

## Fire mediated edge effects in bayhead tree islands

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### Abstract

**Question:** The role edges play in mediating the effects of disturbance is unclear. Bayhead tree islands, which experience above- and belowground fire, contain trees that recover from disturbance by seed (*Pinus elliottii* var. *densa*) and by sprouting (*Gordonia lasianthus*). How does distance-to-edge affect survival and post-fire response of trees with these contrasting life-history strategies?

**Location:** Two bayhead tree islands at Archbold Biological Station, central Florida, North America.

**Methods:** Stem diameter, depth of peat smoldering, char height, resprouting status, and location were recorded for all *Pinus* and *Gordonia* stems  $\geq 8$  cm. Distance to the edge of the tree island was quantified using GIS.

**Results:** The focal species showed contrasting patterns of survival across the edge-to-interior gradient that reflected gradients of fire severity. Survival of *Gordonia* was lowest in the bayhead interior where peat smolder was deepest. Conversely, survival of *Pinus* was lowest near the edges where char heights were greatest. The distinct types of *Gordonia* resprouting (crown versus basal) also showed spatially contrasting patterns. Basal resprouting dominated near the edges and was positively influenced by char height, while crown resprouting was nearly constant across the edge-to-interior gradient and was negatively influenced by char height.

**Conclusions:** The spatial patterns of tree survival and resprouting observed are likely due to gradients in intensity of peat smoldering and aboveground burning, coupled with differential susceptibility to these two types of fire. Despite the rarity of fire in wetland tree islands (compared to uplands) it may

play an important role in structuring the spatial distribution of trees.

**Keywords:** Char height; Fire effects; Fire severity; *Gordonia lasianthus*; Path analysis; *Pinus elliottii* var. *densa*.

### Introduction

A central goal of landscape ecology is to determine how edges influence ecological processes within patches (Weins et al. 1985; Ries et al. 2004). Edges (also termed ecotones or boundaries) are transitional areas with a rapid change in vegetation structure and different diversity than either bordering community (Fraver 1994; Laurance et al. 2002; Harper et al. 2005). Edge permeability to the movement of organisms, material or energy between patches (ecological flows) can influence patch residents (Ries et al. 2004). Edges can amplify, attenuate and/or reflect ecological flows (Strayer et al. 2003; Boughton et al. 2006). Fires moving across a landscape are an example of an ecological flow that can be blocked, filtered or amplified by edges (Gosz 1991). Edges often separate communities with different fire frequency, fuel characteristics and fire severity.

The edge between forested wetland tree islands and more frequently burned adjacent communities represents a dramatic shift in fuel types and fire severity. Forested wetlands in the southeastern USA accumulate thick organic soils that can ignite during dry season fires, smoldering for long durations and causing tree mortality (Ewel & Mitsch 1978; Ryan & Frandsen 1991; Smith et al. 2003). The severity of above- and belowground burning that trees experience during forested wetland fires are not necessarily positively correlated. In boreal forests, the temperature of underground smoldering can vary independently of the severity of the aboveground frontal fire (Schimmel & Granstrom 1996). Spatial studies of fire temperatures have not been conducted in forested wetland tree islands; however, anecdotal accounts of greater char heights along tree island edges (Smith et al. 2003) and greater depth of peat smoldering in the interior (Monk & Brown 1965;

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Coultas & Calhoun 1975; Ewel & Mitsch 1978) suggest that above- and belowground fire severity may be negatively correlated across the edge-to-interior gradient.

The most common division used to classify the post-fire response of trees is to categorize species as either sprouters (recover vegetatively from roots or stems) or seeders (killed by fire; Keeley & Zedler 1978; Bond & Midgley 2001). Generally, sprouters allocate more to belowground structures, produce fewer seeds, have lower seedling recruitment and longer generation times compared to seeders (Bond & Midgley 2003). Sprouters are also favoured in systems with severe and frequent disturbance (Bond & Midgley 2003). Disturbance severity may influence the position on a tree where sprouting occurs; severe disturbance often promotes basal sprouting and mild disturbance promotes sprouting in the tree crown (Bond & Midgley 2001).

We studied the spatial fire-effects of trees in bayhead tree islands and compared the survival of a sprouting species (*Gordonia lasianthus*, (L.) Ellis – from here on *Gordonia*) to that of a seeder (*Pinus elliottii* var. *densa*, Little & Dorman – from here on *Pinus*). Additionally, we compared basal versus crown resprouting of *Gordonia*. Our overall goal was to identify causal pathways responsible for spatial patterns of tree survival and resprouting. Specifically our goals were to:

1. Use path analysis models that incorporate distance-to-edge, above- and belowground fire severity and stem diameter to identify causal pathways influencing tree survival and resprouting.
2. Determine the overall spatial patterning of *Gordonia* and *Pinus* survival across the edge-to-interior gradient and basal versus crown resprouting of *Gordonia*.

