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Regeneration Failure in a Remnant Stand of Pignut Hickory (*Carya glabra*) on a Protected Barrier Island in Georgia, USA

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ABSTRACT: Maritime forest communities on barrier islands along the Atlantic and Gulf coasts have been severely fragmented by a continuous history of human land use and natural disturbance. Isolated populations of certain tree species in maritime forest fragments may now be too small to be viable and their inability to regenerate may result in their eventual elimination from barrier islands. Using an 11-year study of a population of pignut hickory (*Carya glabra*), a common species of remnant maritime forest stands on St. Catherine's Island, Georgia, we present a case study of tree regeneration failure on a barrier island. We found that there has been no recruitment of new hickory individuals into the canopy of this population over the last 65 years. Field evidence of browse and a strong correlation between seedling density distributions and microsite protection from herbivory suggest that this trend in recruitment failure is related to an increased abundance of deer (*Odocoileus*) and pigs (*Sus*) on the island. Using a size class population projection model, we estimated that, if such recruitment failure and mortality rates continue, the hickory population will be extirpated from the maritime forest within 200 years. Tree species that are failing to regenerate within maritime forests represent a special challenge that is not currently being addressed in the long-term management of barrier island biodiversity.

Index terms: barrier island, maritime forest, pignut hickory, remnant stand

INTRODUCTION

Maritime forest communities associated with barrier islands along the Atlantic and Gulf coasts of the United States represent unique assemblages of species whose composition and diversity on a given island are a combined function of: latitude, distance from mainland, island size and orientation, age, topographic heterogeneity, and disturbance history (Art 1976; Bellis 1995). Maritime forests are generally associated with those portions of barrier islands that experience relative long-term protection from storm overwash and shoreline erosion, thus allowing for the establishment and maintenance of long-lived tree populations (Bourdeau and Oosting 1959; Bellis 1995). These island forests are naturally small in size, isolated, and, therefore, particularly prone to fragmentation and the associated loss of biodiversity that follows anthropogenic and natural disturbances (Au 1974; Lopazanski et al. 1988; Wentworth et al. 1992; Smith et al. 1997).

Within these barrier islands, maritime forests are stable relative to their unprotected margins, and because of this they are desirable locations for human activity. Maritime forests often have had a long history of human land use from Native American settlements, centuries of agriculture, timbering and grazing, to the more recent acceleration of coastal development (Bratton and Davison 1987). As a result of this continuous land use, maritime forests that are inherently spatially restricted have become heavily fragmented over time

(Bourdeau and Oosting 1959; Lopazanski et al. 1988). Remnant fragments of original forest are often bounded by a matrix of cleared human development, such as on Bogue Banks in North Carolina (Lopazanski et al. 1988) or, more subtly, by a matrix of former agricultural clearings such as can be found on many Georgia sea islands (Johnson et al. 1974; Bratton and Miller 1994).

During historic times, islands in general have experienced a much higher rate of extinction than mainland areas (Primack 2010). A major cause of local extinction on islands has been anthropogenically driven habitat loss and fragmentation, coupled with invasive species impacts (Primack 2010). In the tropics, research has shown that as forest habitat becomes increasingly fragmented, some short-lived species disappear quickly from fragments while other long-lived species, such as trees, enter a phase of 'latent extinction,' where the population is represented by a slowly declining number of adults that are no longer able to successfully reproduce within their small populations (Janzen 1986; Myers 2003). These 'living dead' species (*sensu*, Janzen 2001) are often not recognized as problems by reserve managers, since the process of adult mortality may extend out over more than a century. In temperate forests, regeneration failure within tree populations has been shown to be driven by various mechanisms, including ungulate overbrowse (deer, Tremblay et al. 2007; moose (*alces*), McLaren and Peterson 1994) and climate-changed in-

duced loss of seed viability (Verheyen et al. 2009).

In this study, we examined the regeneration status of a pignut hickory (*Carya glabra*) population on St. Catherine's Island, Georgia, over the course of 11 years. We hypothesized that these small, remnant pignut hickory populations on St. Catherine's Island are no longer regenerating and, therefore, represent a temperate example of Janzen's (2001) "living dead" phenomenon.

