

Pignut hickory (*Carya glabra*) recruitment failure on a Georgia barrier island¹

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Demographic disruption in pignut hickory (*Carya glabra*) populations, a major canopy species, was observed for 10 years on St. Catherine's Island, GA., and recruitment failure was identified as the central mechanism of local extinction. From 1996 to 2006 there was no recruitment by hickory seedlings into the sapling size class. Tree cores of the youngest adult trees indicate that there has been no recruitment at the study site for over 65 years. Tree cores in 4 other pignut hickory populations indicate similar patterns across the island. Field evidence of browse and a strong statistical relation ($p < 0.0001$) between seedling density distributions and microsite protection from herbivory suggest that this trend in recruitment failure is related to the increasing abundance of deer and pigs on the island. Using a size class population projection model, we estimate that, if such recruitment failure and mortality rates continue, these hickory populations will be extirpated from the maritime forest within 200 years. The decline of this major canopy species will have extensive ecological implications. This study points to the high susceptibility of many hardwood tree species to the current biotic and abiotic conditions that are met within maritime forests on islands with a continuing history of land use.

Introduction

Maritime forest tree populations associated with barrier islands along the U.S. Atlantic coast grow in a highly disturbed, resource-limited environment from which mainland tree populations are often well buffered (Young *et al.* 1995). To establish and survive in these environments, woody species must overcome a variety of abiotic and biotic pressures, the intensities of which are exacerbated in island settings by the dynamic, fragmented nature of insular forests. Island habitats are typically restricted in size and bound by a large area of natural edge habitat. Dynamic environments are known to increase the likelihood of extinction in populations of restricted size (Drake and Lodge 2004), and this plays a significant role in the success or decline of species in perpetually changing island settings. The plant succession of

established island forests can be reset by dune migration (Hippensteel and Martin 1999) and coastal erosion due to transgressing seas (Titus *et al* 1991). Furthermore, tree populations experience blowdowns and defoliation from the annual cycle of high-wind coastal storms, including hurricanes and noreasters (Sallenger 2000, Smith *et al.* 1997). Limited and varying nutrient resources add to this suite of environmental pressures; maritime forest populations experience inconsistent freshwater availability from a dynamic underground lens, soils are typically low in nitrogen, potassium and phosphorus content (Young *et al.* 1995), and coarse coastal sediments generally facilitate soil leaching (Bourdeau and Oosting 1959). Due to their coastal position, barrier island tree species face intermittent inundation, ocean salt spray incursion that results in elevated soil salt content (Wells & Shunk 1938, Easton 1978, Art *et al.* 1974, Young *et al.* 1995) and a transient germinable seed bank (Looney and Gibson 1995).

In this island context, barrier island tree populations are highly vulnerable to local extinction, particularly when they have been and/or still are subject to disturbance patterns that follow human encroachment and development of a landscape (Lopazanski *et al.* 1988). Humans have an acute effect on the stability of island tree populations, both directly as disturbers of habitats and indirectly as agents of invasion (i.e. purposefully or unintentionally transporting plants, insects, rats, snakes, or herbivorous ungulates to islands). Georgia barrier islands have been inhabited by humans for millenia, from pre-agricultural indigenous Americans to Spanish missionaries to industrial modern American (Bratton and Miller 1994, Thomas 1978). American Navy and Merchant Fleets extracted large trees from southeastern maritime forests in the 17th and 18th century (Spence 1985), and large tracts of barrier islands were used as cattle fields and crop land in the 19th and early 20th century (Bratton and Miller 1994). In the last century, increased development pressure on these insular maritime forests has resulted in their overall

decline (Spence 1985). Since the early 1900's, large-scale and piecemeal development has accelerated on many islands on the Atlantic coast, leading to the devastation of maritime forests (Zucchini 1980). Recent management has encouraged the protection of maritime forests surrounding island developments, because the canopy provides unequalled protection from hurricane winds (Zucchini 1980). However, residual forests on developed islands are typically highly altered. These alterations generally result in a thinned understory, reduced resistance to storm winds, and increased salt spray encroachment into the forest (Zucchini 1980).

Understanding the scale and impact of this intensive land use history is considered necessary to studying current island forest ecology and population distributions (Clark 1986). However, the role humans have played as agents of invasion, despite the depauperate historic account of human-induced exotic species invasion, is extensive in terms of ecological impacts on an island's tree populations. Introduced species following habitation of a landscape by humans has strong and damaging effects on native biota, at times causing community- and landscape-level changes (Elton 1958, Mack 1981, Case and Bolger 1991, Simberloff and Stiling 1996, Sax *et al.* 2002). Human-induced invasion of feral ungulates is pervasive throughout the Atlantic coast barrier islands (Donlan and Croll 2002), and the invasion of exotic forest pathogens has been shown to alter forest communities dramatically (Hess *et al.* 2008, Stromayer and Warren 1997). On islands, the introduction and establishment of non-native species are known to facilitate the extinction of natives or previously naturalized species (Steadman 1995, Fritts and Rodda 1998).

The challenges presented by the combination of island settings and human disturbance provide the context of this 10-year study, in which we observed a declining tree population in an insular maritime forest with extensive land use history. St. Catherine's Island, located off of the

southern Georgia coast, was the island on which we conducted our research (Map 1). We focused on pignut hickory (*Carya glabra*) populations heterogeneously distributed throughout the Pleistocene soils of the island. As a slow-growing, non-clonal, late successional broadleaf species that can not resprout and is predated upon both as seeds and seedlings by various herbivores (Smalley 1990), pignut hickory is an ideal species with which to explore island tree populations' susceptibility to decline.