## Methods

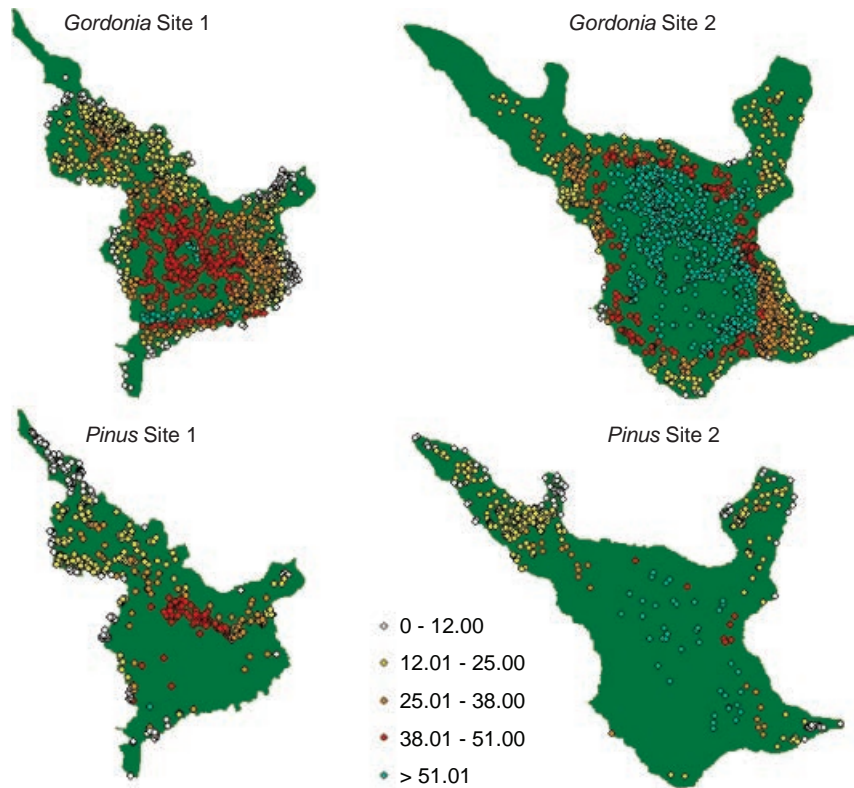
### *Study system*

Bayheads (also baygalls, bayswamps) are an association of broadleaf evergreen trees growing on strongly acidic organic soils found in depressions in central and south Florida (Wade et al. 1980; Abrahamson et al. 1984; Stone et al. 2002). Bayheads get their name from the dominance of broadleaf trees with the common name bay (e.g. loblolly bay – *Gordonia*, red bay – *Persea palustris*, sweet bay – *Magnolia virginiana*). Bayhead tree islands have a well-developed overstorey composed of *Gordonia*

(Theaceae), *P. palustris* (Lauraceae), *M. virginiana* (Magnoliaceae), *Pinus* (Pinaceae), and to a lesser degree, *Myrica cerifera* (Myricaceae) and *Ilex cassine* (Aquifoliaceae; Ewel 1990). The dominance of *Gordonia*, *P. palustris*, and *M. virginiana* distinguishes bayheads from similar vegetation types (Simons et al. 1989). Bayheads have one of the longest hydroperiods and lowest fire frequencies of any forested wetland in Florida ( $\geq 100$  years; Ewel 1990). Most Florida uplands burn periodically (Menges 1999), and prescribed fires in uplands are common. Forested wetlands such as bayheads, which are often transitional communities between upland and aquatic habitats, burn infrequently. The boundary between bayheads and adjacent vegetation is often sharp (Wade et al. 1980) but becomes more blurred as bayhead vegetation invades adjacent communities between fires (Peroni & Abrahamson 1986; Landman & Menges 1999). The peak in fire occurrence during Florida's natural fire regime is May–September (Robbins & Myers 1992). Bayhead soil is organic and deep, and can ignite during dry season fires (October–May). Smoldering of bayhead soil can occur for days, causing significant plant mortality (Wade et al. 1980) and major smoke management problems.

We focused our study on two tree species with contrasting fire response strategies: *Gordonia* (loblolly bay) and *Pinus* (south Florida slash pine). *Gordonia* is found in swamps along the Atlantic Coastal Plain from North Carolina to south Florida (Duncan & Duncan 1988). *Gordonia* is a slow growing, small to medium size evergreen tree reaching 23 m in height on rich soil but is shrubby on poor soil (Gresham & Lipscomb 1990). The canopy structure of *Gordonia* ranges from conical to columnar (Godfrey & Wooten 1981) and the trunk has thin bark (Gilman & Watson 1993). *Gordonia* is shade tolerant (Penfound 1952) and can sprout after fire basally or from branches in the canopy (Cypert 1961).