METHODS

Study Site

The cultural history, physiography, and biota of St. Catherine's Island are typical of barrier islands on the southern Georgia coast (Thomas et al. 1978; Coile and Jones 1988; Bratton and Miller 1994). St. Catherine's is a private, undeveloped island with an interior maritime forest and a long history of land use (Thomas et al. 1978). Most of the island interior was cleared and used to farm Sea Island cotton between 1800 and 1860 (Thomas et al. 1978; Coile and Jones 1988). Cattle (*Bos*) production in the mid-1900s, along with consistently high densities of deer, resulted in a severe browse line across the island (Coile and Jones 1988). Feral pigs (*Sus scrofa*) have also been present on the island since the 1950s and have been increasing in density (Thomas et al. 1978).

Small forested areas between fields were left intact, and today these remnant stands of primary forest exist on low ridges that separate former agricultural fields, interspersed throughout a matrix of second growth that is dominated by second generation pine (*Pinus* spp.) (Coile and Jones 1988). Pignut hickory is a common canopy species in many of these small, isolated primary forest fragments on St. Catherine's Island and other southern Atlantic barrier islands (Coile and Jones 1988; Bellis 1995). The large seeds of this species are poorly dispersed and represent an important food source for feral hogs resident on the island (Wood and Roark 1980). Pignut hickory foliage is also a preferred browse of white-

tailed deer (*Odocoileus virginianus*) (McCarthy 1994). Adult pignut hickory trees are known for their age longevity (300+ yrs, Trimble 1975).

A 100-m x 60-m plot was centered within one of the larger remnant pignut hickory populations located in the island's center. Canopy and subcanopy species included red bay (*Persea borbonia*), American holly (*Ilex opaca*), red cedar (*Juniperus virginianus*), black cherry (*Prunus serotina*), sparkleberry (*Vaccinium arboreum*), and sweet gum (*Liquidambar styraciflua*), but the majority of the canopy was occupied by pignut hickory, which comprised 64% of the total community basal area (23.4 m²/ha) in 2006. The understory of this forest was characterized by patches of saw palmetto (*Serenoa repens*) among areas of grass.

Stand dynamics

Within the plot, all hickory individuals were assigned to one of four size classes: seedling (< 0.5m in height), sapling (≥ 0.5 m ht. but < 5cm dbh), pre-adult (≥ 5 cm dbh but < 30 cm dbh, which corresponded to those individuals that were determined through observation to be non-reproductive within the stand), and adult (≥ 30 cm dbh, reproductive). A stratified random sample of pre-adults and adults (n = 27) were cored using an increment borer and their ages determined from ring counts. Each individual was mapped within 30-m x 10-m subplots (n = 20), and subsequently censused for growth (change in height or dbh), survivorship, and recruitment repeatedly over an 11-year period (1996, 1997, 1998, 2001, 2003 and 2006). Average annual recruitment rates to larger size classes were calculated based on size-class transitions that occurred within the population over the 11-year study period. Recruitment and mortality probabilities, observed throughout the 11 years, were used to calibrate a size class population projection model (Figure 1). By assuming this model's parameter values remain unchanged and external disturbances do not interfere, we were able to calculate the size-class-based abundance trends in the population for the next 200 years.

Seedling microsite association

A representative 300 m² subplot was mapped within the plot, displaying ground cover type and point-locations of all hickory seedlings. Ground cover types included: fallen logs, dense palmetto, grass, and bare ground. A chi-square analysis was used to test whether the actual number of seedlings found within palmetto cover differed significantly from what would be expected given a random spatial distribution, which would suggest microsite protection from hogs and/or deer.

RESULTS

Age determination

A strong correlation ($p = 0.0025$, $R^2 = 0.758$, $n = 27$) was found between hickory tree diameter and age. Using this regression analysis, we estimated the approximate ages of all hickories within the study sites with the following equation:

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

The addition of 10 years at the end of the above equation accounted for the approximate number of years necessary for a pignut hickory sapling to grow to breast height in sandy soils (based on data from Boisen and Newlin 1910). Using this regression, we determined that the youngest hickory (larger than a seedling) at the study site in 1996 (dbh = 5.5cm) was 65 years, and the oldest (dbh = 67.2cm) was 219 years.