To track the regeneration of this species through demographic analysis and to infer abiotic and biotic mechanisms governing these population trends, 10 years of demographic data were collected to evaluate the following three hypotheses: 1) St. Catherine's hickory populations have experienced seedling establishment failure and canopy recruitment failure; 2) initial seedling distribution on the forest floor is associated with microsite protection from seed predators and seedling browse, and 3) projected long-term trends in tree density suggest the major decline of pignut hickory populations on St. Catherine's Island.

Methods

Study Site – The cultural history, physiography, and biota of St. Catherine's Island are typical of barrier islands on the southern Georgia coast (Coile & Jones 1988). St. Catherine's is a private, undeveloped island with an interior maritime forest and a long history of land use (Thomas 1978). This island's history is similar to that of many nearby barrier islands such as Cumberland Island (Bratton & Miller 1994). Most of the island interior was used for the farming of Sea Island cotton between 1800 and 1860, and the effects of this agricultural period are still evident within the maritime forest (Coile & Jones 1988). This agricultural period introduced many plant species to St. Catherine's maritime forests (Coile and Jones 1988). Cattle production

in the mid-1900's, along with consistently high densities of deer, have grazed on nearly every digestible plant on the island (Coile and Jones 1988). Swine (*Sus scrofa*) have also been present on the island since the 1950's (Thomas 1978). Swine are particularly detrimental to native flora, especially large-seeded species like pignut hickory, in that they dig up the roots and nuts (Coile and Jones 1988).

The composition of the Sea Islands' maritime forests has historically varied according to a climatic gradient (Bellis 1995, Helm et al. 1991, Bourdeau & Oosting 1959). In the southern Sea Islands, oak (*Quercus spp.*) and pignut hickory are among the dominant canopy species in this late successional maritime ecosystems are (Bellis 1995). Pignut hickory composes a majority of the canopy on barrier islands from Florida to South Carolina and is an ecologically integral member of the maritime forest in the southern Sea Islands (Smalley 1990).

The forest at our primary study site was the focus of the 10-year study; it was inventoried in 1996, 1997, 1998, 2001, 2003 and 2006. This study site was a 100m x 60m plot located along Backcreek Road at N 31°, 37.623' W 81°, 09.498' (Map 1). The maritime forest at this site is typical of oak-hickory forests of secondary study sites on the island. This forest has a variety of species in the canopy and subcanopy, including red bay (*Persea borbonia*), American holly (*Ilex opaca*), red cedar (*Juniperus virginianus*), black cherry (*Prunus serotina*), sparkleberry (*Vaccinium arboreum*), and sweet gum (*Liquidambar styraciflua*). The hickory population here comprises a large component of the local community structure. 55% of the total community basal area is attributed to this species (523.51m²/ha., Table 1). Although maritime forest canopies typically feature loblolly pine (*Pinus taeda*), this species is not a prominent component of St. Catherine's maritime forests (Bellis 1995). The understory of these forests is characterized by patchy zones of saw palmetto (*Serenoa repens*) among clearings of tall grass and briar.

Stand dynamics - At all study sites 1-5, a representative sample of pignut hickory trees were cored and their ages were determined. Within this plot, the location of each tree (>3m tall) was mapped, its species was identified, and its diameter at breast height (dbh, 1.4m) was recorded. Traces of dead trees (rotting stumps, soil depressions, etc.) were also mapped and identified if possible. Special attention was given to the search for saplings within the study plot. Seedling density was then counted for each subplot. Recruitment rates between size classes were calculated based on size class shifts over the 10-year study period.

Seedling microsite association – At the primary study site, evidence of browse and safe-site blocking agents (e.g. fallen logs, dense palmetto, etc. that may protect seedlings during germination and early growth) was recorded. In 2001, a detailed map of the northeast 300 m² of the study plot was created; this map displayed all hickory seedlings, ground cover type, palmetto area and blocking agent instances within the plot. A chi-square analysis was used to determine the significance of a correlation between microsite protection and seedling location and density. Fluctuating density distribution patterns throughout the study period were analyzed to account for non-random pattern shifts, such as mast cycles.

Population projection model- Using average mortality rates and recruitment probabilities from the 10-year study, we calibrated a population demography projection model we developed in 1996 (Figure 1). This algorithm calculated the projected densities per size class over time within the pignut hickory population at site 1. The population was subdivided into 5 possible size classes: seed (code: 1), seedling (<0.5m, 2), sapling (0.5m < x < 5cm dbh, 3), pre-adult (5 cm < x < 30 cm dbh, 4), adult (<30 cm dbh, 5). Annual recruitment rates (e.g. the probability of a seed surviving to the seedling size class in a given year, code: P₁₂=0.75, based on Bonner and Maisenhelder 1974) and size class stasis rates (e.g. the probability of a pre-adult remaining in the

pre-adult size class within a given year, P44) governed shifting densities over time. The average number of seeds produced by adult hickories was drawn from the 1983 study of three growing seasons in a temperate pignut hickory forest (Sork 1983a).

