EXECUTIVE SUMMARY

ARE WHITE-TAILED DEER AFFECTING THE ECOLOGICAL INTEGRITY OF THE BHI MARITIME FOREST?

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(1) *The key recommendation of this report is to continue culling deer on BHI* after deer populations have returned to levels at or above average levels for the past 5 years. Holding deer populations at low densities will likely result in the inability to detect and measure any effects that deer may be having on forest diversity and regeneration.

Under such 'average' deer population sizes, the precautionary approach of regular culling is recommended. Unnaturally high deer populations have demonstrated negative effects on forest regeneration and biological diversity. As has been documented for all other forests for which data exist, historical deer populations on barrier islands such as BHI were very likely significantly smaller due to less available 'good' foraging habitat and due to the presence of predators such as wolves, bears, coyotes, and foxes.

(2) *Continued systematic studies of plant recruitment dynamics at the population and community levels within maritime forest are essential to future management decisions.*

- Whether or not deer even eat live oak seedlings and saplings on BHI is unknown; future studies must address this issue, yet they would be relatively easy to conduct.

- Whether or not burial of acorns is essential for oak recruitment is unknown for BHI, but studies in other, similar systems strongly point to burial of acorns by squirrels as a necessary component of oak recruitment.

- Research is badly needed to separate past effects of logging and current effects of deer on oak populations. Also necessary is to establish whether oaks will respond to removal of competition from the understory and midstory layers of the forest.

- Natural reproductive variability is unknown but can be monitored; an assessment of reproductive trends in live oak would require monitoring for 5-10 years at least.

(3) *Key findings of this study include:*

- The keystone species for maintaining the structural integrity of a continuous forest canopy – live oak (*Quercus virginiana*) – is experiencing or is under the imminent threat of significant population decline in the BHIFR.

- Deer are likely suppressing oak recruitment by killing (via consumption) acorns directly and by lowering acorn densities, thereby reducing the likelihood of acorn burial by squirrels. Acorn burial preventing burial of acorns

- Whether deer are or are not altering total seedling survival across all species recruitment, or are differentially altering the survival of seedlings of some species cannot be determined at this early point in the research. At least one to two more years of monitoring seedlings will be necessary to detect/measure any effects on seedling populations.

- Some species are also being disproportionately impacted by bucks via antler rubs. Of special concern are the dogwood (*Cornus florida*) and eastern red cedar (*Juniperus virginiana*), which have experienced sharp population declines (from logging and/or disease).

- Lingering effects of logging on forest recruitment and structure are evident. Some woody plant species appear to be responding positively to the general canopy disturbance, and a self-perpetuating cycle of disturbance may have been set in motion from heavy logging in the middle of the 20th century.

ARE WHITE-TAILED DEER AFFECTING THE ECOLOGICAL INTEGRITY OF THE SMITH ISLAND COMPLEX?

PROGRESS AND PRELIMINARY FINDINGS OF THE PROJECT:

A REPORT TO
THE NORTH CAROLINA COASTAL RESERVE PROGRAM, DIVISION OF COASTAL MANAGEMENT

24 JUNE 2008

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INTRODUCTION

Growing scientific evidence supports the hypothesis that high deer populations have predominantly negative effects on the composition, diversity, and abundance of flora and fauna in "natural" and human-dominated landscapes (reviewed by Côté *et al.* 2004). As selective foragers, deer enhance the abundance of unpalatable and browse-tolerant plant species, usually at the expense of the diversity and abundance of preferred species (Côté *et al.* 2004) that otherwise might be competitively dominant. Although their effects on herbaceous species may be important, deer most significantly alter woody vegetation. Consequently, deer effects often include changes in the physical as well as biotic components of ecosystems. Moreover, overabundance of deer may result in unexpected indirect effects, such as changes in the diversity and abundance of birds and other fauna (Casey & Hein 1983, de Calesta 1994), and degradation of the functional properties of soil (Hobbs 1996).

One threat to the ecological integrity of Bald Head Island (BHI) is an overabundance of white-tailed deer (*Odocoileus virginianus*). Overabundance of deer is difficult to define and value-laden unless placed into a specific context (McShea *et al.* 1997). In the context of BHI, deer may be defined as "overabundant" when their population size exceeds carrying capacity of the island *or* the integrity of one or more of the island ecosystems is degraded due to the current deer population levels. Determining whether or not deer populations are overabundant therefore requires setting a target, or reference state by which current ecological conditions are compared.

Unfortunately for maritime forests, habitat disturbance via human development, including the elimination of some natural predators and competitors of deer, as well as the natural variation among "presettlement" maritime forests, preclude the construction of accurate reference systems for deer populations. However, maritime forests are dominated by just a few woody plant species and are not particularly species rich communities in general. One may therefore assume that the ecological integrity – at least in terms of the flora – of the BHI forest reserve can be assessed by measuring deer impacts on key general features of the forest: physical structure, plant species and plant community composition, and the population dynamics of dominant tree plant taxa. The BHI maritime forest is unique in that it is the northernmost example of the "southern variant" of maritime forests of the eastern U.S. (Bellis & Keough 1995). Thus the BHI forest canopy is dominated by the evergreen oaks *Quercus virginiana* L. and *Quercus hemisphaerica* Bartr. ex Willd. Additionally, the palmetto, *Sabal palmetto* (Walt.) Lodd. ex J.A. & J.H. Schultes., and the eastern red cedar, *Juniperus virginiana* L. are significant components of the sub-canopy and canopy forest layers.

The goals of this project are to quantify the effects of deer on vegetation structure and composition, as well as population dynamics of key plant taxa of the BHI Forest Reserve (BHIFR). Due to the high inter-annual variation in conditions for plant recruitment and moderate-to-high variability in deer populations, this project must necessarily be conducted over the long-term (five years minimum) in order for ecologically meaningful conclusions to be reached about the principle research questions.

PRINCIPLE RESEARCH QUESTIONS

What are the effects, if any, of deer populations on the ecological integrity of the plant communities of the Bald Head island Forest Reserve?

More specifically, this study is focused on:

1) Whether current deer populations on the island have a detectable effect on forest vegetation:
   (a) species composition
   (b) species diversity
   (c) species abundance
   (d) physical structure of the vegetation (*e.g.*, canopy height, number of vegetation layers, spatial patterns of growth forms such as lianas).

2) Whether deer affect plant recruitment, especially the recruitment of woody plants including oaks, palmettos, and red cedars via:
   (a) effects on acorn survival relative to other fauna
   (b) effects of browsing and antler rubs on seedlings and juveniles.

These questions address components of physical and compositional forest structure that are likely to have direct and indirect impacts on habitat and food availability for fauna and ecosystem properties (*e.g.*, physical conditions and processes including nutrient cycling and salt-spray inputs), and as such vegetation is an effective indicator of integrity of other components of the ecosystems.

METHODS

PROJECT TIMELINE

With continued support, this project is scheduled for a minimum of five years for three major reasons. First, lag times between herbivory by deer and the manifestations of ecological effects will likely be substantial. For example, consumption of seeds and seedlings of woody species by deer, and the consumption of herb species with considerable seed banks in the soil, may not manifest detectable effects on plant populations for several years. Woody plants are generally well-adapted to tolerating low-moderate levels of herbivory, yet the stress associated with intensive herbivory rarely results in mortality of perennial plants within one growing season. Second, deer effects (if present) on vegetation must be discernable from other "natural" variation in characteristics of plant communities. Seed production of oaks, for example, varies to some extent among individuals and to a large extent with abiotic conditions such as rainfall, disturbance, and light levels. Teasing apart the effects of deer and other natural forces on plant recruitment requires some baseline data on natural variation in plant communities of the island. Third, the relative impact of deer on plant communities may depend on abiotic conditions. For example, water stress due to a particularly dry year may enhance the probability of plant mortality due to buck "rubs" or herbivory by deer. The relative impacts of abiotic and biotic forces on natural communities varies over time and are essential to understanding the extent to which deer may affect ecological integrity.

Site Reconnaissance and Plot Selection and Establishment

Prior to the establishment of this experiment, temporary belt plots ("transects") 2 m x 50 m were used to sample and describe the forests of the three islands of the Smith Island Complex: Bald Head Island (BHI), Middle Island, and Bluff Island. This sampling scheme was used, along with intensive visual assessments, to better understand the variation in forest structure (physical and biological). It must be emphasized that the subsequent plot experiment was designed primarily to sample deer effects in the "regeneration phases" of the maritime forest and not be completely representative of the variation in forest structure. Therefore, most of the plots did not include mature (>30 cm DBH) live oak trees (*Q. virginiana*) for three reasons, although most plots were located within 10 m of mature live oaks. First, the plot number would have had to be doubled at minimum in order to sample variation in the most mature-phase patches of forest. Second, recruitment of trees even without predation of seeds and seedlings is very rare under trees of the stature of mature adult live oaks. Third, deer are physically unable to browse most of the vegetation in mature-phase patches (canopy >5 m and usually >10 m in height). Therefore, plots were located where deer might possibly have an effect on both extant vegetation and recruitment of new individuals. A forthcoming analysis of composition and structure will compare data from the transects and plots with the results of Bourdeau and Oosting (1959).

In order to discern natural variation in vegetation from that which may be due to deer, an exclosure experiment was established in late May and early June of 2007. Vegetation changes over time are dependent on extant characteristics of the vegetation, including species presence, population size, and percent cover, plus abiotic characteristics. The previous system of exclosures on the island is insufficient to address the research question due to limited size, location, and replication; most of the previously exclosed forest areas are subject to edge effects of the fence, are located close to roads (representing edge habitat only), and are limited in number. More importantly the scale of forest dynamics is larger than 9 m^2. Twenty exclosures 12 m x 12 m in dimension were established and paired with open, control plots 10 m x 10 m in forested vegetation. The size of the exclosure removes edge effects from the included 10 m x 10 m area to be censused. Exclosures were constructed of heavy-duty plastic deer fencing, anchored to 3 posts per side (includes corner posts) using plastic ties, and anchored to the ground with ground anchors every 2 m and small openings large enough for access by squirrels and other mammals. The location of each exclosure was recorded with GPS (Figure 1, Appendix 1). Sites for paired plots were chosen to represent variation in the species composition and physical structure of the regeneration phases of the forest, as well as the environmental gradients from southwest to northeast (a gradient direction that includes younger to older dunes and generally increasing moisture availability and decreasing salt spray, respectively). A similar gradient is presumably present from east to west, as the island is bounded by salt water to both the south and east.

Question 1: Deer effects on vegetation structure and composition

Within each plot, all species were identified and measured with respect to percent cover, plus diameter at breast height (DBH) for trees. Vines and lianas were censused by stems ascending into the canopy at 1.3 m above the forest floor, regardless of connectedness among stems. Woody plants were classified and counted as seedlings if

their stems were <130 cm tall. Exceptions included *Prunus caroliniana*, with seedlings < 25 cm not counted due to the carpets of seedlings that appear after seed fall and 90+% of which typically vanish within a year. *Ilex vomitoria* seedlings < 50 cm were not counted due to numbers so high (500-1500 per plot) as to be prohibitively costly (in time) to count accurately. Therefore seedlings counts for these two species are a reflection of recruitment to larger size classes than the remaining species. Additionally, presence/absence of deer browsing was noted. Soil characteristics including % organic matter, N, P, K and micronutrient concentrations will be measured at the beginning of the growing season of 2008.

If deer significantly affect plant communities of the island, then the following results should be expected. Browsing of deer should be disproportionately higher on species known to be preferred by deer. Browsing effects on herbaceous species should have a disproportionately higher effect on total biomass and reproduction of herbaceous, versus woody, species, however, deer should browse more frequently on woody plant species. Relative abundances of plant species should be skewed towards unpalatable plants in control plots compared to exclosures (Anderson & Loucks 1979, Anderson & Katz 1993), resulting in significant compositional and structural differences (below 3 m height) between the control and exclosed plot within five years. Control plots should exhibit lower diversity than exclosures, unless deer are not selective in species browsed. Under the latter scenario, deer will enhance diversity compared to exclosures, by selecting the most abundant species, keeping any one species from dominating the plot.

Data Analyses

It was important to establish that exclosures and control plots were not initially significantly different in biotic and abiotic characteristics, so that any differences that would be detected (if present and detectable) could be attributed to exclusion of deer *per se*, rather than chance similarities of plots chosen for one of the two treatments. For this reason, nonmetric multidimensional scaling was used to ordinate plots for visual inspection of relationships among plots and between treatments. Canonical correspondence analysis (CCA) will be used to further investigate the multivariate relationship between the abiotic variables and compositional relationships among plots and exclosures; however CCA was not applied for the limited variables measured in 2007. Non-parametric multivariate analysis of variance using a permutation procedure (Anderson 2001) was conducted to determine if the two treatments differed in their compositions of trees and seedlings. The same procedure, as well as the Mantel test (Mantel 1967, Sokal 1979), was used to test for differences among plots in composition. Dissimilarity measures such as the complement of Jaccard's index (Jaccard 1908) for presence/absence of species and chord Euclidean distance (Pielou 1984) for distances among plots in relative abundance of species were used. Both approaches have the advantage of not requiring the distributional assumptions of parametric tests, and the Mantel test was specifically developed for non-independent data.

