbf{X}$  represents the design matrix. The logit function is given by  $\text{logit}(\bar{p}) = \log\left(\frac{\bar{p}}{1-\bar{p}}\right)$ . We fit our models using maximum-likelihood in the R statistical software package (<http://www.r-project.org>), and compared the likelihood of different models using Akaike's Information Criterion (AIC, Burnham and Anderson 2002).

We calculated annual relative growth rates ( $G$ ) for all plants in 2007, as a function of initial diameter:  $G = \log\left(\frac{d_{t+1}}{d_t}\right)$ , where  $d_t$  is the diameter measured during



the December 2006 census and  $d_{t+1}$  is the diameter measured during the December 2007 census, after 1 year of growth. This metric accounts for the higher absolute growth rate of larger individuals (Beckage and Clark 2003). We estimated the likelihood that observed relative growth rates  $\bar{G}$  followed a normal distribution  $\bar{G} \sim Normal(\mu_g, \sigma^2)$ , with mean  $\mu_g$  and variance  $\sigma^2$ . We used AIC to compare the likelihood of a model with a single  $\mu_g$  and  $\sigma^2$ , regardless of fire history, to a model with that included a separate  $\mu_g$  and  $\sigma^2$  for plants that had survived fire in 2006.

We modeled the fecundity schedule of Brazilian pepper using a joint likelihood function modified to include plant sex. Our fecundity schedule was dependent on the predicted probability of sexual maturity  $\Theta(d)$ , which increased with diameter  $d$  according to the probit (cumulative normal) distribution:

$$\Theta(d) = \Phi(d; \mu, \sigma^2) \quad (1)$$

where  $\mu$  is the mean and  $\sigma^2$  is the variance of Brazilian pepper diameter upon reaching maturity. We defined the predicted number of fruits  $\lambda(d)$  as a function of the square of diameter (e.g., Clark *et al.* 1998):

$$\lambda(d) = b + ad^2 \quad (2)$$

where the parameter  $b$  allows for size-independent fruit production. We then modeled the probability of a female plant with diameter  $d$  having its observed number of fruits  $f$  as  $\gamma(f | d, k)$ . The fruit set data appeared to be overdispersed, so we modeled  $\gamma$  as a negative binomial distribution with overdispersion parameter  $k$  (Beckage and Stout 2000):

$$\gamma(f | d, k) = \frac{\Gamma(k + f)}{\Gamma(k) f!} * \left(\frac{k}{k + \lambda(d)}\right)^k * \left(\frac{\lambda(d)}{k + \lambda(d)}\right)^f \quad (3)$$

The fecundity schedule is dependent on the plant gender as well as sexual maturity, and so we modeled the joint likelihood of gender and fecundity. A plant producing 0 fruits could either be immature (with gender unobservable), or female and mature but without fruit present. A mature stem that is observed to be male has a 0 probability of producing fruits, but does provide information on the sex ratio. Thus, the joint likelihood of observing  $f$  fruits and gender  $g$  on a Brazilian pepper individual is given by the joint likelihood function:

$$L(f, g | p_\delta, b, d, a, \mu, \sigma^2) = \begin{cases} (1 - \Theta(d)) + (p_\delta * \Theta(d) * \gamma(f | d)); & 0 \text{ fruits, gender unknown} \\ p_\delta * \Theta(d) * \gamma(f | d); & \text{fruits} > 0, \text{ gender female} \\ (1 - p_\delta) * \Theta(d); & \text{fruits} = 0, \text{ gender male} \end{cases} \quad (4)$$

where  $\Theta(d)$  describes the probability of maturity as a function of diameter (Ladeau and Clark 2001). The likelihood of all observations would then be the product of (4) across all individuals.

We examined whether fire affected the predicted maturity schedule  $\Theta(d)$ , the predicted number of fruits  $\lambda(d)$ , or whether both demographic processes. We subset the data into two groups: plants that did not burn, and plants that burned in either 2006 or 2007. For each model (null, different maturity, different fecundity, or both different), we compared the corresponding AIC values for models with separate parameters for burned and unburned stems to the AIC value for a model that did not account for burn history.

### *Simulation model*

We used the demographic parameter estimates to simulate the response of an initial population of Brazilian pepper to different fire-return intervals. We abstract important demographic processes, such as subsequent recruitment of new individuals, to focus on the survival of the founding population. We incorporate these other demographic processes in a spatially explicit model that we are currently developing. We created an initial population of 100 female seedlings with an average diameter of 0.1 cm ( $\sigma=0.01$ ), which was the size of the smallest individual from our field data. Each individual could grow, produce fruits, and die at annual intervals. We simulated fire-return intervals of 16, 8 and 4 years, as well as a no-fire schedule. If a fire was scheduled for a given year, it occurred at the beginning of each yearly time-step, and all plants were assumed to be burned. Then, each individual experienced a probability of mortality  $p$ , as a function of the plant's diameter and of whether or not it burned. We used parameter estimates from our 2007 mortality data (Appendix 1). If the individual survived, we assigned it a relative growth rate  $G$  from a normal distribution with mean  $\mu_g$  and variance  $\sigma^2$ . We allowed  $\mu_g$  and  $\sigma^2$  to vary depending on the initial size of the plant (smaller plants had higher  $\mu_g$ , Appendix 1) and on whether the plant burned. Our growth function for the simulation was  $d_{t+1} = d_t + d_t * (\exp(G) - 1) * (1 - \frac{d_t}{d_{\max}})^2$ , a modification of the discrete logistic growth model (Gotelli 2001), where  $d_{\max}$  is the average maximum diameter of Brazilian pepper stems (10 cm, Ewel *et al.* 1982). At the end of each annual time-step, we calculated the probability of maturity for each

surviving individual as  $\Theta(d_{t+1})$ , from eq. 1, and if mature, each individual produced  $\lambda(d_{t+1})$  fruits (from eq. 2). Following fires, we set the fruit set at 102 for any surviving mature females for two years (Appendix 1), and then allowed them to resume their normal fecundity schedule. We ran each simulation for 50 years and compared the survivorship, average diameter and total fecundity of the cohort under the 4 different fire regimes. While our model does abstract important demographic processes, which we incorporate in a more detailed spatially explicit model, we believe our results are nevertheless useful.

## Results

### *Fire effects on Brazilian pepper*

Fire caused mortality rates of 42% in 2006 and 31% in 2007 among low-density Brazilian pepper populations. A model of mortality that included fire and diameter had the most support in both years (Table 2.2) because mortality from fire was size-dependent, with larger plants less likely to die (Figure 2.1). Depending on the year, the probability of Brazilian pepper mortality from fire was 74%-78% for a plant of diameter 0.1cm, 50%-56% for a plant of diameter 1cm, 21%-34% for a plant of diameter 2cm, and 2%-7% for a plant of diameter 4cm.

Brazilian pepper individuals that survived fire by re-sprouting exhibited rapid growth rates during the year following the fire (Figure 2.2). Because all individuals resprouting from the 2006 fire had small diameters in December 2006 (<1cm), we compared their mean relative growth rate (RGR) to that of unburned plants <1cm diameter, as well as to all unburned plants. The mean RGR was higher among plants recovering from fire (1.06) than it was among unburned plants less than 1cm diameter (0.64), and among all unburned plants (0.22). The model allowing for differences in mean RGRs between burned and unburned plants had more support than the null model of a single mean RGR, both for small plants and for all plants (Table 2.2).

Fire altered the reproductive response of Brazilian pepper, causing a more narrow size range at maturity and lower fecundity (Figure 2.3). We observed 17 flowering Brazilian pepper individuals in 2007, despite having been burned between 6 and 18 months earlier. Our model showed that Brazilian pepper recovering from fire

exhibits an increase in its probability of maturity from less than 20% at 0.8 cm diameter, to more than 80% at 1.2 cm diameter (Figure 2.3A). However, those mature individuals generally produce fewer fruits than do unburned plants of similar sizes (Figure 2.3B). We allowed fecundity to either vary with, or be independent from diameter (eq. 2), and our best model for the fecundity of burned plants was independent from diameter. Our joint likelihood model had the most support when it allowed both maturity and fecundity to be differentially affected by fire (Table 2.2). Single-effect models that allowed either maturity or fecundity, but not both, to be affected by fire, still had more support than a model without any fire effects (Table 2.2).

#### *Simulation model*

Our simulation of a founding female cohort showed that increasing fire-return intervals could lead to the extirpation of the cohort, but that the population stabilized with infrequent fires or in the absence of fires (Figure 2.4). When fire was absent from the system, the cohort stabilized at > 60% of its initial population size within 10 years, by which time total fruit production of this cohort exceeded  $e^{12.5}$ , or  $\approx 268,000$  fruits. Under a 16-year fire-return interval, the initial cohort still had 50% survivorship after 50 years, and fruit production, following an initial post-fire decline, recovered to levels seen in the absence of fire (Figure 2.4B). Under an 8-year fire-return interval, total fruit production was reduced by more frequent fires and a declining population, but > 10% of the initial cohort still persisted after 50 years. However, a 4-year fire-return interval caused the initial cohort to be lost after 25 years, with a dramatic decrease in the

population following the first fire, because plants were still relatively small 4 years after establishment (Figure 2.4D).