Results

Age determination- A strong logistic correlation ($R^2=0.758$) was found between hickory tree widths and their respective ages, determined via random coring of the population ($n=27$) in 1996 (Figure 2). We estimated the ages of all hickories within the study sites by establishing a logistic regression ($p=0.0025$) from this 1996 data with the following equation:

$$\text{age} = 10^{(0.586\log(\text{dbh}) + 1.228)} + (\text{current year} - 1996) + 10$$

The addition of 10 years at the end of the above equation is to account for the approximate number of years it takes for a sapling to grow to breast height (at which the trees were cored). Using this regression, we estimate that the youngest hickory at the study site ($\text{dbh}=5.5\text{cm}$) is 65 years of age, and the oldest ($\text{dbh}=67.2\text{cm}$) is 219 years old.

Recruitment failure- In 1996, the pignut hickory (*Carya glabra*) populations in St. Catherine's maritime forests were conspicuously lacking a sapling size class ($< 5\text{cm dbh}$). No large saplings or adults under the age of 40 were found at any study site, and tree mortality was observed within each site over the course of the study (Figure 2). At our primary study site, a total of 116 living hickories were found in 1996. Of these, 71 were found to be subadults and 45 were adults. The ages of the youngest trees at the site align with the date, provided in Thomas (1978), at which swine were first introduced to the island. No hickory saplings with an age between the seedling age class (1-2 years) and the sub-adult age class (65 – 140.3 yrs.) was present at any study site. Between 1996 and 2006 there was no recruitment from seedling to

sapling size class or from sapling to sub-adult size class. These patterns were also observed at the four other study sites.

Over the course of the 10-year study, 3 sub-adults grew into the adult age class within the study plot. The average rate of recruitment between these age classes is 0.004 trees/yr. Of course, the average rates of recruitment between seedlings and saplings was 0 trees/yr, as was the average recruitment rate between sapling and sub-adult age. 19 of the hickories recorded in 1996 had died by summer 2006; at the end of the study, hickory basal area in the stand (1381.94 m²/ha in 1996) was 523.51 m²/ha, which is 37.9% of 1996 basal area. Individuals that died include 10 sub-adults (14% of 1996 population) and 9 adults (20% of 1996 population). The average survival rate therefore was 0.982 and 0.98 trees/yr for each age class, respectively.

Seedling distribution analysis- Spatial analysis was also used on these datasets to look for statistical patterns that may suggest microsite protection as a variable in the distribution of seedlings. As is expected in tree populations subject to variable annual environment conditions and mast cycles, seedling densities within different areas of the study site differed every year but maintained consistent proportionate densities relative to one another (Figure 4). This lends evidence for the non-random distribution of hickory seedlings in this forest. Using a 300m² map of the forest floor, we found that the actual number of seedlings found in the palmetto differed significantly from the expected number of seedlings found in the palmetto given a random spatial distribution ($\chi^2=1df, n=59. p\text{-value} < 0.0001$).

Future demographic projection- Using average annual seed (*I*) production per adult from Sork 1983a (246 seeds per tree) and a maximum estimate of 75% seed germination success (Smalley 1990), we estimated the seed yield and probability of seed germination per parent adult tree for our site. This average seedling production fit within our range of seedling densities

recorded in 1996, 1997, 1998, 2003 and 2006. Average mortality rates, survival probabilities and recruitment rates were determined (see Table 2) and incorporated into the population demographic projection model. This model indicated a high rate of population decline (Table 3). The model projected that if these recruitment and mortality rates continue, only 5 hickories will still be alive within our study site in 2069, and by 2208, only 1 adult individual will still be standing (Figure 4).

Discussion

The collected data confirmed our three hypotheses. The demographic imbalance in the pignut hickory populations of St. Catherine's Island is due to failed seedling establishment and canopy recruitment failure. The patterns in seedling distribution on the forest floor are correlated to microsite protection, and the recruitment and mortality rates observed from 1996 to 2006 have allowed us to quantitatively predict the future of pignut hickories on St. Catherine's. For the past 65 years at the primary study site, there has been no successful canopy recruitment. The situation in this forest likely reflects the severity of the demographic imbalances within other hickory populations on the island. Continued failure of seedling establishment will broaden this demographic gap as the populations age, reducing the probability of recovery from this pattern.

Ecological pressures, such as increased browse and seed predation by introduced herbivores, can explain these fairly recent trends. Herbivory has been the cause of population decline on many coastal barrier islands with hardwood forests, both on the Atlantic coast and in New Zealand (Wood et al. 1987, Stewart and Burrows 1989). Forest floor disturbance is known to increase germination success for hickory seeds, but intense browse quickly becomes detrimental (Sork 1983b). Deer tend to negatively affect all species within forests, but have

been documented to cause considerable mortality in hickories (*Carya spp.*) (Russell *et al.* 2001 and McCarthy 1994). This is particularly true of island habitats, in which rapid depletion of habitat can leave herbivore populations well above carrying capacity, making their depletion of the remaining forest floor persistent and nearly total. Experimental exclusion studies have substantiated this conclusion (Donlan *et al.* 2002). White-tailed deer populations now exceed historical records (Anderson and Katz 1993, Abrams and Orwig 1996), and the dense population of deer and feral pigs on St. Catherine's Island are the probable source of this detrimental browse pressure. Our results indicate that microsite protection greatly enhances the probability of seed germination success and temporary survival. Our approach provides no direct evidence for the mechanism behind recruitment failure, but strong correlative evidence suggests intense herbivory as the mechanism behind recruitment failure. While in general, heterogeneous seedling distribution in large gravity-dispersed species may simply be a result of similarly variable adult tree distribution, our field observations, which included repeated sightings of half-chewed seedling leaves and prevalent soil disturbance by pigs, and our microsite analysis suggests that microsite protection from herbivory was also a decisive factor on St. Catherine's Island.

