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Population dynamics of the rare threatened gooseberry Ribes echinellum

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An abstract of
A thesis submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

Population dynamics of the rare threatened gooseberry Ribes echinellum

By Joseph Ives Stockert

The Miccosukee gooseberry, Ribes echinellum, is a federally listed shrub endemic to the Southeastern United States. It has an extremely narrow distribution: only two populations are known to exist, one in McCormick County, South Carolina, and one in Jefferson County, Florida. Reports of a possible decline in abundance in the Florida population have emerged from long-term monitoring efforts; however, these findings are difficult to interpret due to a paucity of information on the biology and ecology of the species. Additionally, comprehensive monitoring efforts ceased a decade ago. We established eight permanent plots in each population for the collection of demographic data over multiple years. We identified differences in the rate of reproduction, growth, and survivorship between the two populations, between local habitats within each population, and between plots that were fenced to control herbivory versus plots that were left open. These vital rates will be used to build a model of overall population dynamics, including population growth rate and long-term viability, using an integrated population model approach. The results of this study will ultimately inform efforts to conserve the species.

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Introduction

Biodiversity of Rare Plants

Estimates of the total number of plant species on Earth come with a degree of uncertainty. Some 2,000 new species are named each year (Cheek et al., 2020), while new standards rewrite existing lineages and new methods emerge to collate a massive and distributed set of global species observation data – over 390 million herbarium specimens from 182 countries (Thiers, 2022) – which in and of itself introduces biases due to differential representation and access across regions with varying resources. However, multiple studies over the past two decades have concluded that the total number or known flowering plants is somewhere around 430,000 species (Dirzo & Raven, 2003; Enquist et al., 2019). Out of all known flowering plant species, about 35% of the total number are considered rare (Enquist et al., 2019).

Three criteria have been used to define plant species rarity: limited geographic range, low local abundance, and high habitat specificity (Rabinowitz, 1981). Species are considered more or less rare depending on the degree to which they meet these criteria. Studies on the drivers of rarity have suggested that these three attributes are correlated (Slatyer, Hirst, & Sexton, 2013), and that that local abundance scales with range size. Niche theory suggests that this range size-abundance relationship arises from variation in niche breadth. Generalist species, which can occupy a wider range of habitats, are able to occupy more area in a heterogeneous landscape (Sexton, Montiel, Shay, Stephens, & Slatyer, 2017). Since there is a positive association between range size and long-term species survivorship, it is surprising that species with extremely limited geographic ranges make up a significant percentage of total extant taxa, especially in the plant kingdom.

Relict species fall into two categories: taxonomic relicts or biogeographic relicts. The former refers to surviving members of once-widespread taxa that have largely become extinct, while the latter refers to species whose geographic distribution has become severely contracted by large-scale environmental change (Habel, Assmann, Schmitt, & Avise, 2010). Biogeographic relict species are, by definition, rare, but not all rare species are relictual.

Endemism, a term often used synonymously with rare, refers to species found in a single geographical area (e.g., a particular stream, island, or continent) and can be itself be separated into two categories: paleoendemism and neoendemism (Stebbins & Major, 1965). Paleoendemism is synonymous with biogeographic relicts. Neoendemism, on the other hand, refers to species that have evolved recently and have not achieved a widespread distribution, though they may or may not become more widespread in the future. Not all rare species are necessarily endemic. Using Rabinowitz's (1981) schema to define rarity, it is possible for a species to have a global distribution but limited local abundance (Enquist et al., 2019).

The Southeastern United States is a hotspot for endemic species: 1,817 species are endemic to the Coastal Plain (Noss et al., 2015). Many of the 189 temperate-deciduous forest species endemic to the US are found in the Southern Appalachian Mountains (Erlandson, Bellemare, & Moeller, 2021). The high degree of endemism in the Southeast is likely due to a relatively stable regional climate over the past 10,000 years. At a global level and across many different ecosystem types, there is evidence that climate refugia harbor high numbers of both paleo-and neoendemic species. Environmental stability of such refugia reduces extinction risk while discontinuity with the surrounding landscape promotes speciation (Harrison & Noss, 2017). Braun-Blanquet (1923, cited in Stebbins & Major, 1965) assert that to understand the trajectory of ecological communities, study of endemic species, their distribution, and provenance is a central requirement. Thus, categorizing *Ribes echinellum* and other endemic species as ancient or recently arisen can add evolutionary context to the story of changing landscapes in the Southeastern U.S. Conversely, identifying environmental and ecological features common to the landscapes that support the highest numbers of rare species can foster systematic, land-based conservation decision-making to efficiently address the habitat needs of many species at once (e.g., Critchlow et al., 2022).

Ribes echinellum

The Miccosukee gooseberry, *Ribes echinellum,* has been found in two distinct populations over a small geographic range located in the southeastern United States (USFWS 1985). The populations occur in the physiographic regions of the Red Hills of Florida and lower Piedmont in South Carolina. The two populations cover a total area of less than 12 km^2 (NatureServe 2009).

Ribes echinellum imparts a certain symbolism for the ecology and history of the land, as the plant is indicative of the complex relationships that bind humans and nature together. This connection begins with its common name: Miccosukee gooseberry. The Miccosukee people are an indigenous tribe, part of the Creek Nation. These groups lived on the southeastern coastal for thousands of years prior to European colonization. With increasing settlements and land acquisition by colonists, speakers of the Mikasuki language emigrated to, and still reside in, the Florida Everglades (Miccosukee Tribe, 2023). Associating native species with the indigenous people who shared their environment, either by recognizing ethnobotanical significance of the species or, as in this case, by referring to species by indigenous names (e.g., see Evans, 2020), serves to not only memorialize the original inhabitants in a landscape but also to recognize the rich relationships with the natural world that indigenous cultures cultivated over millennia

(McGregor, 2021). In spite of dramatic changes in the cultural, political and ecological landscape, the tribe, it's language and the gooseberry persist to date, although all three are considered rare and in danger of extinction.

In a more direct sense, the name refers primarily to the species' type locality. Lake Miccosukee is a lime-sink (Harper, 1921); a karst solution depression that funnels rainwater through permeable limestone bedrock layers directly into the Florida aquifer (Ahmed, Ye, Wang, Greenhalgh, & Fowler, 2021). Lake Miccosukee is in the Red Hills physiographic region, which straddles the border between Georgia and Florida and extends south to Tallahassee. The region is underlain by the unconfined, shallow Floridan aquifer which enables a high degree of exchange between surface and groundwater (USGS). Additionally, the Red Hills are home to some of the largest remaining patches of endangered longleaf pine forest, a historically important natural community (C. Frost, 2006) that once covered broad swathes of the Southeastern United States and now provides the last refuges for several highly charismatic endangered species. Land use change, such as clear-cutting longleaf pine for agriculture, has had have dramatic effects on local hydrology (e.g., Scanlon, Reedy, Stonestrom, Prudic, & Dennehy, 2005). Within large-scale aquifer systems such as the North Floridan, the consequences of such ecological change can be telecoupled (Reyers, Folke, Moore, Biggs, & Galaz, 2018), not only to other downstream ecosystems but also to human societies many miles distant, by shared water resources. The exchange between the Red Hills region and the Floridan aquifer serves as one example of the ties between human health and the health of ecosystem. Such connections are embodied, explicitly or implicitly, by efforts to conserve biodiversity broadly and protect rare species such as *Ribes echinellum.* That is, species such as *Ribes echinellum* remind us of our place in, and obligation to, intertwined social-ecological systems.

To those with an eye for aesthetics this plant is a pleasure to look at, perhaps due to the uniqueness of its character among the grays and browns of surrounding hardwood trunks (Coville, 1924). Beneath an explosion of emerald leaves – each blade three-lobed, with a toothy margin, fluttering from a long petiole – the slender woody stems of *Ribes echinellum* are covered in inch long, needle-like thorns. The stems, which grow in clusters of about a dozen, either stand tall, reaching up to one meter above the ground, or spread outward in great arcs. New stems, green, fleshy, and covered in prickly hairs, march out from the center of their parent clump at the end of these arcs; vegetative clones emerge wherever the tip of a stem touches the earth and sends out roots. On larger plants, dozens or even hundreds of pendant flowers dangle from the bows of lateral stems (Figure 1). Several species of bumblebees can be observed clinging, inverted, to the skirts of reflexed green-white petals (Catling, Dumouchel, & Brownell, 1998). In exchange for nectar, they cover their abdomens with pollen from the exposed anthers before moving on to the next flower. Once fertilized, the ovaries, covered in gland-tipped hairs, swell at the base of each flower; by summer, the plant is covered in marble-sized green fruit.

Figure 1: Photograph of *Ribes echinellum* stem in flower at Stevens Creek Heritage Preserve, McCormick County, South Carolina.

The fruits, like the stems, have evolved an intimidating display of spines, though their function is not well understood. Frederick Coville, a preeminent botanist of the day who was the first to describe this species, was inspired to give the epithet *echinellum* because of the hedgehog-like appearance of the fruit (Coville 1924). He postulated that the spines deter small mammals from feeding on the fruit but would allow birds to access the fleshy inside with their beaks. Intuitively, this strategy seems beneficial – birds typically have a larger range further and could provide a better dispersal mechanism than mammals. In reality, however, the spines provide little protection; cotton mice (*Peromyscus gossypinus*) have been observed eating the berries (Engstrom & Radzio, 2014). Seeds eaten by the mice are digested beyond the point of viability, affirming at least a part of Coville's theory.

Botanists first laid eyes on *Ribes echinellum* in 1924 during a visit to a floristically unique site on shore of Lake Miccosukee (Coville, Harper 1925). The community that Roland Harper described following his survey with fellow botanist Herman Kurz is a predominantly hardwood forest reminiscent of more northern latitudes in the Piedmont or Cumberland Plateau (Harper 1925). On a low bluff composed of sandy clay soils, Shumard oak (*Quercus shumardii)*, swamp-chestnut *(Quercus michauxii)*, sweetgum *(Liquidambar styraciflua)*, basswood *(Tilia sp.)*, white ash *(Fraxinus americana)* and Florida maple *(Acer floridanum)* were abundant large tree species. Harper notes the relative lack of mesic species such as live oak *(Quercus virginiana)*. Loblolly *(Pinus taeda)*, and southern magnolia (*Magnolia grandiflora)* were present in the canopy in low numbers; cherry laurel *(Prunus caroliniana)* and holly *(Ilex opaca)* in the mid-story, crossvine *(Bignonia capreolata)* and greenbriar (*Smilax smallii)* in the shrub layer. Late fall and winter sunlight, unimpeded by evergreen leaves, may be a key characteristic of the microhabitat that allows *Ribes echinellum* to persist at Lake Miccosukee. The gooseberry's phenology is unique: plants go dormant in the heat of late summer and begin to leaf out again in October (Harper 1925) as the canopy thins. Data collected by the South Carolina Department of Natural Resources (SC DNR) in Stevens Creek Heritage Preserve (where the second population is located) provide additional evidence that the species' distribution is constrained by sunlight: *Ribes echinellum* is most abundant beneath canopy gaps and areas with fallen trees (USFWS, 2008).

More than three decades after the publication of Coville's description, and 200 miles to the north, a second population of *Ribes echinellum* was discovered by Alfred Radford in another floristically unique setting (Radford, 1959). *Ribes echinellum* was found to be growing in a thick band along a system of rocky bluffs above Stevens Creek in McCormick County, South Carolina. Along with the gooseberry, several other species that had not previously been known to occur in the state were observed on the bluffs (Radford, 1959), including dutchman's breeches (*Dicentra cucullaria*), false-rue anemone (*Enemion biturnatum*), blue-eyed grass (*Sisyrinchium albidum*), heartleaf nettle (*Urtica chamaedryoides*), and tuberous gromwell (*Lithospermum tuberosum*). As with the Lake Miccosukee shoreline, the plant community at Stevens Creek was described a hardwood-dominant mixed mesophytic forest (Radford, 1959): canopy trees included hickories (*Carya sp.*), Florida maple *(Acer floridanum*), oaks (*Quercus sp.*), elms (*Ulmus sp.*), hackberry (*Celtis laevigata*), black walnut (*Juglans nigra*), tulip poplar (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*).