Question 2a: Deer effects on tree recruitment: seed predation

Recruitment limitations for plants are those factors that constrain transitions from the early life history stages. Major limitations for plant recruitment at the local scale are (1) seed availability – determined in large part by predation upon seeds by

herbivores and by dispersal, (2) seedling survival – determined generally by herbivory and/or fungal pathogens, and/or competition from neighboring vegetation, and (3) habitat availability, determined largely by abiotic conditions and disturbance. Regeneration of oak forests, as in all plant communities, is constrained by some degree of recruitment limitation. The relative strengths of constraints imposed by herbivory, dispersal and microhabitat on oak recruitment vary in time and space.

Oak recruitment, especially the younger stage transitions from seed to seedling, and seedling to sapling was singled out for examination due to the strong physical effects that these trees have on barrier islands. This portion of the project focused on *Q. virginiana* P. Mill. and *Q. hemisphaerica* Bartr. ex Willd., key tree species in maritime forests of the southeastern Atlantic Coast. These species are also responsible for generating the principal source of food (acorns and the insects that infest them) for many mammals and some birds during the fall and early winter, when alternative food sources are scarce.

Removal of acorns placed in open and exclosure plots was recorded approximately every two days in order to estimate the relative impacts of types of small and large herbivores on seed survival. Holes at the bases of the exclosed plots to allowed access by small mammals, but excluded deer. Therefore, the difference in the proportions of seeds remaining intact in the exclosed versus open plots is a measure of deer effects on seed survival, assuming exclosures do not hinder access by small mammals. Direct and indirect observations in the plots confirmed that small mammals readily gain access to exclosed plots.

For each oak species, 20 randomly selected acorns were placed in separate grids, with spacing of approximately 10 cm, in the existing exclosures and open plots in densities high enough (20 seeds/species/plot, or 800 seeds/species total) such that intra-plot variation in seed fates could be assessed against inter-plot variation in seed fate. The proportion of the experimental acorns that were removed and dispersed was estimated by tracking fates of marked acorns. We used a method of attaching threads with uniquely coded tags of plastic flagging to the acorns in order to find them upon removal and to distinguish them from natural acorn fall (modified from Brewer & Rejmánek 1999, Brewer & Webb 2001). Insect infestation of acorns was determined by examining acorns with a float test in water. Distances to moved seeds were also measured. Post-dispersal insect infestation was examined at the end of the experiment. Experiments will be repeated annually to assess temporal effects, and possibly fluctuations in deer density, on early recruitment of oaks.

If deer significantly constrain oak recruitment, then exclusion of deer should result in significantly greater seed and seedling survival compared to non-exclosed areas. Furthermore, greater seed survival in the absence of seed should result in a higher amount, but not necessarily higher proportion, of seeds being dispersed by small rodents to “safe sites” for recruitment. Safe sites enhance recruitment to adults because they have more amenable abiotic and biotic conditions for survival, including greater resource availability and/or lower pathogen load, respectively. Seed dispersal also

enhances seedling survival by reducing seedling density and thus the density-dependent forces acting on seedlings, principally competition and disease.

Data Analyses

Removal rates of acorns, as affected by treatment (open control or exclosure), species, and site, were analyzed using survival analysis with Cox regression (Muenchow 1986, Le 1997). This type of analysis has the advantages of accommodating right censored data (*e.g.*, acorns still in exclosures at the end of the study but having unknown total survival times) and/or other data (acorn survival times) that are not normally distributed (*e.g.* Muenchow 1986, Le 1997). Cox regression uses the proportional hazards model for analysis of time until removal of acorns. Predictor variables (covariates) were species of oak and treatment (exclosure, control). The analyses were stratified by site as a technique for separating variation associated with location. Covariates were entered both at once rather than using the stepwise procedure. Interactions between covariates were tested and removed from the final model when statistically insignificant. The effect of treatment and species on likelihood of burial of an acorn was tested using three collapsed fate categories – buried, eaten, and remaining on the surface/intact – in multinomial logistic regression.

Question 2b: Deer effects on tree recruitment: "buck rubs"

For those trees that escape seed and seedling predation, some will be rubbed by male deer (bucks) before the fall rut. Buck rubs typically occur down to non-functioning wood, resulting in the destruction of active xylem and phloem and associated transport processes, as well as the loss of the protective function of bark. Even very old (>1-2 yrs.) buck rubs retain their distinctive markings and are readily identified. In order to establish the significance of buck rubs at the population and inter-specific level of trees, we censused c. 4500 trees located in five 2 m x 150 m transects bisecting the center of the forest reserve plus 38 10 m x 10 m plots scattered throughout the reserve. Trees were identified to species and measured with respect to area and depth of buck rubs (if present), DBH, and diameter at the wound.

Data Analyses

Buck Rub Census and Data Analysis

The buck rub censuses were conducted in November/December 2007 after the male deer had finished dropping their "velvet". Even old (>1-2 yrs.) and shallow buck rubs retain their distinctive markings and were readily identified in the BHIFR. In order to establish the significance of buck rubs at the population and inter-specific level of trees, we censused 4498 trees located in five 2 m x 150 m transects bisecting the center of the forest reserve plus 38 10 m x 10 m permanent plots scattered haphazardly throughout the reserve. All trees with a diameter at breast height (DBH, H= 130 cm) were identified to species and measured with respect to DBH, plus stem diameter at the wound, and area and depth of buck rubs if present. Trees with wounds of uncertain origin (<0.1% of all trees with wounds) were excluded from the analyses.

We used binomial logistic regression (SPSS Inc., 2004) to identify the explanatory categorical variables that were most closely associated with the presence/absence of buck rubs. Species and size class (<1 cm, 1-2.5 cm, 2.5-5 cm, 5-10

cm, 10-20 cm, 20-40 cm, <40 cm DBH classes) were the main factors, both of which were treated as categorical covariates and entered all at once in the regression model in SPSS (SPSS Inc., 2004). The explanatory variables were dummy coded with *Ilex vomitoria* and DBH class 2 (1-2.5 cm) as reference values for tree species and tree size, respectively, as these categories provided the most easily interpreted references and had the maximum numbers of observations. Only significant main factors were included in the final model; as an exploratory procedure, an interaction term between the main variables was initially included, then removed from the final model as it was statistically insignificant ($P > 0.1$) and contributed little (<2% increase) to the area under the Receiver Operating Characteristic curve. The smallest one and largest three DBH categories were eliminated from the dataset during regression analysis of tree species selection, because these size classes accounted for <7% of all rubbed trees and were heavily biased to one species in representation. Elimination of these trees did not alter the conclusions but did increase the power to detect species selection for those size classes of trees that were rubbed.

Figure 1. Satellite views of the Bald Head Woods forest reserve. Points correspond to site locations (see Appendix 1).

RESULTS & DISCUSSION

PHYSICAL STRUCTURE

Few quantitative data exist for undisturbed maritime forests, of which the BHIFR is one of the northernmost representatives of the southern variant (*Sabal palmetto* variant) of "Maritime Evergreen Forest" (Bellis & Keough 1995). However, general size class distribution is fairly typical of forests in general, in that small stems (< 5 cm DBH) comprise >60% of the total stems (Figures 2, 3). Large trees comprise most (> 50%) of the total biomass (as basal area) in the forest but the fewest number of stems because of a space limitation inherent in the stem size-number tradeoff for trees with continuous lateral growth.

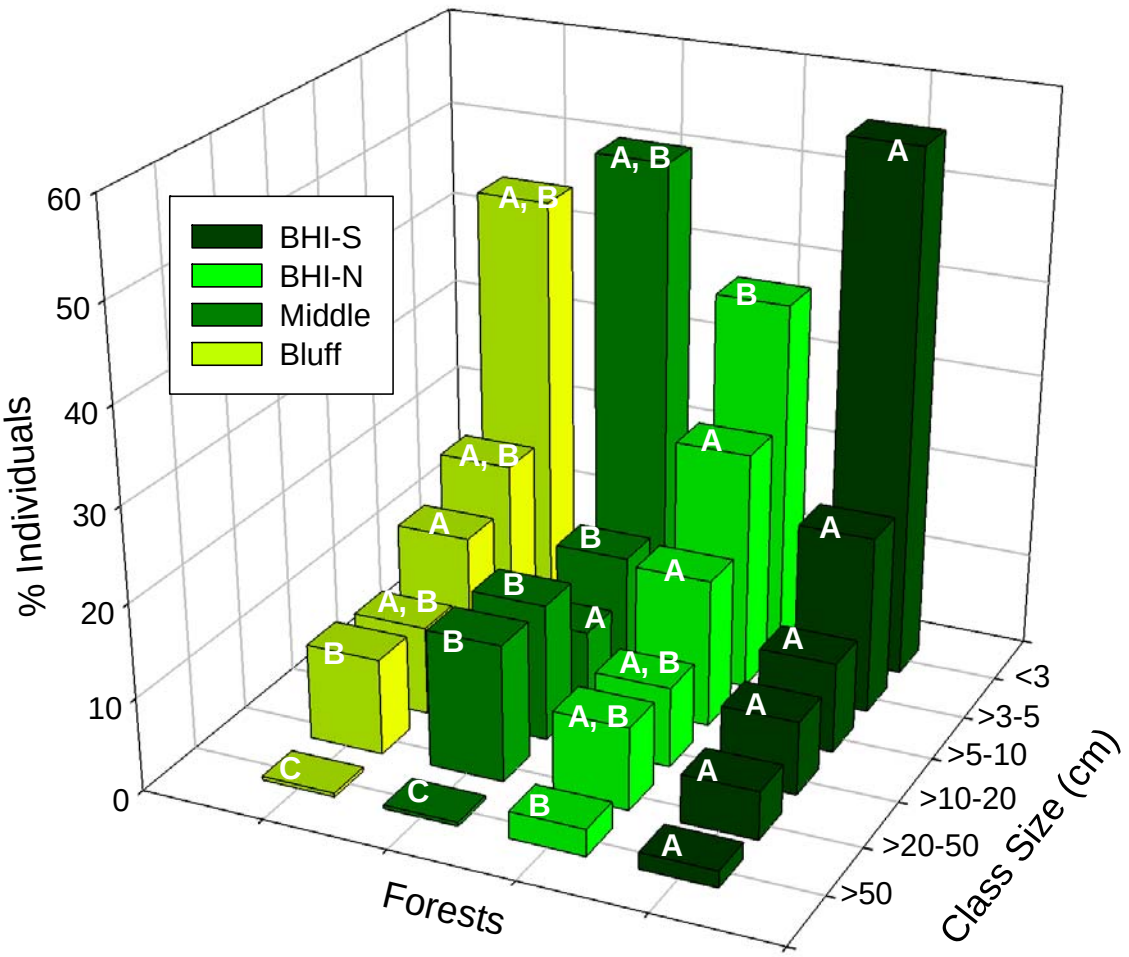

Figure 2. Size class distribution for trees in 2 m wide x 50 m transects distributed in a stratified random fashion among the three island forests. BHI-S and BHI-N refer to south and north side of federal road, respectively.

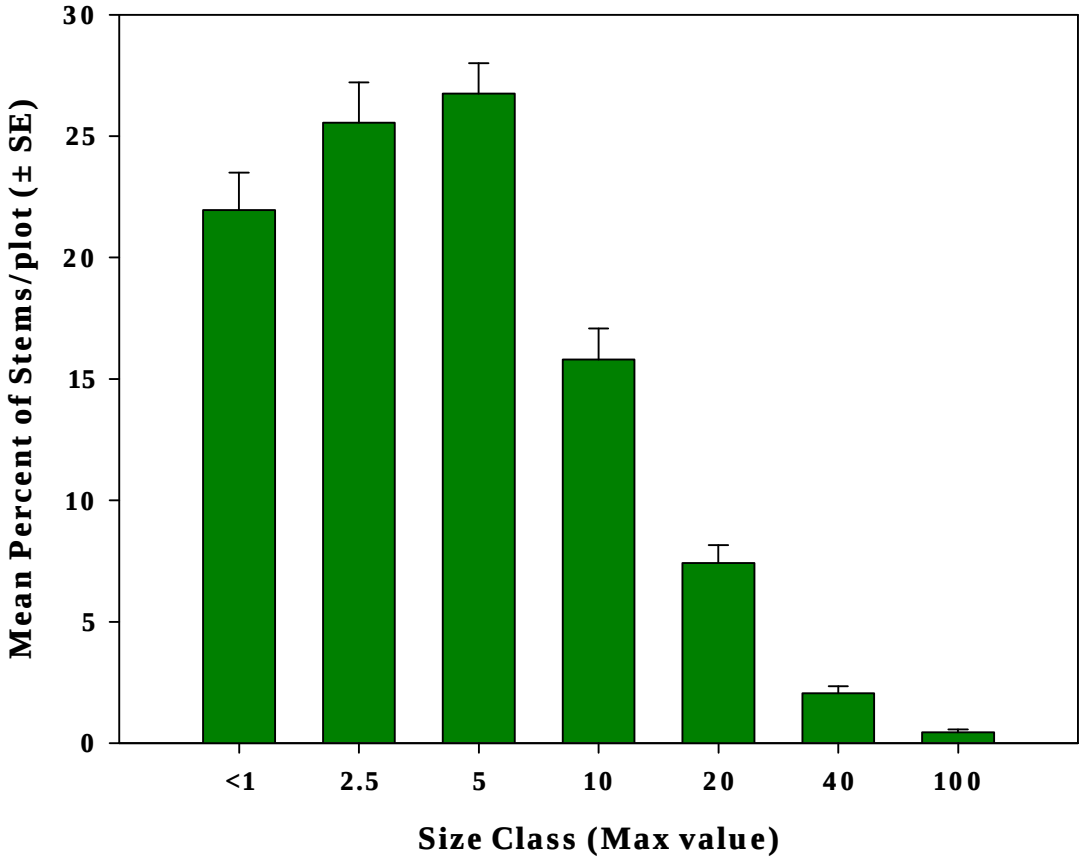

Figure 3. Size class distribution for trees in the 40 plots in the BHI Forest Reserve, by mean percent of stems per plot. Size class ranges are indicated by maximum value.