*Pinus* is found only in central and south Florida where it dominates the tree layer in pine savannas, flatwoods and pine rocklands (Abrahamson et al. 1984) but is also found in flooded sites such as swamps (Lohrey & Kossuth 1990). *Pinus* does not resprout after disturbance, has no seed bank, but possesses several fire-resistant characteristics (Little & Dorman 1954). The trunk of *Pinus* is protected by thick bark and lower branches are rapidly shed, reducing the risk of a canopy fire. In the tussock-like seedling stage the terminal bud is protected when small, followed by rapid growth that elevates the bud above the level of low-intensity fires. Mature *Pinus* can reach 17 m in height (Lohrey & Kossuth 1990).



**Fig. 1.** Maps showing the spatial patterning of the distance-to-edge index for *Gordonia* and *Pinus* in Site 1 (1.94 ha) and Site 2 (2.37 ha). See the Data Collection: GIS section of the methods for a description of the distance-to-edge index.

Our two bayhead sites are located within Archbold Biological Station (ABS) in Highlands County, Florida (27°11'N, 81°21'W). These undrained bayheads are relatively small (Site 1 = 1.94 ha and Site 2 = 2.37 ha), in close proximity to each other (192 m at the closest point), and highly irregular in shape (Fig. 1). In the winter of 2001, fuel conditions in central Florida was dry due to a severe drought (Smith et al. 2003) and late freezes. On 12–16 February 2001 at ABS (Ketch-Byram drought index = 755), a 260-ha fire ignited by a freight train burned both bayhead sites. The fire was of unprecedented intensity (flame lengths 6–18 m), with minimal heterogeneity in most habitats compared to previous fires at ABS (ABS fire report). The aboveground fire burned heterogeneously in both study bayheads, and after it had passed, peat smoldering occurred in the bayheads for 2 weeks, consuming much of the organic soil, until it was extinguished by rain (D. Matlaga and E. Menges, personal observation).

#### *Data collection: field*

We collected fire severity and post-fire response data on all stems  $\geq 8$  cm in basal diameter. The lo-

cation of each stem and the bayhead edge were mapped using GPS (Trimble Pro-XR, Trimble Navigation Ltd, Westminster, CO, USA, 1-m accuracy). Char height (maximum height of blackened trunk), an estimate of aboveground fire severity (Wang 2002), was measured directly for heights  $\leq 5$  m, and indirectly for heights  $> 5$  m using a clinometer (Suunto PM-5/360 PC, Finland). We measured the depth of peat burning ('depth of burn'), an indicator of belowground fire severity (Schimmel & Granstrom 1996), as the vertical distance from the ring of remnant peat on the stem to the present level of burned peat. Stem basal diameter was measured 0.5 m above the ground. Death was recorded for stems that did not display green tissue. We recorded the presence/absence of basal and crown resprouts (crown resprouts includes axillary, branch epicormic and stem epicormic sprouting; Bellingham & Sparrow 2000) for *Gordonia* stems. Time-sensitive variables (depth of burn, death and presence of resprouts) were collected in April and May 2001, 2–3 months post-fire. Time-insensitive variables (basal diameter, char height and spatial location of stems and bayhead edge) were recorded in June–September 2001.

### Data collection: GIS

Edge effects are one of the most extensively studied topics in ecology (Ries et al. 2004), yet empirical research (e.g. Chen et al. 1995; Marchand & Houle 2006) and models (e.g. Laurance & Yensen 1991) typically consider only the distance to the nearest edge. Organisms may experience ‘multiple edge effects’ resulting from more than one edge (Zheng & Chen 2000) because multiple edges can interact additively (Kapos 1989; Fletcher 2005). Models incorporating distance to more than one edge typically have greater explanatory power than those using only the single closest edge (Malcolm 1994, 1998, 2001; Zheng & Chen 2000; Fernández et al. 2002), especially when patches are small and irregularly shaped (Malcolm 2001; Fletcher 2005). Because the bayheads we studied are small (> 3 ha) and irregularly shaped, we chose to quantify the distance to multiple edges, by performing a modification of Mancke & Gavin’s (2000) method, measuring the distance to the four closest edges within quadrants.