Following his visit to Stevens Creek, Radford (1959) proposed a theory to explain the disjunct geographic distribution of *Ribes echinellum* populations: the community found on the bluffs is a relict Pleistocene forest. He asserted that the flora at Stevens Creek is characteristic of communities in the Piedmont during the last glacial maximum and notes that similar relict forests can be found across the region on steep north-facing stream banks (Radford 1959). Fossil pollen collected from White Pond, South Carolina (about 50 miles southeast of Stevens Creek) indicates that the Coastal Plain was characterized by widespread oak-hickory communities, similar to the forest found at Stevens Creek, during a period of glacial retreat occurring between roughly 16,000 and 10,000 years before present (Krause, Russell, Zhang, Williams, & Jackson, 2019) Additionally, the White Pond pollen record provides evidence for a transition starting around 10,000 years before present to the *Pinus*-dominant forests that now cover much of the region as the climate became warmer, drier, and fire frequency increased (C. Frost, 2006; Robert J.

Mitchell, 2009). Following from the Pleistocene-relict scenario, *Ribes echinellum* would have evolved within an environment that did not burn frequently. Monitoring within the Florida population showed an insignificant increase in *Ribes echinellum* density for three years following application of fire (Slapcinsky, Gordon, & Menges, 2010), indicating that the species is not strongly fire-adapted. Species without fire-dependent life history strategies are unusual in the Coastal Plain, where only about 5% of the landscape was protected from fire pre-European settlement (C. C. Frost, 1995). Across the Coastal Plain, contemporary hardwood associations occur only on moist slopes and bluffs that are sheltered from fires in the pine uplands (NatureServe, 2022). These mesic hardwood-type forests may indicate Pleistocene refugia – areas where suitable habitat persists for species that evolved during the Pleistocene within a broader landscape that has largely become unsuitable – due to a microclimate has remained stable through the past 10,000. The cooler winter temperatures and wetter soils characteristic of northern aspect slopes (Fan et al., 2020), such as the bluffs above Stevens Creek and the shore of Lake Miccosukee, may have enabled the hardwood forest, and in turn *Ribes echinellum,* to persist by acting as a buffer against Holocene inter-glacial climate change.

Threats to Ribes echinellum

Biodiversity at the species level is subject to multiple threats including habitat change, invasive species, climate change, pollution, and overharvesting. The risk of extinction for rare and endemic species is much higher relative to taxa with wider distributions. Studies of the fossil record have documented a negative correlation between range size and probability of extinction throughout much of the history of life on Earth (Payne & Finnegan, 2007). In the Anthropocene, habitat loss (including both degradation and destruction) is the primary driver of extinction across taxa (Dirzo & Raven, 2003; Hernández-Yáñez et al., 2016; Pimm et al., 2014). Dirzo &

Raven (2003) estimate that current rates are at least 2 orders of magnitude higher than the background rate of 1 species per million species per year. In the United States and Canada, at least 65 plant species or varieties have become extinct in the past 500 years, 35 of which were known from a single location, including the Parish's gooseberry (*Ribes divaricatum* var. *parishii*) from California (Knapp et al., 2021). Intensive land use, either for recreation, agriculture, mining, housing, or infrastructure, threatens the majority of critically imperiled species in the continental United States, along with encroachment by invasive species or disruption of the natural fire regime (Hernández-Yáñez et al., 2016). However, many species face multiple threats at once, and the interaction of threats can amplify the effects of each (Lienert, 2004). As a result, efforts to conserve individual species need to target the threats associated with the local ecosystem and the target species biology, though land-based conservation should be a prerequisite for most species.

Conservation and management of *Ribes echinellum* populations are complicated because they are found on both public and private lands. Portions of the South Carolina population is found within the Sumter National Forest, which is managed by the US Forest Service. Other portions are found within Stevens Creek Heritage Preserve, which was established with the explicit intention to safeguard the site's unique flora and is managed by the South Carolina Department of Natural Resources. The Florida population spreads across three adjacent private ownerships. One landowner unit has recently come under conservation easement (USFWS, 2015), meaning that the rights to engage in intensive land use practices are restricted in the interest of protecting wildlife (Farmer, Meretsky, Knapp, Chancellor, & Fischer, 2015). A second landowner unit is managed by a timber company. While federal agencies are prohibited from engaging in activities that result in damage or destruction of threatened and endangered plants under the Endangered Species Act (ESA), no protections exist for listed plants on private property (Havens, Kramer, & Jr., 2014). When *Ribes echinellum* was listed as threatened under the ESA in 1985 (USFWS, 1985), uncertainty about possible development of the private parcels was considered a primary concern for the species; five-year reviews as recent as 2021 recognize that development is still a concern (USFWS, 2022).

As a listed species, the US Fish and Wildlife Service has reviewed the status, trends, and threats to *Ribes echinellum* at five-year intervals, beginning in 2008. Herbivory by white-tailed deer, seed predation by cotton mice, and rooting by feral hogs are ongoing threats (USFWS, 2008, 2015, 2022). White-tailed deer (*Odocoileus virginianus*) are more abundant now than any other time on record in the U.S. due to decreases in hunting pressure and the abundance of predator species (Côté, Rooney, Tremblay, Dussault, & Waller, 2004). Deer directly impact plant fitness during foraging by consuming leaves or fruits. The impacts of deer herbivory have been observed at the community level; presence of deer is negatively correlated with understory cover and richness, particularly for woody species (Habeck & Schultz, 2015). Importantly, white-tailed deer can reduce the reproductive capacity of rare plant populations (Darl Fletcher, Shipley, McShea, & Shumway, 2001). Like deer, feral hogs (*Sus scrofa*) damage plants and disrupt communities through foraging behaviors. Feral hogs are descended from escaped livestock and are considered invasive; their foraging involves overturning soil to access food sources below the surface (Felix, Orzell, Tillman, Engeman, & Avery, 2014). Like deer, feral hogs have been shown to negatively impact cover, composition, and structure of herbaceous plant communities (Gray et al., 2020).

Inbreeding depression, where an increase in inbreeding has a negative effect on fitness, may also pose an additional threat to the persistence of both *Ribes echinellum* populations. The impact of genetic drift increases as population size decreases, leading small populations to lose genetic diversity faster than large populations (Ouborg, Vergeer, & Mix, 2006). Oleas, von Wettberg, and Negrón-Ortiz (2014) performed the only genetic study conducted on *Ribes echinellum*, in which they analyzed DNA from 102 individuals in Florida and 28 individuals in South Carolina to assess the genetic structure of each population. They found that genetic diversity (measured by number of alleles at seven loci and number of heterozygotes) was low in both populations, but especially in South Carolina; they also identified nine clonal individuals in each population and evidence that the Florida population has recently gone through a population bottleneck. The interpretation of these data paint an interesting picture when field observations are taken into account: 1) plants in South Carolina appear to be growing more vigorously and set more fruit than plants in Florida (see Results), which could indicate a recent switch from asexual to sexual reproductive strategies in response to the genetic paucity caused by vegetative growth (García, Ávila, Quesada, & Caballero, 2013) or to an environmental stressor. 2) In his description of the species, Coville (1924) theorized that the Florida population was recently established (though he did not provide evidence for this theory). The finding of a bottleneck in the Florida population (Oleas et al., 2014) could provide support for Coville's theory and point to a founder effect, meaning the South Carolina lineage is ancestral to the Florida lineage.

Of immediate conservation concern is the impact of low genetic diversity on *Ribes echinellum* population dynamics. Negron-Ortiz (2018) found that neither population produced viable seedlings, possibly indicating the species is already impacted by inbreeding depression, though environmental variables may also have contributed: the study found evidence of self-incompatibility through hand-pollination experiments, which could negatively impact seedling fitness in the absence of a pollinator. Additionally, they note that abnormally low soil moisture during the Spring germination period may have also contributed to the absence of seedlings. However, in the same study, Negrón-Ortiz (2018) estimated *Ribes echinellum* abundance at Lake Miccosukee by re-sampling permanent transects that were established by The Nature Conservancy (TNC) in 1992 and used to count *Ribes echinellum* individuals until 2001. Comparing the new counts to the results of the original survey, Negrón-Ortiz (2018) identified a significant change in abundance between 1992 and 2012, though the direction of change was ambiguous: the total number of *Ribes echinellum* patches decreased by 51% in the southern portion of the Florida population, but doubled in the northern portion. The study (*op cit*) was not able to definitively link changes in abundance to the lack of viable seedlings.

Conservation of *Ribes echinellum* is hindered because of a lack of information on whether the populations are increasing or decreasing and incomplete information on processes that influence population changes (Schemske et al. 1994). To address these knowledge gaps, the USFWS set a number of priorities for research, including 1) establishing permanent monitoring plots to collect baseline estimates of abundance and population dynamics, 2) fencing areas within each population to reduce the impacts of deer and hogs, 3) assessing and mitigating the impacts of invasive plant species including privet (*Ligustrum sinense*) and honeysuckle (*Lonicera japonica*), and 4) conducting additional reproductive biology studies (USFWS, 2022). To fill these gaps, the USFWS has established a collaborative partnership with the personnel at the Conservation and Research department of the Atlanta Botanical Garden. This partnership resulted in the present study, which aims to use demographic data and modeling tools to describe *Ribes echinellum* population dynamics.

Dynamics of plant populations

Demographic approaches are well-suited to the study of rare species because they can be used to predict species persistence into the future and shed light on specific biotic or abiotic interactions that define a species' ecology (Griffith, Salguero-Gomez, Merow, & McMahon, 2016). Demography has been used to study plant populations since at least the 1970s (Werner & Caswell, 1977), though multiple demographic models have been continuously developed throughout the past 3.5 centuries (Caswell, 2001). Together, they form a statistical framework for analyzing rates of births, deaths, and migrations (termed vital rates) in order to identify larger patterns of overall population growth, stable population parameters, and long-term population behavior (Caswell, 2001).

Most modern demographic analyses build on Leslie matrices; matrices containing probabilities of transitioning from one age- or size-class to another can be constructed from graphical models of a species' life cycle and data collected repeatedly on individuals over multiple years. Eigen analysis of the resulting transition matrix provides estimates for the transient population growth rate $\boldsymbol{\lambda}$ corresponding to the dominant eigenvalue, while the size and structure of the population in year $t+1$ can be projected by multiplying the transition matrix by the population size in year t. Matrix population models have been widely applied to the study of rare plant population dynamics; studies have used matrix models to assess the population dynamic effects of deer herbivory, habitat variation (Bermingham, 2010), inbreeding depression (Bladow, Bohner, & Winn, 2017), clonality (Berg, 2002; Lin, Miriti, & Goodell, 2016), fire, and management regimes (Gross, Lockwood, Frost, & Morris, 1998).

However, the use of matrix models for plants is problematic, in a statistical sense (Doak et al., 2021), because most studies of plant demography use measurements of size as the state variable that indicates an individual's position in their life cycle and in turn defines the probability that an individual grows, reproduces, or dies. To fit the structure of a matrix model, wherein transitions occur between discrete states, these continuous measurements must be discretized; selection of size classes can rest on incomplete knowledge of complex life cycles (Ellner & Rees, 2006) or rely on algorithm that make contested assumptions about the acceptable error within classes (i.e., Moloney, 1986). Additionally, matrix models preform worse for small datasets, which are inherent to studies of rare species with few populations or low abundance (Ramula, Rees, & Buckley, 2009).