The BHIFR forest appears to be atypical in other structural characteristics of what might be expected for anthropogenically "undisturbed" maritime forests. Openings or large gaps dominate the mature-phase canopy (Figure 4). Maritime forests of large as well as small stature typically have been described in the past (*e.g.*, Oosting 1954, Bourdeau and Oosting 1959) as having rather continuous and tight canopies, with few openings. Unfortunately degrees of openness of maritime forest canopies have not previously been published. Fortunately hemispherical photography (see figure 4) provides an accurate measure of understory light conditions; actual photosynthetic photon flux densities and canopy openness are strongly related (Becker *et al.* 1989, Rich *et al.* 1993).

Light transmission to the forest floor is directly affected by stand density, leaf-area index, tree spacing, crown closure, and basal area (Reifsnyder & Lull 1965). Canopy openness in this study averaged 17.6% (SD = 4.4%, n = 40), which is considerably higher than reported values from other forests in North America, which range typically around 2%-3%, to 6% in unusual cases (Horn 1971, 2.9% in a New Jersey Piedmont forest; March and Skeen 1976, 3% in a Georgia hardwood pine forest; Hutchison and Matt 1977, 2.2% in 50-yr-old yellow-poplar stands in Tennessee; Floyd *et al.* 1978, 2% in a mixed-oak forest during several phenological stages; Baldocchi *et al.* 1984, 1986, <3% in

an uneven-aged oak-hickory stand in Tennessee; Lorimer et al. 1994, 1% in closed-canopy oak forests of southwestern Wisconsin). Plots may not accurately represent average canopy openness for the forest, therefore further light sampling will take place in summer of 2008: n = 40 is a fairly low sample size for a forest of this size, and plots were rarely located under mature live oaks.

Figure 4. Hemispherical photographs of the forest canopy: from top to bottom a relatively small canopy opening and a relatively closed canopy for the BHIFR.

Nevertheless, through this small sample and visual assessment of the forest, it is immediately apparent to the experienced eye that the BHIFR has a high proportion of "broken canopy", with a large proportion of the forest experiencing unusually high light levels and dense understory/sub-canopy layers. Lopazanski *et al.* (1988, p. 92) made the same observation nearly 20 years ago. They attributed the physical structure of the BHIFR area to hurricanes and blow downs. However, Lopazanski *et al.* (1988) apparently failed to consider how resistant maritime forests are to hurricane impacts (Conner 1998). Dominant tree taxa such as *Q. virginiana* and *S. palmetto* are quite resistant to and resilient from the effects of hurricanes and their associated stresses of increased salt-spray inputs (Conner *et al.* 2005). Furthermore, despite observing clear evidence of logging from the 1920's, Bourdeau and Oosting (1959) pointed out the near-continuous nature of the forest canopy on BHI, although they observed some openings in the canopy as well. Their study was actually conducted one year before the most significant hurricanes of the century for the Cape Fear area (Cat. 4 Hazel, 15 November 1954; Cat. 3 Helene 27 September 1958). These hurricanes are comparable to the Category 4 Hugo (21 September 1989), which had relatively low impact on live oaks (Smith *et al.* 1997). In fact, Smith *et al.* (1997) found that the proportion of total basal area represented by live oak increased over an order of magnitude following Hurricane Hugo. In a preliminary analysis (data analyses are ongoing), live oak representation in the BHIFR has actually decreased – although is still a dominant component – since Bourdeau and Oosting's fieldwork in 1953.

Two hypotheses for the sparse canopy on BHI are (1) hurricanes and storms have opened up the canopy more so than would be found in comparable mature-phase maritime forest (as suggested by Lopazanski *et al.* 1988), or (2) logging effects combined with effects of salt-spray and/or major storms and hurricanes have either perpetuated the openings cause by logging or have interacted with openings caused by logging to increase the proportion of the canopy that is open. My professional opinion supports the latter hypothesis, based on Bourdeau and Oosting's pre-hurricane observations of a nearly continuous canopy except for some openings. Certainly these ecologists with vast experience in coastal ecosystems would have remarked about the broken nature of the canopy were it similar in openness as it is now. Moreover, Bourdeau and Oosting (1959) found dense populations of live oak seedlings (stems <2.5 cm DBH) on BHI under canopy openings which should have recruited into the understory and/or subcanopy by 1988 following Hurricane Hazel. There has been a general recruitment failure by live oaks, however, as noted below. Apparently these canopy openings have not been filled by longer-lived and/or larger statured tree species such as live oak, although populations of laurel oak and red cedar (*Q. hemisphaerica, J. virginiana*, respectively) appear to have benefited from the disturbed canopy, as both of these species are to some extent disturbance dependent in recruitment and respond rapidly to increased light availability. Were the BHIFR forest of much higher diversity and functional redundancy, other larger taxa would replace live oaks to fill in the canopy disturbance. The extreme abiotic conditions of barrier islands, however, filter out most of the potential colonizing species from the nearby mainland forests.

Species Composition

For woody plants, only eleven arborescent species and six vine or liana species were found in the plots (Table 1, Figure 5). Herbaceous cover was generally very low (<2 %) and represented by only six species (data forthcoming). Very low diversity of all species in the BHIFR equates to very low functional redundancy (if any). This means is one species is removed from the forest, few if any species will be able to the roles of lost species. As systems become more species diverse, types of functional roles and functional redundancy increase, leading to greater ecological stability of the system.

As is common in plant communities, the BHIFR is dominated by an oligarchy of species. *Ilex vomitoria* dominates the understory with over half of small stems (<5 cm DBH, <5 m tall). *Prunus caroliniana* dominates the middle story and subcanopy with over half of all stems 5 cm – 10 cm DBH, while *Q. hemisphaerica*, *Q. virginiana*, and *J. virginiana* dominate the larger size classes. In terms of biomass, as represented by basal area, *Q. virginiana* and *P. caroliniana* take up nearly 80% of the woody biomass in the forest (data from transects). The lack of herbaceous cover is normal for maritime forests, where poor, dry soils, low light, and salt spray are too extreme for the survival of most of the regional herbaceous species pool.

Species composition of trees, lianas, and seedlings were not significantly different between exclosures and control plots (Table 2, Figures 6-9), regardless of method (perMANOVA or Multi-Response Permutation Procedure) or distance measure used. Analyses shown in Table 2 were performed using relative abundance of species as a measure of differences among plots. The first two growth forms were not expected to be different between treatment types, as most individuals are too large to be removed by deer. By chance, some species represented by seedlings were rare and present either only in exclosures or control plots (Figure 8). No actual seedlings of *Q. virginiana* were observed, however stump, root, and underground-stem sprouts ("suckers") of seedling size were recorded for the seedling size class. These sprouts are capable of becoming separate stems if the parent tree dies or if separated from the parent. How much these stems contribute to recruitment is unknown.

The lack of difference between control and exclosure plots was attributed to the spring and summer drought, the recent implementation of the exclosures, both of which suppressed normal recruitment and survival of new seedlings in the understory and ground layer. Effects of exclosures on seedling survival may not be visible for one or two more years, after the deer population has rebounded and enough seedlings recruit into the ground layer of the forest.

Finally, observations indicate certain taxa seem likely to suffer proportionate damage by deer browsing. Clearly favored are *Smilax bona-nox*, *P. caroliniana* (especially stump sprouts and "root suckers", both of which are vegetative means of reproduction), to a lesser extent new growth of *I. vomitoria* and *S. palmetto*. However, based on preliminary analyses (results not shown) *P. caroliniana* appears to be increasing in proportional basal area in the BHFR. *Sabal palmetto* is showing very strong recruitment – possibly due to a greatly expanded regeneration niche due to canopy disturbance – and appears poised to become a canopy co-dominant species within c.

150-250 years. Red bay (*Persea borbonia*, incl. *Persea palustris* here), has a high density of stems in the seedling class that are being growth-suppressed by the red bay ambrosia beetle, *Xyleborus glabratus* Eichhoff. This beetle was first detected in the U.S. in 2002 (Rabaglia 2005) and is causing extensive damage to *P. borbonia* in the BHIFR. The effects on population dynamics of *P. borbonia* in the BHIFR are unknown, but are likely to reduce the abundance of this dominant understory tree.

TABLE 1. Total abundance of woody species by N stems/ size class and by total basal area ("BA", cm^2), a proxy for biomass for the 40 10 m x 10 m plots. *Sabal* was not represented in the plots in tree form, therefore abundance of non-"seedlings" are represented (seedlings were classified as having only unlobed leaves) under "Trees".

	<5	5-10	10-20	>20	N	%	BA	%
Trees								
Ilex vomitoria	1869	137	4	0	2010	56.8	11800	9.6
Prunus caroliniana	238	178	129	23	568	16.0	40506	32.8
Carpinus caroliniana	36	47	11	1	95	2.7	5876	4.8
Quercus hemisphaerica	23	28	13	24	88	2.5	21969	17.8
Persea borbonia	67	14	11	4	96	2.7	5338	4.3
Osmanthus americanus	9	13	13	3	38	1.1	3960	3.2
Juniperus virginiana	15	4	3	10	32	0.9	7576	6.1
Ilex opaca	5	2	6	2	15	0.4	2016	1.6
Cornus florida	3	4	3	0	10	0.3	73	0.1
Quercus virginiana	0	0	1	8	9	0.3	24337	19.7
Sabal palmetto	NA	NA	NA	NA	580		NA	
Total	2265	427	194	75	3541		123451	
Vines & Lianas								
Vitis rotundifolia	156	5	0	0	161	47.2	771	40.0
Toxicodendron radicans	136	2	0	0	138	40.5	413	21.4
Smilax bona-nox	17	0	0	0	17	5.0	175	9.1
Parthenocissus quinquefolia	13	1	0	0	14	4.1	535	27.8
Berchemeria scandens	8	0	0	0	8	2.3	27	1.4
Gelsemium sempervirens	3	0	0	0	3	0.9	5	0.3
Total	2598	435	195	83	341		1926	

Seedlings (N only)			
Persea borbonia	4197	*Vitis rotundifolia*	17
Ilex vomitoria	3112	*Gelsemium sempervirens*	11
Sabal palmetto	924	*Callicarpa americana*	8
Prunus caroliniana	645	*Berchemeria scandens*	4
Smilax bona-nox	174	*Juniperus virginiana*	4
**Quercus virginiana*	156	*Osmanthus americanus*	2
Quercus hemisphaerica	20	*Parthenocissus quinquefolia*	1
Toxicodendron radicans	45		
Total			9620

**Quercus virginiana* stump sprouts and root suckers were not true seedlings, but were placed in the seedling size class.