To quantify the location of each stem in relation to four bayhead edges, we digitally mapped the bayhead boundaries and stems using ESRI ArcGIS 9.1. We generated a 3m × 3-m grid on each digital bayhead polygon, and then overlaid the stem coverage on the grid, assigning a grid cell to each stem. Similar to the point-quarter technique, we divided each 360° universe of a grid cell into four quadrants based on compass direction, and measured the distance from the centre point of the grid cell to the closest edge within each quadrant (NWc, SWc, NEc, SEc (‘c’ denotes the closest edge in each quadrant)). These four distance-to-edge values for each grid cell were assigned to all stems within the cell. We calculated the mean distance-to-edge by taking the mean of the four values ((NWc+SWc+NEc+SEc)/4).

### Analysis

We tested each variable for normality and homogeneity of variance and applied transformations as needed. We compared spatial location of *Gordonia* and *Pinus* stems using a one-way ANOVA and Tamhane’s post-hoc tests to detect significant differences in distance-to-edge.

We used path analysis models (Wright 1934, 1960) to evaluate the importance of specific variables along a variable pathway affecting survival and resprouting. This technique places a set of correlations into an assumed cause-and-effect flow chart. Using regression coefficients, path analysis

helps to define direct and indirect effects, and to evaluate the importance of different variables (Wright 1960; Scheiner & Gurevitch 2001). Historically, the final dependent variable in path analysis needed to be continuous but more recently a framework for binary dependent variables has been developed (Eshima et al. 2001). We evaluated the relationships among independent (char height, depth of burn, stem diameter and distance-to-edge) and dependent variables (survival and resprouting). Analyses of resprouting were restricted to *Gordonia* because *Pinus* does not resprout. Path coefficients were calculated using the demo version of *Mplus* 3.11, which allows for binary dependent variables (Muthén & Muthén 2004). In our path analyses, the final dependent variables were treated as binary (presence/absence of survival, basal resprouting and crown resprouting).

We constructed a path model judged to be most realistic for our system based on past research. In our model, distance-to-edge has a direct effect on the intermediate variables – stem diameter, char height and depth of burn. Each intermediate variable has a direct effect on the final dependent variable – survival, basal resprouting or crown resprouting. The only indirect effect is that of distance-to-edge on the final dependent variable. Path models were constructed for *Gordonia* and *Pinus* survival in both sites, and *Gordonia* basal and crown resprouting in both sites. Path coefficients (standardized partial regression coefficients) were calculated and we evaluated the strength of the overall model by calculating *U*, the error of estimation due to causes outside the path model ( $U = (1 - R^2)^{1/2}$ ; Mitchell 1993). The models for survival of *Gordonia* (Site 1  $\chi^2 = 25.322$ ,  $df = 3$ ,  $P = 0.092$ ; Site 2  $\chi^2 = 33.253$ ,  $df = 3$ ,  $P = 0.102$ ) and *Pinus* (Site 1  $\chi^2 = 14.582$ ,  $df = 3$ ,  $P = 0.201$ ; Site 2  $\chi^2 = 12.127$ ,  $df = 3$ ,  $P = 0.162$ ) as well as *Gordonia* basal resprouting (Site 1  $\chi^2 = 25.934$ ,  $df = 3$ ,  $P = 0.114$ ; Site 2  $\chi^2 = 22.325$ ,  $df = 3$ ,  $P = 0.107$ ) and crown resprouting (Site 1  $\chi^2 = 12.442$ ,  $df = 3$ ,  $P = 0.087$ ; Site 2  $\chi^2 = 14.282$ ,  $df = 3$ ,  $P = 0.0944$ ) fit the data. Note that a nonsignificant  $\chi^2$  test indicates a good fit between model and data (Mitchell 1993).

To visualize the overall trends of survival and resprouting across the edge-to-interior gradient, we first performed logistic regressions using distance-to-edge as the independent variable and survival and resprouting (presence versus absence) as dependent variables. From these regressions we saved the probability of surviving and resprouting and plotted these against distance-to-edge.

**Results**

*Survival*

The two focal species differed in the variables that affected their survival. Survival of *Gordonia* was negatively affected by depth of peat burning (Path coefficients:  $-0.294$  and  $-0.196$ , Sites 1 and 2, respectively; Fig. 2) and distance-to-edge ( $-0.156$  and  $-0.280$ ) but char height and diameter did not have an effect (Fig. 2). In contrast, *Pinus* survival was negatively affected by char height ( $-0.317$  and  $-0.398$ ) and positively effect by diameter ( $0.237$  and  $0.592$ ), but depth of burn did not have an effect and the effect of distance-to-edge was inconsistent between sites ( $0.274$  and  $-0.270$ ).

The influence of distance-to-edge on the intermediate variables (char height, depth of peat burning and diameter) was remarkably consistent between species (Fig. 2). Distance-to-edge had an opposite effect on the two fire intensity variables. Char height was negatively affected by distance-to-edge for *Gordonia* ( $-0.194$  and  $-0.494$ ) and *Pinus* ( $-0.641$  and  $-0.257$ ). In contrast, depth of peat burning was positively affected by distance-to-edge for *Gordonia* ( $0.315$  and  $0.267$ ) and *Pinus* ( $0.637$  and  $0.531$ ). Stem diameter was positively affected by distance-to-edge for *Gordonia* ( $0.335$  and  $0.248$ ) and *Pinus* ( $0.322$  and  $0.316$ ).