Our results indicate that persistent recruitment failure effectively induces population decline and leads to eventual extirpation. According to population demographic projection model, this population will be extirpated from the island within 200 years if recruitment failure and mortality rates continue as they have for the last 10 years. And without a quantitative analysis of all parameters influencing the stand's survival, this estimation is likely a substantial underestimation of the risk of local extinction (Saether *et al.* 2000). Generally, wind-pollinated plant species like *Carya glabra* can be sustained at very lower population numbers by receiving pollen from distant populations, but in a zero-recruitment situation wind pollination does not

offer a solution. As pignut hickory density decreases to scrub or grassland habitat levels, the chances of pollination for stranded surviving trees diminish greatly. This is especially true in a coastal setting in which prevailing winds blow from the east, preventing the pollination of coastal hickory populations by mainland pollen stock. Furthermore, the chances of a large, heavy hickory seed “rafting” across the salt marshes that divide the barrier island and the Georgia mainland are negligible. It seems that both the establishment and extinction of a species like *Carya glabra* in an insular maritime forest are susceptible to events stochastic in nature. The extirpation of this tree species from St. Catherine’s island would be a significant loss that would alter the ecological dynamics of its maritime forests. Differential browse preference by white-tailed deer is known to influence relative seedling densities in the forest, consequently changing future forest composition (Liang and Seagle 2002). The large seeds of this species serve as a food resource for forest rodents, which often provide a mechanism for local dispersal within the forest, as well as for over 100 insect species, wild turkey (*Meleagris gallopavo*), songbirds, foxes, raccoons and rabbits (Hall 1977, Martin *et al.* 1961). Because a thinning canopy amplifies the volume of salt spray accessing previously protected salt-sensitive species (Zucchini 1990, Spence 1985), populations of other woody and herbaceous plant species will likely respond to the decline of a major canopy species like pignut hickory (Clark 1986). As pignut hickory populations continue to decline, they will probably be replaced by browse-tolerant or unpalatable species (Husheer *et al.* 2005).

It is important to view this declining population on St. Catherine’s within the context of declining state of southeastern maritime forests as a whole. Sparse seedling and sapling size classes is a common pattern in maritime forests throughout the Southeast, particularly within live oak (*Quercus virginiana*) and loblolly pine (*Pinus taeda*) populations (Bourdeau & Oosting

1959, Stromayer & Warren 1997). Prevalent recent pressures in addition to the overbrowse of pigs and deer include the recent massive decline in red bay due to the southern range shift of the ambrosia beetle (*Xyleborus glabratus*) (Hess *et al.* 2008), the severe effects of the Southern pine beetle (*Dendroctonus frontalis*) on susceptible forest species (Helm *et al.* 1991), the increasing development pressures on the southeast Atlantic coast (Bellis 1995) and accelerated landward movement of unstable dune communities due to rapid sea level rise (Titus *et al.* 1991). As the sea encroaches onto barrier islands and pushes their forests westward, pignut hickory is not likely to remain a major canopy species given its high susceptibility to insular environmental conditions and reduced capacity for regeneration in herbivore-populated forests. When assessed in the light of these changes, the imminent extirpation of hickory populations from these oak-hickory forests may be another indicator of the uncertain future of maritimes forests of the Sea Islands.

St. Catherine's intensive land use history and the current inundation of introduced herbivorous ungulates pose a threat to the island's maritime forests. It is now well understood that size and distance from the mainland, the life history of a species, and a suite of environmental and ecological factors govern the success or extinction of a species in an island context (Beissinger 2000, Owens and Bennett 2000). As this study has shown, demographic patterns, as well as the anthropogenic factors driving the ecological conditions that govern them must also be considered when explaining local extinctions on barrier islands. While these barrier islands may seem overwhelmed with a suite of detrimental pressures, recruitment failure due to feral ungulate overpopulation is a threat that can be easily managed. On several islands, management utilizing temporary exclusion has successfully re-established a seedling and sapling size class in forest sites (Anderson and Katz 1992). Efforts to restore this oak-hickory forest

must involve the control or exclusion of introduced ungulates from these threatened forest systems on St. Catherine's Island.

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Tables and Figures



Map 1. Georgia Coast. The inset shows St. Catherine's Island, with the study site marked.

Table 1. Age class densities and basal area statistics for the pignut hickory population within the primary study site.

| Age Class | Density (indiv. per ha.) | Basal Area (m²/ha.) |
|--------------------------|---------------------------------|---------------------------------------|
| Seedlings (2) | 2111.52 | |
| Saplings (3) | 0.00 | 0.00 |
| Subadults (4) | 96.28 | 176.43 |
| Adults (5) | 64.74 | 347.08 |
| Total | 2272.54 | 523.51 |
| All Other Species | 142.76 | 434.90 |
| % of Community | 94% | 55% |

Table 2. Input values for population demographic projection model. F51= average seed production per adult tree; P12= annual recruitment rate of seed to seedling size class; P23= annual recruitment rate of seedling to sapling size class; P33= annual survival rate of saplings, P34= annual recruitment rate of sapling to pre-adult size class; P44= annual survival rate of pre-adults; P45= annual recruitment rate of pre-adults to adult size class; P55= annual survival rate of adult trees).

| INPUT | VALUE |
|---|-------|
| F51= | 246 |
| P12= | 0.75 |
| P23= | 0 |
| P33= | 0 |
| P34= | 0 |
| P44= | 0.982 |
| http://terraserver-usa.com /P45= | 0.004 |
| P55= | 0.98 |