## Discussion

We show that low-density populations of Brazilian pepper generally exhibit a negative response to fire. Fire causes Brazilian pepper mortality rates to increase significantly, up from less than 5% overall in the absence of fire to more than 30% overall following fire. The increase in mortality rate is size-dependent (Figure 2.1), suggesting that frequent fires may strongly regulate juveniles and newly established populations, and prevent them from recruiting into reproductive size classes. Furthermore, fire causes a decrease in fecundity at all sizes for at least 1.5 years following fire (Figure 2.3), in large part because reproductively mature individuals that survive fire tend to re-sprout. Thus, while large, reproductively mature Brazilian pepper might be more likely to survive fire, they still suffer negative demographic consequences.

Reduced fecundity alone might be sufficient to cause a decrease in population growth rates of invasive plants following fire. Emery and Gross (2005) showed that summer burns reduced flowering among the invasive forb *Centaurea maculosa*, which reproduces in the autumn. This reduction in flowering was enough to cause negative population growth, even though these fires did not significantly increase mortality (Emery and Gross 2005). Similarly, in our study Brazilian pepper was burned prior to its flowering season, which is generally September through November (Ewel *et al.* 1982), and the negative effects of fire on fecundity extend at least a year beyond the date of fire. Therefore, we expect that the combination of high mortality among small individuals, and reduced fecundity among larger individuals should produce an overall



negative demographic response to fire among low-density Brazilian pepper populations.

Plant responses to fire often exhibit tradeoffs in different demographic processes. Bond and Midgely (2001) suggest that species adapted to frequent fire may occupy a “persistence niche”, in which post-fire populations are primarily composed of fire-survivors rather than new recruits. Such species, which have high survivorship through resprouting following fire, tend to have relatively low growth rates and fecundity levels in the absence of fire, because they allocate resources to root storage (Bond and Midgely 2001). For example, Keith et al. (2007) showed that the fire-adapted Australian shrub *Epacris barbata*, exhibited low (< 6%) mortality following fire, and had low relative growth-rates in the absence of fire (< 0.03). We show that Brazilian pepper exhibits an opposite response, with high (> 30%) mortality following fire, and in the absence of fire had a high relative growth rate (0.21), and high fecundity (Figure 2.2). Furthermore, Brazilian pepper which survive fire by resprouting have exceptionally high growth rates the year following the fire (mean = 1.06, Figure 2.2), but have low fecundity (mean = 101.5 fruits, Figure 2.3). These results suggest a possible tradeoff between post-fire growth and fruit production (*sensu* Keith et al. 2007). The demographics of Brazilian pepper indicate that it is not adapted to fill a persistence-niche as defined by Bond and Midgely (2001); however, high growth rates, especially during the year following fire, suggest that Brazilian pepper populations can still persist following fire unless additional fires continue to cause mortality and suppress fruit production by survivors.

We explicitly modeled population persistence of Brazilian pepper to variation in fire regimes using a simple simulation model. We simulated the demographics of a founder population of Brazilian pepper juveniles in a pine savanna system using our estimated demographic parameters. We have shown that in the absence of fire, the founder population is able to persist, with mortality concentrated in early years (Figure 2.4A). The corresponding increase in the average reproductive output of this cohort would be expected to translate into increased population growth, especially in the absence of continuous mortality (Jacquemyn *et al.* 2005). Low-frequency fires with a 16-year return interval (Figure 2.4B) caused substantial mortality, but the initial cohort appears to recover biomass between fire events, and thus future fires cause relatively little mortality because of declining fire-related mortality associated with increasing stem diameter. When the fire-return interval was as short as 4 years, however, the initial fire following colonization caused a 53% decrease in cohort size, and the rapid fire-return caused comparable mortality in each successive fire, eliminating the original cohort within 25 years. Thus, repeated short-interval fires appear to be effective at controlling low-density populations of Brazilian pepper, and should also be effective at preventing large-scale colonization events.

While it is common for fire disturbance events to promote invasion by fire-tolerant plants (D'Antonio 2000), we have shown that fire may also be effective at controlling low-density populations of invasive plants. Brazilian pepper is moderately fire-intolerant at low-densities, exhibiting both increased mortality and decreased fecundity following fire. Thus, in ecosystems such as pine-rockland savannas, which

naturally experience fires every 3-7 years (Beckage *et al.* 2003), restoring the historical fire regime may be sufficient to prevent invasion by fire-intolerant plants (Keeley 2006). However, infrequent fires might allow for sufficient growth during the inter-fire period to reduce the effectiveness of fire for controlling Brazilian pepper (i.e. Figure 2.4B). Furthermore, if Brazilian pepper populations can grow to high enough densities, between 4-6 plants per 5 meters, they might suppress future fires entirely (Stevens and Beckage 2008). Therefore, while single fires can have a negative impact on Brazilian pepper, frequent fires are required to effectively prevent invasion.

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**Chapter 3: Fire feedbacks facilitate invasion of pine savannas by Brazilian  
pepper (*Schinus terebinthifolius*)**

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## Abstract

Exotic plants can modify existing disturbance regimes, potentially initiating a positive feedback that facilitates their continued invasion. Species that are susceptible at low densities to disturbances, such as fire, may successfully invade if they reach a minimum density threshold to inhibit subsequent fires. 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 U.S. Prescribed burns caused significant Brazilian pepper mortality at low densities, and savannas with more frequent fires were less likely to be invaded. High densities of Brazilian pepper, however, reduced fire temperature up to 200°C, and reduced mortality by more than 80%. We use a cellular automaton model to show that frequent fire may control low-density populations, but Brazilian pepper may reach a density threshold during fire-free periods, initiating a positive feedback and converting the savanna to an exotic-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 to occur, the probability of disturbance at invaded sites must be different from the probability of disturbance at uninvaded 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 re-colonization through propagule pressure from the abundant exotic species (Buckley *et al.* 2007). This is an

example of a conditional invasion dynamic (Eppstein & Molofsky 2007), where an exotic population will successfully invade if its population growth rate exceeds that of native competitors only above a critical density threshold, due to a positive environmental feedback. 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, the minimum density threshold for invasion (i.e. the Allee threshold; Taylor & Hastings 2005) is the density at which the invasive suppresses future disturbance. When the density of the invasive is above this threshold, its population growth exceeds its native counterparts, and invasion occurs. When the density is below this threshold, repeated fire-disturbance will reduce the invasive population growth-rate relative to the native community, provided that fire negatively affects the invasive at low-densities. 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 in a pine savanna ecosystem in south Florida, initiated through the suppression of fire by the invasive shrub Brazilian pepper (*Schinus terebinthifolius* Raddi.). 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 and 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 low mortality in the absence of fire, 3) Brazilian pepper should reduce the intensity and spread of fire more at high-densities than at low-densities, and 4) Pine savannas that are burned frequently should have less Brazilian pepper invasion than unburned savannas. We use a cellular automaton model to suggest the potential for a coupled vegetation-fire feedback that could facilitate invasion of pyrogenic savannas by a fire-suppressing invasive shrub.

## 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, Florida, 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 years at 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 more than 90% of original pine rockland savanna lost to development, LPK is the largest remaining tract in southern Florida (Figure 3.1), and has been managed under a system of prescribed burns since 1958 (Snyder *et al.* 1990; DeCoster *et al.* 1999). 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 is an exotic hardwood shrub that has successfully invaded much of southern Florida (Ewel *et al.* 1982). Introduced by plant collectors during the late 1890's, Brazilian pepper had extensively invaded the region by the late 1970's (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 blocks”, with different schedules of prescribed fire (Slocum *et al.* 2003). We established one transect 20 m wide in each of six burn blocks, three of which would be burned in either 2006 or 2007 (Figure 3.1). In each transect, we surveyed for Brazilian pepper individuals, stopping every 20 m to conduct a 5-minute 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 elsewhere in the burn block 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.

To examine the effects of fire on low-density populations of Brazilian pepper, we conducted a pre-burn census of each plant during the summer of two years (July

2006 and June 2007). Burn blocks were burned by Everglades Fire Management in late July of each year, and we re-censused all previously tagged plants approximately five months following the fires, in December of 2006 and 2007. For each census, we measured basal diameter, mortality and resprouting. Resprouting individuals contained old charred stems and new stems generally less than 0.5m tall.

We used temperature-sensitive paints to investigate the potential for Brazilian pepper individuals in low-density populations to reduce local fire temperature. We painted ten different temperature-sensitive paints by Tempilaq (Tempilaq, Tempil Division, Air Liquide America Corporation, South Plainfield, New Jersey, USA) on a stainless steel tag and suspended the tag from an 8-inch garden stake. Each of the ten 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). We covered each tag with tinfoil to keep water out, and inserted the stakes at the base of all Brazilian pepper individuals in burn blocks I2 and B prior to their prescribed burns (Figure 3.1). We put another tag 3 meters to the north of these individuals as a control.

We also examined whether high-density populations of Brazilian pepper could reduce fire intensity and their subsequent mortality, the necessary conditions for a feedback. We established three additional transects across a density gradient at the southern end of burn block B (Figure 3.1). 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 block

B, and continued to the north until no Brazilian pepper individuals were found for 40 meters. Transects were 2 meters wide, and we tagged every individual 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-meter, 5-meter and 10-meter radius. We again used temperature-sensitive paints to examine the effects of high-density populations on fire temperature. Assembling temperature-sensitive paints on stakes as described above, we put one stake every 10 meters in the middle of the transect, and inserted the last stake 10 meters 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 above.

To assess fire-temperatures following the prescribed burns, we returned to all low-density and high-density transects in August 2007, approximately 2 weeks 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.

