Final Project Report 2:

Effects of herbivory on oak seedlings and understory vegetation on Jekyll Island, Georgia

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<u>About this report:</u> This report explains a suite of experiments that used fenced exclosures to investigate the effects of deer herbivory on the understory vegetation community, on naturally-occurring oak seedlings, and on planted live oak seedlings. Because of large vegetation changes, likely driven by major storm disturbances, we were not able to detect impacts of deer on Jekyll Island. We present our study in four sections:

Background and Rationale → Research Design and Methods → Findings → Conclusions and Management Implications

Background and Rationale

Deer Herbivory and Forest Composition

The Maritime Live Oak (MLO) forest is the most iconic and dominant forest type on Jekyll Island. MLO forests are complex systems, in which many physical and biotic factors act to steer and shape the assemblage of life we see. Factors such as hurricanes, fires, and herbivores can be seen as stressors that limit the growth, survival, and reproduction of some species, and thereby alter the composition and functioning of forests. But at the same time, disturbances are inherent to these ecosystems, and as agents of change, they are in fact key to the maintenance of biodiversity over time. Nevertheless, some changes are more desirable to us than others. Jekyll Island's maritime forest communities are globally rare, unique to barrier islands, foundational to the island's ecological health, and cherished for their aesthetic and recreational values. This creates a strong impetus for conserving the characteristic composition of these forests.

Ecological research can help us understand how current levels of disturbance are affecting different species in forest ecosystems, and if those effects are likely to cause long-term change in forest composition. But because stressors and subsequent changes in forests can occur at grossly different time scales, from days to decades, and numerous conditions are always changing at once, it is a challenging and long-term process to isolate and clearly determine the impacts of any given stressor on the future trajectory of forests. Yet that is often the most valuable evidence-based knowledge that managers, land stewards, and stakeholders seek to inform action and policy.

One reason for current concern about the future condition of Jekyll's MLO forests is the observed rarity of live oak (*Quercus virginiana*) seedlings and saplings. Oak regeneration failure is a major concern not only in maritime forests, but has been a challenge in numerous oak woodlands and forests around the U.S. and the world.

Deer and other ungulates are well known to browse on oak seedlings and have been implicated in oak regeneration failures (see Holladay et al. 2006). But a number of studies that simultaneously examined deer and other factors, have found that the net effect of deer on regeneration can be more complex, and sometimes contradictory. For example, deer may stunt the growth of a target seedling species, but they may also consume competing vegetation, so that when deer are removed, target seedlings suffer even greater mortality due to shading and competition from other faster-growing species (Bobiec et al. 2011; Dalgleish et al. 2015). In some study areas, impacts of deer have far exceeded those of small mammals (e.g., Blossey et al 2017), while in other studies, the exact opposite trend has been observed (e.g., MacDougall 2010). Another study found that deer and rabbit had no effect on forest regeneration and composition after 10 years of monitoring, despite the animals' browsing activity (Holladay et al. 2006).

Study Objectives

Our broader research program has investigated different possible stressors that affect forest composition and limit live oak regeneration, as well as restoration strategies that may facilitate regeneration. In this component study, we sought to examine the effects of deer herbivory on (a) the understory vegetation community, (b) naturally occurring oak seedlings, and (c) planted live oak seedlings. This study was also replicated on Ossabaw, St. Catherines, and Sapelo Islands, to explore whether deer effects differ from island to island, and to provide additional insights into the trends and unique characteristics of Jekyll Island's MLO forests.

In efforts to distinguish effects of deer from effects of other potential stressors, we employed the classic experimental design of herbivore exclosure treatments. The design consists of multiple replicated, medium sized plots (10 x 10m), half of them fenced to exclude deer, and the other half unfenced. Effects of deer on vegetation are seen by comparing fenced and unfenced plots over time. Other factors may also cause vegetation changes over time, but are expected to affect both fenced and unfenced plots similarly.

From 2017 to 2020, we monitored paired plots, which were either unfenced or fenced to exclude deer, to assess the following questions:

- Does deer exclusion affect density or composition of **understory vegetation**?
- Does deer exclusion affect **naturally occurring oak seedlings** in particular?
- Does deer exclusion affect growth or survival of **planted live oak seedlings**?

Figure 1: Two photos of forest plots, illustrating the kinds of vegetation composition in the MLO forest.