Table 3. Linear algebraic projection model of demography dynamics for hickory population at study site, based on average recruitment probabilities and mortality rates observed between 1996 and 2006.

| Age Class | | Year | | | | | | | | | | | |
|--------------|---|-------|-------|-------|-------|-------|------|------|------|------|------|------|------|
| | | Code | 1996 | 2000 | 2006 | 2010 | 2025 | 2050 | 2075 | 2100 | 2150 | 2200 | 2206 |
| Seed | 1 | 11070 | 10419 | 9508 | 8944 | 7095 | 4795 | 3219 | 2141 | 943 | 409 | 370 | 357 |
| Seedling | 2 | 8303 | 7814 | 7131 | 6708 | 5322 | 3596 | 2415 | 1606 | 707 | 307 | 277 | 268 |
| Sapling | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sub-Adult | 4 | 56 | 52 | 47 | 43 | 33 | 21 | 13 | 8 | 3 | 1 | 1 | 1 |
| Adult | 5 | 45 | 42 | 39 | 36 | 29 | 19 | 13 | 9 | 4 | 2 | 2 | 1 |
| TOTAL | | 19473 | 18327 | 16725 | 15731 | 12479 | 8432 | 5660 | 3765 | 1657 | 719 | 650 | 628 |

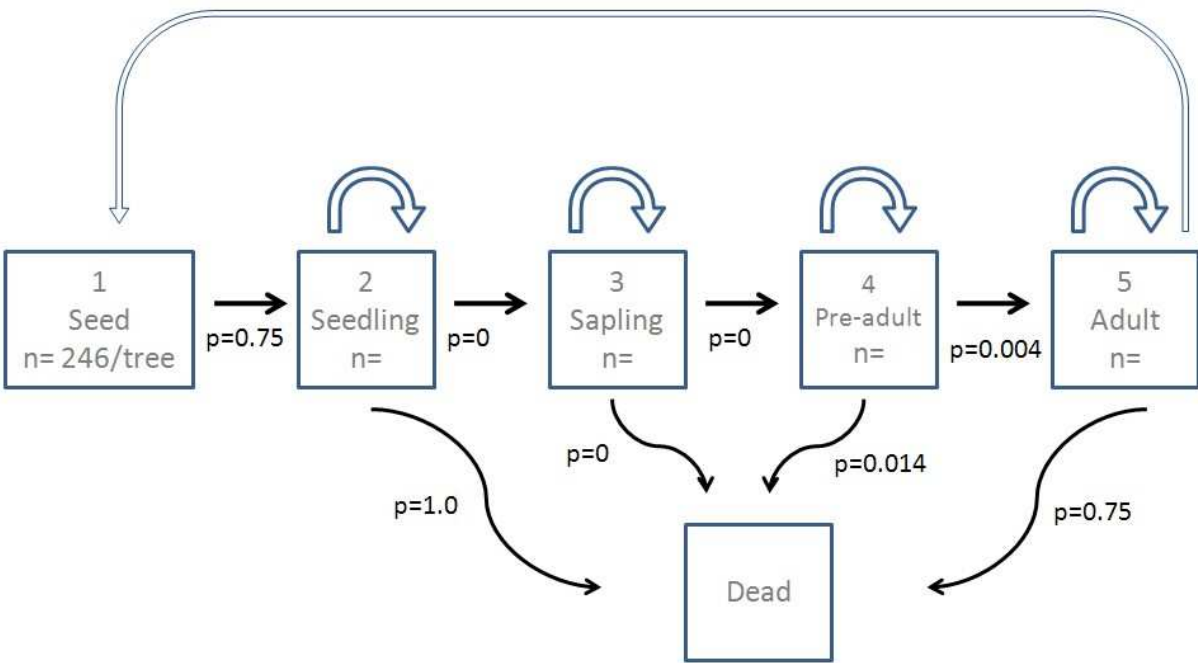


Figure 1. Illustration of population demography projection model for pignut hickories at site 1, with mortality and recruitment rates determined over course of 10 year study. Average seed production per adult hickory was taken from Sork 1983a.

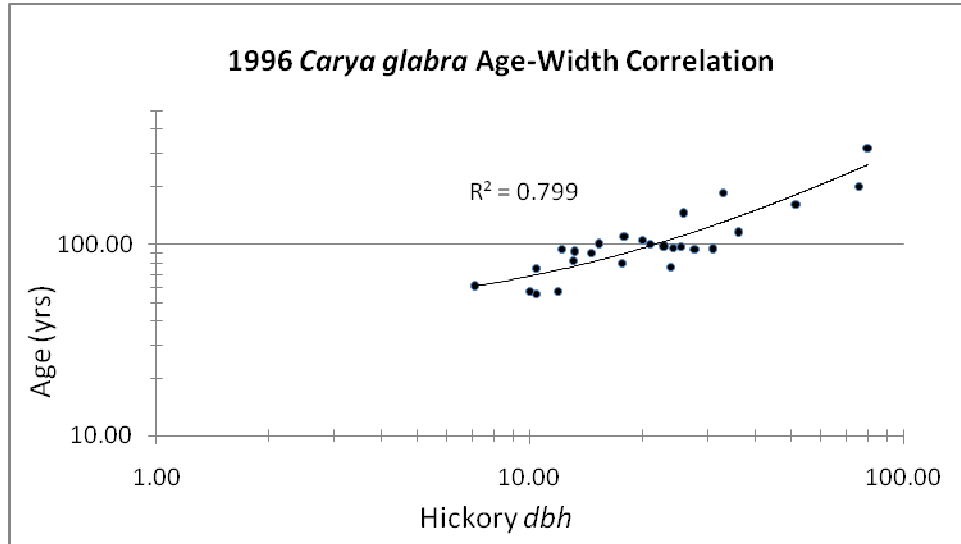


Figure 2. A strong logarithmic regression ($R^2=0.799$, $p<0.001$) of *Carya glabra* tree width-to-age based on a random core sample ($n=27$) of the primary study site hickory population in 1996 (Jackson et al 1996).