The indirect effect of distance-to-edge on *Gordonia* survival was weakly negative ( $-0.150$  and

$-0.026$ ) and combined with the stronger negative direct effects ( $-0.156$  and  $-0.280$ ) producing a strong negative total effect of distance-to-edge on *Gordonia* survival ( $-0.312$  and  $-0.306$ ). The probability of *Gordonia* surviving decreased from nearly 70% at the bayhead edge to less than 30% in the interior (Fig. 3a).

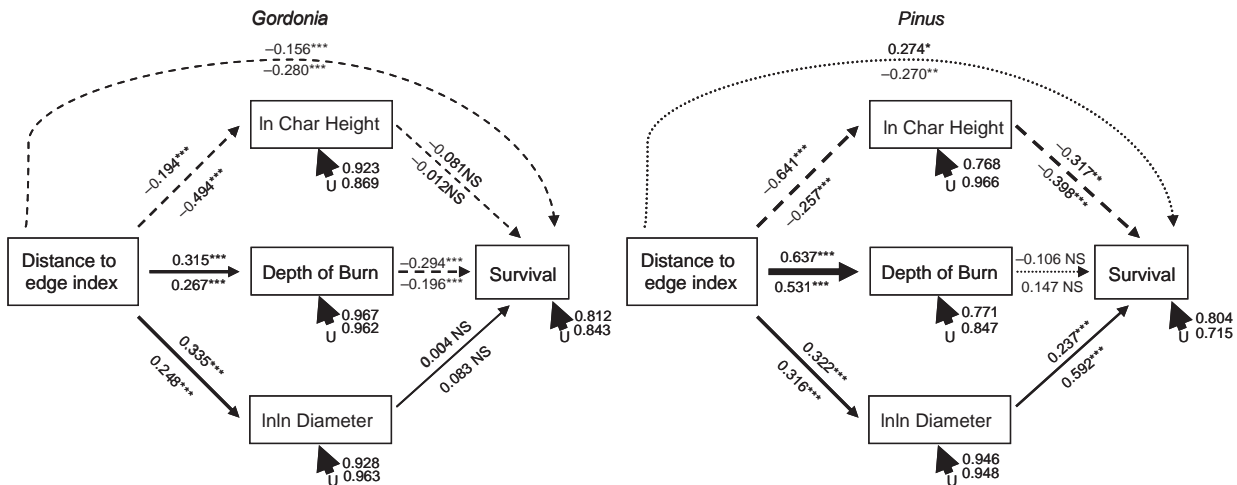
The indirect effect of distance-to-edge on *Pinus* survival was positive ( $0.211$  and  $0.367$ ) and combined with the inconsistent direct effect ( $0.274$  and  $-0.270$ ) to produce a total effect that was positive but inconsistent in its strength between sites ( $0.485$  and  $0.097$ ). The probability of *Pinus* surviving was nearly 0% at the edge and increased dramatically towards the bayhead interior, to almost 60% in Site 1, but the increase in Site 2 was less dramatic, reaching only 35% in the interior (Fig. 3a).

*Spatial location of species*

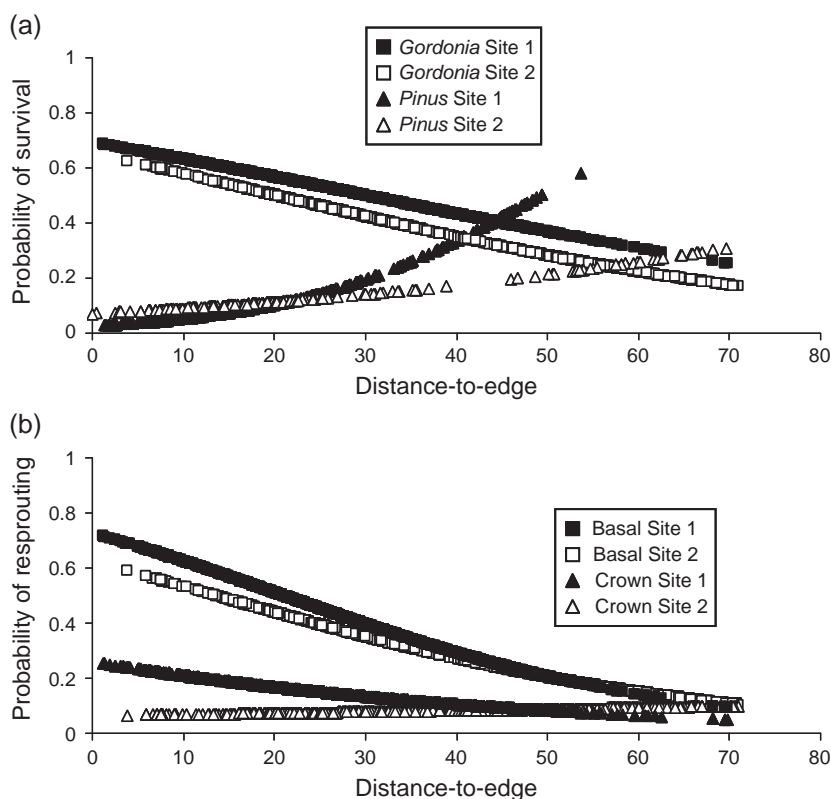
*Gordonia* was located in more interior areas of both bayhead sites, compared to *Pinus*, which was predominantly found near bayhead edges (Fig. 1). On average, *Pinus* had lower distance-to-edge values (Fig. 1; Site 1  $F_{29,1713} = 40.831$ ,  $P = 0.0001$ , Site 2  $F_{2,1684} = 214.631$ ,  $P = 0.0001$ ) compared to *Gordonia*.