We analyzed the effect of fire on low-density Brazilian pepper individuals using a binomial model of plant mortality:  $\bar{M} \sim Binomial(\bar{p})$  where  $\bar{M}$  is the vector of observed mortality (1=died, 0=survived) and  $\bar{p}$  is a vector of predicted mortality probabilities defined by  $\text{logit}(\bar{p}) = \mathbf{X}\bar{\beta}$ . The vector of estimated parameters  $\bar{\beta}$  corresponds to the design matrix  $\mathbf{X}$ , which contains the diameter and burn status of each



plant. The logit function is given by  $\text{logit}(\bar{p}) = \log\left(\frac{\bar{p}}{1-\bar{p}}\right)$ . We fit our model using maximum-likelihood in the R statistical software package (<http://www.r-project.org>). We distinguished between alternative models of plant mortality using the Akaike information criterion (AIC; Burnham and Anderson 2002).

To assess the effects of Brazilian pepper on fire temperature in the low-density transects, we calculated the mean difference  $\bar{\Delta T}$  in observed fire temperature between a tag at the base of each Brazilian pepper and the control tag 3 meters adjacent to the stem. We calculated the likelihood of the observed temperature differences  $\Delta \bar{T}$  given a predicted mean difference of  $\bar{\Delta T}$  compared to 0, using the model  $\Delta \bar{T} \sim \text{Normal}(\mu_t, \sigma^2)$ , where  $\mu_t$  is the predicted mean fire temperature difference and  $\sigma^2$  describes the variance. We compared the two models using the likelihood ratio  $L_{\bar{\Delta T}}/L_0$ , where  $L_{\bar{\Delta T}}$  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  $\bar{\mu} = \beta_0 + \beta_1 * \bar{D}$ , where  $\bar{\mu}$  is the vector of predicted mean fire temperatures,  $\beta_0$  is the intercept, and  $\beta_1$  is the parameter estimate for the effect of Brazilian pepper density  $\bar{D}$  on temperature. We calculated the likelihood of the observed temperature values  $\bar{T}$  in the high-density transects using the model  $\bar{T} \sim \text{Normal}(\bar{\mu}, \sigma^2)$  to obtain best-fit 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- meters), 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:  $\bar{M} \sim Binomial(\bar{p})$ , where  $\bar{M}$  is the vector of observed mortalities from our high-density populations. We estimated  $\bar{p}$ , the predicted probabilities of mortality, as a function of density, using the link-logit function  $\text{logit}(\bar{p}) = \beta_0 + \beta_1 \bar{D}$ , where  $\bar{D}$  is the conspecific density around each plant in the high-density transects, at one of three different radii (2, 5, and 10 meters). We compared the likelihoods of the three density models, and a null model, again using AIC.

#### *Landscape invasion patterns*

We analyzed digital aerial photographs 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, [www1.labins.org](http://www1.labins.org)). These images were taken in 2005, have 1 m<sup>2</sup> 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 (Figure 3.1), 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, personal communication). 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 ERDAS Imagine® (ERDAS 2007) using the GCPs as training sites to identify a unique spectral signature for each vegetation class. We subsequently 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 (Appendix 2).

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, where each variable contained 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. We defined seven site-factors to explain the probability of invasion and severe invasion by Brazilian pepper. These included the variables 1) fire occurrence, 2) number of fires, 3) distance (in km) to downtown Miami, 4) area of the burn unit (in km<sup>2</sup>), 5) perimeter of the burn unit (in km), 6) area:edge ratio (in km<sup>2</sup>/km), 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 also for a gradual decrease in elevation with increasing distance to Miami (Snyder *et al.* 1990).

We defined the land cover surrounding each site as either 1) pine savanna, 2) agricultural land, 3) suburban/residential development, or 4) urban development.

We used Bayesian model averaging to select the site factors which best explained the probability of a site being invaded or severely invaded (e.g., Platt *et al.* 2002). We estimated the probability  $p_i$  of each site being invaded above the given threshold as  $\text{logit}(\bar{p}_i) = \mathbf{X}\bar{\beta}$ , where  $\bar{\beta}$  is a vector of parameters corresponding to 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

$$\Pr(M_j | \text{Data}) = \frac{\Pr(\text{Data} | M_j)\Pr(M_j)}{\sum \Pr(\text{Data} | M_j)\Pr(M_j)} \quad (1)$$

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

## Results

### *Feedback dynamics of Brazilian pepper*

Fire caused 30-45% mortality among low-density populations of Brazilian pepper, compared to 0-4% in the absence of fire. Our best model of mortality, as judged by AIC, accounted for both fire and initial plant size (2007  $\Delta$ AIC values: null=23.8, fire=5.5, fire+diameter= 0; see Appendix 3A for 2006 values). Fire killed more small plants (51%; diameter <2 cm) than large plants (20%), and all surviving small plants resprouted, while larger plants tended to retain some live foliage (Figure 3.2). 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 from the temperature recorded at a paired control location just 3 meters away. The mean temperature of the fire under Brazilian pepper individuals was 107° C, compared to 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 (Figure 3.3a). Linear regression models of temperature on density at all three distances, 2 m, 5 m, 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 ( $\Delta$ AIC values: null= 21.5, 10 m= 8.4, 5 m= 6.7, 2 m= 0; parameter estimates are given in Appendix 3B). When there

was no Brazilian pepper within 2 meters, average fire temperature ranged from 128° C to 229° C, while at high densities of 3 plants within 2 meters, the fire temperature never exceeded 68° C, and in some cases fire was apparently absent (Figure 3.3a).

Brazilian pepper individuals in high-density populations also had lower probability of mortality in a fire (Figure 3.3b). Density at all distances was again a better predictor of mortality than a null model, with the 5m model the best fit ( $\Delta$ AIC values: null= 24.3, 10m= 5.7, 5m= 0, 2m= 9.2; parameter estimates are given in Appendix 3C). Among individuals with fewer than two neighbors within 5 meters, 88% (8 of 9 plants) were killed by fire. Conversely, when individuals had more than two neighbors within 5 meters, only 6% (2 of 31 plants) were killed by fire (Figure 3.3b). High density also reduced the extent of the fire: 89% of surviving plants that had fewer than 4 neighbors per 5 meters were burned and resprouted, while 100% of plants with more than 6 neighbors per 5 meters did not burn (Figure 3.3b).

#### *Landscape invasion patterns*

Fire was the strongest predictor variable of Brazilian pepper invasion extent into pine savanna fragments, determined by our remote sensing analysis. The binary occurrence of fire was the best model to explain both the probability of invasion and the probability of severe invasion by Brazilian pepper (Table 3.1). The number of fires over a 20-year period was the second best model, with more frequent fires reducing the probability of invasion (Table 3.1). In particular, savannas that were burned more than once experienced a steep decline in Brazilian pepper abundance compared to unburned savannas (Figure 3.4), with a 42% decline in sites classified as invaded and a 31%

decline in sites classified as severely invaded. Other than fire occurrence and number, additional site-factors had little support in our models. No non-fire site-factor had greater than 10% posterior probability of being in the best model (Table 3.1).

## Discussion

We found strong evidence that Brazilian pepper reduces fire intensity and spread, facilitating its invasion into pine savannas through a positive feedback. Brazilian pepper is an apparent disturbance suppressor (D'Antonio 2000; Brooks *et al.* 2004; Buckley *et al.* 2007), capable of reducing the intensity of fire to the point of complete fire suppression, with increasing density (Figure 3.3). The interaction of Brazilian pepper and fire meets the requisite conditions for a disturbance-suppressing feedback: the exotic species successfully invades in the absence of disturbance (Figure 3.4), it experiences significant mortality in response to disturbance (Figure 3.2), and it is able to reduce disturbance when it exceeds a minimum-density threshold. It is this reduction of the disturbance regime that allows for the increase in the exotic species' population growth above that of its native competitors, allowing for conditional invasion (Eppstein & Molofsky 2007). We show that the minimum-density threshold for disturbance-suppression by Brazilian pepper in pine savannas is likely between 2 and 6 plants per 5 meters (Figure 3.3b). The scale of this threshold is important, as shown by Eppstein and Molofsky (2007), because a small population that exceeds this density can initiate the feedback process locally, and spread outward through continued disturbance suppression.

Variation in Brazilian pepper density can affect fire temperatures at a very small scale, while mortality is most strongly affected by density at a slightly larger scale (Figure 3.3). Brazilian pepper can reduce 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-meter 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 population to impede fire progress, due to the low flammability of Brazilian pepper stands (Loope & Dunevitz 1981). Therefore, density at a 5-meter radius best explained variation in Brazilian pepper mortality, because some dense stands did not burn at all.

The disturbance-suppressing feedback between Brazilian pepper and fire that we identified as operating at local scales resulted in landscape level patterns. Given that fire has a suppressive effect on low-density Brazilian pepper populations, frequent fire should reduce the probability of Brazilian pepper invasion into pine savannas. Furthermore, because Brazilian pepper can suppress fire at high densities, severely invaded savannas should experience fewer fires. We show that the occurrence of fire and the number of fires experienced were the two strongest predictors of Brazilian pepper abundance within a given burn unit (Table 3.1). Frequent fire appears to be particularly important in preventing severe (>25%) invasions by Brazilian pepper, with no sites burned more than once reaching the severe invasion threshold, while more than 30% of unburned sites were severely invaded (Figure 3.4). The high preponderance of invasion at unburned sites shows that Brazilian pepper can successfully invade in the absence of disturbance (e.g., Loope & Dunevitz 1981), a necessary condition for a disturbance-suppressing feedback. Furthermore, there is evidence from our remote-

sensing data that in some savannas with high Brazilian pepper abundance, fire failed to penetrate these sites despite burning adjacent sites with less invasion (Stevens 2008). Thus, the landscape-scale pattern of fire and Brazilian pepper invasion appears to support the predictions of the disturbance-suppressing feedback model.