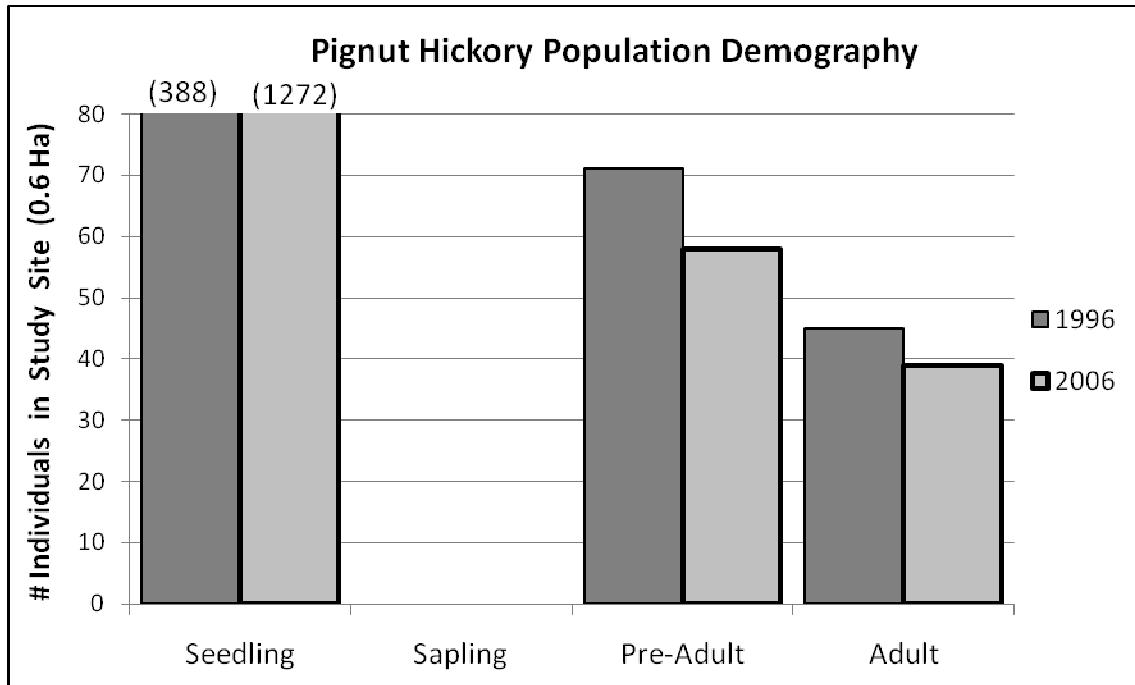


Figure 3. Age class distribution within hickory population at study site, showing clearly the complete lack of a sapling age class. All trees within a 100m x 60m plot were counted and measured.

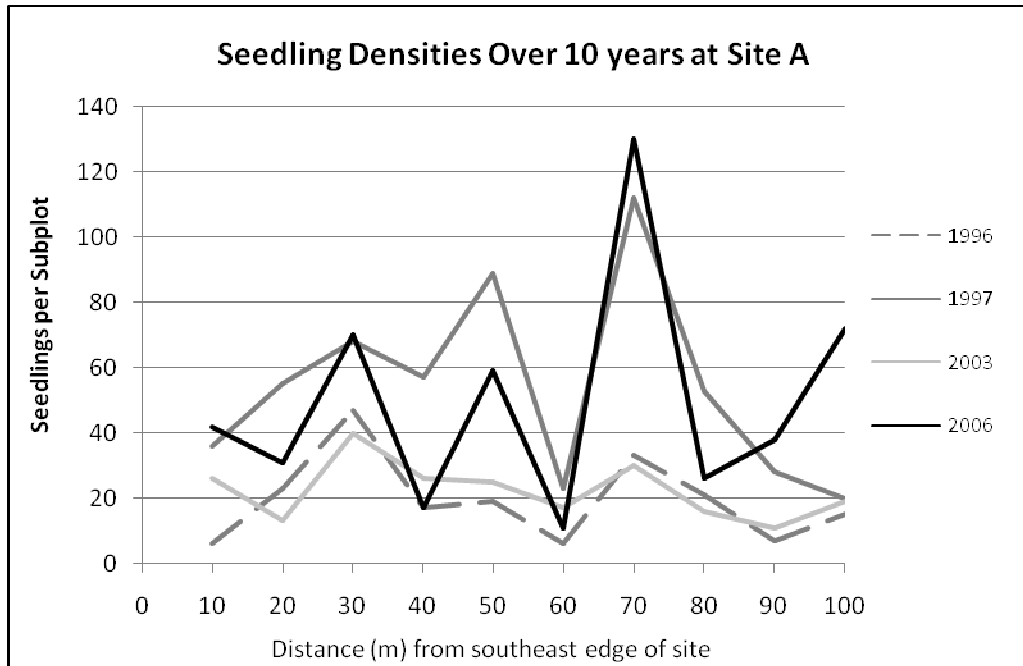


Figure 4. Differential seedling densities across a transect of the primary study site, at four different years (1996, 1997, 2003 and 2006). All seedlings within a 10m x 30m subplot were counted at each transect point (10m apart). The synchronicity of density spikes on each spatial distribution suggests non-random seedling distribution.