Recruitment failure

In 1996, the pignut hickory populations in St. Catherine's maritime forests were conspicuously lacking a sapling size class (< 5cm dbh), and a total of 116 living hickories were found. Of these, 71 were found to be pre-adults and 45 were adults (Figure 2). The ages of the youngest trees at the site align with the date, provided in Thomas et al. (1978), when hogs were first introduced to the island (1950s). Between 1996 and 2006, there was no recruitment from seedling to sapling size class or from the sapling to pre-adult size class. No seedling

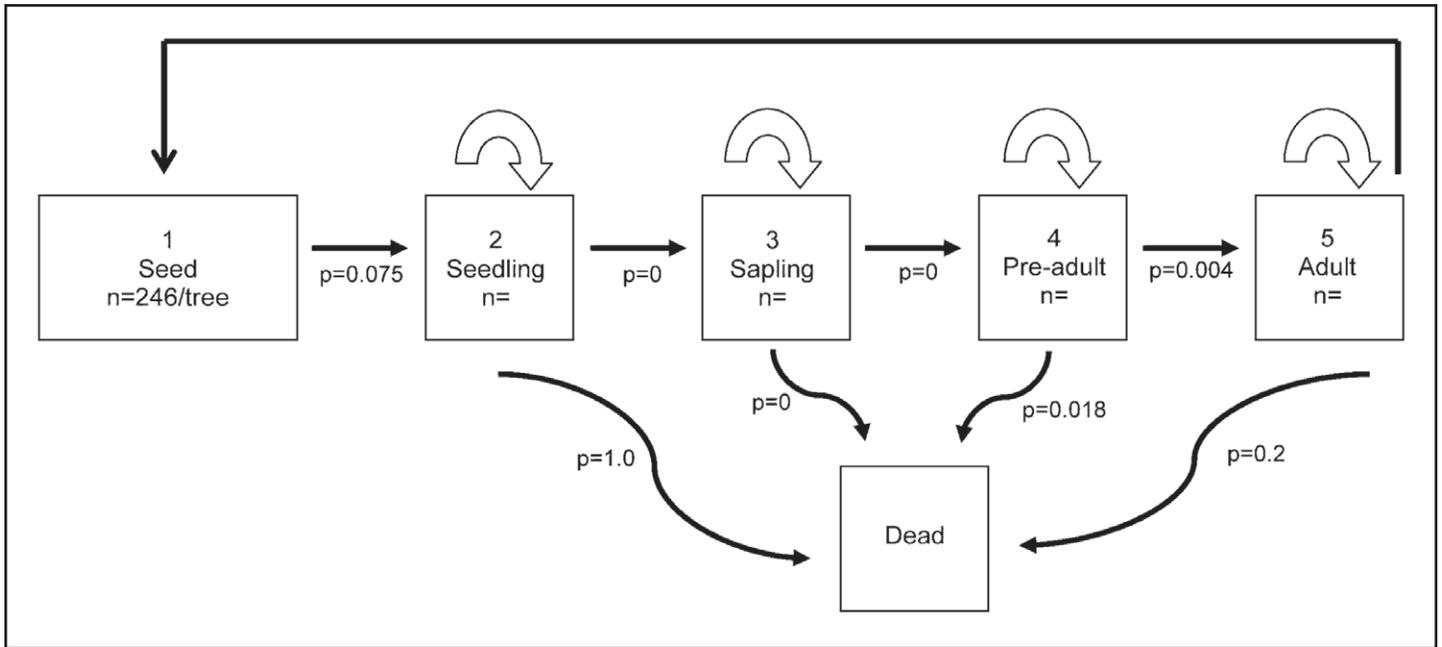


Figure 1. Illustration of size class projection model for pignut hickories, with mortality and recruitment rates determined over course of 10-year study. Average seed production per adult hickory ($n = 246/\text{tree}$) taken from Sork (1983).

survived longer than four years.

Over the course of the 11-year study, three pre-adults grew into the adult age class within the study plot. The average rate of recruitment between these age classes was 0.004 trees/yr. Of the pre-adult and adult hickories recorded in 1996, 19 had died by summer 2006, reducing hickory basal area in the stand from 17.4 m^2/ha in 1996 to 14.9 m^2/ha in 2006. Individuals that died included 10 pre-adults (14% of 1996 population) and nine adults (20% of 1996 population). The average survival rate, therefore, was 0.982 and 0.980 trees/yr for these two size classes, respectively.