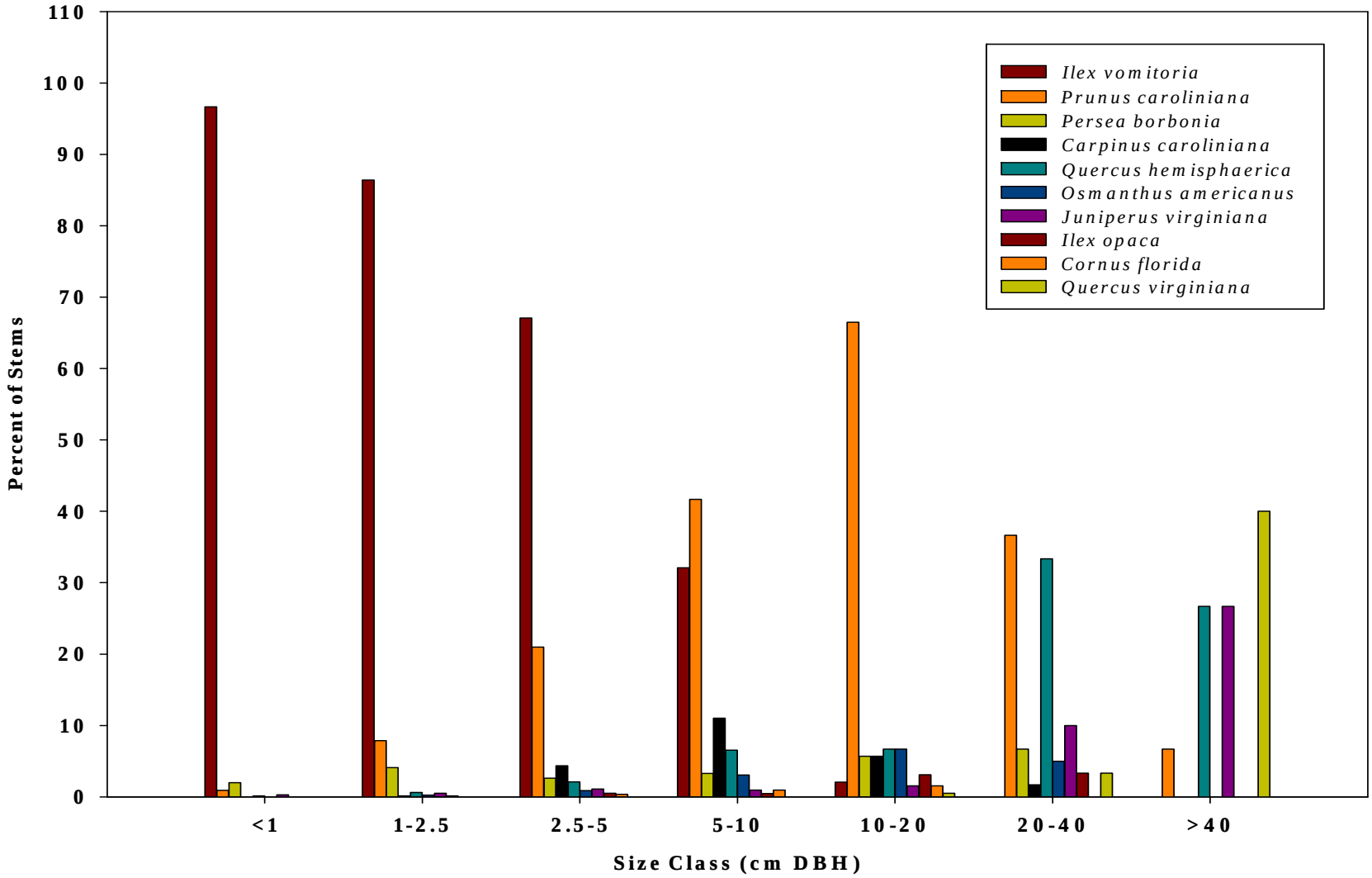

Figure 5. Size class distribution by tree species, ordered from left to right, and top to bottom in the legend, by total stems across all plots. Lower limits of size classes shown are minimum sizes included.

TABLE 2. Permutation MANOVA (multivariate analysis of variance) testing the null hypotheses of so difference between treatments (exclosure, control) or among sites in species composition of seedlings and trees.

SEEDLINGS	d.f.	SS	MS	F	p
Site	19	3.4268	0.18036	1.5698	0.013400
Treatment	1	0.15786	0.15786	1.3740	0.213800
Residual	19	2.1829	0.11489		
Total	39	5.7676			

TREES	d.f.	SS	MS	F	p
Site	19	2.8846	0.15182	1.0756	0.316800
Treatment	1	0.10596	0.10596	0.75069	0.664400
Residual	19	2.6818	0.14115		
Total	39	5.6724			

Ordination showed little clustering of groups of woody species (Figure 10). Lianas tended to be randomly dispersed in ordination space, suggesting no positive associations between lianas and any particular tree species. These results might be expected given that lianas are most responsive to light. Therefore access to light rather than a particular species of "host" tree likely drives the distribution of lianas, which constitute a growth form adapted to competition for light. *Prunus caroliniana, S. palmetto, P. borbonia,* and *I. vomitoria,* and to some extent *Q. virginiana,* appear to be positively associated in Figure 10. *Gelsemium sempervirens* and *Toxicodendron radicans* are lianas and vines that appear to be positively associated, perhaps due to shared light requirements or dispersal vectors.

Mantel tests tended to show significant positive associations of tree and seedling *composition* within plots based on species presence and absence (Table 3). No significant associations of tree and seedlings within plots based on *relative abundance* of species resulted from the Mantel tests. Species compositions of the seedling and canopy layers are essentially correlated, but abundance of species in the canopy layers does not determine the abundance of seedlings of species in the seedling layer. These phenomena are fairly common in low-diversity forests, although seedling and tree compositions are often decoupled in tropical forests (S. J. Wright, pers. comm.).

TABLE 3. Mantel tests of correlation (r) between differences among plots in tree species composition with differences among plots in seedling species. Measures of abundance used were individuals (N) and basal area (BA) for trees, and individuals for seedlings. Measures of distance included presence/absence only (using Jaccard's index) and chord Euclidean distance, which is a measure of proportional abundance of species' seedlings and trees. P values < 0.05 indicate significant correlations between the matrices. Results using the Monte Carlo approach are shown.

Comparison	Standardized Mantel r	p (type I error)
Measure = Presence/Absence		
BA Trees vs. N Seedlings	0.21	0.005
Positive association between matrices		
N Trees N Seedlings	0.15	0.038
Positive association between matrices		
Measure = Relative Abundance		
BA Trees vs. N Seedlings	0.12	0.082
Marginally positive association		
N Trees N Seedlings	0.090	0.16
No association between the matrices		

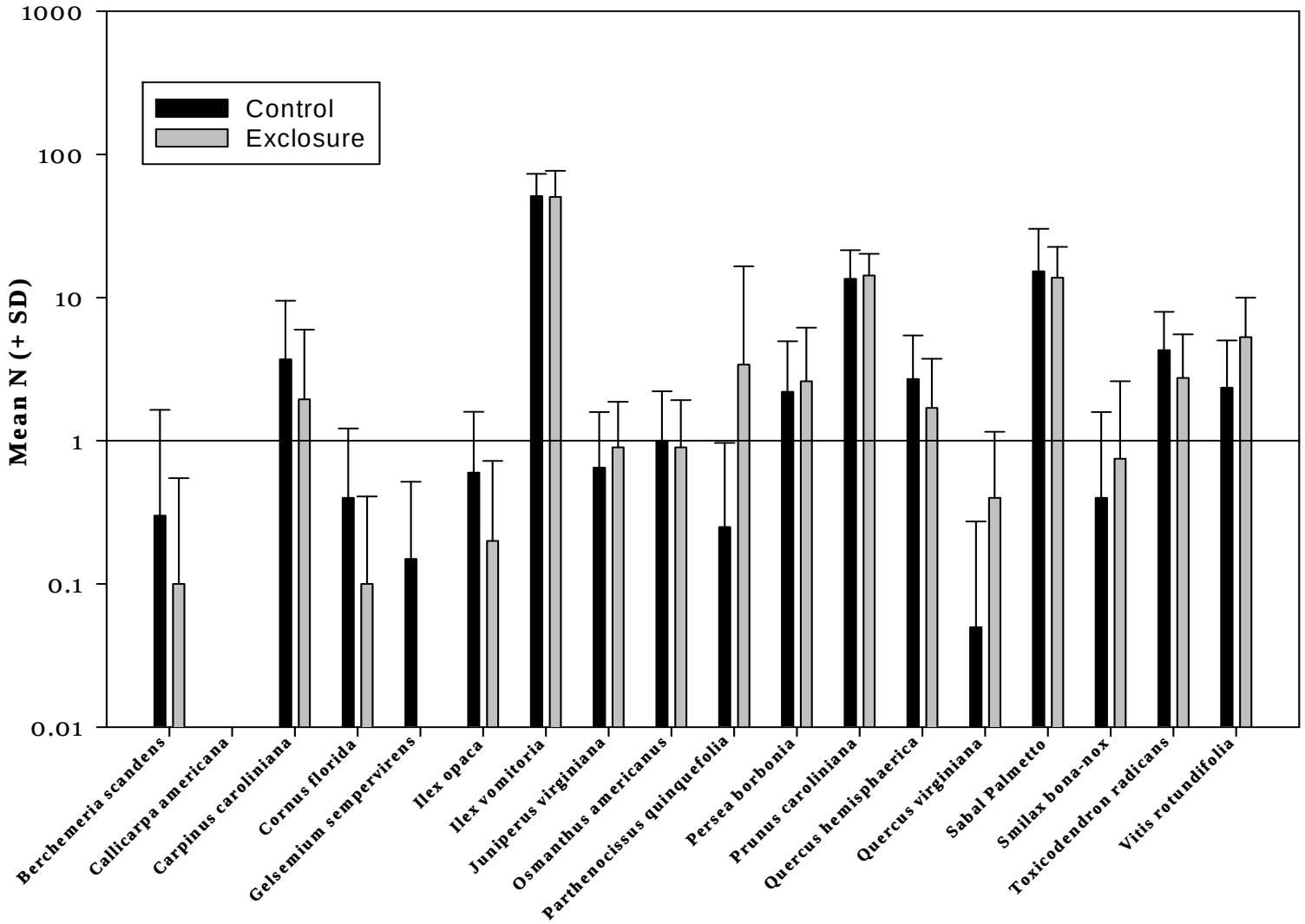

Figure 6. Log mean number of individuals (N) per species, between treatments (paired t-tests, all differences $P > 0.05$).

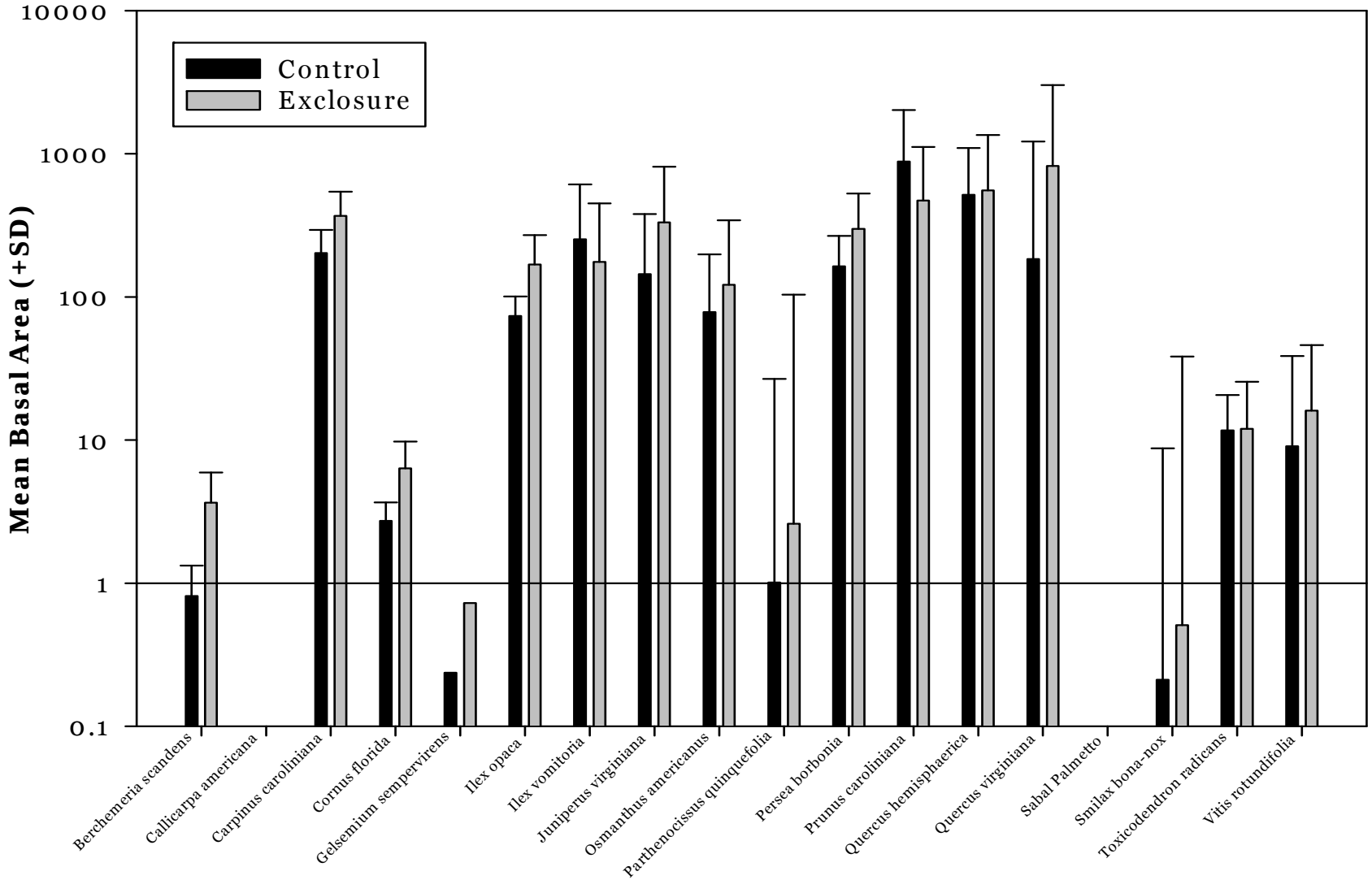

Figure 7. Log mean basal area per species, between treatments (paired t-tests, all differences $P > 0.05$).