The feedback between Brazilian pepper and fire has the potential to create ecological thresholds and abrupt transitions in community state (Beckage and Ellingwood 2008). An initial reduction of fire frequency through either climate change (e.g., Beckage et al. 2003) or a change in anthropogenic prescribed fire policy could provide the opportunity for initial establishment of Brazilian pepper, and the perpetuation of a fire-free regime. This feedback may lead ultimately to a rapid population expansion of Brazilian pepper and invasion by other fire sensitive woody species (Loope & Dunevitz 1981; Rose & Fairweather 1997), while suppressing pine recruitment and reducing herbaceous diversity (Loope & Dunevitz 1981; Platt *et al.* 2002). We used a cellular automaton model to show the potential for these feedbacks to create sensitivity to fire frequency that results in rapid transitions between invaded and un-invaded states with small changes in fire regime. The cellular automaton model of pine savanna dynamics was developed by Beckage and Ellingwood (2008) and was forced by varying lightning intensity (strikes per unit area) as a proxy for fire frequency. In our simulations, Brazilian pepper exhibits a minimum density threshold for invasion across a range of lightning frequencies, but the location of this threshold shifts to lower densities when lightning frequency decreases (Figure 3.5). Thus, community transitions between invaded and un-invaded states might be sensitive to any

factors affecting fire regimes, including landscape fragmentation and climate change (Knick & Rotenberry 1997; D'Antonio 2000; Beckage *et al.* 2006).

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, there are few empirical examples to date of invasion through fire suppression (D'Antonio 2000). In this study, we show that the invasive shrub Brazilian pepper may invade by just such a mechanism. Small populations of Brazilian pepper may be susceptible to fire, and frequent fire may keep it at low densities. However, large populations may establish in the event of fire suppression, and have the ability to reduce fire temperature and spread, facilitating invasion and irreversibly converting pine savannas to Brazilian pepper thickets.

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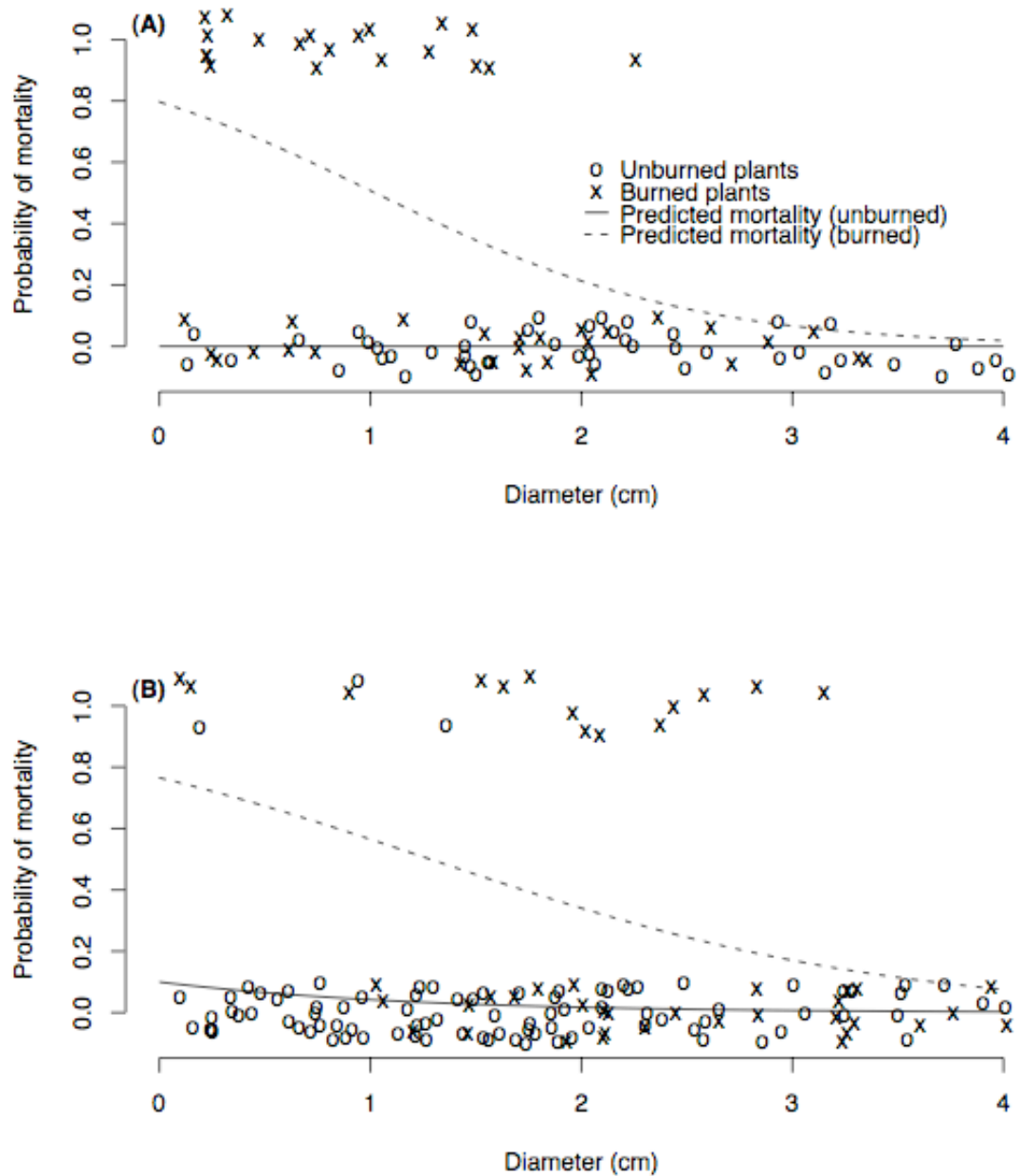
**Table 2.1:** Transects used for Brazilian pepper (BP) sampling. Three transects burned and three did not. Not all plants in each transect burned. 47 of 61 plants burned in 2006. 45 plants of 61 burned in 2007. Density is given as (plants/1000 m<sup>2</sup>), where each transect was 20 m wide.

<b>Transect Name</b>	<b>Transect Length (km)</b>	<b>Year Burned</b>	<b>BP</b>	<b>BP burned</b>	<b>BP density</b>
H	1.5	2006	61	47	2.03
I2	2.15	2007	31	31	0.72
B	2.6	2007	30	14	0.58
A	2.25	NA	13	0	0.29
F1	1.5	NA	21	0	0.70
E	2.25	NA	8	0	0.18
<b>Total:</b>			164	92	

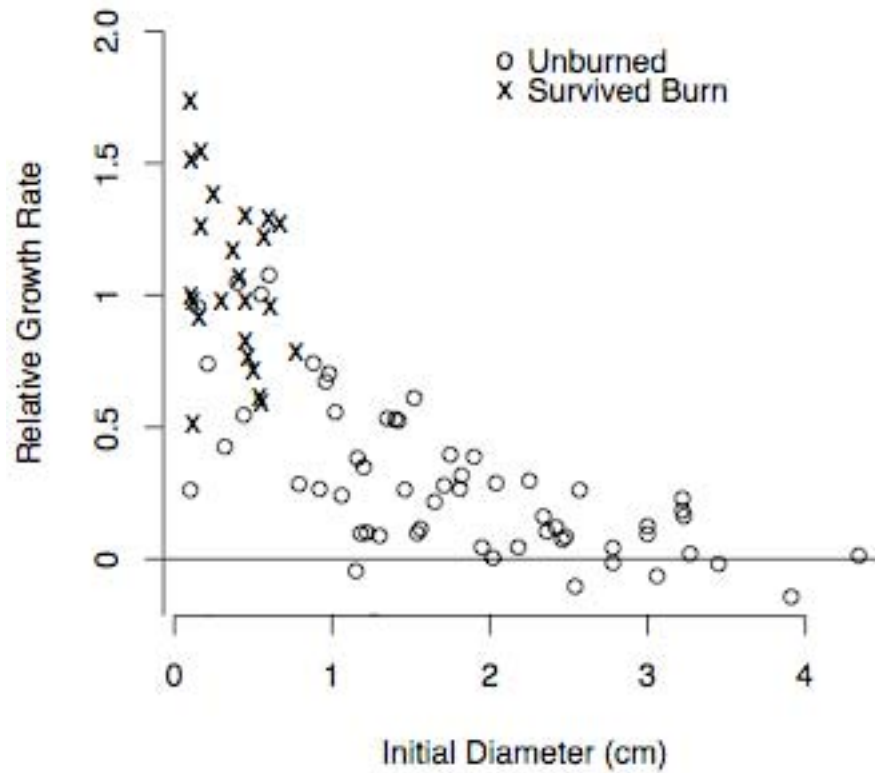
**Table 2.2:** AIC values for all models.

Model(s) with the most support (where  $\Delta$  AIC <2) are in bold. Model parameter estimates are given in Appendix 1.