*Gordonia lasianthus* resprouting

Both basal and crown resprouting of *Gordonia* were affected by char height and stem diameter;



**Fig. 2.** Path diagram of *Gordonia* (Site 1  $n = 1267$ ; Site 2  $n = 1238$ ) and *Pinus* (Site 1  $n = 389$ ; Site 2  $n = 318$ ) survival. Strength of the weakest path coefficient between the two sites is represented by the arrow width. Path coefficient for Site 1 is above the arrow, and Site 2 is below. Positive effects are shown by solid lines, negative effects by dashed lines, and inconsistencies in the sign of the path coefficient between sites by dotted lines.  $U$  represents all unmeasured variables affecting the dependent variable, Site 1 is above and Site 2 below. The natural logarithm is abbreviated as ln. Symbols: \*\*\* $P < 0.001$ ; \*\* $P < 0.01$ ; \* $0.01 < P < 0.05$ ; NS =  $P > 0.05$ .



**Fig. 3.** Survival and resprouting trends across the edge-to-interior gradient. a) Probability of survival for *Gordonia* and *Pinus*, calculated from the logistic regression relationship of survival and distance-to-edge (*Gordonia* Site 1  $\chi^2 = 38.98$ ,  $df = 2$ ,  $P < 0.0001$ ; Site 2  $\chi^2 = 73.59$ ,  $df = 2$ ,  $P < 0.0001$ ; *Pinus* Site 1  $\chi^2 = 48.14$ ,  $df = 2$ ,  $P < 0.0001$ ; Site 2  $\chi^2 = 6.56$ ,  $df = 2$ ,  $P = 0.008$ ). b) Probability of basal and crown resprouting for *Gordonia*, calculated from the logistic regression relationship of resprouting and distance-to-edge (Basal resprouting Site 1  $\chi^2 = 103.54$ ,  $df = 2$ ,  $P < 0.0001$ ; Site 2  $\chi^2 = 90.48$ ,  $df = 2$ ,  $P < 0.0001$ ; Crown resprouting Site 1  $\chi^2 = 18.76$ ,  $df = 2$ ,  $P = 0.05$ ; Site 2  $\chi^2 = 1.21$ ,  $df = 2$ ,  $P = 0.25$ ).