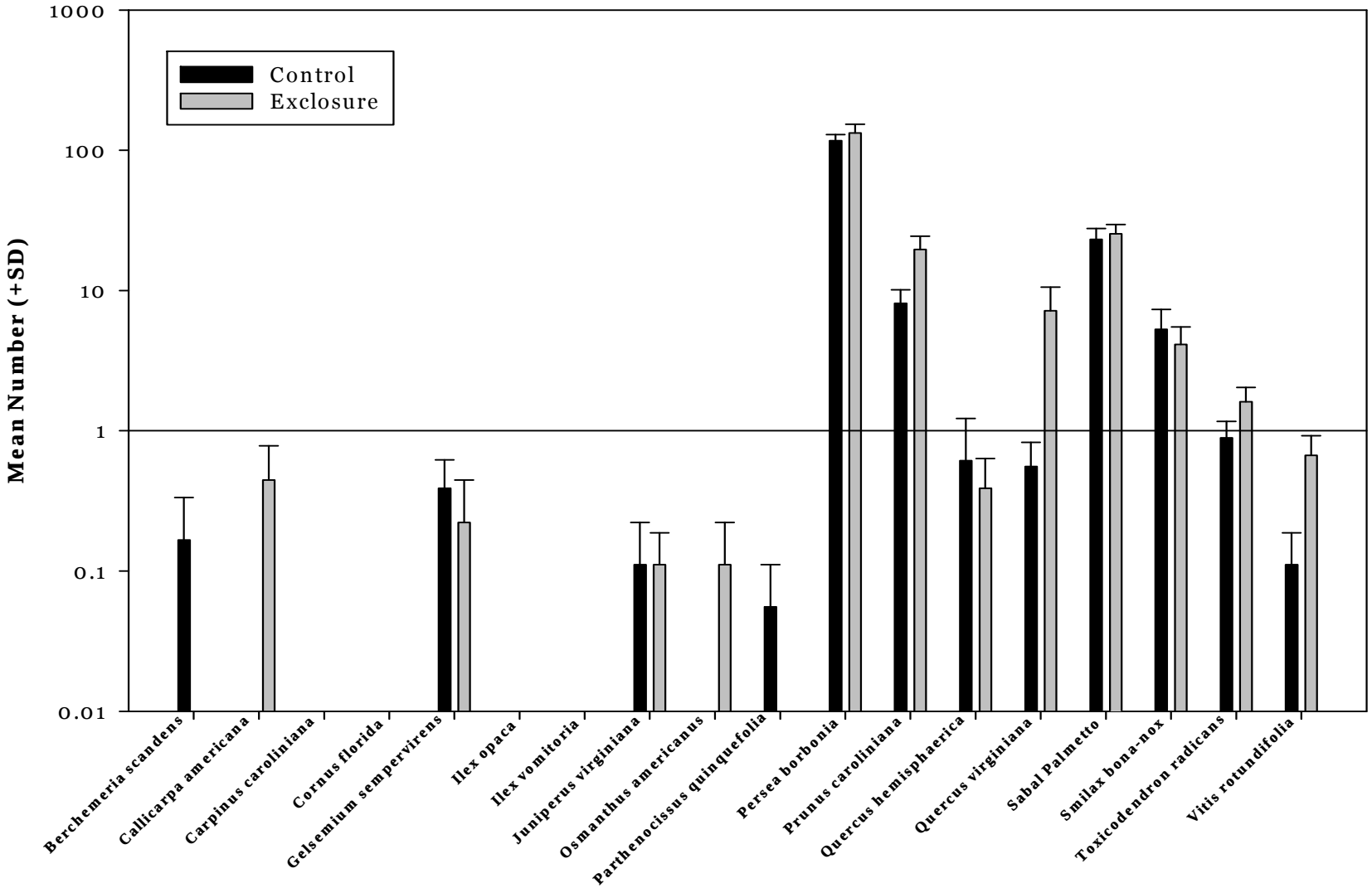

Figure 8. Log mean number of seedlings per species, between treatments (paired t-tests, all differences $P > 0.05$). *Q. virginiana* "seedlings" are seedling-sized stems adventitious on roots and underground portions of stem.

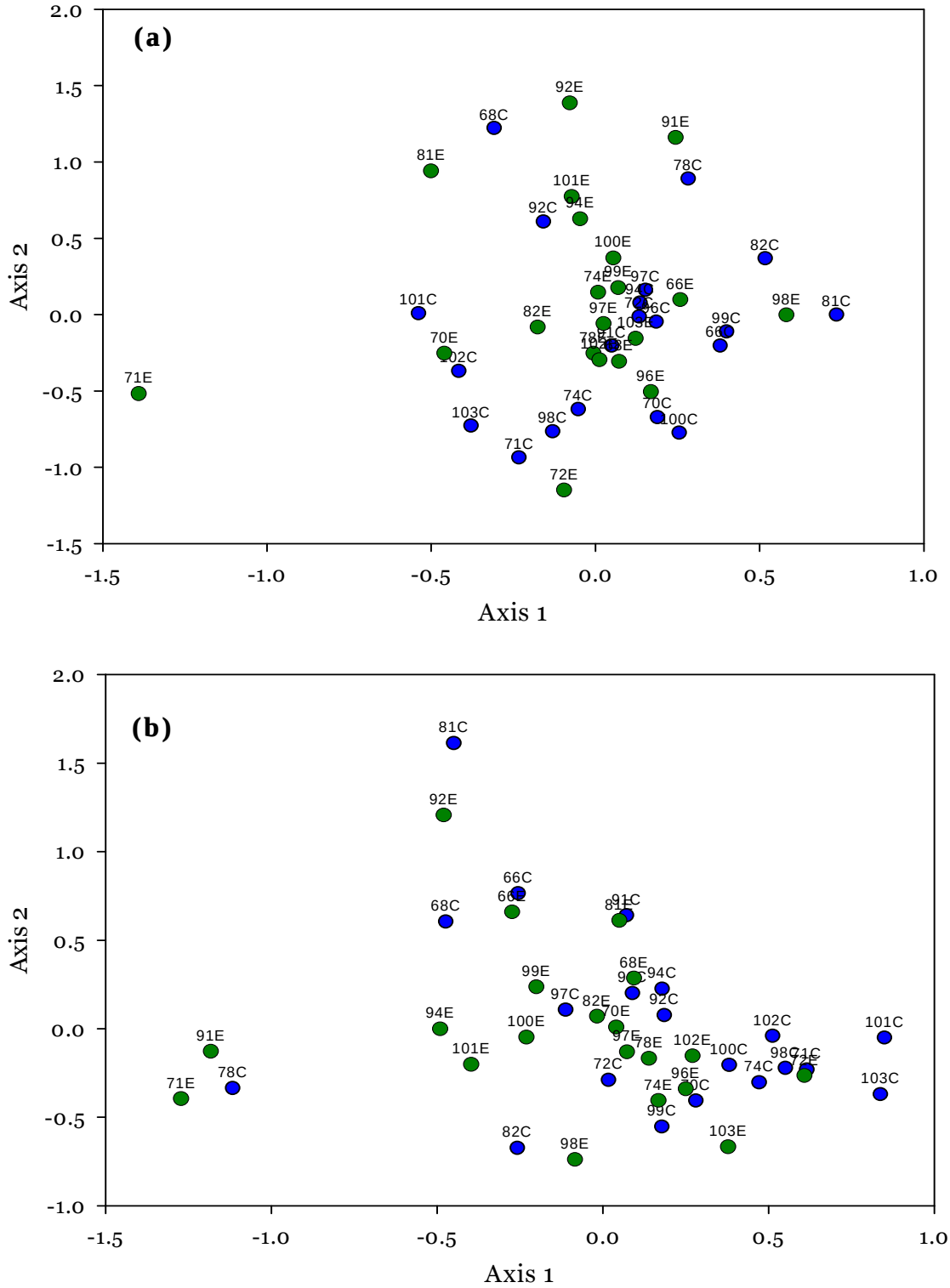

Figure 9. Non-metric multidimensional scaling of plots using tree (a) species presence/absence and (b) relative species abundances in measures of distance.

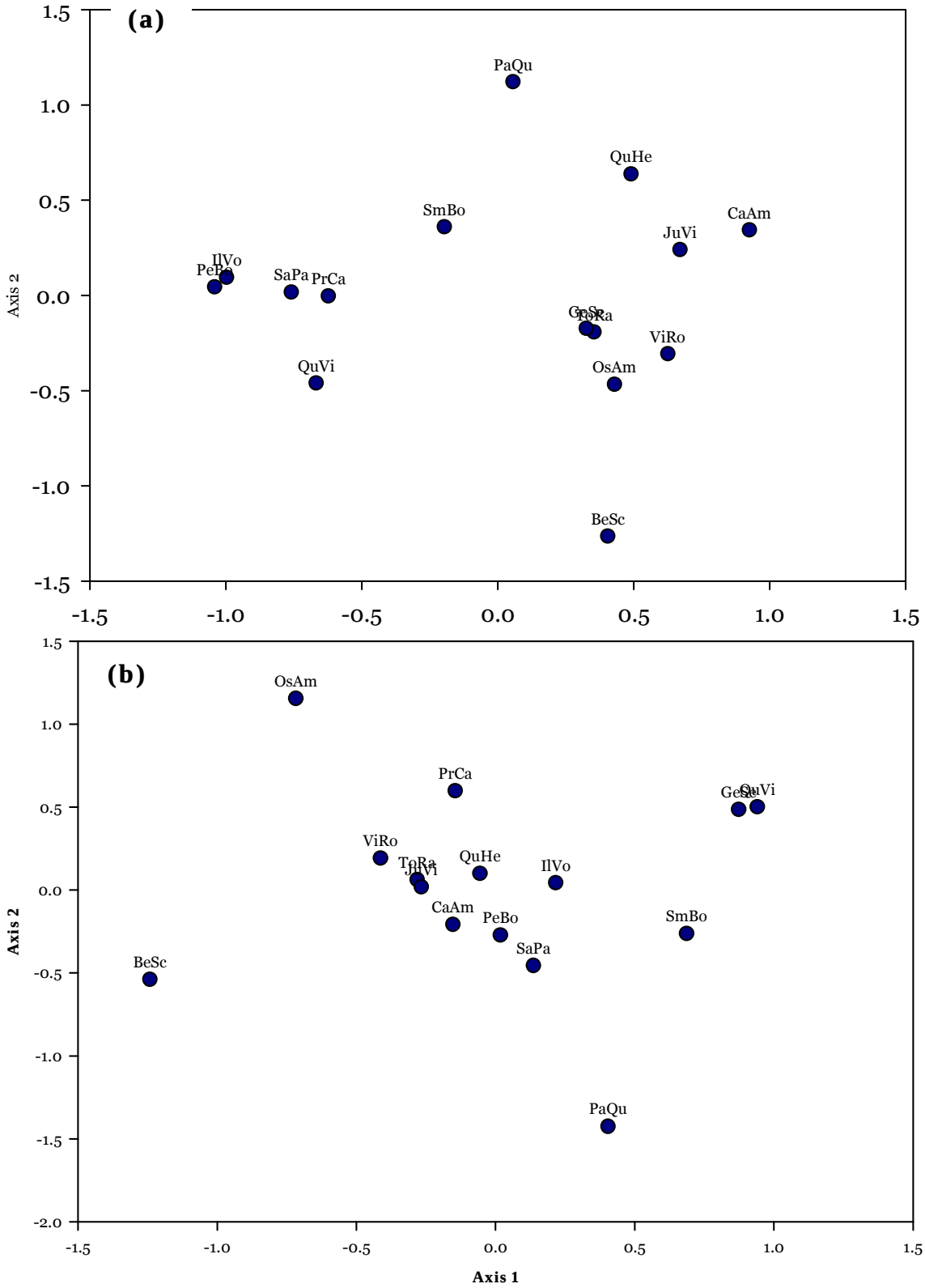

Figure 10. Non-metric multidimensional scaling of species in plot space using (a) species presence/absence and (b) relative species abundances in measures of distance. Species codes correspond to the first two letters of the genus name and specific epithet.