Research Design & Methods

We conducted this study in the MLO forest between Horton House and Horton Pond. In January / February 2017, we established two large "macro-plots," each 100x200m, at the site. One slopes downhill toward the east, and the other slopes down to the west. We used a random stratified strategy to place 8 plot pairs (fenced and unfenced) in each macroplot, ensuring that they spanned the elevational gradient. Once the 10 x 20m area for the plot pair was located, we randomly chose which side to enclose with 8ft tall plastic mesh deer fencing.

In March / April 2017, we began a monitoring protocol to assess the understory plant community and naturally occurring seedlings in 3 permanently marked subplots within each plot. First, we visually assessed percent cover of vegetation in the understory zone (0 to 1.5 m in height), for each species with 5% cover or more. Second, the total abundance and species of naturally-occurring oak seedlings was also counted in each subplot. Third, we tagged 12 randomly-chosen oak seedlings (all were laurel oak) to serve as “focal seedlings” for more intensive individual monitoring of seedling length, stem diameter, and survival. With three subplots, we had a total of 36 focal seedlings per plot. Vegetation monitoring, total seedling counts and focal seedling measurements were repeated in May / June of 2018, 2019, and 2020.

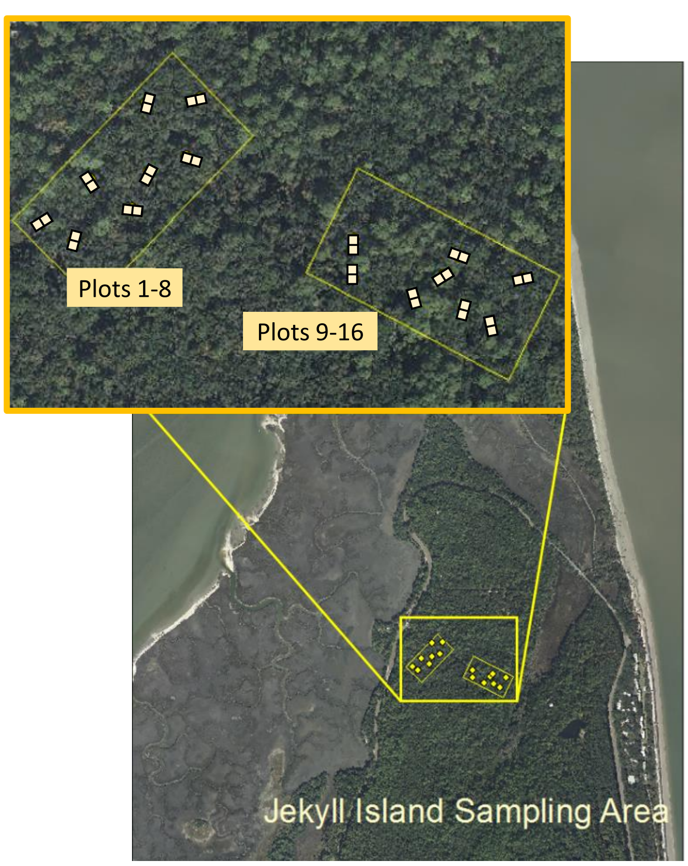


Figure 2: Locations of study plots on northern end of Jekyll Island. The squares on the enlargement represent pairs of fenced and unfenced plots.

There were not enough naturally-occurring live oak seedlings to feasibly investigate deer herbivory effects on live oaks. So in the spring of 2018 we planted live oak and sand live oak *(Q. geminata*, a closely related sister species) seedlings in 8 of the 16 plot-pairs. A total of 590 live oak and sand live oak seedlings were planted in 8 paired (fenced / unfenced) plots on Jekyll Island in April of 2018.

The monitoring protocol involved measuring seedling length, stem diameter, assessing extent and source (deer, rabbit, insect, or other) of herbivore damage, and an index of leaf browning or loss due to water stress. The deer exclosures and planted seedling study was also replicated on three other islands, Ossabaw, St. Catherines, and Sapelo.

Figure 3: Examples of subplots, showing variation in understory vegetation density, from almost bare, to a blanket of laurel oak seedlings, to young palms.

Findings

Figure 4: Aftermath of Hurricane Irma, which struck the Georgia Coast in September 2017, about 6 months after the establishment of the experiment. Left: large tree trunk crushed side fence of deer exclosure. Center: a view upwards of a large canopy gap. Right, falling branches also brought down tangles of vines from the canopy, crushing fences and also burying understory vegetation in dense debris and foliage. Below: two more plots with large limb/trunk damage and mounds of leaves, moss, and vines. Posts of plots are marked in red for clarity.