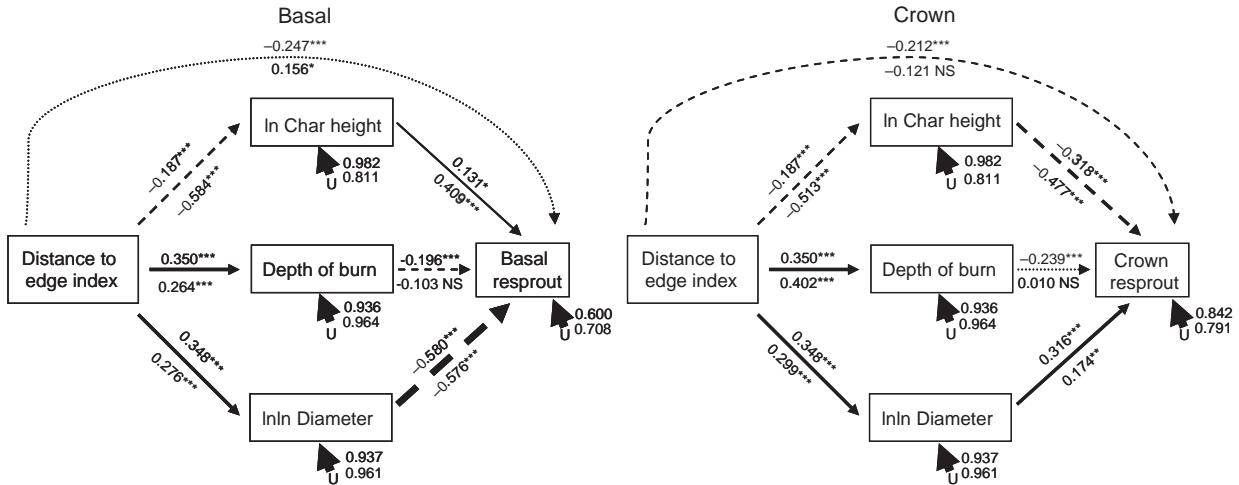
however these variables influenced types of resprouting differently. Char height had a positive effect on basal resprouting (0.131 and 0.409; Fig. 4) and a negative effect on crown resprouting ( $-0.318$  and  $-0.477$ ). Diameter had a strong negative effect on basal resprouting ( $-0.580$  and  $-0.576$ ) and a positive effect on crown resprouting (0.316 and 0.174). Depth of peat burning negatively effected basal ( $-0.196$ ) and crown resprouting ( $-0.239$ ) in Site 1 but did not have a significant effect in Site 2 (Fig. 4).

The indirect effects of distance-to-edge on resprouting were stronger and more consistent than the direct effects. The direct effects of distance-to-edge on basal resprouting were inconsistent between sites ( $-0.247$  and  $0.156$ ) but the indirect effects were strongly negative ( $-0.294$  and  $-0.425$ ) and combined to produce a strong negative total effect ( $-0.541$  and  $-0.269$ ). The probability of basal resprouting was almost 70% near the edge and decreased to almost 10% in the interior (Fig. 3b). In contrast, the direct effects of distance-to-edge on

crown resprouting were consistently negative ( $-0.212$  and  $-0.121$ ) and the indirect effects were positive but the strength was not consistent between sites (0.035 and 0.227). The total effect of distance-to-edge on crown resprouting was weak and inconsistent between sites ( $-0.177$  and  $0.106$ ). The probability of crown resprouting across the edge-to-interior gradient was inconsistent between sites. In Site 1, the probability of crown resprouting was nearly 25% at the edge and decreased to 5% in the bayhead interior, while in Site 2 the probability of crown resprouting was approximately 10% across the entire edge-to-interior gradient (Fig. 3b).

## Discussion

Our results indicate that the ability of a tree to survive and respond to fire is highly dependent on its spatial location within the tree island. They also highlight that spatial location does not similarly influence all tree species, or types of post-fire response.



**Fig. 4.** Path diagram for *Gordonia* basal and crown resprouting (Site 1  $n = 644$ ; Site 2  $n = 412$ ). Path coefficient for Site 1 is above the arrow, and Site 2 is below. Strength of the weakest path coefficient is represented by the arrow width. Positive effects are shown by solid lines, negative effects by dashed lines, and the inconsistencies in the sign of the path coefficient between sites are shown by dotted lines.  $U$  represents all unmeasured variables affecting the dependent variable, Site 1 is above and Site 2 below. The natural logarithm is abbreviated as ln. Symbols: \*\*\*  $P < 0.001$ ; \*\*  $P < 0.01$ ; \*  $0.01 < P < 0.05$ ; NS =  $P > 0.05$ .

We observed distinct trends across the edge-to-interior gradient of bayhead tree islands in the survival of *Pinus* versus *Gordonia*, and in basal versus crown resprouting of *Gordonia*. On their own, these trends are evidence that natural edges have the potential to differentially impact species population dynamics within patches. Results from our path analysis models provide a deeper understanding of these spatial patterns by suggesting causal pathways that include specific types of fire severity. We argue that specific causal pathways are favoured for species or types of resprouting due to their differential susceptibility to either above- or belowground fire and the range of locations they occupy. We place the results from this dry season fire within the larger context of fire seasonality and the successional trajectory of bayhead communities.

The disparate trends observed in *Gordonia* versus *Pinus* survival can be understood in the larger context of sprouter versus seeder regeneration strategies. Although it has been suggested that sprouters have the potential for near immortality (Bond & Midgley 2003), like seeders, they also have the potential to be killed by disturbance. Due to the suite of functional traits of sprouters versus seeders, it is likely that they are differentially vulnerable to above- and belowground disturbance.