Acorn Removal and Fate

Oak species typically "mast", producing heavy crops of acorns once every 4-5 years, probably as a means of saturating seed predators and facilitating dispersal by burial (reviewed by Kelly & Sork 2002). Oak reproduction, however, is highly variable among individual trees in time and space even during mast years (Beck 1993). The 2007 year was a mast year for oaks in many parts of mainland Brunswick County (Brewer pers. obs.), however the BHIFR experienced low acorn production for live oaks (*Q. virginiana*). Laurel oak (*Q. hemisphaerica*), however, experienced a heavy acorn crop throughout the county including BHIFR. Laurel oak produces acorns take two years to mature, while live oak acorns develop from flower to acorn within one year, therefore the conditions between the two species for fruiting success are experienced one year apart. It is possible that the spring drought combined with the characteristic sandy and poor soils on BHI severely hampered live oak acorn production, compared to mainland Brunswick County.

Fates of experimental acorns could be determined for all but 0.75% of *Q. virginiana* acorns and 2.0% of *Q. hemisphaerica* acorns; these are exceptionally high recovery rates, due in part to the lack of long-distance dispersal and lack of burrowing or cryptic rodents. Removal rates were rapid and nearly complete for both oak species, with most acorns removed within 10 days (Figure 11). No significant difference in survival probabilities was detected between exclosure and control plots (Wald statistic = 0.32, df = 1, r = 0.00, p = 0 .5732), however *Q. virginiana* acorns were removed significantly faster than *Q. hemisphaerica* acorns (Wald = 13.8, df = 1, r = 0.03, p = 0 .0002). The interaction term between the two covariates was not significant, therefore the removal rate of a given species did not depend on treatment (Wald = 0.18, df = 1, p = 0.67).

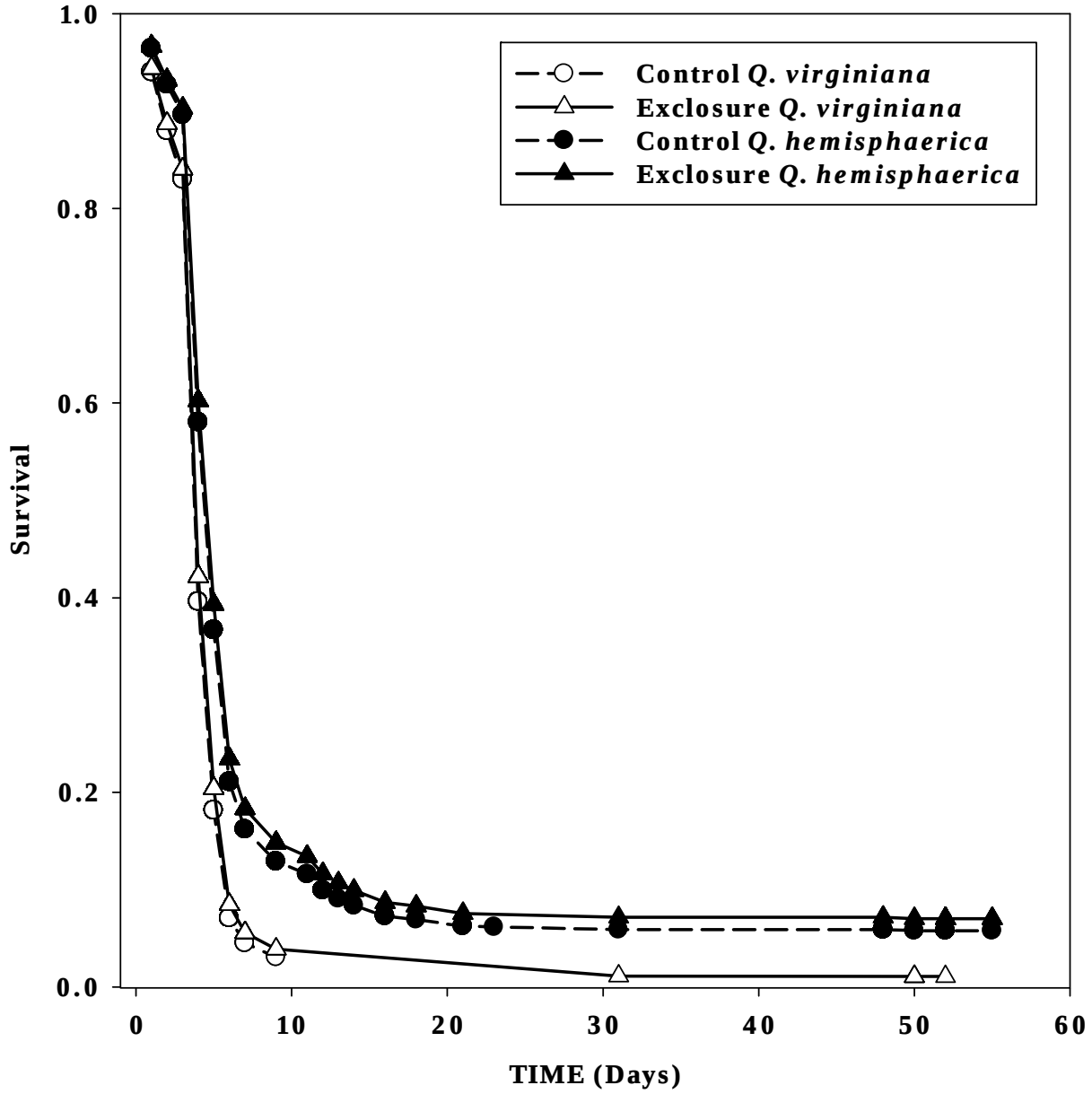

Figure 11. Survival functions for control plots (circles, dashed lines) and exclosures (triangles, solid lines): *Q. virginiana* (open symbols), *Q. hemisphaerica* (solid symbols).

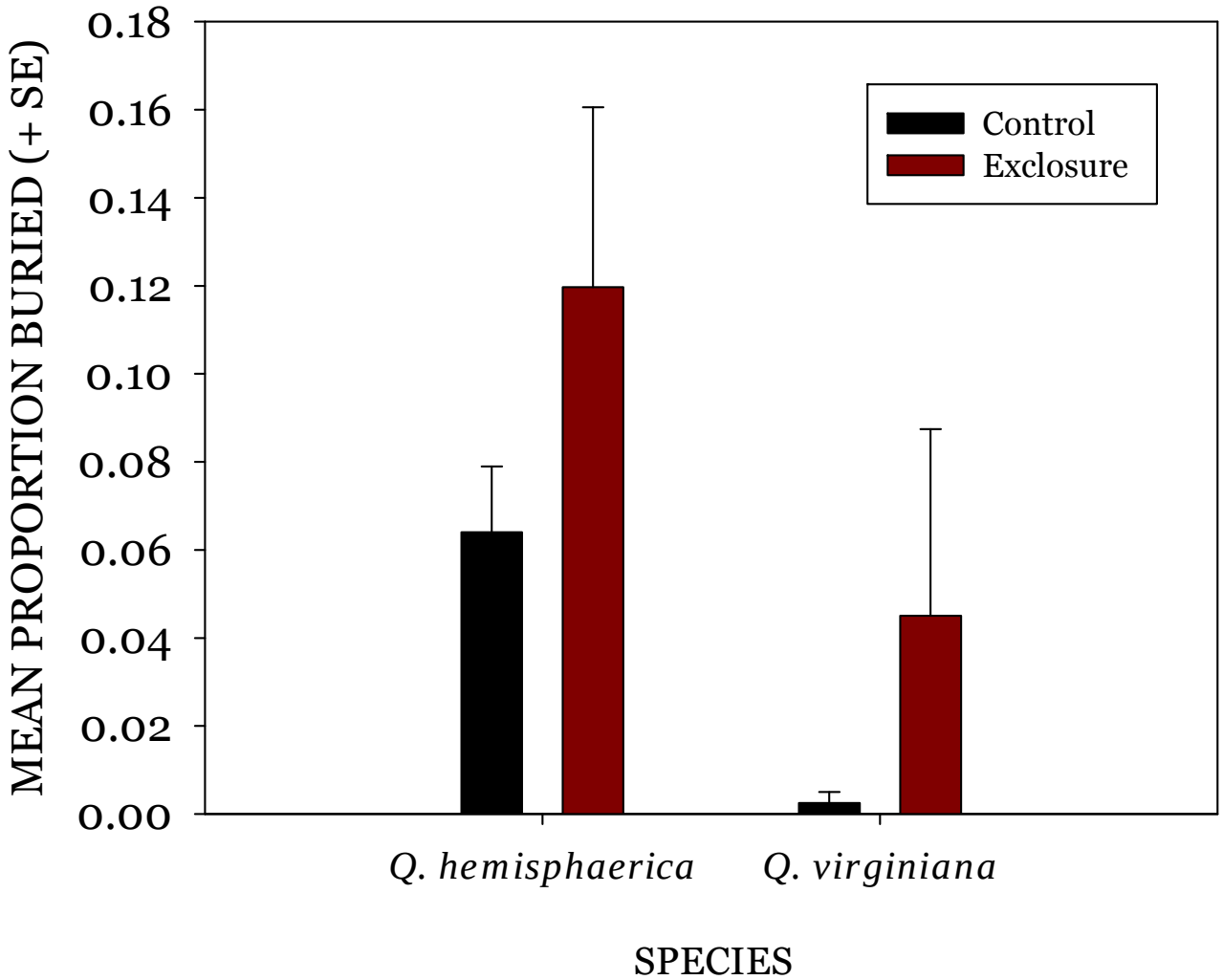

Figure 12. Mean proportions of acorns *Quercus* species buried by animals in control and exclosure plots.

Vertebrates killed 83.3% of *Q. hemisphaerica* acorns and 98.9% of *Q. virginiana* acorns used in the experiment, however some acorns were buried by rodents. Burial of acorns was significantly more likely for *Q. hemisphaerica* than *Q. virginiana* (Figure 12; Wald = 4798.8, df = 1, $p < 0.001$). Burial was also significantly more likely for acorns placed in exclosures than control plots (Wald = 6.80, df = 1, p = 0 .009). Of the two factors, species was more important than treatment in likelihood of burial (Figure 12). Rodents may be especially influential in seed survival because of their tendency to disperse seeds by burying them (*e.g.*, Price and Jenkins 1986). Caching behavior potentially enhances plant recruitment by decreasing the probability of predation of seeds, maintaining seed viability, and promoting seedling establishment (VanderWall 1990, Thorn and Tzilkowski 1991). Scatter hoarding behavior benefits the scatter hoarding rodent by giving that individual better or exclusive access to seed resources compared to a competitor that is ignorant of the locations of cached seeds (Stapanian & Smith 1984, Smith & Stapanian 2002, Steele & Smallwood 2002, Smith & Reichman 1984, Brewer & Webb 2001).

Potential predators of acorns include almost exclusively white-tailed deer (*Odocoileus virginianus*) and gray squirrels (*Sciurus caroliniensis*). Eastern woodrats (*Neotoma floridana floridana*) are documented for the island (Hayes & Richmond 1993) but were apparently extirpated from the Smith Island Complex in 1966 (D. Webster pers. comm.). As an inhabitant of some barrier islands of the southern Atlantic coast, the cotton mouse (*Peromyscus gossypinus*) is a possible predator of acorns in the BHIFR (D. Webster pers. comm.; Bellis & Keough 1995), although no know records exist for this species on BHI. The turkey (*Meleagris gallopavo*) has not been documented for the island in modern times (BHI Conservancy pers. comm.). Birds such a blue jays (*Cyanocitta cristata*) are known predators of acorns, however no evidence of bird predation was discovered, and no jays were observed feeding on acorns in the BHIFR.

The lack of a treatment effect on removal rates is evidence of intense predation pressure on acorns in the BHIFR regardless of the seed predator responsible for removal. However, significantly greater burial rates for both oak species in exclosures demonstrate that deer have proportionately stronger negative effects on acorn survival. Deer populations were relatively low in 2007, by as much as 75%, therefore higher densities of deer will have greater effects on acorn survival. Moreover, acorns in maritime forests likely require burial – a fate given only by squirrels – for survival to the seedling stage, and perhaps beyond. Desiccation and/or attack by isopods apparently kills all acorns left on the soil surface, and burial of acorns is known to be required for germination and survival of acorns in other systems (Darley-Hill & Johnson 1981, Crow 1988, Deen & Hodges 1990). Future studies of burial effects on acorns in the BHIFR are necessary to determine more precise estimates of the effects of squirrels vs. deer on oak recruitment to the seedling stage. Finally, live oaks are at a competitive disadvantage with laurel oak for safe sites for germination and recruitment, as evidenced by lower rates of survival and burial of live oak acorns, few numbers of acorns produced per tree (Brewer pers. obs.), and possibly lower lifetime production of acorns in number. Greater burial of laurel oak supports the conclusions of Smallwood and colleagues (Smallwood & Peters 1986, Hadj-Chikh *et al.* 1996) that oaks in the red oak group (section *Erythrobalanus*) are less likely to be eaten immediately and are more likely to be cached than acorns from species in the white oak group (section *Quercus*, formerly *Lepidobalanus* or *Leucobalanus*). Red oaks have higher fat (a reward) and tannin (a cost in terms of digestion) than white oaks, and white oaks germinate almost immediately compared to the delayed germination of red oaks. The combination translates into adaptive behavior that favors immediate consumption of white oak seed to avoid germination and loss of food content, and caching of red oak acorns that are less perishable via dormancy (Smallwood *et al*. 2001).