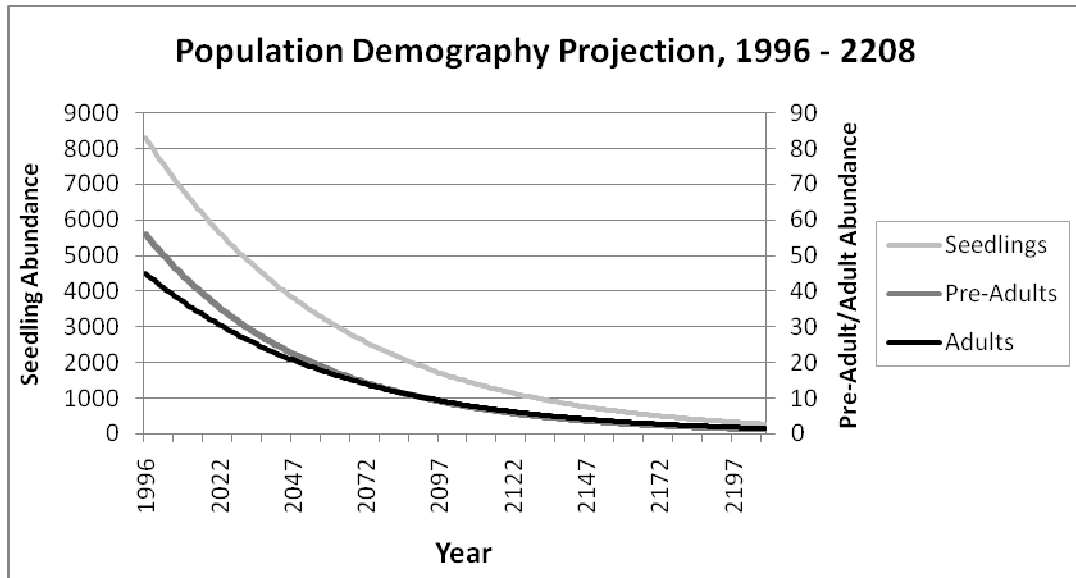


Figure 5. A projection of pignut hickory density (indiv./0.60 ha) at this site into the next 200 years, using a linear algebraic model (developed by Evans in 1998), calculated with recruitment probabilities and mortality rates based on 1996-2006 data. The primary left axis represents predicted numbers for seed and seedling age classes; the secondary right axis pertains to the sub-adult and adult age class.

LITERATURE CITED

- Abrams, M.D. and D.A. Orwig. 1996. A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA. *Journal of Ecology* 84:353-363.
- Anderson, R.C., and A.J. Katz. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. *Biological Conservation* 63: 203-208.
- Art, H.W., F.H. Bormann, G.K. Voigt, and G.M. Woodwell. 1974. Barrier island forest ecosystem: role of meteorologic nutrient inputs. *Science*. 184: 60-62.
- Beissinger, Steven R. 2000. Ecological mechanisms of extinction. *Proceedings of the National Academy of Sciences*. 97(22):11688-11689.
- Bellis, V.J.. 1995. Ecology of Maritime Forests of the Southern Atlantic Coast: A Community Profile. *Biological Report 30*. U.S. Department of the Interior, National Biological Service. Washington, DC 20240
- Bonner, F.T., and L.C. Maisenhelder. 1974. *Carya* Nutt. Hickory. In Seeds of woody plants in the United States. p. 262-272. C.S. Schopmeyer, tech. coord. U.S. Department of Agriculture, Agriculture Handbook 450. Washington, DC.
- Bourdeau, P. and H. Oosting. 1959. The Maritime Live Oak Forest in North Carolina (in Notes and Comment). *Ecology*, 40(1): 148-152.

- Bratton, S. and S. Miller, 1994. Historic field systems and the structure of maritime oak forests, Cumberland Island national seashore, Georgia. *Bulletin of the Torrey Botanical Club*, 121(1): 1-12.
- Case, T.J. and D.T. Bolger. 1991. The role of introduced species in shaping the abundance and distribution of exotic birds. *Biological Conservation* 78:69-96.
- Clark, J.S. 1986. Coastal forest tree populations in a changing environment, southeastern Long Island, New York. *Ecological Monographs*, 56(3): 259-277.
- Coile, N.C. and S.B. Jones, Jr. 1988. Checklist of the Vascular Flora of St. Catherine's Island, Georgia. *American Museum Novitates*. 2920:1-14.
- Donlan, J., B. Tershy and D. Croll. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. *Journal of Applied Ecology*. 39: 235- 246.
- Drake, J.M. and D.M. Lodge. 2004. Effects of environmental variation on extinction and establishment. *Ecology Letters* 7 (1): 26–30.
- Eaton, T.E. 1978. Natural and artificially altered patterns of salt spray across a forested barrier island. *Atmospheric Environment*. 13: 705-709.
- Elton, C.S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.