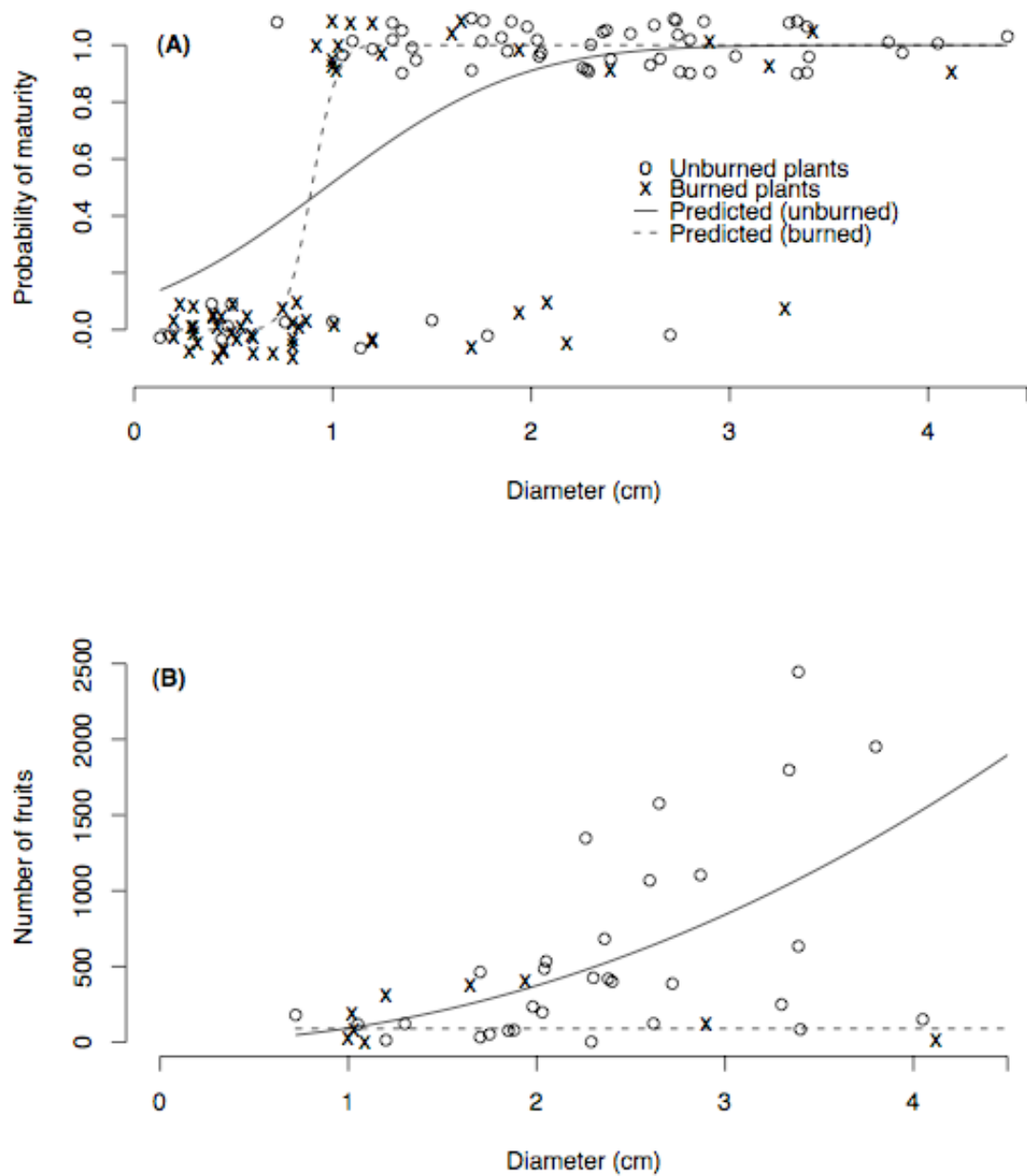
Demographic response	Year	Model	- log likelihood	$\Delta$ AIC
Mortality	2006	No effect of fire or diameter.	48.7	40.7
		Fire	32.1	9.5
		<b>Fire + diameter</b>	<b>26.3</b>	<b>0</b>
	2007	None	51.2	23.8
		Fire	41.1	5.5
		<b>Fire + diameter</b>	<b>37.3</b>	<b>0</b>
Growth rate of all plants	2007	No effect of fire.	70.3	61.1
		<b>Fire</b>	<b>38.7</b>	<b>0</b>
Growth rate of small plants	2007	No effect of fire.	17.9	6.3
		<b>Fire</b>	<b>13.7</b>	<b>0</b>
Maturity and Fecundity	2007	No effect of fire.	372.0	19.3
		<b>Fire</b>		
		Affects maturity	368.4	16.2
		Affects fecundity	369.7	16.8
		<b>Affects maturity and fecundity</b>	<b>357.3</b>	<b>0</b>



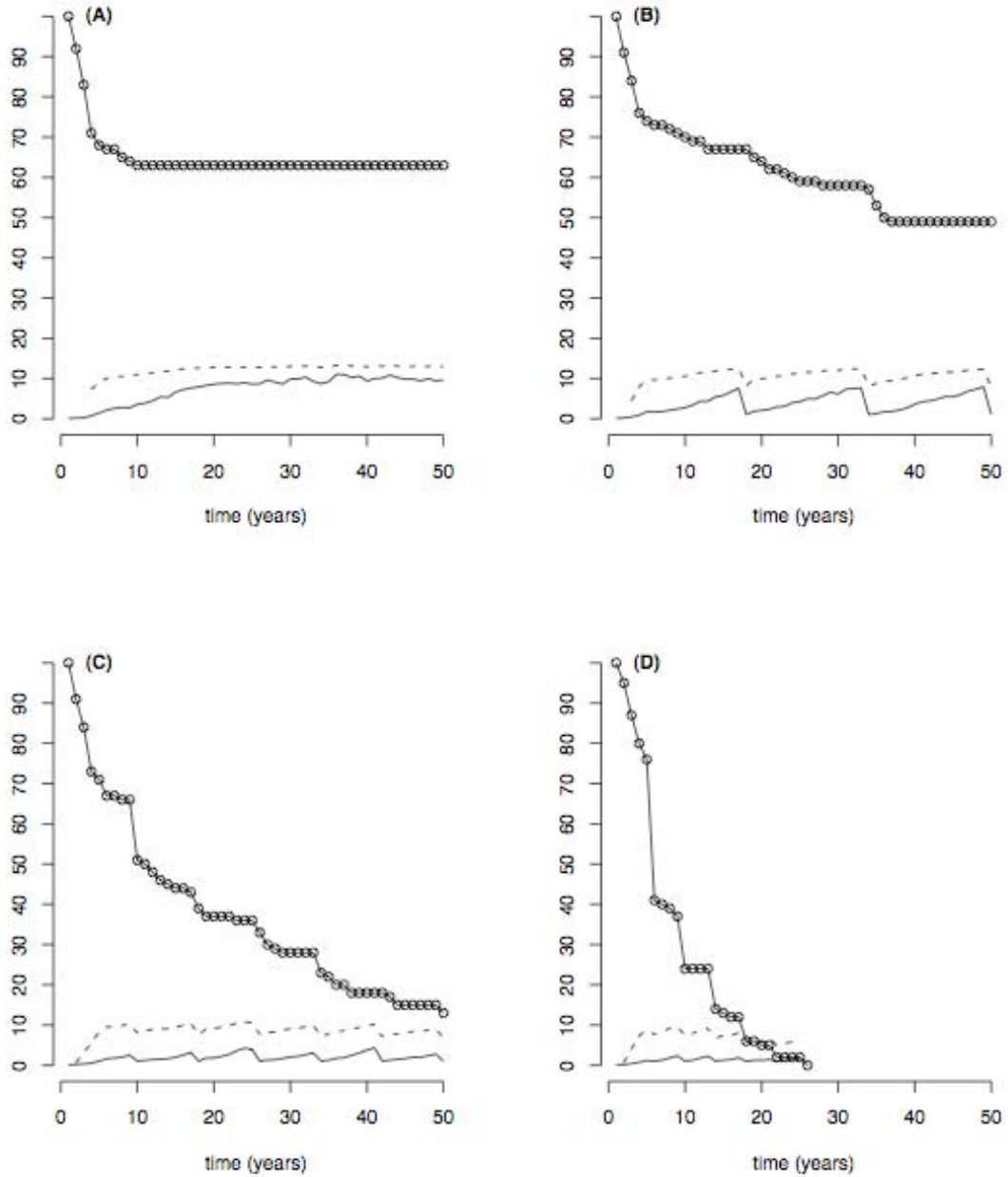
**Figure 2.1:** Size-dependent mortality of Brazilian pepper in (a) 2006 and (b) 2007. Points represent individual plants, 1 represents mortality and 0 represents survival. Curves represent predicted probability of mortality of both burned and unburned plants, using logistic regression models derived using maximum likelihood. Points were jittered in the y-direction for clarity.



**Figure 2.2:** Fire effects on growth rate of Brazilian pepper. Relative growth rate was calculated for 2007. The mean relative growth rate for burn-surviving plants (1.06) is higher than that of unburned plants, both for all diameters (0.21) and at diameters less than 1 cm (0.65). Negative RGRs are likely small positive values affected by measurement error in either 2006 or 2007.