Insect predation differentially affected the two oak species in the BHIFR. Acorns randomly gathered from the forest floor were significantly more likely than expected to be infested with *Curculio* sp. (weevil) larvae if they came from *Q. hemisphaerica* than from *Q. virginiana* ($\chi^2 = 275.4$, df = 1, $p < 0.00001$). Infestation resulted in destruction of acorn embryos. Only 19% (of N = 355) of *Q. virginiana* acorns were infested, but 67% (of N = 1326) of *Q. hemisphaerica* acorns were infested.

Invertebrate and fungal and/or bacterial predation killed 6.4% of *Q. hemisphaerica* acorns that passed the float test (i.e. were initially intact) but were not removed by vertebrates. All acorns (2.4%) of *Q. hemisphaerica* that remained on the forest floor at the end of the study were destroyed by a combination of desiccation and predation by terrestrial isopods ("sow bugs" or "pill bugs" of the sub-order Oniscidea of Isopoda).

Effects of "Buck Rubs" on Juvenile Trees

Bucks rub trees during and after dieback of the external tissue ("velvet") on their antlers as early as late August for as long as three months. This behavior is well-documented in the literature, although the significance of buck rubs appears to be a continued source of speculation, ranging from velvet removal, practice for male-male antagonistic behavior, and signposting or scent-marking (see references in Marchinton and Hirth 1984, Benner and Boyer 1988, for example). Physical characteristics of trees (*e.g.*, smoothness of bark, size class, height of first branch; Kile & Marchinton 1977, Nielsen *et al.* 1982) and the purported aromatic qualities of some woody species (Kile & Marchinton, 1977) have been associated with trees that deer selected to rub. What is considered "aromatic" however is speculative, as the secondary plant compounds that may or may not be actually detected and possibly preferred or avoided by deer is unknown. Most of the buck rubs in BHIFR were from one or more previous years, due to low buck densities in 2007. Most of the rubbed tree wounds were healing as their bark and vascular cambium and tissue began to grow onto the wound.

Trees between 1 cm and 10 cm DBH comprised 93.2% of all rubbed stems but only 58.3% of all stems total. Trees between 1 cm and 5 cm DBH were rubbed at a higher frequency than expected (Table 4, Figure 13). Trees 5-10 cm DBH were about as equally likely to be rubbed as not (Figure 13). Only one tree > 10 cm DBH (0.4% of rubbed stems) was rubbed by bucks. Trees ≤1 cm DBH comprise 33% of all stems in the samples, but only 6.4% of those that had been rubbed, significantly less frequently than their proportional representation across all stems <20 cm DBH (Wald t =14.65, df = 1, $p < 0.001$; Figure 13).

Mortality was significantly associated with the presence of rubs (logistic regression, Pearson's $\chi^2 = 26.8$, df = 1, $p < 0.0001$) for trees within the target size (≤10 cm DBH) for rubbing. The number of rubbed trees that were dead (31) was more than twice the number expected (13) if the number of dead and bucked-rubbed trees were independent. Due to low sample size of dead trees per species, any potential interaction of buck rubs and tree species on likelihood of mortality could not be assessed with confidence.

Trees of *Ilex vomitoria* (the reference species) were about equal in percent of rubbed trees (51.5%) as proportionate representation of *I. vomitoria* among all trees in the sample (62%) of trees of target size (Figure 14, Table 4). Compared to the reference species, *Cornus florida* was about 26 times as likely to be classified as being rubbed by bucks, followed by *Callicarpa americana* (24 times), *Juniperus virginiana* (23 times), *Osmanthus americana* (5.5 times), *Ilex opaca* (5.4 times), *Prunus caroliniana* (2.7 times), and *Persea borbonia* (1.2 times) (Table 4). *Quercus hemisphaerica* was 70% as

likely as *I. vomitoria* to be rubbed and no stems of *Carpinus caroliniana* in the sample were rubbed (0.7% as likely as the reference species).

Variation in proportions of rubbed trees in the 40 experimental plots was not significantly associated with variation in total stem density ($R^2 = 0.05$, $p = 0.16$), or the density of stems ≤ 10 cm DBH ($R^2 = 0.04$, $p = 0.23$, Figure 15). Few quantitative data on size-class distributions exist for undisturbed maritime forests, however, the size class distribution for the BHIFR seems comparable to evergreen maritime forests in general (Brewer, pers. obs.), in that small stems (< 5 cm DBH) comprise >60% of the total stems. Large trees comprise most (> 50%) of the total basal area in the forest but the fewest number of stems because of a space limitation inherent in the stem size-number tradeoff for trees.

TABLE 4. Logistic regression with size class (cm DBH) and species as independent variables and condition (rubbed or not) as the dependent variable. Exp(B) is the odds ratio. Species codes are derived from the first two letters of the genus and specific epithet. Variables with a "**+**" beside their name are rubbed more frequently than expected, and significant or marginally significant variables are in boldface type.

Variable	Wald t	df	P	R	Exp(B)
SIZE CLASS	41.23	2	<0.0001	0.15	
1-2.5	39.26	1	<0.0001	0.15	4.56
2.5-5	16.05	1	0.0001	0.09	2.48
SPECIES	137.7	9	<0.0001	0.27	
Caam	22.79	1	<0.0001	0.11	24.13
Caca	0.620	1	0.43	0.00	0.071
Cofl	28.25	1	<0.0001	0.13	25.83
Ilop	12.13	1	0.0005	0.078	5.39
QuHe	0.1756	1	0.68	0.00	0.7358
Juvi	74.53	1	<0.0001	0.021	23.25
Osam	14.18	1	0.0002	0.086	5.55
Pebo	0.3062	1	0.58	0.000	1.24
Prca	34.24	1	<0.0001	0.14	2.69
Constant	32.1938	1	<0.001		

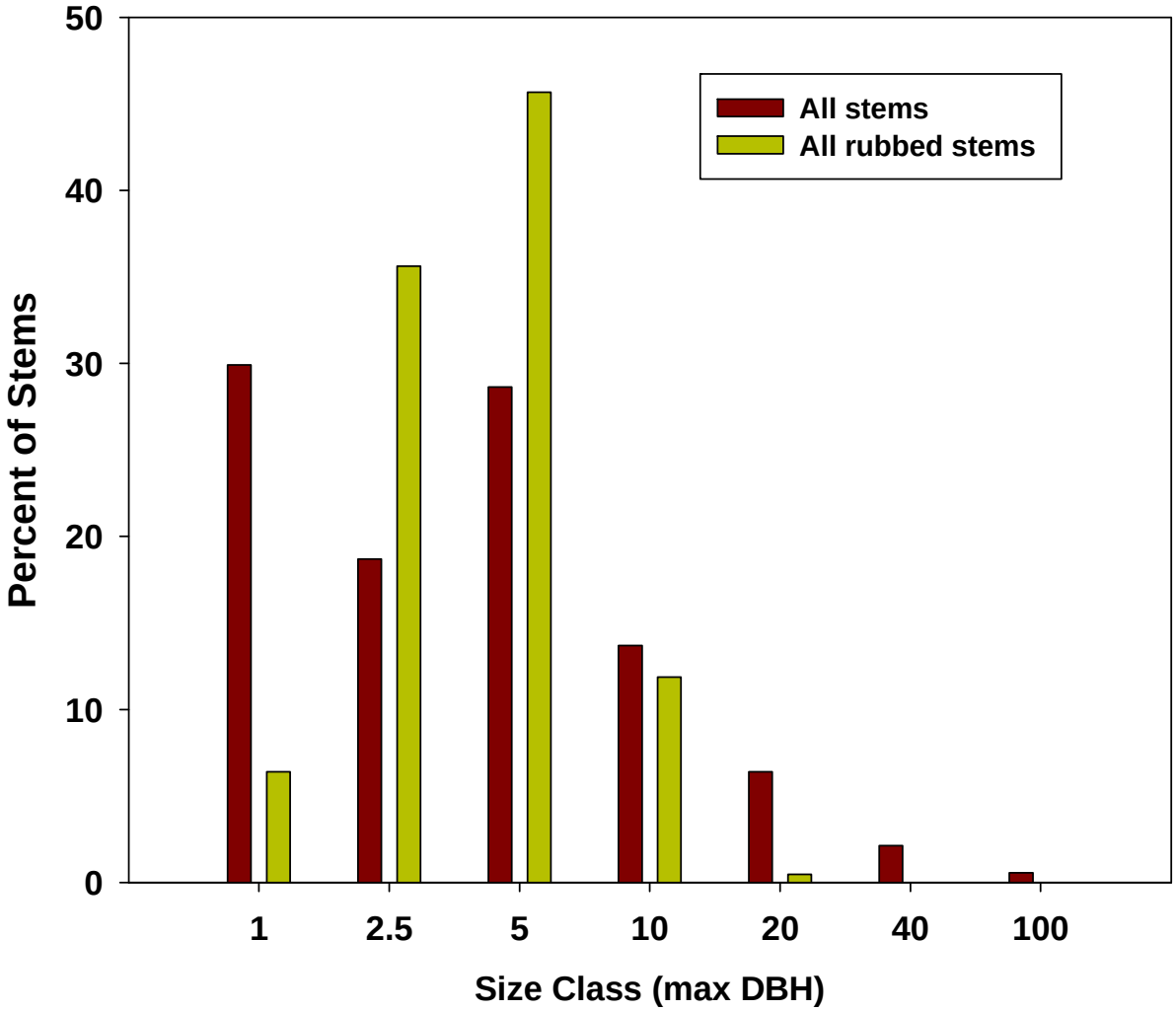

Figure 13. Number of stems by each size class (maximum DBH of the size class shown) as a percent of all stems (red) and all rubbed stems (yellow).

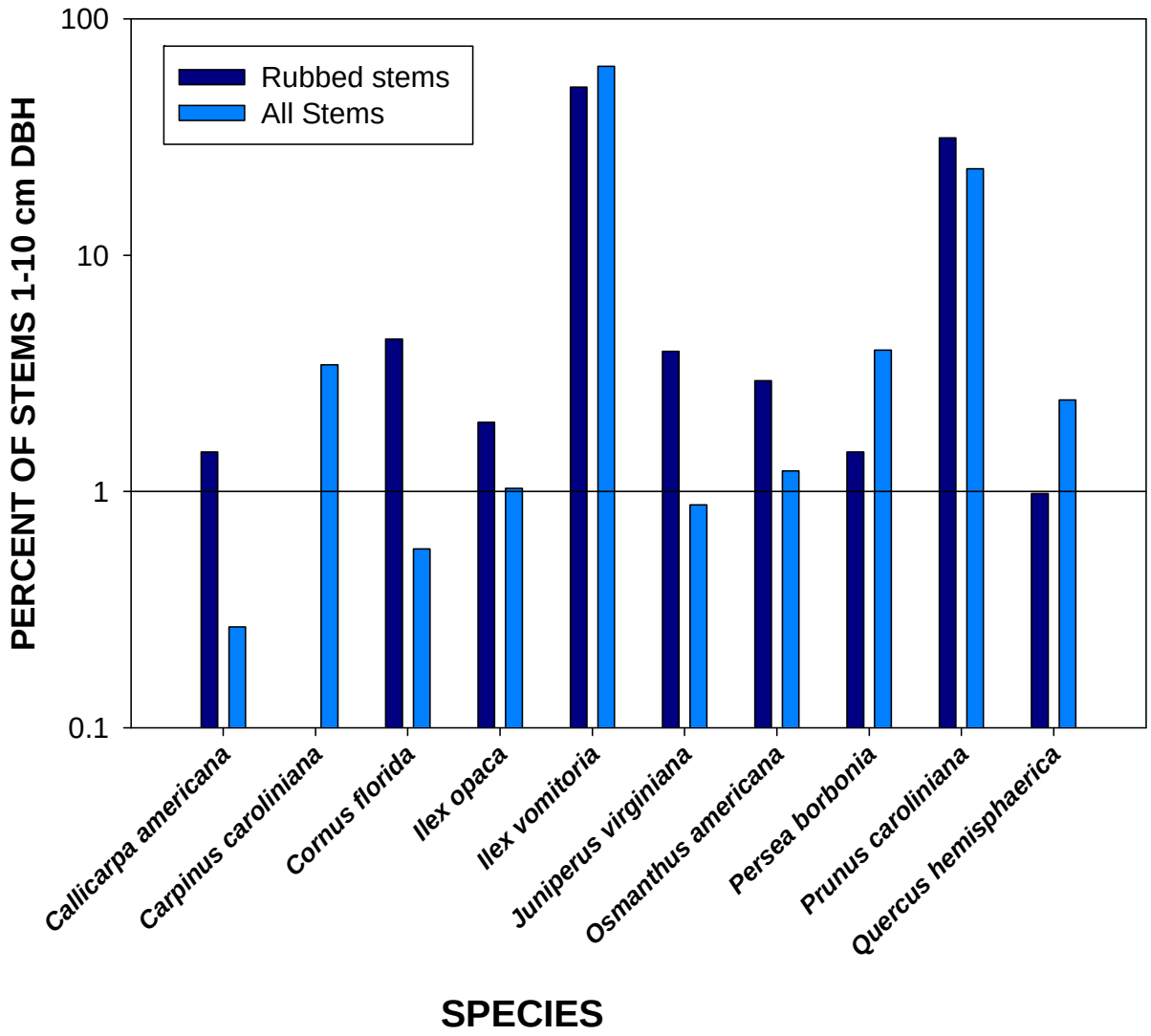

Figure 14. Relative abundance of species in stems as a percent of all trees 1-10 cm DBH sampled in the BHIFR (light blue bars; N = 4105) and percent of trees rubbed by bucks (dark blue bars n = 217). Note Y-axis is on log scale.