Easterling, Ellner, & Dixon (2000) proposed a new type of demographic model, known as integral projection models (IPMs) that are better suited to the use of continuous state variables such as size. IPMs are built on a probability density function, called a *kernel*, that takes the general form:

$$K(z', z) = P(z', z) + F(z', z) \quad \text{(eq. 1)}$$

where *z* represents the state of the individual, generally specified as a measure of size, at time *t* and *z'* represents the state at time $t + 1$. *P(z',z)* is called the survival kernel component and describes the combined probability of survival from time *t* to *t + 1* given an initial state *z*, and the probability of transitioning from state *z* to a state *z'*. These probabilities are parameterized as functions *s(z)* and *G(z',z);* the survival kernel component can be written as*:*

$$P(z', z) = s(z) * G(z', z) \quad \text{(eq. 2)}$$

The reproductive kernel component *F(z', z)* describes the probability of producing recruits of state *z'* given a parent state *z*. Whereas the survival component generally takes the form in equation 2 regardless of species, specification of the reproductive component is more variable; reproductive kernels for plant species can be particularly complicated because complex life history traits, such as seed bank persistence across multiple years, must be accounted for (Ellner & Rees, 2006). As an example illustrating the specification of a reproductive kernel with species-specific model parameters, Ellner & Rees (2006) define *F(z',z)* for the thistle *Onopordum illyricum* as:

$$F_{a,k,j}(z',z) = \alpha_j \varphi_0(z') S(z,a,k) \tag{eq. 3}$$

where α describes the fraction of seedlings in quality class j, φ describes the seedling size probability density, and S describes a per-parent fecundity based on size, age a, and quality class k.

Multiplying the kernel by *n(z,t*), or the number of individuals of state *z* at time *t,* and then integrating the product over a range of states provides an estimate of the population size and structure at time *t+1* (Rees, Childs, & Ellner, 2014):

$$n(z',t+1) = \int_L^U K(z',z)n(z,t)\,\mathrm{d}z \tag{eq. 4}$$

where L and U are minimum and maximum values for the state variable *z.* Iteration over many time steps results in a simulation of population dynamics, including changes in abundance and convergence around a stable state distribution. IPMs provide more flexibility in comparison to matrix models because the vital rate functions that make up each component kernel (e.g., the functions *s(z)* and *G(z',z)* in the survival kernel) can be parameterized from a variety of different models, including general linear models (GLMs), and can incorporate discrete or continuous state variables, or combinations of state variables. IPMs have been leveraged to analyze demographic data from complex experimental designs assessing spatially-variable habitat suitability (Diez, Giladi, Warren, & Pulliam, 2014), impacts of climate (Dalgleish, Koons, Hooten, Moffet, & Adler, 2011), and drivers of demographic variation between populations (Römer et al., 2021).

The goal of this study was to contribute to the understanding of factors that influence population changes of *Ribes echinellum,* especially rates of growth, flowering, germination, and survivorship. Establishing monitoring plots in both populations will allow for repeated measures of survival, growth, and reproduction of individuals, these data can be used to estimate population vital rates and population growth rates. Comparing vital rates and growth rates between the Florida and South Carolina populations, effects of grazing and intrapopulation variability will point to key genetic or ecological conditions that facilitate positive population outcomes.

This thesis describes the process of estimating vital rates, which are key parameters of *Ribes echinellum* population model. This work is an essential first step toward the goal of building an IPM that describes overall population dynamics. To avoid the pitfalls of model overfitting, this study attempts to establish relationships among vital rates and population, site, or herbivory effects so that these variables can be appropriately included in a demographic model. Data were collected over two years using a study design that captured variation between populations, spatial variation across microhabitats within populations, and the effects of an herbivore exclusion regime. Hence, three hypotheses were evaluated in this thesis.

H_1: Vital rates and population growth rates are significantly different between the Florida and South Carolina population. This variation implies a population-level effect, such as genetic diversity, on vital rates.

H_2: Vital rates vary between sites within each population. This variation implies an environmental constraint on vital rates, such as soil nutrients, slope angle, hydrology, or light availability.

H_3: Vital rates are affected by herbivory. This variation implies that herbivore pressure is limiting population growth and management interventions may improve species viability.

Methods

Study sites

Populations in Florida and South Carolina were sampled (Figure 2). The Florida population spans three separate private landowner parcels: Norias Plantation, Mays Pond Plantation and the van Reed property. The South Carolina population spans two separate public landowner units; Stevens Creek Heritage Preserve and Sumter National Forest. In both cases, the boundaries between landowner units correspond to a midline between each population's northern and southern halves.

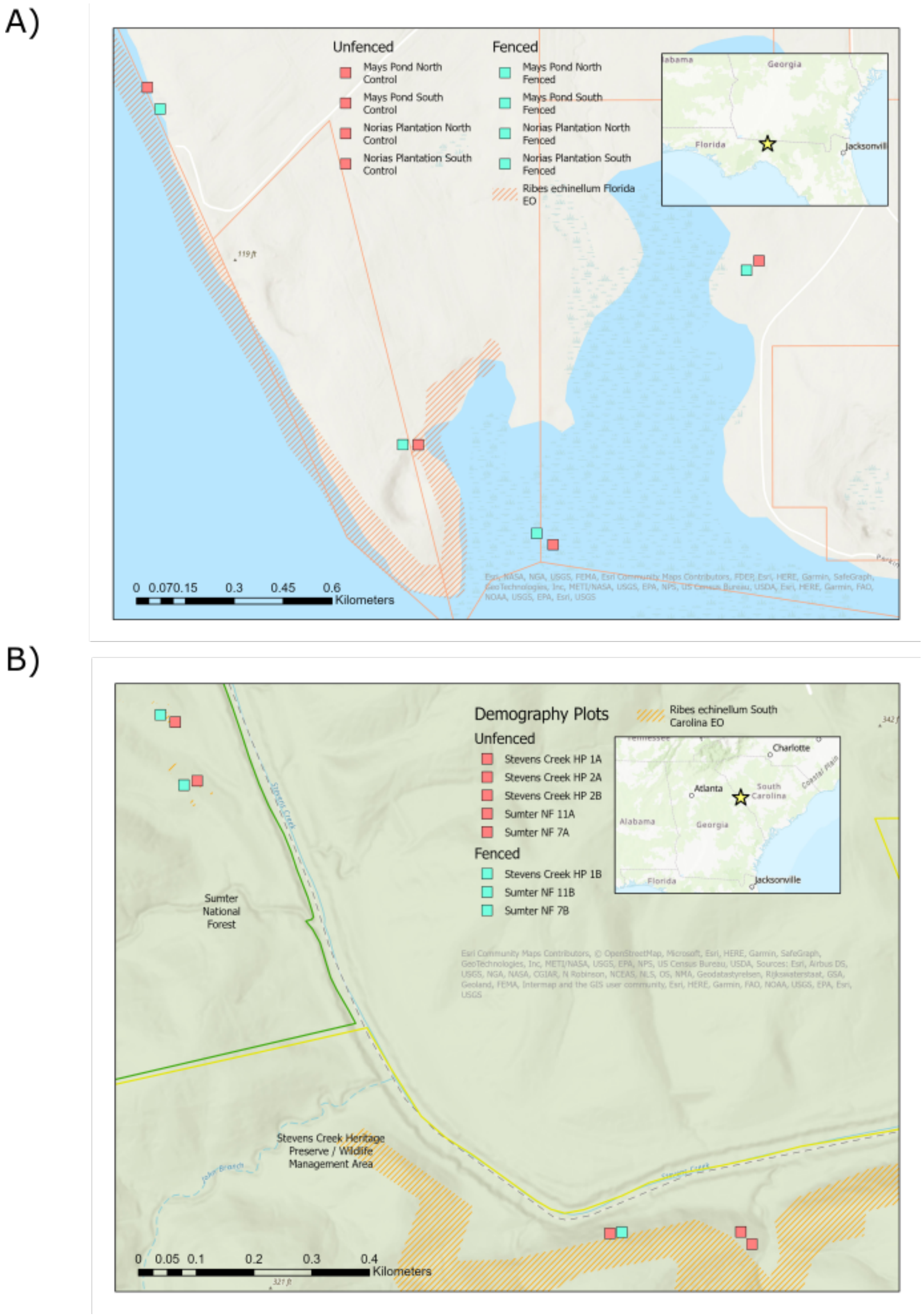

Figure 2: Locations of *Ribes echinellum* populations in (A) Jefferson County, Florida and (B) McCormick County South Carolina. Element Occurrence (EO) data provided by the USFWS are shown as orange hatched polygons and represent the boundaries of contiguous areas where *Ribes echinellum* is known to occur. Lines on the map represent boundaries between landowners. Colored squares represent location of paired demography sample plots; blue squares are fenced plots; red squares are unfenced plots.

Study sites were chosen opportunistically, located in areas of the highest plant density within each landowner unit. Each plot had different environmental features, such as vegetation community, topography, soil composition, or management history. Plots were placed in the northern and southern areas of both populations, resulting in a roughly even north-south distribution of plots. The following is a brief description of the environmental features at each site of the four study sites:

Stevens Creek Heritage Preserve is characterized by a system of granitic bluffs. Plots were located on steep north-facing slopes with mineral, and organically rich, rocky soil. The organic layer is slightly alkaline, while the soil within an inch of the underlying syenite is highly acidic (Radford, 1959). Two plots were installed along a drainage about 100 meters south and 10 meters above Stevens Creek. This area was characterized by the densest patches and largest individuals of *Ribes echinellum* and the highest herbaceous cover of any study site in South Carolina. Two plots were installed on a bench about 5 meters above Stevens Creek.

Sumter National Forest is characterized by a lower slope angle, sandier soil, and an absence of visible rock. The patches of *Ribes echinellum* that are generally smaller and less continuous than at Stevens Creek. Patches in SNF are found along wide berms between seasonal drainages feeding into Stevens Creek. The forest around the patches in SNF is more typic hardwood with a high abundance of river cane (*Arundinaria sp.*). Two plots were installed on a flat, open area, while the other two were installed on a low slope.

Mays Pond is characterized by low-lying hardwood hammocks surrounding seasonally wet bald cypress (*Taxodium distichum*) sloughs. The midstory in MP is dense with young trees, shrubs, and grapevine, though one plot (MPSA) was installed in a more open area under mature canopy trees.

Norias Plantation is characterized by low slopes near white-tailed deer feed lots. Two plots were installed under hardwood forest with an open midstory on a west-facing slope above

Lake Miccosukee. The soil at this site is slightly acidic and rocks are absent within 3 feet of the surface (Harper, 1925) The other two plots were installed on an east-facing slope above a slough with a dense shrub layer and midstory composed of cherry laurel (*Prunus caroliniana*) and grapevine (*Vitis* sp.).

Demography surveys

Two pairs of 5-meter by 5-meter plots were established at each of the four study sites for a total of eight plots within each population. Plots were situated to sample approximately 400 individuals from each population, following field sampling protocols for matrix population model development (Halbritter et al. 2020).

To assess whether deer herbivory posed a threat to the stability of *Ribes echinellum* population dynamics, 7-foot exclusion fences were erected around the perimeter of one plot from each pair (see Figure 3 for experimental design schematic). However, fencing was not permitted around either of the plots visible from the Stevens Creek Heritage Preserve hiking trail both to reduce interruption to the visitor experience and to reduce the risk of tampering. Additionally, motion-activated game cameras were located at each unfenced plot to confirm that white-tailed deer are browsing on *Ribes echinellum*.