Changing environment during study period

The first two years of the study span a time following three major disturbances – two hurricanes and an ice storm – that damaged mature trees and thus likely increased sunlight on the forest floor. The first Spring and Summer of the study followed the landfall of Hurricane Matthew in October 2016. Between the first and second monitoring bouts, Hurricane Irma and an ice storm brought down even more branches and trees.

Canopy gaps are a very important phenomenon for live oak regeneration, because they offer the higher light environment that live oak seedlings and saplings require in order to ascend toward the canopy. However, other vegetation can also take advantage of increased light penetration, and can potentially outcompete juvenile live oaks. Also, the huge quantity of leaves and branches cleared from the canopy were deposited on the ground below, which in places dramatically changed the immediate ground-level light environment, as well as delivered an unusually large input of organic matter that is expected to enrich soils as it decays. Lacking pre-storm measurements needed to quantify any of these large environmental changes, we can only consider their potential correlations to observed vegetation changes effects based on ecological principles rather than data.

Understory plant community

We examined the density of cover in the understory (below 1.5m) created by vegetation in different categories of plants: tree species, palms, shrubs, vines, forbs, and graminoids (grasses and sedges). We evaluated year to year changes and looked for differences between the fencing treatments, shown in Figure 5.

Overall, the total amount of understory vegetation changed from year to year, but didn't differ between the fencing treatments (Figure 5a). We also saw found significant year to year variation in the cover of palm species (and graminoids. **Only one group, vines, showed a difference between fenced and unfenced plots**, where deer exclusion was associated with a greater abundance of vines. Other than vines, none of the other vegetation groups showed a response to fencing.

The most notable patterns we see across the vegetation groups are general increases in cover from 2017 to 2018. By our informal observations, we hypothesize that these increases are in response to the noticeable increase in light penetration through the canopy.

Regardless of the cause, **the year to year variability in general is quite large, and plot-to-plot variability was also large.** These circumstances of high variability make it hard to detect more subtle or more gradual changes in vegetation due to herbivore exclusion. The effect of deer would have to be quite consistent and greater than the background variation in order for us to be able to detect it. **Thus, we cannot answer the question of whether deer do, or do not, affect understory vegetation.**