- Evans, J.P., and R. E. Shaw. 1988. An Assessment of maritime forest resources on the north carolina coast. *North Carolina Department of Natural Resources and Community Development, Division of Coastal Management.*
- Fritts, T.H., and G.H. Rodda. 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics* 29:113-140.
- Halls, Lowell K., ed. 1977. Southern fruit-producing woody plants used by wildlife. USDA Forest Service, General Technical Report SO-16. Southern Forest Experiment Station, New Orleans, LA. 235 p.
- Helm, A. C, N. S. Nicholas, S. M. Zedaker and S. T. Young. 1991. Maritime forests on Bull Island, Cape Romain, South Carolina. *Bulletin of the Torrey Botanical Club.* 118(2): 170-175.
- Hess, M., J.P. Evans and N. Hollingshead. 2008. The effect of an introduced ambrosia beetle (*Xyleborus glabratus*) on red bay (*Persea borbonia*) mortality in maritime forest communities of St. Catherine's Island, GA. Accepted by *For. Ecol. Man.* In press.
- Hippensteel S.P. and R.E. Martin. 1999. Foraminifera as an indicator of overwash deposits, Barrier Island sediment supply, and Barrier Island evolution: Folly Island, South Carolina. *Paleogeography, Paleoclimatology, Paleoecology.* 149(1): 115-125(11).
- Husheer, S.W., D.A. Coomes, and A.W Robertson. 2003. Long-term influences of introduced deer on the composition and structure of New Zealand *Nothofagus* forests. *For. Ecol. Manag.* 181:99-117.

- Liang, S. and S. Seigel, 2002. Browsing and Microhabitat effects on Riparian Forest Woody Seedling Demography. *Ecology*. 83(1): 212-227.
- Looney, P.B. and D.J. Gibson. 1995. The relationship between the soil seed bank and the above-ground vegetation of a coastal barrier island. *Journal of Vegetation Science* 6:825-836.
- Mack, R.N. 1981. Invasion of *Bromus tectorum* into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145-165.
- Martin, A.C., H.S. Zim, and A.L. Nelson. 1961. American wildlife and plants: a guide to wildlife food habits. Dover Publications, New York. 500 p. Unabridged republication of 1st (1951) edition.
- McCarthy, B. 1994. Experimental studies of hickory recruitment in a wooded hedgerow and forest. *Bulletin of the Torrey Botanical Club*, 121(3): 240-250.
- Owens, I. and P. Bennett. 2000. Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences*; 97(22).
- Russell, F., D.B. Zippin and N.L. Fowler, 2001. Effects of White-tail deer on Plants, Plant Populations and Communities. *American Midland Naturalist*. 146(1): 1-26.
- Sax, D.F., S.D. Gaines and J.H. Brown. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist* 160(6): 766-783.

- Saether, B.E., S. Engen, R. Lande, P. Arcese and J.N.M. Smith. 2000. Estimating the time of extinction in an island population of song sparrows. *Proceedings of the Royal Society*. 267(1443): 621-626.
- Sallenger, A.H., Jr. 2000. Storm Impact Scale for Barrier Islands. *Journal of Coastal Research*, 16(3): 890-895.
- Simberloff, D., and P. Stiling. 1996. Risks of species introduced for biological control. *Biological Conservation* 78:185-192.
- Smalley, G.W. 1990. "Carya glabra (Mill.) Sweet, Pignut Hickory" *Silvics of North America*. Volume 2, Hardwoods. Ed. Russell M. Burns and Barbara H. Honkala. *Agriculture Handbook 654*. Forest Service (USDA) Washington, DC.
- Smith, G.F., N.S. Nicholas and S.M. Zedaker. 1997. Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. *Forest Ecology and Management* 95:275-283.
- Sork, V.L. 1983a. Mammalian seed dispersal of pignut hickories during three fruiting seasons. *Ecology*, 64(5): 1049-1056.
- Sork, V.L. 1983b. Distribution of pignut hickories (*Carya glabra*) along a forest to edge transect, and factors affecting seedling recruitment. *Bulletin of the Torrey Botanical Club*. 110(4): 494-506.
- Steadman, D.W. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. *Science* 267:1123-1130.

- Stewart, G.H. and L.E. Burrows. 1989. The impact of white-tailed deer *Odocoileus virginianus* on regeneration in the coastal forests of Stewart Island, New Zealand. *Biological Conservation* 49: 275-293.
- Stromayer, K.A.K. and R.J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin*, 25(2): 227-234.
- Thomas, D.H., G.D. Jones, R.S. Durham, and C.S. Larsen. 1978. The anthropology of St. Catherines Island. I. Natural and cultural history. *Anthrop. Pap. Am. Mus. Nat. Hist.* 55: 155-248.
- Titus, J., R. Park, J. Weggel, M. Greene, P. Maunsell, S. Brown, G. Gaunt, M. Trehan and G. Yohe. 1991. Greenhouse Effect and Sea Level Rise: The Cost of Holding Back the Sea. *Coastal Management*, (19): 171-204.
- Wells, B.W. and I.V. Shunk. 1938. Salt Spray: An Important Factor in Coastal Ecology. *Bulletin of the Torrey Botanical Club*, 65(7): 485-492.
- Wood, G.W., M.T. Mengak and M. Murphy. Ecological importance of feral ungulates at Shackleford Banks, North Carolina. *American Midland Naturalist*. 118(2): 236-244.
- Young, D.R., G. Shao and J.H. Porter. Spatial and Temporal Growth Dynamics of Barrier Island Shrub Thickets. *American Journal of Botany* 82(5): 638-645. 1995.
- Zucchini, L.R. 1980. Development Planning for Barrier Island Maritime Forests. *Carolina Planning*. 6(2): 14-21.