Demographic data were collected in early spring of 2022 and 2023 while *Ribes echinellum* was in flower. The South Carolina population was visited during the week of March 6th in both years. Data from the Florida population was collected during the week of March 15 2022. Flowers were fading, pollinated (ovaries swollen) or falling from the plants (petioles present without flowers), so the 2023 survey was conducted two weeks earlier, during the week of February 27 2023, to coincide with the peak flowering period.

During the 2022 surveys, all individuals within each plot were marked using aluminum tags stamped with a unique number. The tags were placed onto sod staples, which were driven into the soil on the north side of each individual. The growth pattern of *Ribes echinellum* made it difficult to distinguish one individual from another, as stems emerge from rhizomes underneath the soil and stolons connect new vegetative growth to parent plants. To address this ambiguity, any stems that fell within 10cm of their nearest neighbor were considered to be part of a single individual, or conversely, individuals were separated by a minimum distance of 10cm. This definition was used during previous *Ribes echinellum* monitoring studies in Florida (Negrón-Ortiz, 2018).

For each individual, the number of woody stems, the number of green stems, the number of flowers were counted. The length of the longest stem, the width of the individual at its widest point, and the maximum height above ground were all measured using a tape measure.

During the 2023 survey, tagged plants were located using a metal detector wand. If a tag was recovered and either all stems were dry and leafless or no stems were found, the individual was considered to be dead. Some tags came out of the ground (possibly pulled up by animals). For these tags, data from the previous year and best judgement were used to re-identify the associated individual. Untagged individuals that could have either emerged within the past year or fractured off another individual were assigned new tag numbers. 26 tags placed in 2022 were either not found in 2023 or unable to re-identify the associated individuals. These plants were excluded from further analysis.

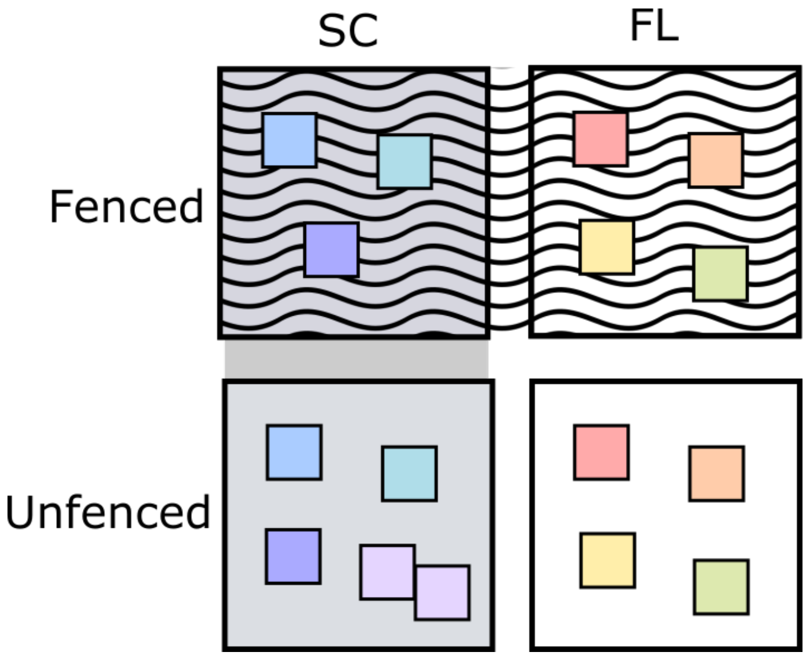

Figure 3: Schematic of the demography survey experimental design. Together, the large grey boxes (upper and lower left) represent the total population in South Carolina, while the large white boxes (right) represent the total population in Florida. The patterned boxes (upper left and right) represent the subset of demography plots that were fenced to control herbivory. Each colored square represents a single demography plot; same-colored boxes (within each population) indicate pairs of plots that were installed at the same site. The treatment variable is nested within sites, which are nested within each population, so interaction effects between site and population, treatment and population, and treatment and site were analyzed along with the effect of each variable independently.

Germination trials

To assess fecundity, 16 ripe fruits from 5 plants near the Norias Plantation North site in Florida were harvested on May 18 2022. The seed were extracted from the fruit and used for germination trials at each Florida plot over the course of ten months. The seeds were separated from each fruit by rubbing the pulp across a mesh screen and washing with water. The number of seeds per fruit was recorded. The seeds from all fruits were pooled. Five seeds were selected randomly from the pool and placed into organza bags. On the outside of each demography plot, four bags were placed under about 2cm of soil, tying each bag to a sod staple with an aluminum tag. A 0.5m diameter wire cage, constructed of chicken wire capped with plastic mesh fencing material was placed over each bag. On June 15 2022, 13 fruits were harvested from eight plants located near the Heritage Preserve 1A site South Carolina. All sites were revisited during the 2023 field survey dates listed earlier. The number of seeds that had germinated, as indicated by the presence of cotyledons or hypocotyls was recorded.

Data analysis

All data cleaning, exploration, analyses, and visualization were conducted using R version 4.4.2 (R Core Team, 2022). The number of individuals in that survived or died were compared between populations or treatments using Chi-squared tests of independence; comparisons between sites or plots were performed using Fisher's exact tests because the number of dead individuals was often less than five. The number of plants that flowered or not were compared between populations, treatments, sites, and plots using Chi-squared tests of independence. The number of seeds that germinated or not were compared between populations, sites, and plots using Fisher's exact tests.

Survival rates were calculated by dividing the number of survivors in 2023 by the total number of individuals tagged in 2022, and mortality rates were calculated by dividing the number of dead individuals in 2023 by the total number of individuals tagged in 2022. Germination rates were calculated by dividing the number of seeds in each organza bag that germinated by the total number of starting seeds, which was 5 in all cases.

Point-biserial Pearson correlations were calculated comparing survival outcome with each of the size variables (number of green and woody stems, length of longest stem, height, width, and volume).

Plants size varied among the plots (Figure 4A), so to make comparisons between the size of individuals that survived and the size of individuals that died, each measurement was normalized by dividing by the median within each plot (Figure 4B). Non-parametric statistical tests were to analyze height data because height data were positively skewed, a Shapiro-Wilks test for normality rejected the null hypothesis that height data are normally distributed ($p < 0.001$), and a Levene's test for homogeneity of variance likewise rejected the null hypothesis that variance between height measurements was equal across groups ($p < 0.001$). Wilcoxon rank-sum tests were used to compare both normalized heights and number of flowers across two groups (e.g., between populations or between treatments) while Kruskal-Wallis one-way analysis of variance was used to compare multiple groups; pairwise comparisons were evaluated using Dunn's test for multiple comparisons with Bonferroni correction.

Model Fitting

Generalized linear models (GLMs) were used to estimate vital rates as a response of height. For each GLM, variables for population, treatment, site, and interactions were added only if a significant effect on a given vital rate was detected (Table 1). Models for survival $s(z)$, growth $G(z',z)$, and probability of flowering $P_r(z)$ (referred to as "reproduction"), and germination P_g were fit using the package 'lme4' (Bates, Machler, Bolker, & Walker, 2015). The model for the number of flowers produced (flowering) was fit using the package 'glmmTMB' (Brooks et al., 2017). Survival, reproduction, and germination are both binary outcomes; that is, a plant can either survive or not, a plant can either reproduce or not, and a seed can either germinate or not, and each can be represented by a 1, denoting the positive outcome, or a 0, denoting the negative outcome. Thus, the binomial-family GLM for survival, reproduction, and germination used a logit link function. Because height data violated assumptions of normality, a gamma-family GLM for growth also used a log link function. Flowering data was zero-inflated, so the flowering model contained a correction for zero-inflation and was fit as a Poisson-family GLM, which is more appropriate for count data.

Results

In 2022, a total of 856 plants were found in the sampled areas; 471 individuals were found in South Carolina plots and 385 were found in Florida plots. The average population density was 2.4 individuals per m^2 in South Carolina and 1.9 individuals per m^2 in Florida. In 2023, a total of 47 untagged individuals were identified. At least one untagged individual plant was found in each plot, with a range from 1 to 15 untagged plants per plot. A total of 56 individuals, or 6% of the overall population died between 2022 and 2023.

In the four sections to follow, results of exploratory analyses on survival, growth, flowering, and germination are presented. Differences in vital rates were compared between populations, between fenced and unfenced plots, and among sites within each population. Understanding the relationships is an essential step toward ultimately specifying realistic and useful population models (Table 1).

Table 1: Summary table of differences in components vital rates. A checkmark indicates a significant difference was found in that vital rate when compared between populations (Florida and South Carolina), treatment (Fenced vs Unfenced), and among sites. Interaction effects of treatments within populations, sites within populations, and treatments within sites are notated as T:P, S:P, and T:S, respectively. For example, a significant difference in survival was detected among site sites, but not between populations or fencing treatment. Significance and strength of effects are discussed in following paragraphs. Significant effects of variables and interactions between variables indicate that they should be included in the specification of vital rate GLMs. The resulting models are combined to form the IPM kernel.

Vital rate terms in IPM kernel	Vital Rate	Population	Herbivore exclusion (fencing)	Site	T:P	S:P	T:S
	Survival			✓			
$s(z)$	Height:Survival	✓	✓	✓	✓		
$G(z',z)$	Growth		✓	✓	✓	✓	✓
	# of Flowers	✓		✓			✓
	Reproduction	✓	✓	✓			
$P_r(z)$	Height:Reproduction	✓		✓		✓	
$F(z)$	Height:# of Flowers	✓					
P_g	Germination	✓	NA		NA		NA

Survival

Survival rates were not significantly different between the Florida and South Carolina populations (Chi-Squared), treatments aggregated between population ($p = 0.94$), treatments across populations (fenced $p = 0.23$, unfenced $p = 0.16$), treatments within populations (SC $p = 0.28$, FL $p = 0.13$), sites in South Carolina (Fisher's exact test $p = 0.83$), or plots in South Carolina ($p = 0.50$). Survival differed between sites ($p = 0.007$) and plots in Florida ($p = 0.01$); the MPS site had a lower survival rate (84%) than MPN (97%, $p = 0.01$) and NS (95%) though the latter comparison was weakly significant ($p = 0.07$). Likewise at the plot level, MPSB had a lower survival rate (77%) than MPNA (96%) or MPNB (98%), though again both comparisons were weakly significant ($p = 0.07$)

Survival appears to be positively related to plant size. All size measurements were positively correlated with survival ($p < 0.05$) except for number of green stems ($p = 0.19$). Height was most strongly correlated with survival ($r = 0.21$, $p < 0.001$), followed by length of longest stem ($r = 0.18$, $p < 0.001$), and number of woody stems ($r = 0.16$, $p < 0.001$).