Sprouters typically rely on resources stored belowground to survive and recover from disturbance (Chapin et al. 1990; Iwasa & Kubo 1997) and therefore may be vulnerable to smoldering peat,

which can damage or completely destroy these stores (Wein 1983; Ryan & Frandsen 1991). Survival of our sprouting species, *Gordonia*, was strongly affected by peat smoldering and had lowest survival in the bayhead interior where smoldering was deepest. Additionally, the thin bark of *Gordonia* (Gilman & Watson 1993) likely provided little insulation from smoldering peat. Similarly, others have observed high post-fire mortality of the sprouting, thin-barked species *Taxodium distichum* in the interior of tree islands (Cypert 1961; Ewel & Mitsch 1978) where peat smoldering is deepest (Monk & Brown 1965; Coultas & Calhoun 1975). Sprouting species are often capable of recovering from high severity aboveground disturbance (Bellingham & Sparrow 2000), and our results showing that *Gordonia* had highest survival near the bayhead edge where char heights were greatest, agree with this generalization.

*Gordonia* is able to recover from aboveground disturbance by sprouting, and our results are consistent with the view that sprouting is strongly influenced by aboveground disturbance severity. We found that char height positively effected basal resprouting but negatively effected crown resprouting. This is consistent with the generalized view that low-severity disturbance causes little crown damage and promotes canopy resprouting, while high-severity disturbance severely damages tree crowns and promotes basal resprouting (Bellingham & Sparrow 2000). Crown resprouting is beneficial for trees be-

cause it allows leaf area that intercepts maximum light to be regained faster than from basal sprouting (Hodgkinson 1998). Trees typically resprout from the crown unless damage to the crown is so extensive that basal resprouting is the only option (Romberger 1963).

Compared to sprouters, seeders have fewer belowground reserves, and when their aboveground tissues are extensively damaged, they die (Bond & Midgley 2001). Seeders often have taller stems than sprouters (Midgley 1996), possibly serving to protect their crowns from damage during disturbance (Stephens & Finney 2002; Keyser et al. 2006). Survival of our seeder species, *Pinus*, was affected by the interplay between aboveground fire severity (char height) and stem size. Char height strongly decreased *Pinus* survival and, on bayhead edges where char heights were tallest, *Pinus* survival was lowest. This is consistent with other studies showing that charring damages tree crowns (Stephens & Finney 2002; Ordóñez et al. 2005) and increases mortality (Weber et al. 1987; Menges & Deyrup 2001) in seeder conifer species. Survival increased with stem diameter for *Pinus*, perhaps because a larger diameter leads to less crown damage, which has also been found in other conifers (Van Wagner 1965; Stephens & Finney 2002; Keyser et al. 2006). Stem diameter can also be associated with bark thickness (Hengst & Dawson 1994; Van Mantgem & Schwartz 2003), which can insulate the cambium from lethal temperatures, thus increasing survival.

Fire may shape both the species composition and spatial structure of the tree community in bayhead tree islands. The overall percentage survival of *Gordonia* (49.2% and 33.3%; Sites 1 and 2, respectively) and *Pinus* (15.9% and 18.6%; Sites 1 and 2, respectively) demonstrates that this dry season fire drastically altered the canopy layer of the community. Fire may shift the relative spatial distributions of trees within the bayhead. *Gordonia* was found in the more interior locations of the tree islands; however its survival was highest closest to the edges. Similarly, *Pinus* was found predominantly near tree island edges but its survival was slightly higher in the interior. Our results suggest that the distribution of trees within bayhead tree islands is likely to be dynamic over time due to the spatial pattern of mortality brought about by fire.

Between fires, bayhead vegetation increases in spatial extent and invades several adjacent vegetation types (Peroni & Abrahamson 1986; Landman & Menges 1999). During this expansion, the representation of *Pinus* in the tree community likely increases as the edges of the bayhead expand. The

season in which fire occurs in bayheads determines if this disturbance merely alters the existing vegetation association or results in an entirely different association. Fires that occur during the wet season, when the bayhead interior is saturated with water, typically burn only the aboveground portions of the edges, pruning back the spatial extent of the bayhead (Peroni & Abrahamson 1986), and likely reducing *Pinus* representation. During a wet season fire, we would likely observe significantly less *Gordonia* mortality due to the lack of smoldering peat. During dry season fires, all of the peat can be consumed by fire down to the mineral soil, creating a depression that fills with water, resulting in an aquatic or semi-aquatic vegetation association (Wade et al. 1980). The fire studied here can be viewed as an intermediate between the extremes of wet and dry season fires. Our fire occurred during the dry season, but the smoldering peat was extinguished before it could consume all of the organic soil. If the peat had continued to smolder, it is likely that we would have observed complete or near complete mortality of *Gordonia* and a shift to an aquatic vegetation association. Our results suggest that community composition and spatial distribution of trees within bayhead tree islands is likely to be dynamic over time, with the frequency and seasonality of fire playing a large role in these dynamics.

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