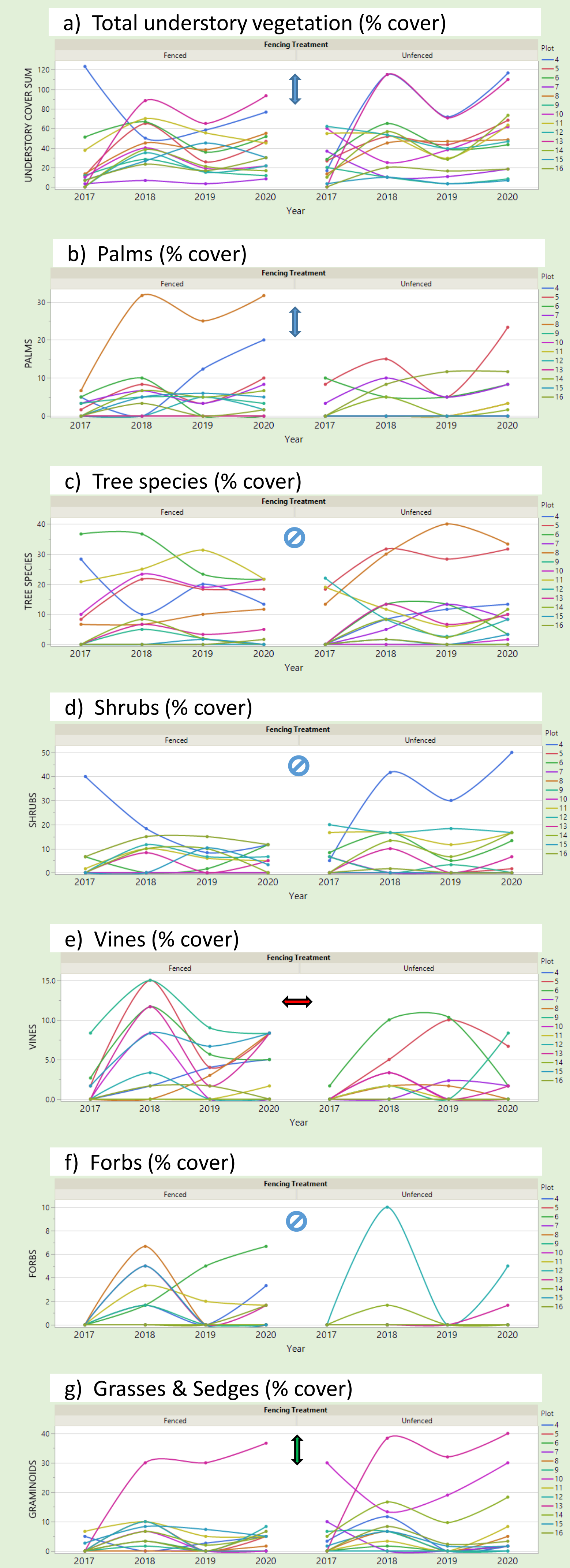


Figure 5. These graphs show the percentage of cover in the understory zone, i.e., from the ground up to 1.5m. Cover of each species present was estimated in three subplots, and the mean is graphed for each plot. Species that had at less than 5% cover in the subplot were considered zeroes. We conducted four annual censuses, in late spring or early summer each year. Graph (a): the sum of cover for all species; Graphs (b-g): sum of cover for all species in each vegetation category. Graphs on the left show cover trends in fenced plots (no deer), and graphs on the right show unfenced plots (deer access.)

⇕ indicates that vegetation cover changed significantly from year to year.

⇔ indicates that vegetation cover was different between the fenced and unfenced plots.

⊘ indicates that vegetation cover did not change significantly with either time fencing treatment.

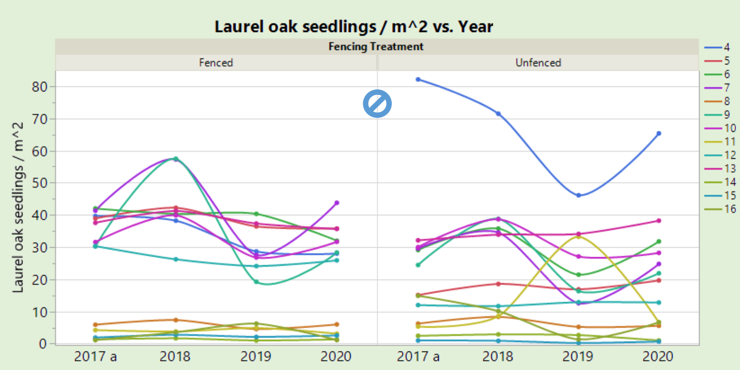
Naturally occurring seedlings

None of our subplots contained live oak seedlings as focal seedlings. Therefore our entire study of naturally occurring seedlings is addressing laurel oak seedlings, not live oak seedlings.

When examining the density of naturally occurring laurel oak seedlings, the first trend visible in Figure 6 is that densities in plots were highly variable to start with. Also, in a few plots, laurel oak density increased and decreased over time, while in other plots, density remained relatively constant. **With this high degree of background variability, we saw no effects of fencing on changes in seedling density.**

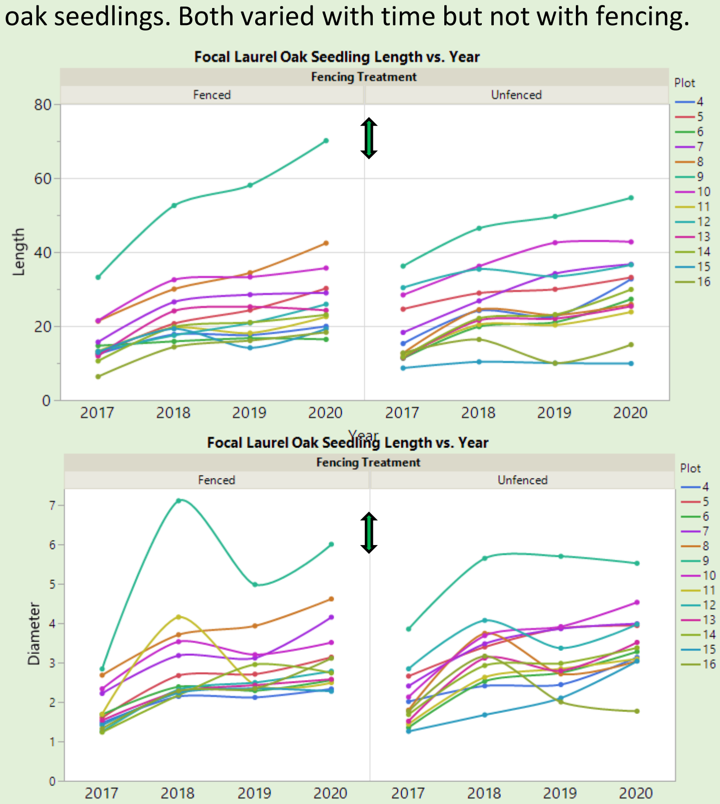
When we examined the growth of focal seedlings (Figure 7), we found that seedlings grew more rapidly in the first year, both in terms of length and stem diameter, then growth slowed in subsequent years. **There were no detectable effects of deer fences on growth rates.**