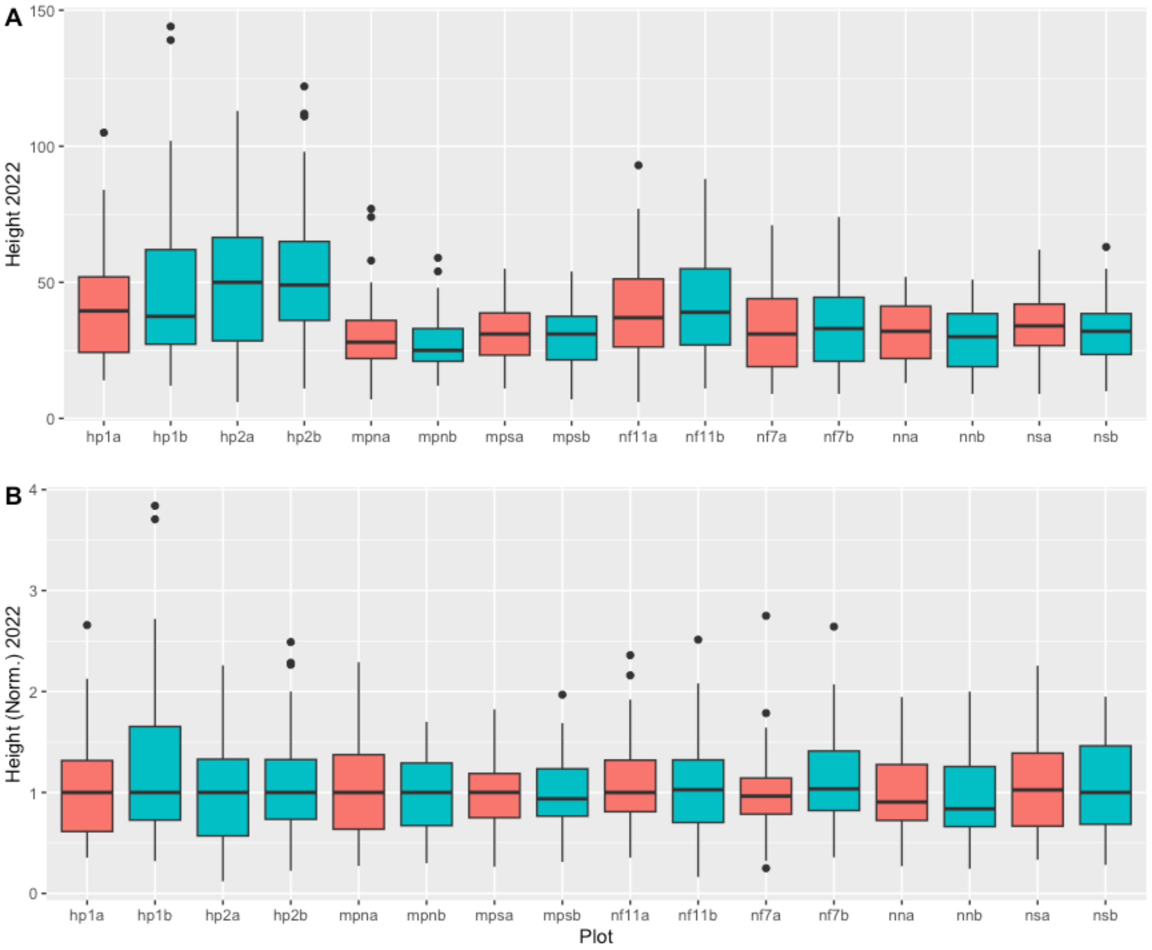

Figure 4. A) Mean height of *Ribes* in each of 16 study plots sampled in 2022. Boxes represent the second and third quartiles for height and whiskers represent the first and fourth quartiles. B) Height data normalized by subtracting plot median from observations. Red boxes represent fenced sites, blue boxes unfenced sites.

Pooling data from both populations, individuals that survived were significantly taller than individuals that died (Wilcoxon $p < 0.001$, Figure 5). The same relationship was found in the South Carolina population ($p < 0.001$) but not in the Florida population ($p = 0.10$). Survivors were taller than individuals that died in unfenced plots with populations combined ($p = 0.004$) and in South Carolina ($p < 0.001$) but the height difference between individuals that survived or died was not significant in unfenced plots in Florida ($p = 0.08$) or in fenced plots in either population ($p > 0.36$). Dead individuals were taller in fenced versus unfenced plots in South

Carolina (p =0.03, Figure 6) but not in Florida (p = 0.39). Height of individuals that died differed between sites (Kruskal-Wallis p = 0.002) and plots (p = 0.03) but no pairwise comparisons between sites or plots within a population were significant (Dunn's test, Bonferroni $1 \geq p \geq 0.30$).

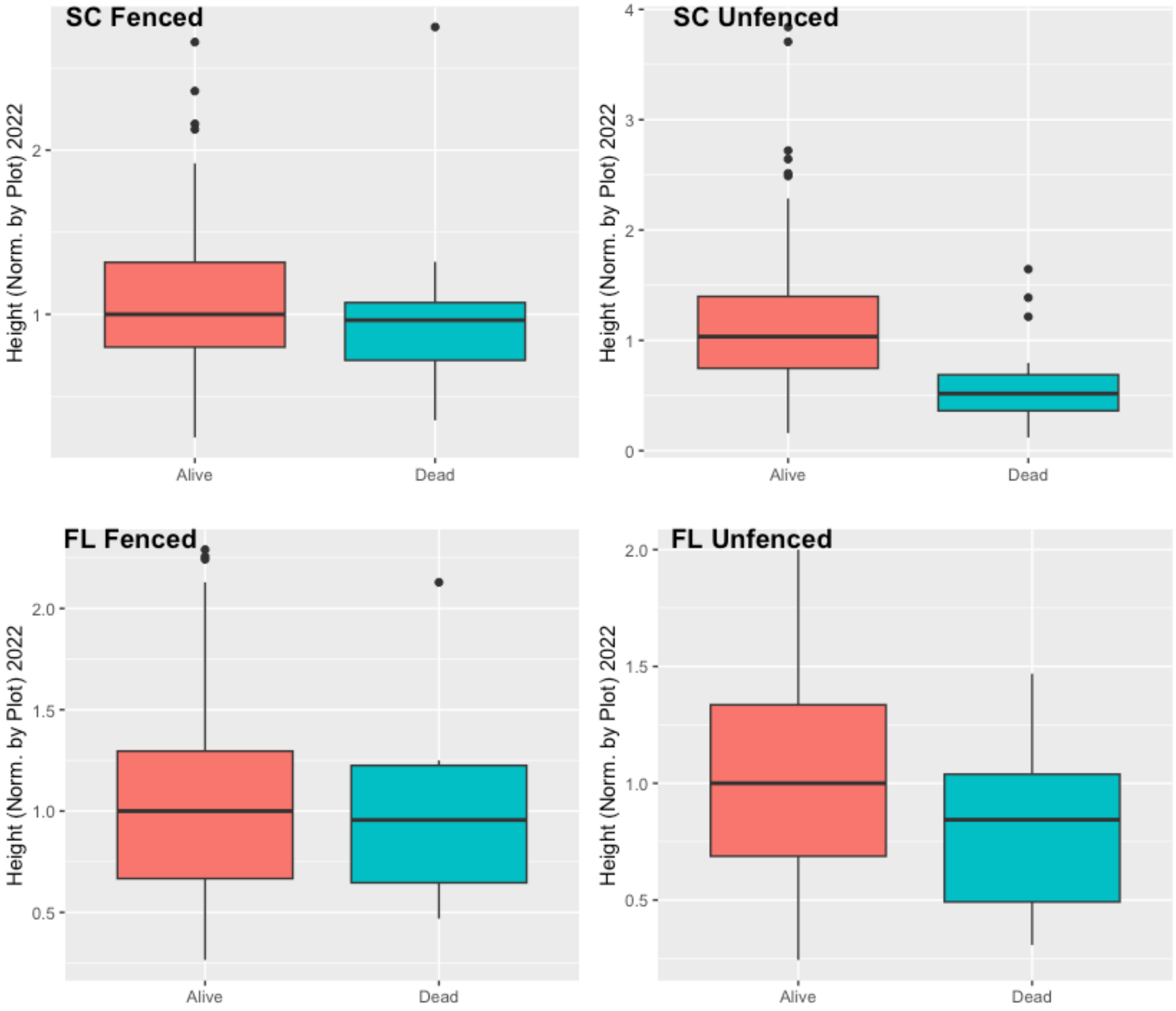

Figure 5. Mean normalized heights of living and dead plants in South Carolina (top panels) and Florida (bottom panels) in fenced plots (left panels) and unfenced plots (right panels). A significant difference in height of surviving and dead plants was found only in the unfenced South Carolina sites (top right panel).

Figure 6: Normalized heights of individuals that died between 2022 and 2023 in fenced and unfenced plots in South Carolina and Florida. Violin plots show the frequency of height measurement within each group; height data appear to be more centrally distributed around the mean in SC than in FL.

Growth

Plant height was greater in South Carolina than in Florida in both years (Kruskal-Wallis $p < 0.001$). In the combined populations, plant height was greater in unfenced plots than in fenced plots in 2022 ($p < 0.001$) but not in 2023. The same difference between treatments held for the South Carolina population, but not for the Florida population. Height varied among sites in South Carolina in both years but was significantly different between Florida sites only in 2022. Similarly, height varied among plots in South Carolina in both years, but did not vary among plots in Florida in either year. At one site in South Carolina, the difference in height was significant in 2023 ($p = 0.004$) but not in 2022 ($p = 0.36$), and at the next closest site, NF7, the difference in height was weakly significant in 2023 ($p = 0.08$) but not in 2022 ($p = 0.76$).

Plants that survived grew more in fenced plots than unfenced plots overall ($M_{Fenced} = 7.56$ cm, $M_{Unfenced} = 2.37$ cm; Wilcoxon $p < 0.001$) and in fenced plots within the South Carolina population ($M_{fenced} = 10.8$ cm, $M_{unfenced} = 0.52$ cm, $p < 0.001$), but the change in height was not significantly different between populations ($M_{FL} = 5.54$ cm, $M_{SC} = 3.94$ cm, $p = 0.63$) or between treatments within the Florida population ($M_{fenced} = 5.25$, $M_{unfenced} = 5.94$, $p = 0.67$). Change in height differed between sites in South Carolina (Kruskal-Wallis $p < 0.001$) and between plots within each population (Kruskal-Wallis $p \geq 0.02$). Only one set of paired plots (Figure 7) showed a significant difference between changes in height, with greater positive change in the fenced plot: SNF 11A and 11B ($M_{11A} = 14.8$, $M_{11B} = 0.851$; Dunn's test, Bonferroni $p < 0.001$). Change in length was positive in all plots except two unfenced plots in South Carolina: SCHP 1B ($M = -2.98$) and SNF 11B ($M = -0.98$).