**Figure 2.3:** Effects of fire on reproductive maturity (a) and fecundity (b). The curves in (A) represent predicted probability of reproductive maturity as a function of diameter  $d$ , according to a probit model. Points represent observed maturity, where 1 represents a mature plant that produced flowers; points are jittered in the y-direction for clarity. Plants recovering from fire have a narrow maturity threshold diameter of  $\sim 1$ cm, above which they are more likely to produce flowers than unburned plants of the same size. The curves in (B) represent best-fit models of fecundity, as a function of  $d^2$  if unburned (solid line), and independent of  $d$  if burned (dashed line). Plants recovering from fire generally exhibit lower fecundity than unburned plants of the same size. Plants were burned between 6 and 18 months prior to the fruit census.



**Figure 2.4:** Simulated population models using demographic parameter estimates. Circles represent surviving members of the original cohort of 100 individuals at each annual time step. Solid lines indicate mean basal diameter (in cm) of the population. Dashed lines represent total fecundity of the initial cohort, calculated as  $\ln(\sum \text{fruits/individual})$ . Fire return intervals are (A) never, (B) 16-year, (C) 8-year, and (D) 4-year. All initial cohort members have been lost after 25 years under a 4-year fire return interval.

**Table 3.1:** Bayesian logistic model selection of factors predicting Brazilian pepper invasion extent.

The probabilities of invasion and severe invasion extents 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.

Probability of invasion (Brazilian pepper > 10%)							
Site-factors	Mean( $\bar{\beta}$ ) <sup>‡</sup>	SD	Odds Ratio <sup>§</sup>	Pr( $\bar{\beta} \neq 0$ ) <sup>¶</sup>	Model <sup>††</sup>		
					1	2	3
Burned	-1.893	1.110	0.15	0.84	*		*
# Fires	-0.193	0.474	0.82	0.16		*	
Distance <sup>†</sup>	-0.002	0.010	0.99	0.10			*
Area (km <sup>2</sup> )	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
$\Delta$ BIC					0	3	4
Probability of severe invasion (Brazilian pepper > 25%)							
Site-factors	Mean( $\bar{\beta}$ ) <sup>‡</sup>	SD	Odds Ratio <sup>§</sup>	Pr( $\bar{\beta} \neq 0$ ) <sup>¶</sup>	Model <sup>††</sup>		
					1	2	3
Burned	-1.582	1.517	0.21	0.56	*		*
# Fires	-1.106	1.403	0.33	0.44		*	
Distance <sup>†</sup>	0.000	0.000	1.00	0.00			
Area (km <sup>2</sup> )	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
$\Delta$ BIC					0	0	4

<sup>†</sup> Distance to downtown Miami, measured in km

<sup>‡</sup> Average parameter value estimated across all models containing that parameter, weighted by model probability

<sup>§</sup> Odds ratio is  $\exp(\bar{\beta})$ , the relative expected difference in probability of invasion caused by a unit increase in a given site-factor.

<sup>¶</sup> Probability of parameter being included in the best model

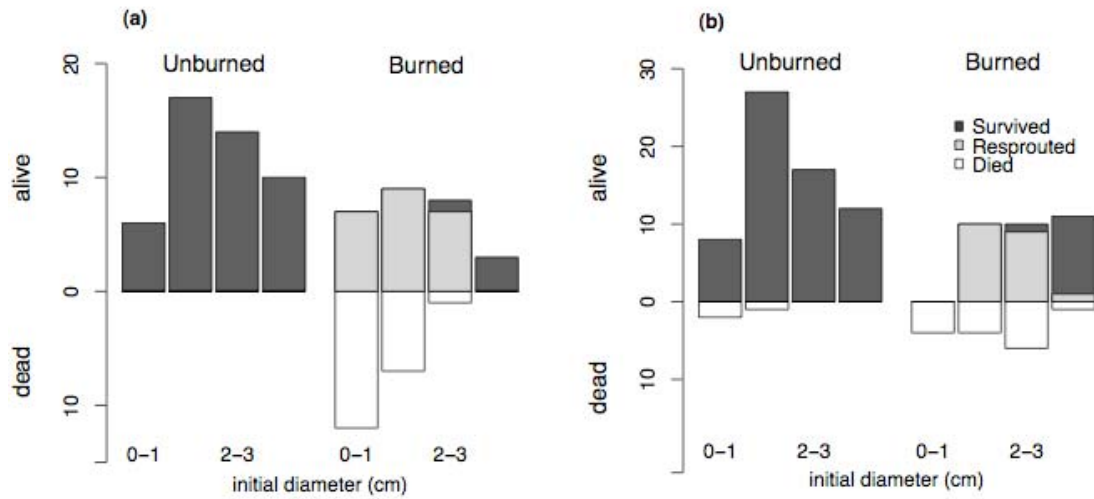
<sup>††</sup> Variables with asterisks have high (>0.05) probability of being in a given model



**Figure 3.1:** The locations of field (a) and remote-sensing (b) study sites, located in southeast Florida (c).

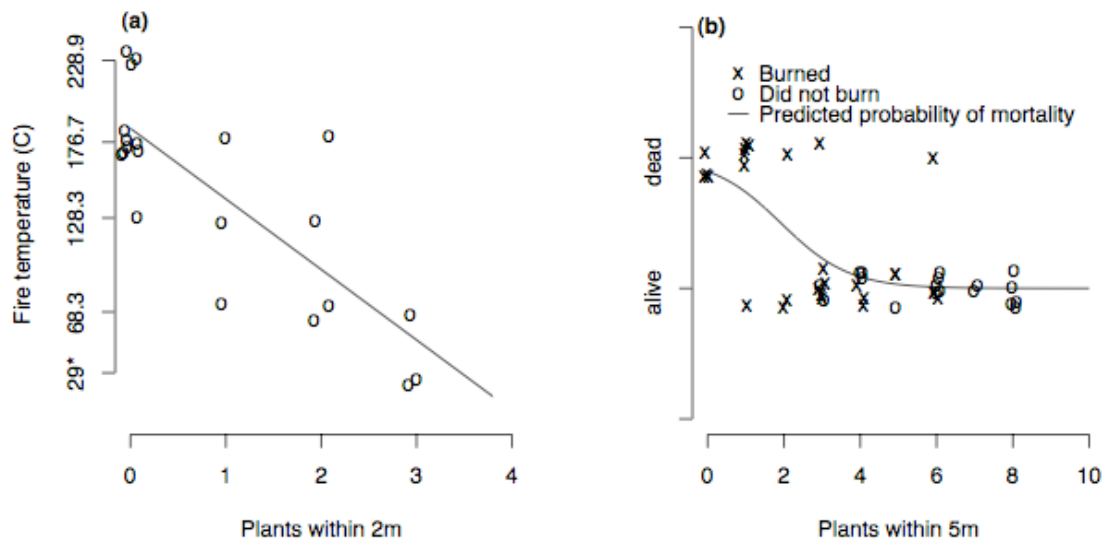
(a): Within Everglades National Park (ENP), low density transects are the 11 thin lines running N-S in six burn blocks at Long Pine Key. High density transects are the 3 thick lines at the southern edge of burn block B. Burn blocks with cross-hatch were burned in 2006; those with stipple were burned 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 (b), numbers 1-26 indicate the locations of our remote-sensing study sites (listed in Appendix 2). Major roads and cities are shown.



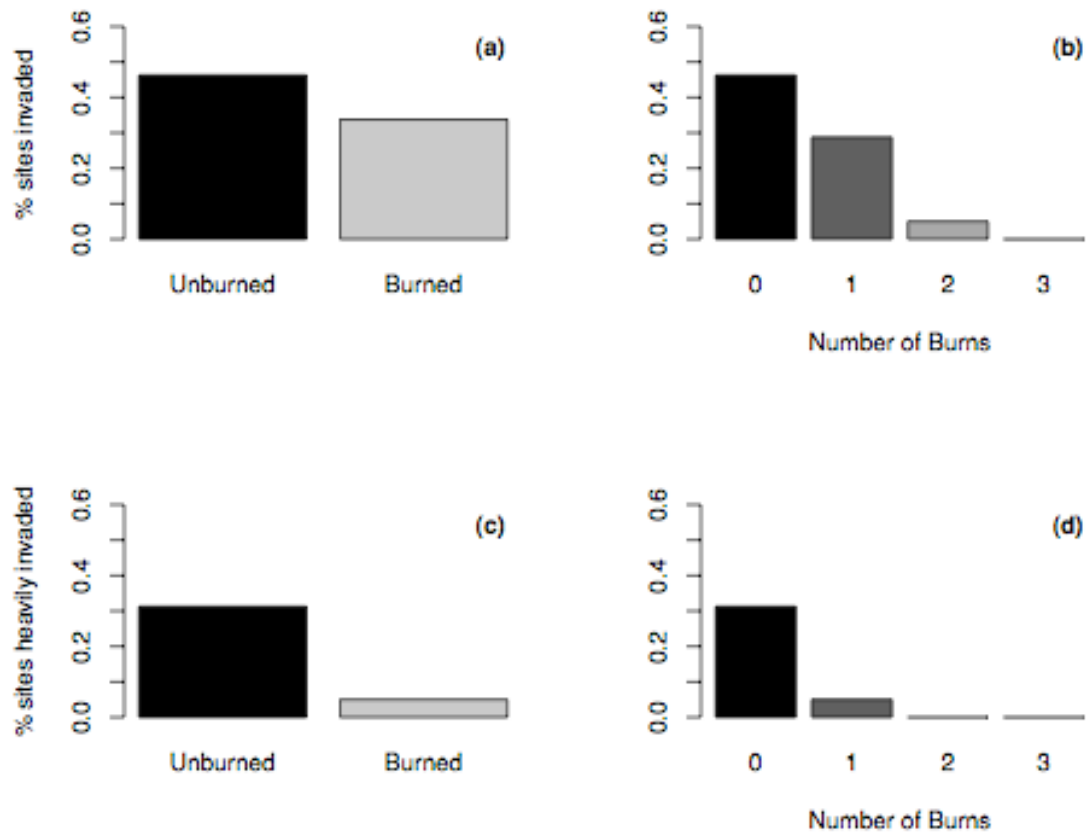


**Figure 3.2:** Brazilian pepper survivorship in (a) 2006 and (b) 2007.

In each panel, the left group of bars are unburned plants, and the right group of bars are burned plants. Mortality was measured in the winter census of each year, where all plants were alive during the summer census of that year. Bars above 0 indicate the number of surviving plants at each size class, where gray bars indicate the number of individuals that re-sprouted, and black bars indicate the number of individuals that retained live foliage since the summer census. White bars below 0 indicate the number of plants in each size class that died between censuses.