Figure 6: Estimated density of naturally occurring laurel oak seedlings in plots over time. Density did not differ significantly between fencing treatments or years.



(a)

Figure 7: Repeated lengths and stem diameters on focal laurel oak seedlings. Both varied with time but not with fencing.



Planted live oak seedlings

In Spring, 2018, we planted 576 live oak seedlings into 8 of the paired plots. Within about 2 weeks, we observed that 44 seedlings had been dug up (Figure 8a). We did not see significant water stress or mammal herbivory on the seedlings on Jekyll, both of which we had seen on Ossabaw and St. Catherines Island in the weeks after planting.

By October of 2018, only 70 seedlings, 12% of the total planted, were still alive. We found 415 seedlings had been dug up or were missing, and an additional 71 seedlings were dead, presumably to water stress. It appeared that these seedlings were dug up by squirrels to get to the root bulb of the seedlings. In December of 2018, we began two studies to monitor seedlings with cameras, and confirmed that squirrels were indeed responsible.

The remining 70 seedlings were not an adequate sample size to reliably detect differences between fenced and unfenced plots even if they existed. Any findings about seedling responses to fencing would be misleading because of a lack of statistical power. Thus, we discontinued measuring the planted seedlings.

On other islands, there was virtually no small mammal damage, and we did see deer exclosure effects on seedling growth. Other islands also had much less understory vegetation, so the relation between dense understory and live oak seedling herbivory remains an important research question for both conservation and restoration practice.

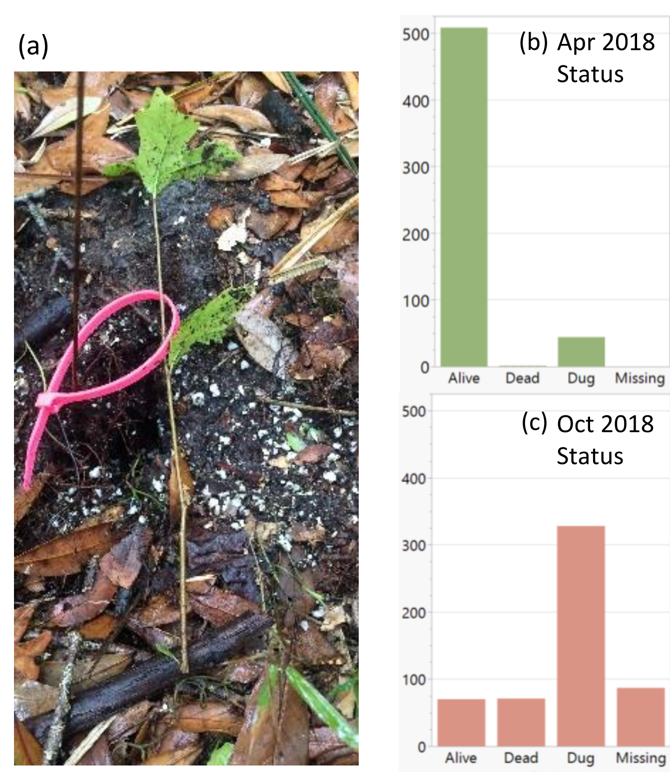


Figure 8: (a) Live oak seedling (with pink zip tie wrapped around its stem and an upright pin flag) that was dug up. The white flecks are from the seedling's nursery potting mix.. Status of planted seedlings: (b) 2 weeks after planting, and (c) 4 months after planting, demonstrating extent of losses.