Seedling distribution analysis

Our analysis of spatial patterns of seedling distribution suggested microsite protection as an important factor in seedling survival. Using the 300- m^2 detailed map, we found that the actual number of seedlings found within palmetto cover differed significantly from that expected given a random spatial distribution (Chi-square goodness of fit of a Poisson distribution. $\chi^2_{0.05,1}$, $n = 59$. $p\text{-value} < 0.0001$). The strong, positive association from this chi-square test indicates that microsite protection greatly enhanced the probability of seed germination success and temporary survival. We observed

that most seedlings showed evidence of repeated deer browse. There was also

widespread soil disturbance throughout the plot caused by feral pig activity.

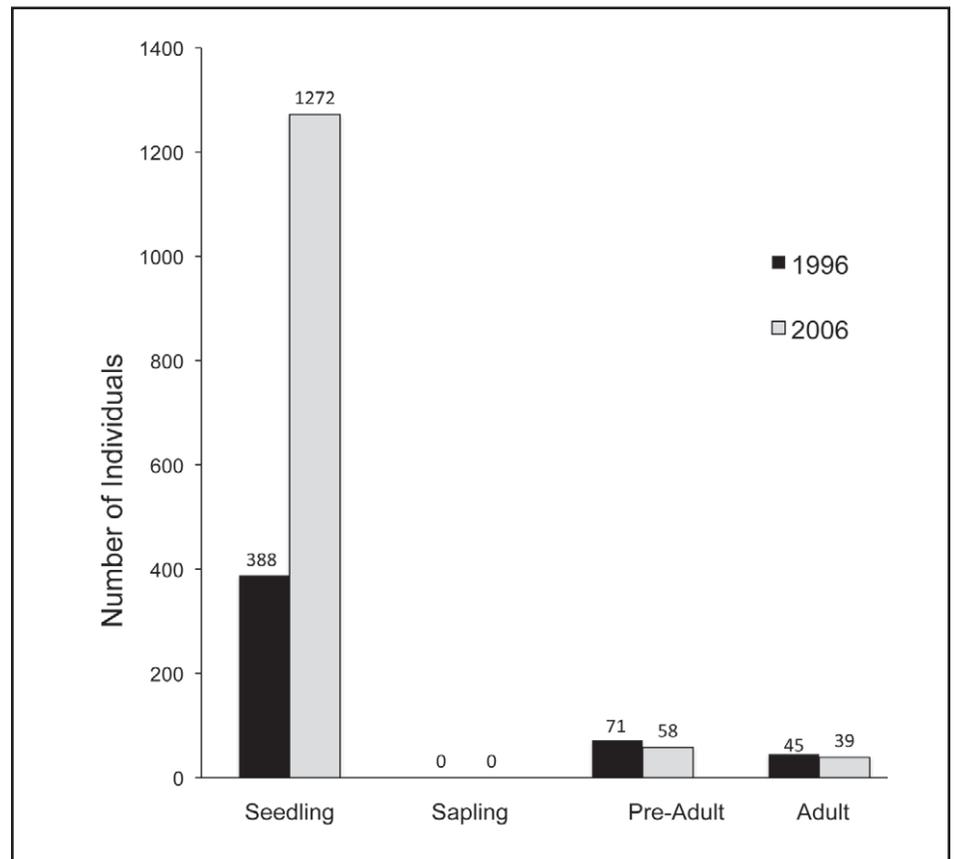


Figure 2. Comparison of pignut hickory size class distribution within the 0.6 hectare study plot population, comparing 1996 to 2006.

Future demographic projection

Average mortality rates, survival probabilities, and recruitment rates were calculated from the 11-year demographic analysis and incorporated into the population demographic projection model (Figure 1). Using an average annual production of 246 seeds per adult tree (Sork 1983), and the average annual establishment of 20.6 seedlings per adult tree, we calculated that there was a 7.5% probability of a seed becoming established as a seedling each year within the plot.

The model projected a high rate of population decline (Figure 3), indicating that if these recruitment and mortality rates continue, less than 20 pre-adult and adult hickories will remain in 2050; by 2112, approximately five will be left within our study site. As pre-adult individuals recruit into the adult class without sapling recruitment to compensate, the decline of the pre-adult size class will be relatively more precipitous than that of the other size classes.