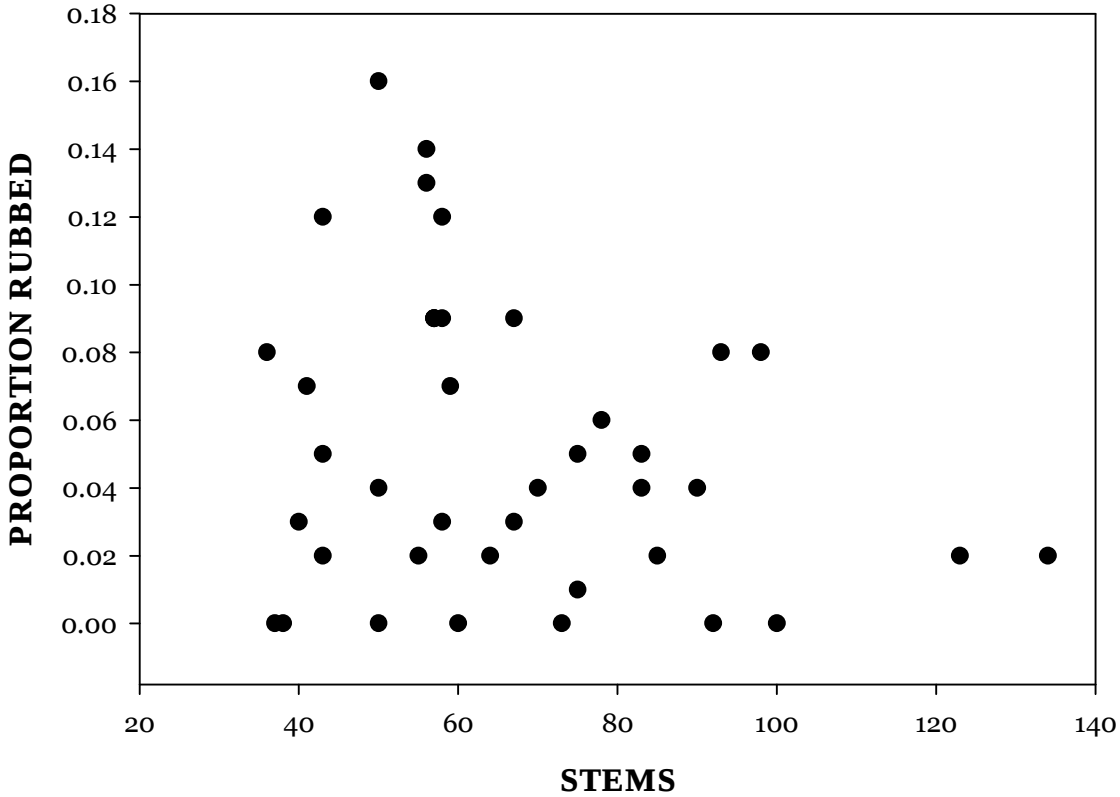

Figure 15. Proportions of stems rubbed by bucks within 10 m x 10 m plots and total stems within the plots. The relationship is not significant with simple linear regression ($R^2 = 0.023$, df = 38, p = 0.35).

CONCLUSIONS AND CONSERVATION SIGNIFICANCE

Recruitment Pressures at Different Life-History Stages

This study is designed to examine some ecological components of the effect of deer on plants at different plant life-history stages. As with virtually all plant species, insects account for a high proportion of the seed predation of acorns. Of the vertebrates currently in the forest, deer have the largest and most significant negative effect on the survival of acorns. Although squirrels have a negative impact on acorn survival, they likely enhance oak recruitment by burying seeds and promoting survival and germination of some oak seeds. Deer reduce the probability of burial of acorns and therefore strongly affect a vital step in the recruitment of acorn seedlings. Their effect on acorns is dominant because of large body mass and nutritional requirements, high reproductive rates, and ability to range widely in the search for acorns. Therefore when given equal access to acorns, deer dominate acorn removal from the BHIFR. Given the relatively low deer populations during the course of the acorn fate experiment, the effect of "normal" deer populations on acorn survival is probably severe. Whether or not higher deer population sizes affect the small proportion of acorns that are buried will require further seed-fate studies.

Whether deer have a negative impact on oak seedling composition cannot presently be determined, as experimental transplanting of seedlings in control plots and exclosures is necessary. The failure to find live oak seedlings in the understory of the BHIFR by Lopazanski *et al.* (1988) and Brewer (2006-7 pers. obs.), in contrast to Bourdeau & Oosting's (1959) observations of dense patches of oak seedlings, may simply reflect the periodic nature of oak seedling recruitment (4-5 year cycles of masting). Possibly it reflects some unusually intense negative influences on acorn production and/or increased consumption pressure that has surfaced since the 1950's, although such a conclusion would not be the most parsimonious one. Long-term recruitment studies of oaks in the BHIFR must be conducted to begin to determine the recruitment pressures on oaks and their proportion impacts.

For seedlings and saplings, some species are being disproportionately impacted through browsing ("high": *S. bona-nox*, *P. caroliniana*; "low-moderate": *Sabal palmetto*; "low" to none (?): *Ilex vomitoria*), however the precise effects of deer browsing on these and other species is unknown. Particularly needed are studies of proportionate impacts on individual species' population dynamics under various deer densities.

Some species are also being disproportionately impacted by bucks via antler rubs. Of special concern are the dogwood (*Cornus florida*) and eastern red cedar (*J. virginiana*), both of which are at a numerical disadvantage due to intensive logging (and disease for the former species) in the past century. What effects buck rubs have on growth and mortality, and timing of reproduction, of trees will require much further study and long-term investigations.

Recruitment Failure of Live Oak

It appears that the keystone species for maintaining the structural integrity of a continuous forest canopy – *Q. virginiana* – is experiencing or is under the threat of significant decline in the BHIFR. The decline of oaks is a widespread phenomenon in eastern forests (Smith 1993) for which causes appear to be multiple if elusive (Lorimer 1993). Recruitment of oak seedlings and saplings in the understory of many hardwood forests are apparently inadequate to maintain oaks as dominant canopy species (Abrams 1992, 1998, 2003; Christensen 1977), although xeric and sub-xeric sites seem to be experiencing less oak decline than mesic sites.

Oak recruitment failure in general also appears to be a rather recent phenomenon, for the past 50 years or so, which is well within the lifespan of most adult oak trees (Lorimer 1993). General declines in oak regeneration appear to be caused by one or more of : (1) available seed limitations caused by poor or variable production and high rates of seed predation by deer , rodents, and insects; (2) predation of seedlings, primarily by deer; (3) poor recruitment to larger size classes due to heavier-than-normal competition from surrounding vegetation; (4) fire suppression and therefore an increase in shade-tolerant and competing vegetation; (5) long- or short-term climate change resulting in unfavorably dry spring conditions.

The large-scale logging of dogwood and cedar, along with oaks (pers. obs. of stumps) during the first half of the twentieth century, appears to have had a significant and long-

lasting role in oak recruitment in the BHIFR. With logging and the subsequent increase in light levels, oaks would be at a relative disadvantage in recruitment. Although shade-intolerant to mildly shade-tolerant, most oak species are poor competitors in the understory and therefore are hindered in recruitment by competing midlevel and understory species that devote more resources to growth (*e.g.*, Johnson & Jacobs 1981; Janzen & Hodges 1985 ; Beck & Hooper 1986; Hix & Lorimer 1990, 1991). As Bourdeau & Oosting (1959) noted, a dense layers of seedlings belies a lack of continuous recruitment from seeds; oak stands on BHI for example are even-aged. Therefore it seems reasonable to presume that a significant component of recruitment failure of live oaks in the BHIFR is a dense understory that suppresses oak recruitment through competition for water, light, and possibly nutrients. What conditions therefore hinder and promote live oak recruitment on BHI have not been tested, although some speculation is in order.

It appears that oaks on BHI require some periodic disturbance favorable for recruitment in the form of eliminating competing understory vegetation. On BHI, such natural disturbances may be fire or salt spray after large-scale catastrophic events or during geographical shifts in the island's location. The principal competitor for oaks in the understory of BHIFR would be *I. vomitoria*, which is sensitive to fire (Fralish & Franklin 2002), while the other species, with the exception of *J. virginiana*, are sensitive to salt spray. It must be emphasized that research is necessary to establish whether oaks will respond to removal of competition from the understory and midstory layers, and whether a disturbance such as prescribed burning is a viable means of releasing oak seedlings (or seeds) from recruitment suppression.

Finally, some species appear to be responding positively to the general canopy disturbance. Most of these are the fast-growing "r-selected" or "ruderal" species, especially yaupon holly (*Ilex vomitoria*) and Carolina cherry (*Prunus caroliniana)*. These species appear to be growing in proportionate representation as well as absolute density in the forest. *Sabal palmetto*, on the other hand, is abundant as individuals in the seedling and establishment (a phase of palm growth similar to the "pole" juvenile stage of dicotyledonous trees) phases, but rare to uncommon as reproductive adults of 5+ m stature.

FUTURE STUDIES & CONSERVATION RECOMMENDATIONS

Given the currently low populations of deer on BHI, it would be advantageous from an applied scientific perspective to suspend culling for several years to allow deer populations to grow to large levels. Such a decision would facilitate the detection and measurement of the effects of short-term differences in deer densities on plant recruitment and extant vegetation. It would also likely result in lower short-term costs of culling. The disadvantage of taking such an approach may be the political costs of appeasing pro-culling advocates, renewing efforts to educate and persuade anti-culling advocates of the ecological and social values of culling, and the disturbance of the aesthetic quality of the island via noise from gunfire during culling.

In the absence of a decision to temporarily suspend deer culling for scientific purposes, the precautionary approach of regular culling is recommended. Historical accounts and

the scientific literature on deer-plant interactions certainly demonstrate that deer can and usually do have significant effects on forest vegetation.

Any other conclusions about the effects of deer on the forest vegetation of BHI must be considered preliminary, as the gaps in what is known about maritime forest ecology are large and many. Perhaps the largest gaps are in what we understand about the ecology of the most important woody taxon on the island – live oak. For example, whether or not deer even eat live oak seedlings and saplings on BHI is unknown; future studies must address this issue, yet they would be relatively easy to conduct. Natural reproductive variability is also unknown, however an assessment of reproductive trends in live oak would require monitoring over decades.

Less tractable are the controlling forces of live oak recruitment at the community level, and the importance of deer within this context. The maritime forest appears to be in a state of arrested succession, whereby a dense understory is suppressing the recruitment of live oaks. This dense understory appears to be at least partly due to anthropogenic forces, primarily from logging and associated disturbances. Like other species experiencing pulse recruitment and even-aged stands, live oaks may depend upon narrow windows in time whereby catastrophic disturbance enhances recruitment. Would the presence of deer effectively close this window by removing potential recruits from the understory? The answer to this question lies in systematic studies of plant recruitment dynamics at the population and community levels within maritime forest. The relative importance of natural processes versus anthropogenic forces (especially historical logging) should be a priority of future studies in order to better understand how deer may be relevant to live oak recruitment.

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Appendix 1. Coordinates (WGS 84) of the 12 m x 12 m exclosure sites used in this study. Control plots are located within 5 m of the exclosures. Site numbers correspond to original waypoints.

SITE NUMBER	LATITUDE	LONGITUDE
66	N33.85300	W77.97519
68	N33.85479	W77.97759
70	N33.85600	W77.97921
71	N33.85407	W77.98130
72	N33.85547	W77.97995
74	N33.85298	W77.97899
78	N33.85167	W77.97551
81	N33.85411	W77.97834
82	N33.85473	W77.98093
91	N33.85326	W77.97212
92	N33.85394	W77.97314
94	N33.85397	W77.97395
96	N33.85099	W77.97614
97	N33.85091	W77.97595
98	N33.85035	W77.97287
99	N33.85010	W77.97166
100	N33.85012	W77.97220
101	N33.85364	W77.97271
102	N33.85406	W77.97297
103	N33.85452	W77.97442