Conclusions and Management Implications

Maritime Live Oak (MLO) Forest Composition

The composition of vegetation in MLO forests defines their visual and aesthetic character, as well as their ecological functioning. The abundance and proportions of different plant species are constantly shaped by a variety of stressors, disturbances, and ecological interactions among species. Disentangling various environmental influences – for instance of storms, herbivores, hydrology, pollinators, and fire regimes – is a challenge for ecological research, but can provide the scientific knowledge needed to understand whether, and how, current forest composition may change in the future.

The rarity of young live oak trees may limit the ability of these forests to maintain their characteristic composition over time. If herbivory by Jekyll's abundant deer population is a contributing factor, this is useful information for the stewardship of these iconic ecosystems.

Deer are just one component of a complex system of ecological interactions. We know that deer can and do browse on live oak seedlings and saplings. We must look beyond the simpler question of, "Do deer affect oak seedlings?" **The more important question is, "What is the *relative importance* of deer herbivory in the wider scheme of all the factors that shape forest composition?"**

Isolating the impact of deer herbivory

Targeted, structured experiments are ecologists' best tool for isolating and teasing apart the effect of one causal factor in a complex system. This is the reasoning behind the use of fenced exclosures and multiple, replicated plots. By intentionally changing just one variable (deer access), repeatedly, in slightly different contexts (plot locations and forest densities throughout the site), we increase the ability to detect the effect of that focal variable, against a backdrop of all sorts of things that can affect vegetation composition. The other sources of variation become background 'noise,' through which the measurements try to detect the specific 'signal' of change caused by deer.

In this study, we were largely unable to detect 'signals' of deer browsing impacts through the 'noise' of complex, varying patterns of vegetation change that were seen across the study plots from 2017 to 2020.

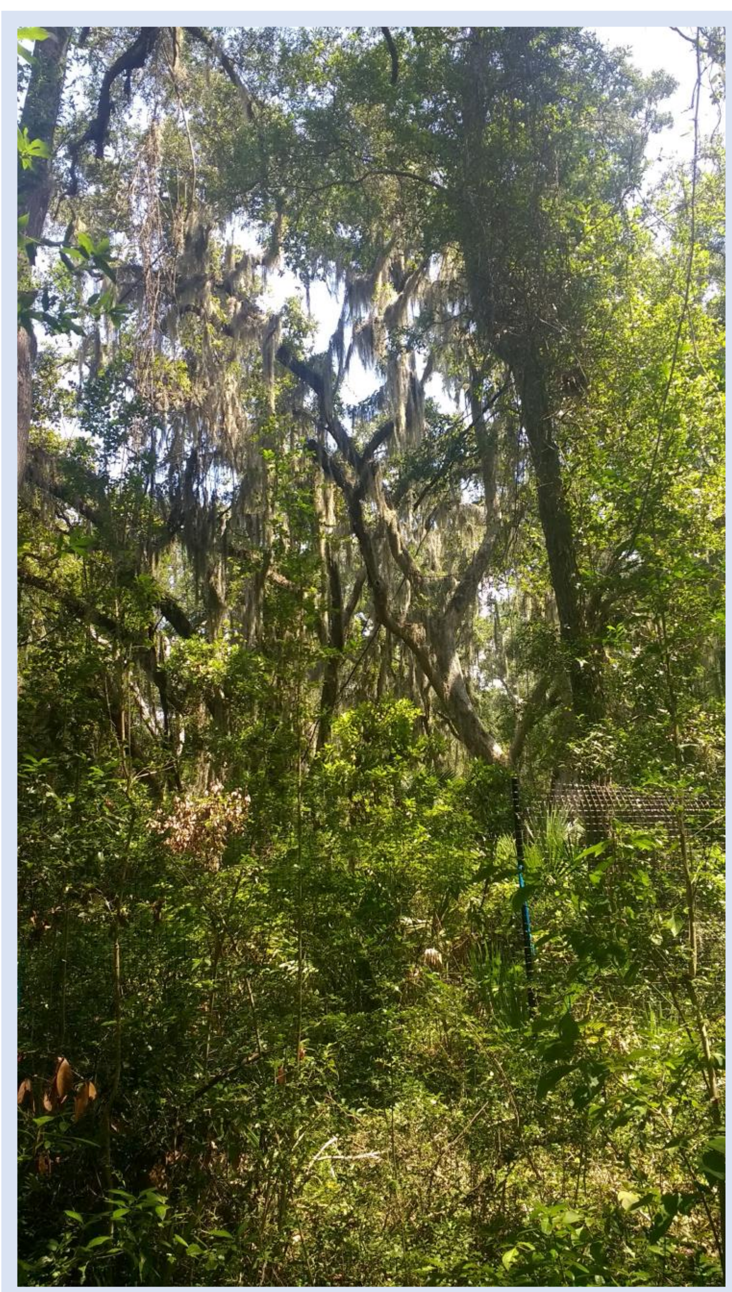
Comparing the findings on Jekyll to the other three study islands – Ossabaw, St. Catherines, and Sapelo – Jekyll Island's forests contain much greater understory cover, biomass, and diversity. This may be due to the history of fire suppression on Jekyll, while the sparse understory cover on other islands may be due to combined effects of fire history and deer herbivory. Lacking the yards and golf courses of Jekyll, those other islands' vegetation offers limited forage availability, particularly in winter. The pruning effects of deer browsing and hog foraging are quite evident. Further monitoring will help determine whether Jekyll's dense understories buffer the impacts of deer, or just make them harder to observe. This question certainly merits continued research.