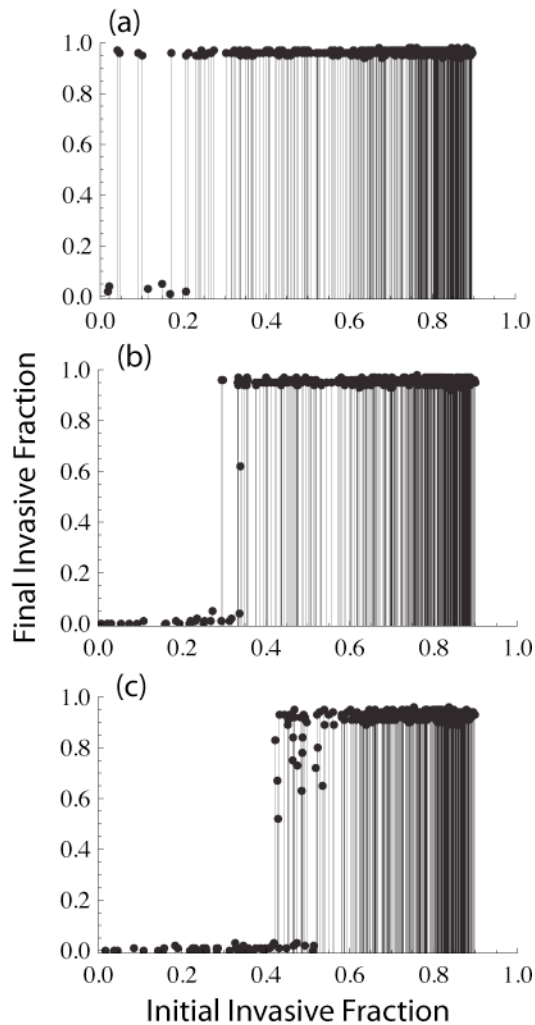


**Figure 3.3:** High densities of Brazilian pepper reduce fire temperature (a) and probability of mortality (b). Intraspecific density at a 2-meter radius was the best model to explain variation in fire temperature (a). Density at a 5-meter radius was the best model to explain variation in Brazilian pepper mortality (b). 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.



**Figure 3.4:** Invasion extent of Brazilian pepper from remote sensing of savanna fragments.

The top row indicates the observed proportion of savanna fragments that were invaded (sites with >10% Brazilian pepper), where the best model of invasion extent was the occurrence of fire (a), and the second best model was the number of fires (b). The bottom row indicates the observed proportion of sites that were severely invaded (>25% Brazilian pepper), where the two best models again were occurrence of fire (c) and number of fires (d).



**Figure 3.5:** Final state of the ecological community as a function of increasing abundance of the invasive and lightning intensity.

Increasing initial abundance of a fire-suppressing invasive leads to an ecological threshold with an abrupt transition between a natural 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). 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. The simulations were conducted using the cellular automaton model of pine savanna dynamics in Beckage and Ellingwood (2008) modified to include an invasive. The invasive has a low probability of burning at high abundances, similar to the characteristics of Brazilian pepper.

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**Appendix 1:** Demographic parameter estimates for fire-effect models. Models in bold had the most support (Table 2.2).

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Mortality response to fire	
<u>2006</u>	
Null:	$\text{logit}(p) = -1.31$
Fire ( $f$ ):	$\text{logit}(p) = -13.01 + 12.71 f$
Diameter ( $d$ ):	$\text{logit}(p) = 0.68 - 1.50 d$
<b>Fire and Diameter:</b>	$\text{logit}(p) = -14.59 + 15.96 f - 1.34 d$
<u>2007</u>	
Null:	$\text{logit}(p) = -1.95$
Fire ( $f$ ):	$\text{logit}(p) = -3.38 + 2.58 f$
Diameter ( $d$ ):	$\text{logit}(p) = -1.54 - 0.23 d$
<b>Fire and Diameter:</b>	$\text{logit}(p) = -2.20 + 3.38 f - 0.92 d$

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Growth response to fire	
<u>All plants</u>	
Null:	$\mu_g = 0.45, \sigma = 0.06$
<b>Fire (<math>f</math>):</b>	$\mu_g = 0.21 + 0.85 f, \sigma = 0.09$
<u>Small plants (<math>d &lt; 1</math>)</u>	
Null:	$\mu_g = 0.94, \sigma = 0.07$
<b>Fire (<math>f</math>):</b>	$\mu_g = 0.65 + 0.41 f, \sigma = 0.14$

---

Maturity and Fecundity response to fire	
(eq. 1, 2)	
No effect of fire:	$\Theta(d) = \Phi(d; \mu = 0.94, \sigma^2 = 0.18);$ $\lambda(d) = 73.8 d^2$
Maturity affected	$\Theta(d, \text{unburned}) = \Phi(d; \mu = 0.86, \sigma^2 = 0.25);$
by fire:	$\Theta(d, \text{burned}) = \Phi(d; \mu = 0.89, \sigma^2 = 0.0012);$ $\lambda(d) = 73.8 d^2$
Fecundity affected	$\Theta(d) = \Phi(d; \mu = 0.94, \sigma^2 = 0.18);$
by fire:	$\lambda(d, \text{unburned}) = 85.1 d^2;$ $\lambda(d, \text{burned}) = 102$
<b>Both affected by</b>	$\Theta(d, \text{unburned}) = \Phi(d; \mu = 0.86, \sigma^2 = 0.25);$
<b>fire:</b>	$\Theta(d, \text{burned}) = \Phi(d; \mu = 0.89, \sigma^2 = 0.0012);$ $\lambda(d, \text{unburned}) = 85.1 d^2;$ $\lambda(d, \text{burned}) = 102$

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**Appendix 2:** Study sites used in remote sensing analysis.

Site numbers correspond with Figure 3.1. Study sites with more than one burn unit have burn units listed below name. BP: Percent of pixels classified as Brazilian pepper. Fires: Number of fires experienced by burn unit since 1985. Area of burn unit in ha; Edge: length of burn unit edge in km. SLC: Surrounding land cover, where A=Agriculture, P=Pineland, U=Urban, S=Suburban. Latitude and longitude are given in UTM Zone 17N coordinates, WGS 1984 datum.

<i>Site Name</i>	<i>BP</i>	<i>Fires</i>	<i>Area</i>	<i>Edge</i>	<i>SLC</i>	<i>Lat</i>	<i>Long</i>
1 Palm Drive	0.07	1	7.8	1.1	A	2814989	546556
2 Navy Well #39	0.22	0	7.6	1.1	A	2813821	551955
3 Sunny Palms							
snp_1b	0.07	0	13.2	1.8	A	2812578	548509
snp_ne_2b	0.06	2	3.1	0.7	AP	2812584	548503
Navy Wells Pineland							
4 Preserve							
nw1_1b	0.27	1	8.2	1.4	AP	2814213	549797
nw2_1b	0.25	1	4.8	1.1	P	2814195	549907
nw2_ub	0.46	0	11.9	1.5	AP	2814207	550113
nw3_ub	0.31	0	10.3	1.4	AP	2813817	550101
nw4_2b	0.14	1	3.8	0.8	P	2813584	549861
nw4_1b	0.18	1	14.7	2.0	AP	2813621	550112
nw5_1b	0.26	1	18.9	1.9	AP	2813564	550112
nw6_ub	0.69	0	1.4	0.7	UP	2813551	549589
nw6_1b	0.16	1	13.1	1.7	AP	2813507	549043
nw6_2b	0.08	1	3.2	0.8	AP	2813132	549489
nw7_1b	0.11	1	6.6	1.1	AP	2813312	549246
nw8_ub	0.30	0	13.3	1.5	AP	2813663	549361
nw9_ub	0.28	0	8.3	1.5	AP	2813833	549427
nw10_ub	0.47	0	22.0	1.9	AP	2814201	549487
5 Rock Pit #39	0.27	0	3.7	1.0	SA	2815427	550106
6 Florida City							
fc_ub	0.13	0	9.8	1.4	U	2814465	551464
fc_b	0.01	1	0.5	0.3	UP	2814227	551345
7 Navy Wells #23	0.52	0	11.4	1.9	S	2813821	551955
8 Fuchs	0.28	0	9.1	2.5	A	2818447	548968
9 West Biscayne W	0.34	0	3.3	0.7	SA	2820459	550257
10 West Biscayne E	0.29	0	3.2	0.8	SA	2820282	550587
Seminole Wayside							
11 Park							
semw_2b	0.07	1	0.8	0.4	P	2819178	554954
semw_1b	0.26	0	5.8	1.5	SP	2819436	554982
semw_ub	0.21	0	5.2	2.3	U	2819442	554985
12 Ingram	0.54	0	3.9	0.9	SA	2820230	553960