DISCUSSION

The recruitment of new hickory individuals into the canopy of this population ended more than 60 years ago. The absence of saplings and the complete lack of recruitment of seedlings into saplings over the 11-year study period indicate that the sapling stage is the bottleneck that is preventing stand regeneration. The strong relationship in our study between seedling distribution and protected microsites (e.g., palmetto thicket), as well as the observed evidence of browse, suggest that herbivory may be the limiting factor preventing sapling recruitment within this remnant stand. These factors have been identified in similar cases in the literature. For example, Forrester et al. (2006) found that white-tailed deer were responsible for recruitment failure in a number of hardwood species on Fire Island National Seashore, New York. They predicted that deer overbrowse would lead to major changes in forest composition within this maritime forest over time. Tremblay et al. (2007) found an inverse exponential relationship between deer

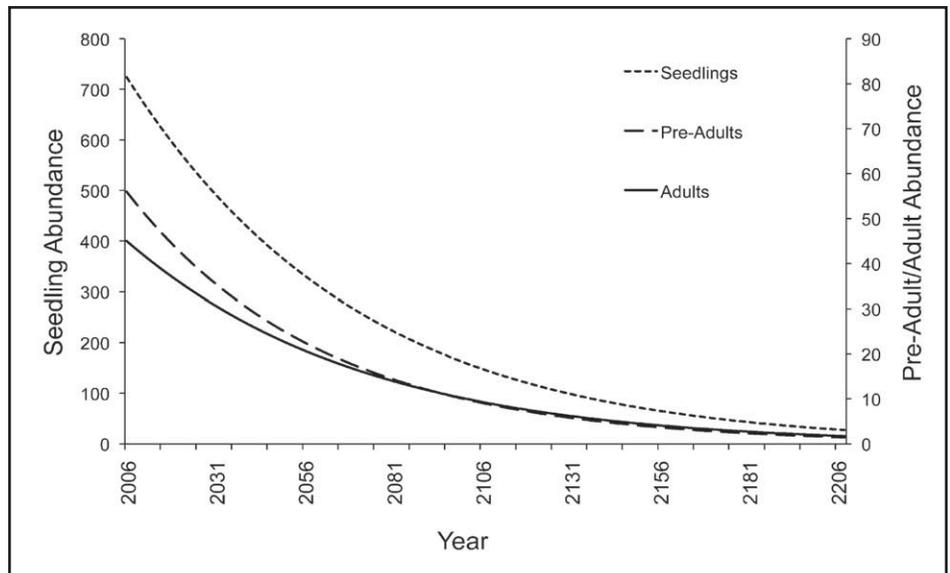


Figure 3. A projection of pignut hickory density (indiv./0.60 ha) at this site into the next 200 years, using a size class projection model, parameterized with recruitment probabilities and mortality rates based on 1996 - 2006 data.

density and regeneration rates in the boreal forests of Anticosti Island, Quebec. White-tailed deer, which have a strong presence on St. Catherine's Island, have been documented to browse preferentially for hickories (McCarthy 1994; Russell et al. 2001). The regular removal of seeds by feral hogs may also be contributing to the regeneration failure by limiting seedling establishment to a restricted set of microsites within the stand.

Possible alternative mechanisms for this decline could include habitat changes caused by drought or light limitation within the understory. However, given the variable patterns of rainfall experienced on the island over the past 60 years, it is unlikely that there have failed to be windows of opportunity for successful sapling recruitment due to water limitation. Light availability in the understory has only increased over this time period as canopy trees have died and have not been replaced. Exclosure experiments (such as employed by Forrester et al. 2006) were not possible for this study, but would be valuable in the future for providing further quantitative evidence of the effect of herbivory as a mechanism for tree regeneration failure.

Without significant action on the part of the manager, it is unlikely that deer or

hogs will be effectively controlled on St. Catherine's Island. The model we present in this study represents a conservative depiction of this population's rate of decline. As noted above, the model assumes that recruitment and mortality rates would remain unchanged for the next two centuries. It is more realistic to expect that, given the stochasticity of disturbances on barrier islands such as associated with hurricanes, there will be higher mortality rates in certain years.