Management Implications

Based on this study, we cannot conclude that deer have no effects on understory vegetation or oak seedlings. Nor can we judge whether their effects may ultimately be important for forest composition change. We can only conclude that we were not able to detect effects during the duration of this study, with the number of experimental plots, in the locations they were set up.

Yet there are still valuable lessons learned from this study. Since our interest is in the issue of young oak dynamics, one clear finding is that seedlings must survive and compete in a highly variable environment. This is itself informative for management. **Restoration and management strategies should take into consideration very local site-specific conditions, and the potential for large year-to-year differences in conditions for plant success.**

We hypothesize that the up-and-down changes through time, and inconsistent patterns seen across plots, reflected vegetation responses to new light conditions following tree-damaging storms. Fallen leaves, branches, and trees created thinnings and gaps in the canopy, and deposited massive amounts of debris in the forest, but those impacts are patchy, not uniform, across the site, and they can change in a few weeks, months, or years after an initial disturbance. **Canopy-damaging disturbances are likely to become more frequent with climate change.** Single point-in-time vegetation assessments are not necessarily representative of the conditions that oak seedling will experience as they try to survive and establish. **Wherever possible, management should utilize multi-year monitoring to allow adaptive management and possible course corrections.**



Complexities worth considering

This study is a helpful reminder of the challenge of navigating the complexities of dynamic ecosystems. We conducted experiments designed to isolate variables so that we could understand direct interactions between two species of management interest on Jekyll Island – live oaks and white-tailed deer. But instead, the lessons learned were about the complexities and variability that actually generate the forest composition we seek to conserve.

One informative example is **the only significant effect of deer exclusion that we detected -- an increased density of vines in exclosures.** Grapes (*Vitis rotundifolia*) are one of the most dramatic responders to canopy light gaps. Our other study of deer herbivory, in a mixed pine-hardwood forest near Shell Road on Jekyll Island, also showed increased grape abundance in deer exclosures.

The implications of this findings are uncertain, and worth further consideration. Deer appear to consume and reduce the density of grapes, which is a native species and an important food source for many species of wildlife. But from the perspective of a live oak seedling, it is a formidable, fast-growing competitor in light gaps, and light gaps are a live oak seedling's opportunity to reach maturity. We therefore speculate that **deer herbivory may be directly negative for live oak seedlings, but it may also benefit them indirectly if it limits a key competitor**. So, there may be a tradeoff. These complexities are important reminders that ecological relationships need to be considered from a holistic perspective.

Another lesson comes from the levels of variability in forest understory composition that we saw. Management plans seek to specify a clear course of action for a period of time into the future. Yet, the appropriateness of that plan may actually change may not have full ecological understanding of how an ecosystem will respond to management, because it may depend on the environmental context, which is ever-changing. Adaptive management is a particular management approach and methodology, designed to cope with this dilemma. By conducting research while implementing different management strategies, we can account for new conditions and continuously improve our knowledge and management success. We therefore **recommend that JIA's Conservation Program utilize adaptive management whenever possible to help navigate the complexities inherent in MLO forest dynamics.**

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