**Appendix 2, continued**

<i>Site Name</i>	<i>BP</i>	<i>Fires</i>	<i>Area</i>	<i>Edge</i>	<i>SLC</i>	<i>Lat</i>	<i>Long</i>
13 Camp Owiassa Bauer							
camp_bauer_ub	0.32	0	11.3	3.6	AP	2814495	542430
camp_bauer_1b	0.10	1	8.0	2.6	SP	2807838	548254
14 Silver Palm	0.17	0	9.0	1.4	A	2826513	558353
15 Goulds							
goulds_ub	0.19	0	9.0	1.8	U	2826827	561568
goulds_sw_1b	0.13	1	2.1	0.7	S	2826471	561567
goulds_ne_1b	0.17	0	5.0	0.9	UP	2826887	561627
16 Med South	0.60	0	1.3	0.5	S	2828729	560201
17 Eachus	0.29	1	5.2	1.7	U	2831412	558120
18 Miami MetroZoo							
mz_lp_median_n	0.16	2	0.6	0.5	SP	2831641	559656
mz_lp_median_s	0.30	1	0.2	0.2	SP	2831463	559665
mz_lp1	0.14	1	3.5	0.9	P	2831938	559369
mz_lp2east	0.11	1	3.6	1.1	P	2831523	559487
mz_lp2south	0.25	0	4.0	0.9	UP	2831344	559547
mz_lp2_lp3	0.21	0	17.1	3.5	UP	2831463	559368
mz_lp4	0.20	1	7.5	1.7	SP	2831582	560081
mz_lp6	0.08	0	8.5	1.2	UP	2831285	560319
mz_lp7	0.17	1	0.7	0.4	P	2831340	560599
mz_lp7_ub	0.31	0	4.6	1.2	SP	2831404	560557
mz_lp9_medium	0.13	2	4.1	0.9	SP	2832285	561211
mz_lp9_10_large	0.14	2	10.0	3.4	SP	2832355	561152
mz_lp9_small	0.08	3	0.4	0.3	P	2832473	561211
mz_lp11_ub	0.67	0	3.0	0.7	SP	2831582	560617
mz_m1	0.20	1	3.7	1.1	UP	2832236	559190
mz_m2	0.09	1	21.0	3.6	P	2832711	559428
mz_m3_nw_ub	0.17	0	15.8	1.7	UP	2832592	559071
mz_m3_sw	0.15	1	2.6	0.7	UP	2832414	558893
mz_m4_ub	0.25	0	6.7	1.9	SP	2832414	559547
mz_m5_ub	0.28	0	6.9	1.4	UP	2832235	559428
mz_zoo_1to7	0.24	2	37.9	2.6	SP	2832473	560854
mz_zoo8_ub	0.73	0	6.9	1.2	SP	2831998	560795
mz_zoo9_ub	0.76	0	1.0	0.4	SP	2833365	561092
mz_zoo9	0.26	0	9.4	1.4	SP	2833602	561151
mz_zoo10	0.20	1	11.9	1.9	SP	2833246	560973
mz_zoo17	0.22	0	3.0	0.8	SP	2833959	561092
mz_u_miami	0.10	1	21.8	2.0	SP	2833127	561389
19 Boystown	0.28	0	27.3	3.2	US	2830393	560557
20 Nixon Smiley	0.07	1	49.8	3.2	U	2837228	559784
21 Tamiami Addition	0.19	0	12.0	1.5	U	2836479	561191



**Appendix 2, continued**

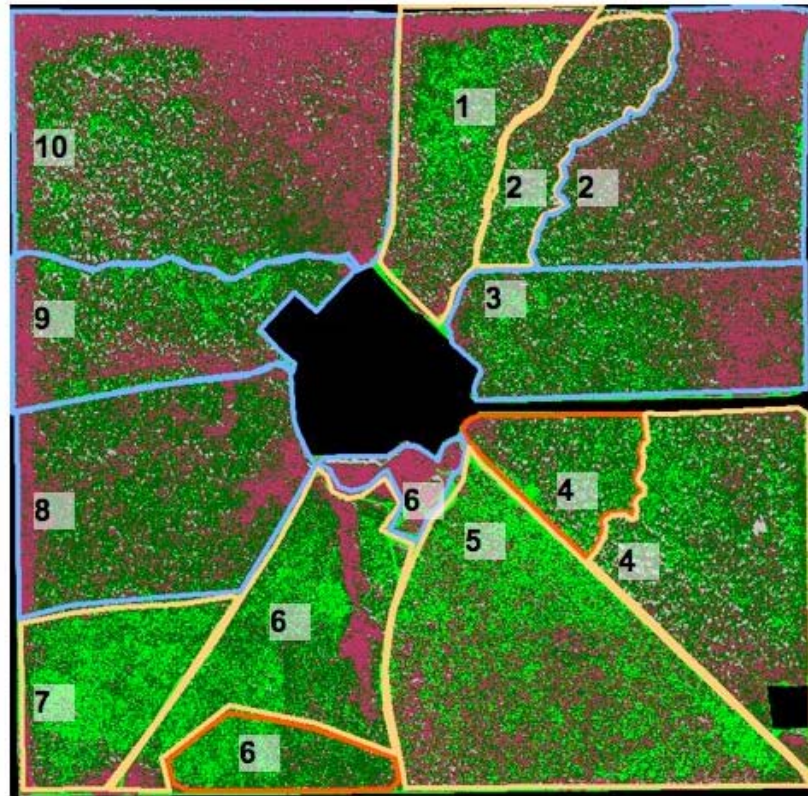
<i>Site Name</i>	<i>BP</i>	<i>Fires</i>	<i>Area</i>	<i>Edge</i>	<i>SLC</i>	<i>Lat</i>	<i>Long</i>
22 Pine Shore Park							
ps_0500_1b	0.14	1	0.5	0.4	P	2837203	562875
ps_1297_1b	0.15	1	0.4	0.4	SP	2837234	562853
ps_0399_1b	0.23	1	0.1	0.1	SP	2837231	562896
ps_ub	0.24	0	2.1	1.3	S	2837237	562900
23 Rockdale							
rd_s_1b	0.08	1	1.3	0.6	UP	2835002	566201
rd_m_1b	0.15	1	7.2	1.4	US	2835486	566325
rd_n_1b	0.09	1	3.6	0.8	SP	2835560	566372
rd_ub	0.33	0	2.7	1.4	UP	2835569	566440
24 Ned Glenn	0.09	1	4.6	0.8	S	2830512	566917
25 Deering Estate North							
dn_2b	0.04	2	18.2	2.3	P	2834562	569550
dn_1b	0.04	1	10.4	2.9	SP	2834800	569531
dn_ub	0.51	0	6.8	1.4	SP	2834383	569888
Matheson Pineland							
26 Preserve	0.04	0	1.8	0.5	SP	2839130	572384

**Appendix 3:** Parameter estimates and AIC values for Chapter 2 models. Model(s) with the most support (where  $\Delta AIC < 2$ ) are in bold.

<i>Model parameters</i>	$\beta$	<i>Odds Ratio ¶</i>	$\Delta AIC$
A.) Effects of fire on mortality			
<u>2006</u>			
Null	-	-	40.7
Fire	12.7	$3.3 \times 10^5$	9.5
<b>Fire; Diameter</b>	<b>16.0; -1.3</b>	<b><math>3.3 \times 10^6</math>; 0.33</b>	<b>0</b>
<u>2007</u>			
Null	-	-	23.8
Fire	2.6	13.5	5.5
<b>Fire; Diameter</b>	<b>3.4; -0.9</b>	<b>30.0; 0.41</b>	<b>0</b>
B.) Effects of density on temperature			
Null	-	-	21.5
<b>Plants per 2m</b>	<b>-11.6</b>	-	<b>0</b>
Plants per 5m	-21.3	-	6.7
Plants per 10m	-45.0	-	8.4
C.) Effects of density on post-fire mortality			
Null	-	-	24.3
Plants per 2m	-0.6	0.55	9.2
<b>Plants per 5m</b>	<b>-1.1</b>	<b>0.33</b>	<b>0</b>
Plants per 10m	-2.1	0.12	5.7

¶ Odds ratio is  $\exp(\beta)$ , the relative expected difference in probability of mortality caused by the presence of fire (A) or by a unit increase in diameter (A) or density (C).

**Appendix 4:** A classified image from Navy Wells Pineland Preserve



**Appendix 4:** A classified image from Navy Wells Pineland Preserve (study site # 4, Figure 3.1 and Appendix 2). Pink pixels were classified as Brazilian pepper, dark green pixels as pine trees, light green pixels as grass, and gray pixels as shadow. Lines indicate perimeters of burn units. Numbers refer to Navy Wells burn unit identification; replicate numbers belong to the same burn unit but had different fire histories. Burn units with orange edges were burned two times, those with yellow edges were burned once, and those with blue edges were not burned at all. The eastern portion of unit 2, and the northern portion of unit 6, were unburned, indicating a possible inhibition of fire spread by Brazilian pepper.