While the loss of a dominant canopy species could, in other circumstances, enable the proliferation of less competitive trees, in this case the decline of pignut hickory may be detrimental to the other species within the community. As the canopy within the hickory stand thins, there is potential for an increased volume of salt spray to reach the maritime forest floor, causing a decline in salt intolerant species (Eaton 1978; Zucchini 1980). Community composition will also change as the high level deer and pig activity within the hickory stand selects for more browse-tolerant or unpalatable species (Clark 1986; Husheer et al. 2003; Sherrill et al. 2010), such as *Pinus taeda* or *Sabal palmetto*, which are both increasing in abundance on the island (J.P. Evans, unpubl. data).

The conservation of biological diversity in barrier island maritime forests requires the maintenance of constituent small populations. Relative to most mainland forests, maritime forests are limited in size and are also isolated. While fragmented forests may function ecologically as islands (*sensu*, MacArthur and Wilson 1967), those of actual islands also harbor unlikely species assemblages, composed of species that co-exist either because of vicarious colonization events over time or because they have had continuous occupancy since the Pleistocene (Bellis 1995). Much of the unique diversity and conservation interest in these forests is manifest in the unique combinations of species that vary in composition from island to island. Many of these species, in a given forest, are represented by small, isolated populations. The conservation of representative maritime forests, therefore, requires special attention to the status of these isolated populations.

On the island level, the inherently limited coverage of maritime forests adds another dimension to the task of prudent conservation. Most barrier islands experience too frequent a disturbance interval (hurricanes, shoreline erosion, overwash) to allow extensive forest cover to be maintained. Maritime forests exist only as patches on portions of certain barrier islands that experience long-term stability (Bellis 1995). However, as noted, it is this relative stability that has made maritime forests particularly safe places for prolonged human land use, and this has further fragmented what are already inherently small, isolated forest patches on barrier islands (Lopazanski et al. 1988).

The recent acceleration of maritime forest loss along the Atlantic coast due to coastal development has prompted the acquisition of major natural area reserves in recent years (for example, state acquisitions by the North Carolina state government in Buxton Woods, Kitty Hawk Woods, Bald Head Woods, etc). While the main conservation goal for these reserves has been to set them aside from coastal development, they still face problems from internal pressures such as: feral animals (Taggart 2008), deer overbrowse (Forrester et al. 2006; Sherrill

et al. 2010), introduced pathogens such as red bay wilt (Koch and Smith 2008), invasive plants (Smith et al. 1997), and lack of fire (Bratton and Davison 1987). Due to the isolation and fragmentation of these island forests, the influence of these internal pressures is often amplified compared to the mainland. Because such small populations are particularly vulnerable to both external and internal pressures, Bratton (1986) suggested that in order to be effective, fire and feral ungulate management on barrier islands require policies that are more specific to maritime forests than general statewide protocols.

Maritime forest tree species that dominate the canopy of small stands, such as pignut hickory on St Catherine's Island, give the illusion of persistence when, in actuality, they may represent populations that are headed toward local extinction. Janzen (2001) referred to such species with long generation times that become reduced to small patches and have no reproductive future as "the living dead." Regeneration of tree species in tropical forest fragments tend to suffer from limitations in pollination and seed dispersal due to a break-down of mutualisms (Janzen 1986). In the case of pignut hickory of St. Catherine's Island, canopy individuals still produce viable seeds and seedlings; however, the regeneration bottleneck in this population is entirely a function of sapling recruitment failure.

It would appear from this study that rescuing this species and others like it from the fate of the "living dead" requires both a recognition of the problem and an active, *adaptive* management program that would control for the effects of deer overbrowse and hog disturbance, allowing saplings the opportunity to survive in the forest understory. It is not sufficient to simply set aside lands from the coastal development and assume that the species have been protected from human interference. Natural area management of maritime forests requires an understanding of internal pressures that are often a manifestation of historical land-use practices such as the establishment of feral animals and the overabundance of native herbivores (Bratton 1986; Wood et al. 1987; Sherrill et al. 2010).

Here we propose that tree-size-class distributions can serve as an indicator of population health in maritime forests, and we recommend the collection of baseline demographic data on focal tree species. Demographic data suggesting regeneration failure can be followed up with enclosure experiments to confirm the effect of herbivore impacts. Results from such studies should be used to inform adaptive management policies and justify potential mitigation measures. The tracking of small populations enables managers to have their finger on the pulse of stand dynamics in these forest fragments and to allow them to effectively conserve their biodiversity.

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