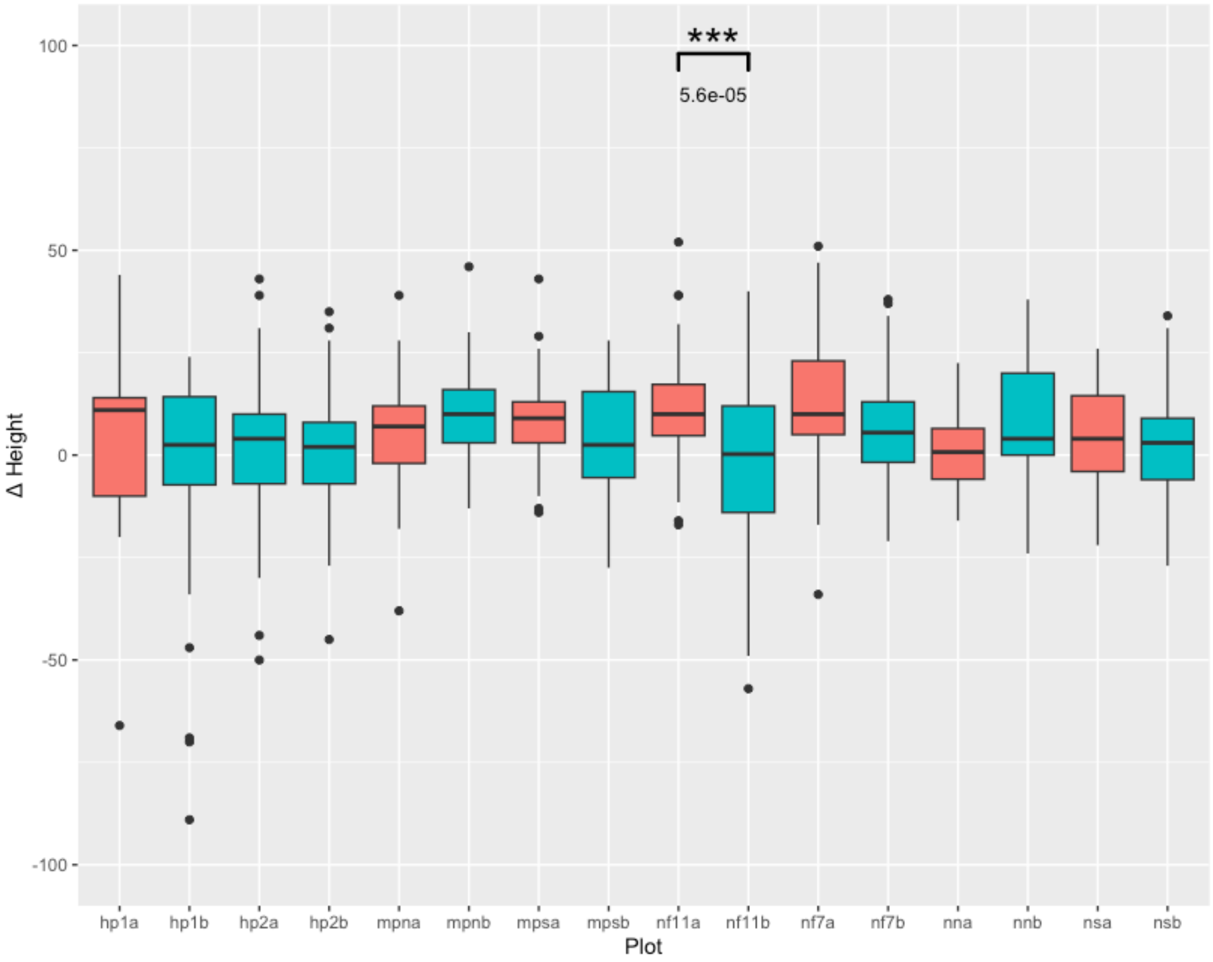

Figure 7: Change in height of the plant's tallest point above ground from 2022 to 2023, by sample plot. Red boxes represent fenced plots, blue boxes represent unfenced plots. One treatment effect (paired comparisons of fenced and unfenced height changes) was significant.

Flowering

There were more flowering individuals in South Carolina than in Florida in both years (Chi-squared test, $p < 0.001$). In 2022, there were 113 flowering individuals in the South Carolina population and 54 flowering individuals in the Florida population. In 2023, 154 flowering plants were found in South Carolina while only 36 were found in Florida. In South Carolina, 25 plants only produced flowers in 2022, 67 plants only produced flowers in 2023, and 87 plants produced flowers both years. In Florida, 18 plants produced flowers in 2022, 23 plants produced flowers in 2023, and 13 plants produced flowers in both years. Number of flowering individuals was significantly different between all sites in South Carolina (Dunn's test, Bonferroni $p < 0.02$) and between all sites in Florida ($p < 0.02$) except when comparing MPN to NN ($p = 1.0$). Number of flowering individuals also differed between plots within each population ($p < 0.001$), and many pairwise comparisons between plots at the same site were significant. With populations combined, the number of individuals that produced flowers increased between 2022 and 2023 in unfenced plots ($M_{2022} = 10.6$, $M_{2023} = 16.9$; $p = 0.02$) but not in fenced plots ($M_{2022} = 0.76$, $M_{2023} = 2.6$; $p = 0.13$). This pattern held for unfenced ($p = 0.008$) versus fenced ($p = 0.14$) in South Carolina, but there was no difference in Florida ($p > 0.62$). The number of flowering individuals increased from 2022 to 2023 at two sites: HP2 in South Carolina ($p < 0.001$) and MPS in Florida ($p = 0.04$).

More flowers were produced in 2023 versus 2022 in South Carolina (Wilcoxon $p < 0.001$) but not in Florida (Figure 8) In South Carolina, the number of flowers increased in both fenced and unfenced plots ($p < 0.004$). The number of flowers increased between years at three sites: SCHP 2 ($p < 0.001$), SNF 7 ($p < 0.001$), and MPS ($p = 0.01$). Within SCHP 2, number of flowers increased in both fenced and unfenced plots ($p < 0.02$), while in SNF 7 and MPS, number of flowers increased in fenced plots ($p < 0.02$) but not in unfenced plots ($p > 0.15$).

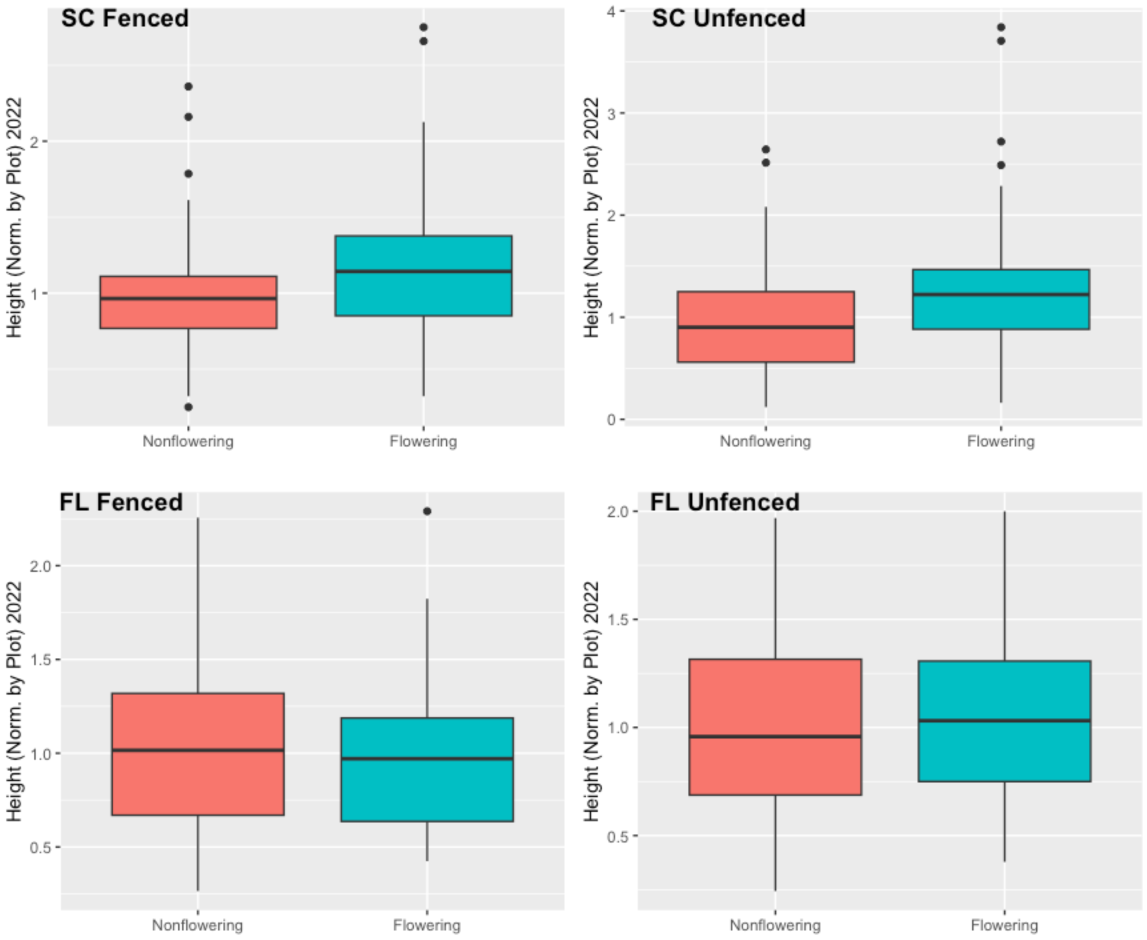

Figure 8: Height of individuals that produced flowers versus those that did not in fenced and unfenced plots across both populations. Difference in height between flowering and non-flowering plants was significant in both fenced and unfenced in South Carolina (top panels).

Reproductive status (flowering or not) was strongly correlated with height in the same year ($0.46 < r < 0.51$, $p < 0.001$), height in the previous year ($r = 0.49$, $p < 0.001$), and length of longest stem in either year ($0.46 < r < 0.62$, $p < 0.001$). Number of woody stems was also correlated with reproductive status, albeit weakly and only in year 1 and ($r = 0.14$, $p < 0.001$). For consistency with the analysis of survival rates, to facilitate population growth model specification, and in absence of a physiological mechanism relating a specific size measurement to flowering capacity, only the relationship between height and flower production was evaluated.

Individuals that produced flowers were significantly taller (with height normalized by plot) in South Carolina than in Florida (Wilcoxon $p = 0.008$). Flowering individuals were taller than non-flowering individuals in the combined populations ($p < 0.001$, Figure 9) and within the South Carolina population ($p < 0.001$) but not within the Florida population ($p = 0.83$). Flowering individuals were taller than non-flowering individuals in fenced plots ($p = 0.01$) and unfenced plots in South Carolina ($p < 0.001$) but the height difference between individuals that flowered or not was insignificant in both treatments in Florida ($p > 0.43$). Height of individuals that produced flowers differed between sites (Kruskal-Wallis $p < 0.001$) and plots ($p = 0.001$) in South Carolina, but not in Florida. Flowering individuals in SCHP site 1 were significantly taller than flowering individuals in any of the other South Carolina sites (Dunn's test, Bonferroni $p < 0.001$, Figure 9).

Number of flowers produced was correlated with height with all data combined ($r = 0.46$, $p < 0.001$), and within both treatment groups across populations ($r > 0.38$, $p < 0.001$). The correlation was stronger within the South Carolina population ($r = 0.48$, $p < 0.001$) than within the Florida population ($r = 0.18$, $p = 0.001$) and stronger for the unfenced treatment in South Carolina ($r = 0.43$, $p < 0.001$) than the fenced treatment ($r = 0.22$, $p = 0.006$). However, height was not correlated with number of flowers in either treatment group in Florida ($p > 0.16$). The correlation between height and number of flowers produced was significant in all South Carolina sites ($0.67 \geq r \geq 0.24$, $p \geq 0.002$). The number of seeds per fruit collected in South Carolina and Florida were not significantly different ($M_{SC} = 16.7$, $M_{FL} = 12.5$, One-way ANOVA $p = 0.14$).

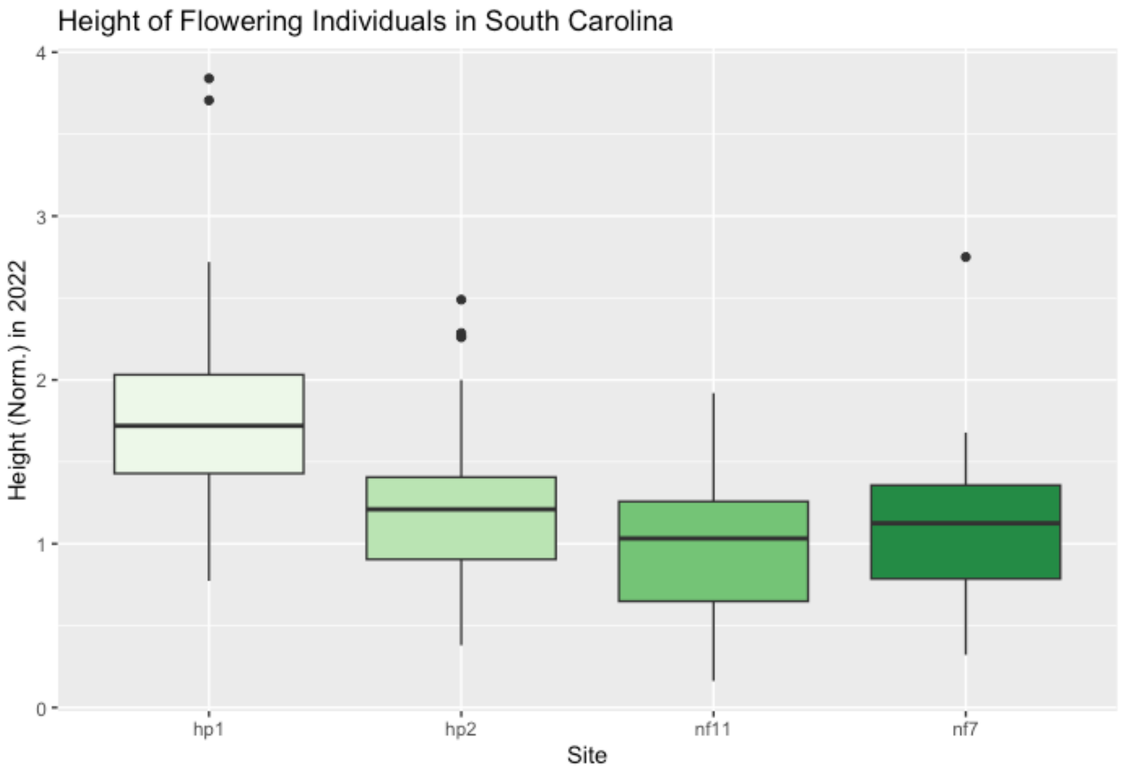

Figure 9: Mean height (represented by dark horizontal lines, with boxes showing second and third quartiles and whiskers showing first and third quartiles) of flowering individuals, normalized by plot medians, in the four sites in South Carolina. Flowering plants in SCHP site 1 were significantly taller than flowering plants at the three other sites.

Germination

Overall, mean germination rate was significantly higher in South Carolina (48%) than in Florida (31%; Fisher's p =0.004). Germination rates did not differ between sites or plots within the South Carolina population. No significant difference was found in germination rate among Florida sites, nor were there any significant pairwise comparisons between sites. Germination rate did differ among plots ($p = 0.002$) in Florida. Specifically, germination rate was lower at NSB compared to five out of the seven other plots ($p \leq 0.05$), although this is unsurprising given that NSB was the only plot at which no seeds germinated. No other pairwise comparisons between Florida plots were significant ($p \geq 0.10$).

Vital Rate Models

Model predictions for each vital rate are shown in Figures 10-14.

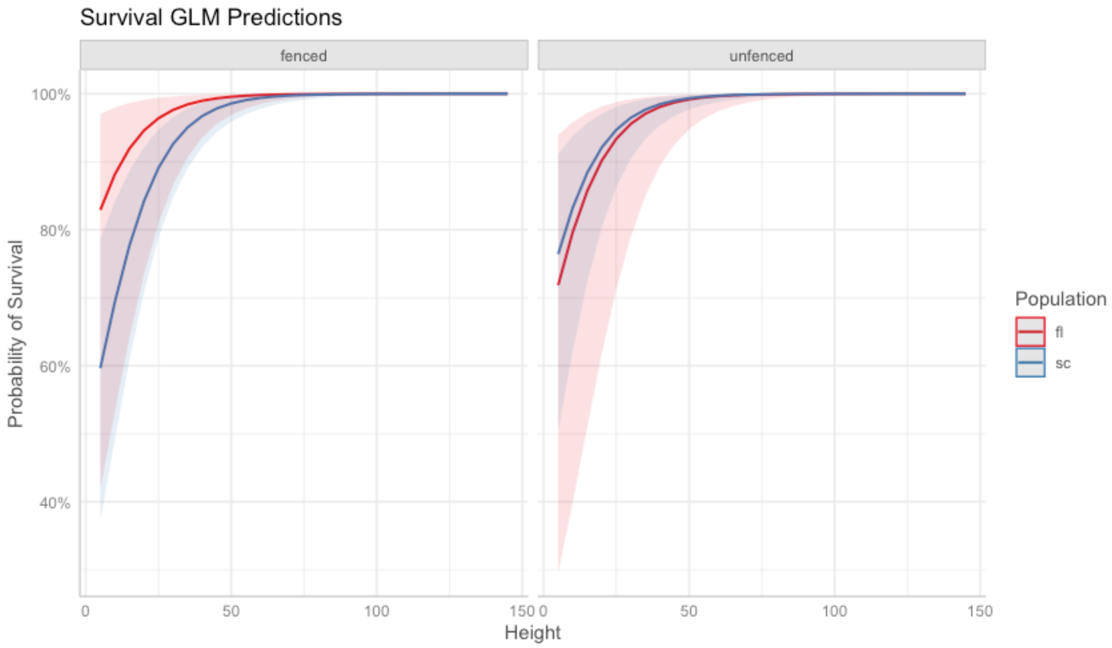

Figure 10: Predicted probability of survival based on height in the previous year, herbivore fencing, and population. Shaded areas represent 95% confidence intervals around predictions. Survival was modeled as a binomial-family GLM with height, population, treatment, site, and treatment-population interaction as fixed effects.

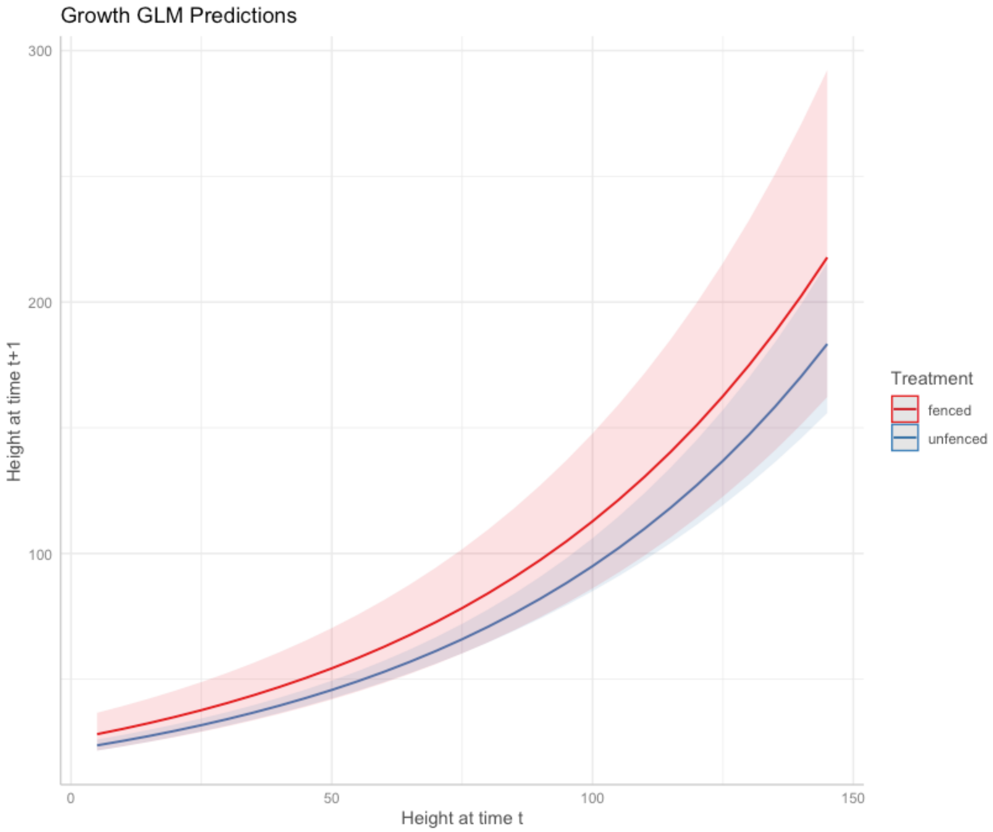

Figure 11: Predicted height based on height in the previous year and herbivore fencing. Shaded areas represent 95% confidence intervals around predictions. Growth was modeled as a gamma-family GLM with height, treatment, site, treatment-population interaction, site-population interaction, and treatment-site interaction as fixed effects.

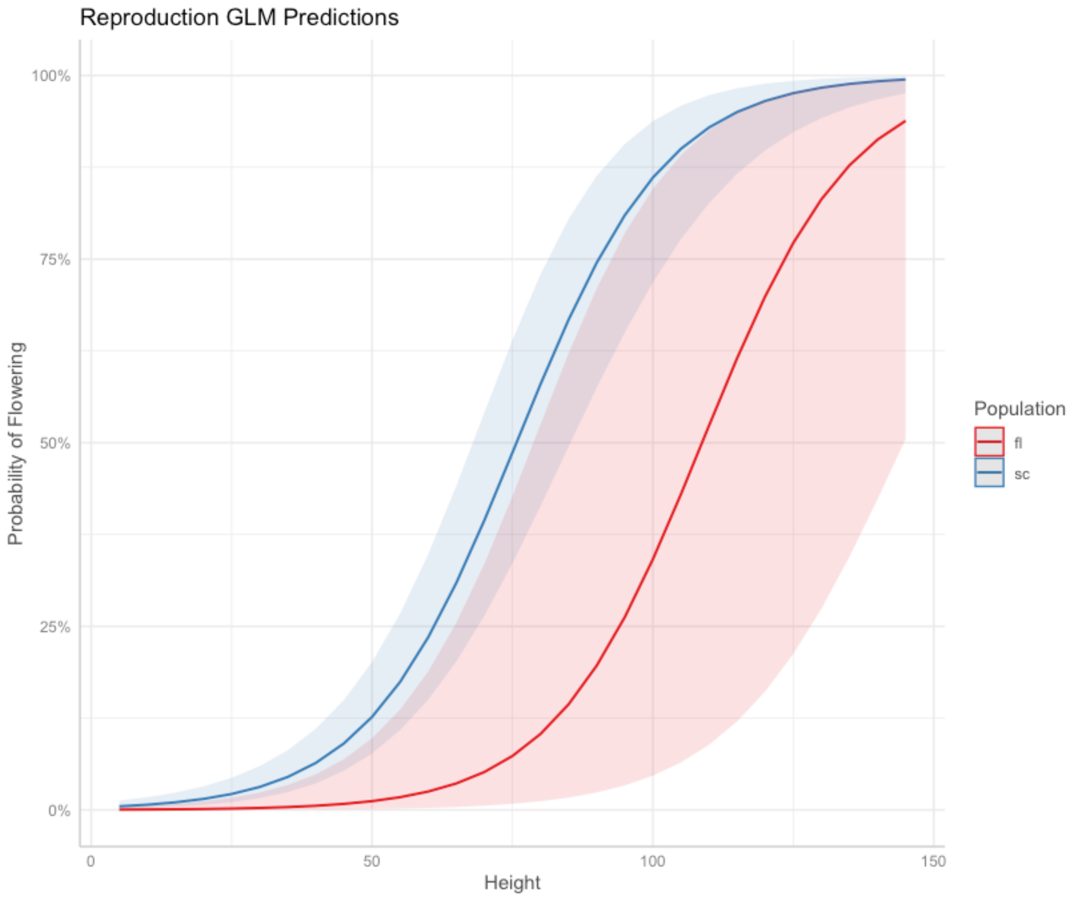

Figure 12: Predicted probability of flowering based on height in the same year and population. Shaded areas represent 95% confidence intervals around predictions. Reproduction was modeled as a binomial-family GLM with height, population, site, and site-population interaction as fixed effects.

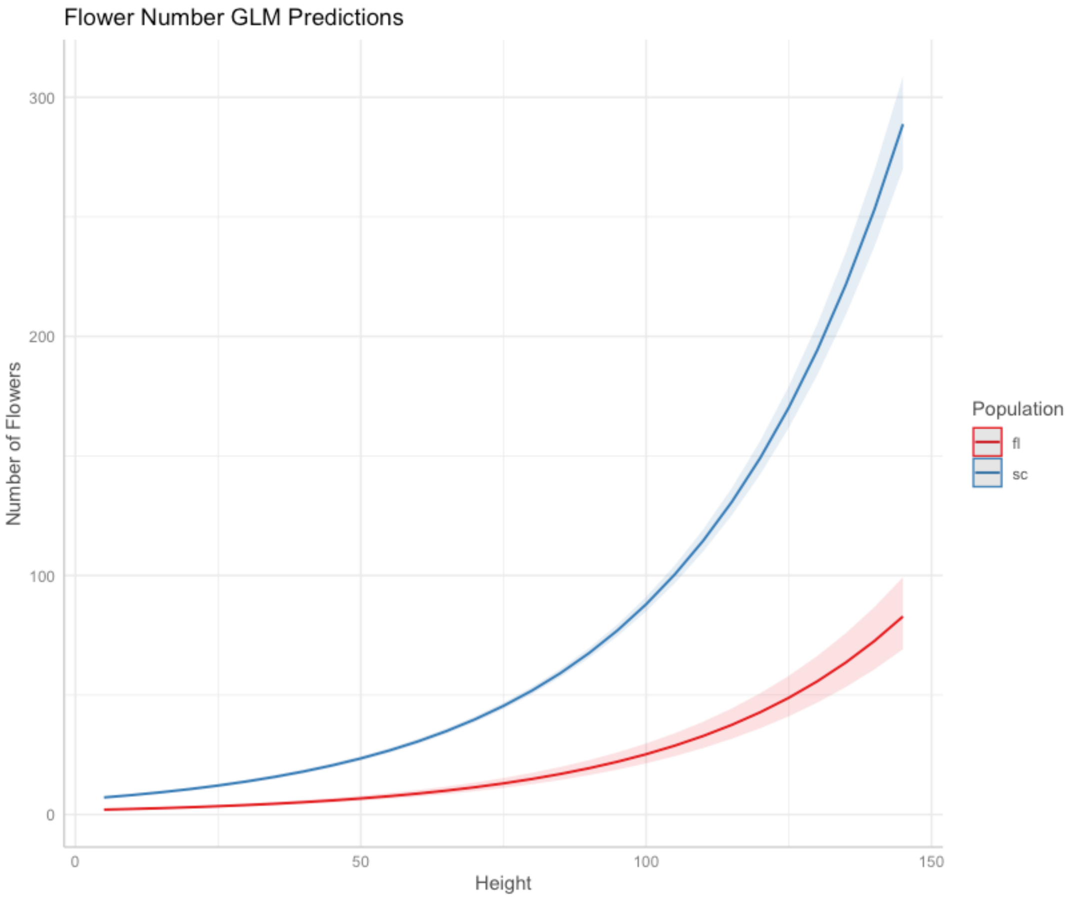

Figure 13: Predicted number of flowers based on height in the same year and population. Shaded areas represent 95% confidence intervals around predictions. Flowering was modeled as a zero-inflation corrected Poisson-family GLM with height, and population as fixed effects.

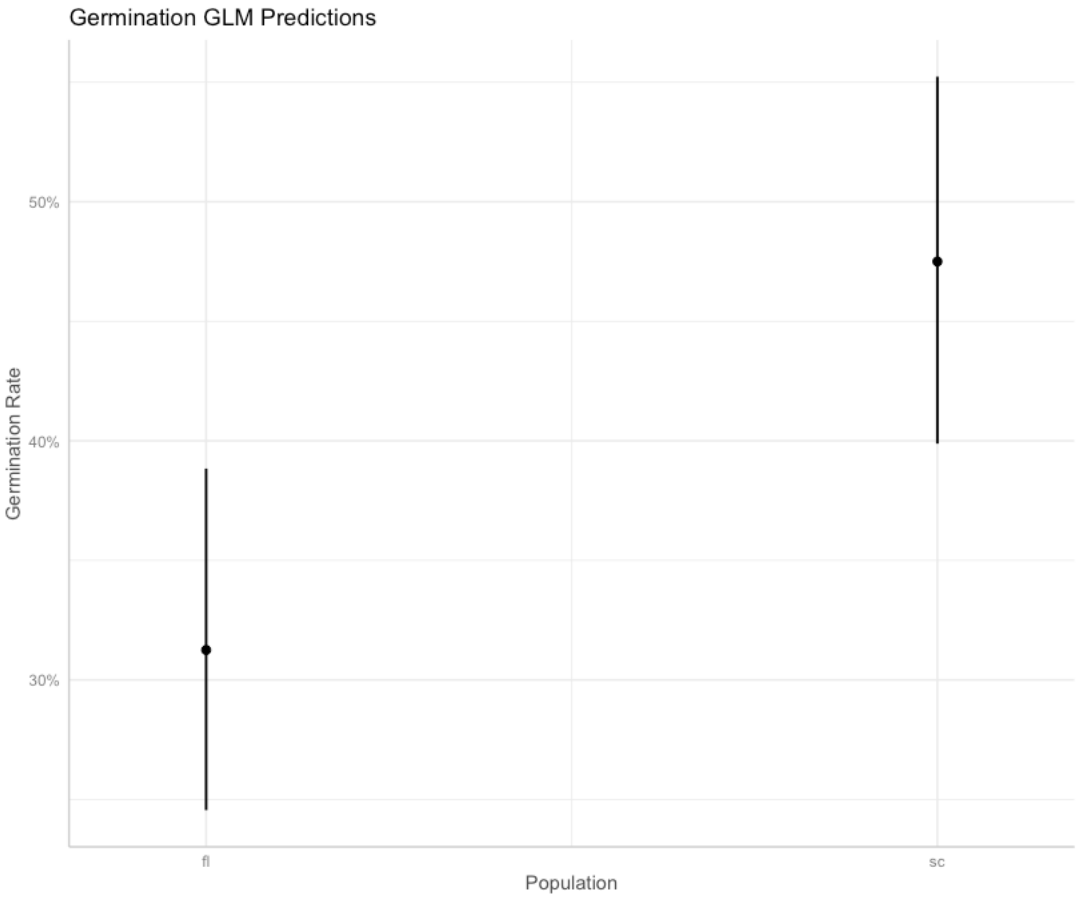

Figure 14: Predicted per-seed probability of germination based on population. Observed average germination rates were 31% in Florida and 48% in South Carolina. Vertical lines around point estimates represent 95% confidence intervals. Germination was modeled as a binomial-family GLM with population as the only fixed effect.

Discussion

High-resolution demographic data were collected from the two known *Ribes echinellum* populations to quantify rates of individual survival, growth, and reproduction. Vital rates of *Ribes echinellum* varied between the two populations. Number of flowering plants, number of flowers per reproductive individual, and germination rates were significantly higher in the South Carolina population. Height of the plants influenced survival, reproduction, and number of flowers in both populations. Six of the eight vital rates (Table 1) varied by site, indicating the effect of local environmental factors among the sites. Growth, reproduction, and height/survival rate were higher within the herbivore exclusion plots (Table 1).

The proportion of plants that died between 2022 and 2023 was equivalent between populations and between paired plots, but survival rate varied between sites. This pattern was mostly driven by single site in Florida, Mays Pond South, that had lower survivorship compared to any other site. Future visits to the Florida population should focus on identifying deleterious ecological interactions, such as light competition with invasive species, and abiotic factors, such as suboptimal soil or hydrological conditions, that are driving the observed decrease in survivorship at this site.

The size difference between plants that survived or died, however, varied between populations, between sites, and between plots with or without fences. Specifically, in unfenced plots in both populations, plants that died were the same size as plants that survived, whereas in fenced plots in the South Carolina population, plants that died were smaller. Given that size does appear to be related to probability of survival, and that growth increased in fenced plots in South Carolina, it follows that plants in fenced plots in South Carolina, once released from herbivory, were able to grow to some threshold size beyond which their chances of survival became much greater. While herbivory does not appear to be a direct driver of mortality (since mortality rate was similar between fenced and unfenced plots), it does appear to indirectly decrease survivorship by limiting plants to a more vulnerable size. Further, given that the probability of flowering and the number of flowers produced appear to be related to size, release from herbivory should increase the number of flowering individuals and total seed set in the South Carolina population. That this pattern is not present in the data may indicate a time-lag between growth and flowering; it is likely that successive demographic surveys will show an increase in the number flowering individuals. Ultimately, population dynamic models should show an increase in the population growth rate for fenced plots in South Carolina due to the increase in plant growth.

These finding provides concrete evidence that herbivore exclusion is a tractable management strategy for increasing the health and size of *Ribes echinellum* populations. Though this study did not attempt to quantify herbivore damage directly, the soft new growth at the tips of stems were consumed by deer. No browse was noticed on the woody stems, which are covered in sharp spines, or the leaves on woody stems. New growth appears to harden in the first year (*personal observation*), so seasonal gains in plant size due to the application of herbivore exclusion fences should become concrete over a short time span. This management strategy could therefore be effectively applied in a transient manner, trading short-term effort on the part of stakeholders for long-term increases in population health. However, no conservation approach should be treated as a panacea and questions remain about the duration of these effects, the site-specific factors that lead to a response in plant growth due to herbivore exclusion, and any negative community-level impacts of installing fences. Investigation of stem longevity would clarify the appropriate timing of herbivore management; if stems are long lived, then fences would only need to be installed once, but otherwise, periodic management may be more suitable. Additionally, if plant size has a ceiling, then management for herbivores may be a wasted effort at sites where plants are already large; additional years of demography data would demonstrate whether growth increases asymptotically to a certain threshold beyond which herbivore exclusion is unnecessary.

The absence of an herbivory effect on growth or survivorship in the Florida population indicates that either deer are not browsing on *Ribes echinellum* to a significant extent or other environmental drivers are driving mortality rates for all plants, regardless of size. Puzzling out the specific environmental factors that maximize *Ribes echinellum* survivorship will allow stakeholders to identify and conserve key habitat where the species can persist long-term; additionally, this will narrow the range of environmental inputs into a systematic survey for new populations.

The reproductive vital rate data demonstrates a real potential to maintain *Ribes echinellum* genetic diversity. Germination of seed from in both populations and indicates the seeds produced in both populations are viable. This suggests that seed collection is a tenable approach to safeguarding the species and plants could be grown *ex-situ* from seeds to maintain genetic lines. Additionally, recruitment is occurring in both populations, pointing towards the hopeful conclusion that the populations are regenerating, in contrast to previous studies on *Ribes echinellum* breeding systems (Negrón-Ortiz, 2018). This study only considered seed production and germination, and failed to consider that the species reproduces vegetatively. No identification of putative recruits as vegetative ramets or true seedlings was done. This shortcoming underestimates reproductive rates, limiting the usefulness of the proposed population growth models.

The reproduction component of the IPM kernel, $F(z)$, is comprised of terms to estimate the probability $P_r(z)$ that an individual produces flowers, the number of flowers produced by an individual at a given size $f(z)$, the average number of seeds per fruit n_s, the probability P_g that a given seed germinates, the average number of recruits n_r and the size distribution of recruits $G_r(z',z)$, such that $\boldsymbol{F(z) = P_r(z) * \frac{n_r}{f(z) n_s P_g} * G_r(z', z)}$. The middle term provides an estimate of the number of recruits produced by an individual of size z. In the case where all observed recruits were clonal ramets and not unique genets, this kernel would significantly overestimate the true rate of sexual reproduction. A better IPM kernel would include an additional component for clonal reproduction, although this would require data differentiating the true seedling establishment rate versus the rate of clonal recruitment.

Ultimately, this work increases understanding of the population biology of this rare and unique Southern species as well as highlighting threats to its survival and opportunities for its conservation. The demographic data collected in this study can be used for the development and parameterization of an integrated population model for *Ribes echinellum*. In less than two years, this approach provided evidence that will direct effective on-the-ground management efforts. Demographic data collected in the coming years can only bring further insight.

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