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Population Trends, Demography, and Seed Ecology of the Florida Scrub Endemic *Chrysopsis highlandsensis* (Asteraceae: Astereae)

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ABSTRACT

Chrysopsis highlandsensis (Highlands Goldenaster; Asteraceae) is a state endangered herb found primarily within pyrogenic scrub communities in south-central Florida. Little is known of its ecology, including population trends, demography, response to fire, and seed ecology. Here, we report on the first detailed demographic study of *C. highlandsensis* over 24 years of field monitoring across 10 populations (6,456 plants) and supplemental surveys and experiments to investigate (1) population trends and vital rates in scrub and roadside habitat, (2) seed ecology, and (3) rangewide population trends. Seedling recruitment occurred year-round, primarily during the winter dry season following flowering (Dec–Mar), and large recruitment events were not associated with fire or mechanical disturbances. Although burning reduced survival, 39% of individuals (>1 year old) that experienced fire survived. Roadside vegetative plants transitioned to reproductive adults at smaller sizes (rosette diameter) than did those in the scrub. Reproductive individuals lived a mean of 4.3 years (max. 12 years). Mortality occurred following the first reproductive event in 87% of individuals, indicative of a largely monocarpic life cycle. Viability of intact seeds was estimated at 20%. Across five field germination experiments, germination ranged from 1.0–8.6%, and the maximum observed seed bank duration was five years. Seed predation by vertebrates accounted for a 23% decline in seed numbers. Rangewide surveys showed significant declines in five of seven sites from 2005–2020. Together, these findings indicate that populations are generally declining, and that several factors, particularly low reproductive output and seedling recruitment, likely limit population growth.

Key words: demography, endangered plants, fire management, seedling recruitment, semelparity

INTRODUCTION

Chrysopsis highlandsensis DeLaney & Wunderlin (Highlands Goldenaster; Asteraceae, tribe Astereae) is a state endangered herb restricted to the pyrogenic scrub habitat of south-central Florida. It is one of 15 native *Chrysopsis* taxa in the southeastern United States, of which 14 occur in Florida, six are endemic to the Florida peninsula, and four are Florida state-listed as endangered (Wunderlin et al. 2024; Weakley et al. 2025). Following an earlier monograph of the *Chrysopsis* genus (Semple 1981), *C. highlandsensis* was described by Delaney and Wunderlin (2002) and later confirmed as a distinct species based on chromosome counts (Semple et al. 2015). *Chrysopsis highlandsensis* is endemic to the southern Lake Wales Ridge and the nearby Bombing Range Ridge, a distribution that spans Highlands, southern Polk, and northern Glades counties (Figure 1) and that occurs within a region of exceptionally high endemism (Christman and Judd 1990; Dobson et al. 1997; Estill & Cruzan 2001). The climate in the region is subtropical, typically with hot, rainy summers and cool, mild winters (Abrahamson et al. 1984). *Chrysopsis highlandsensis* grows in fire-prone Florida scrub (i.e.,

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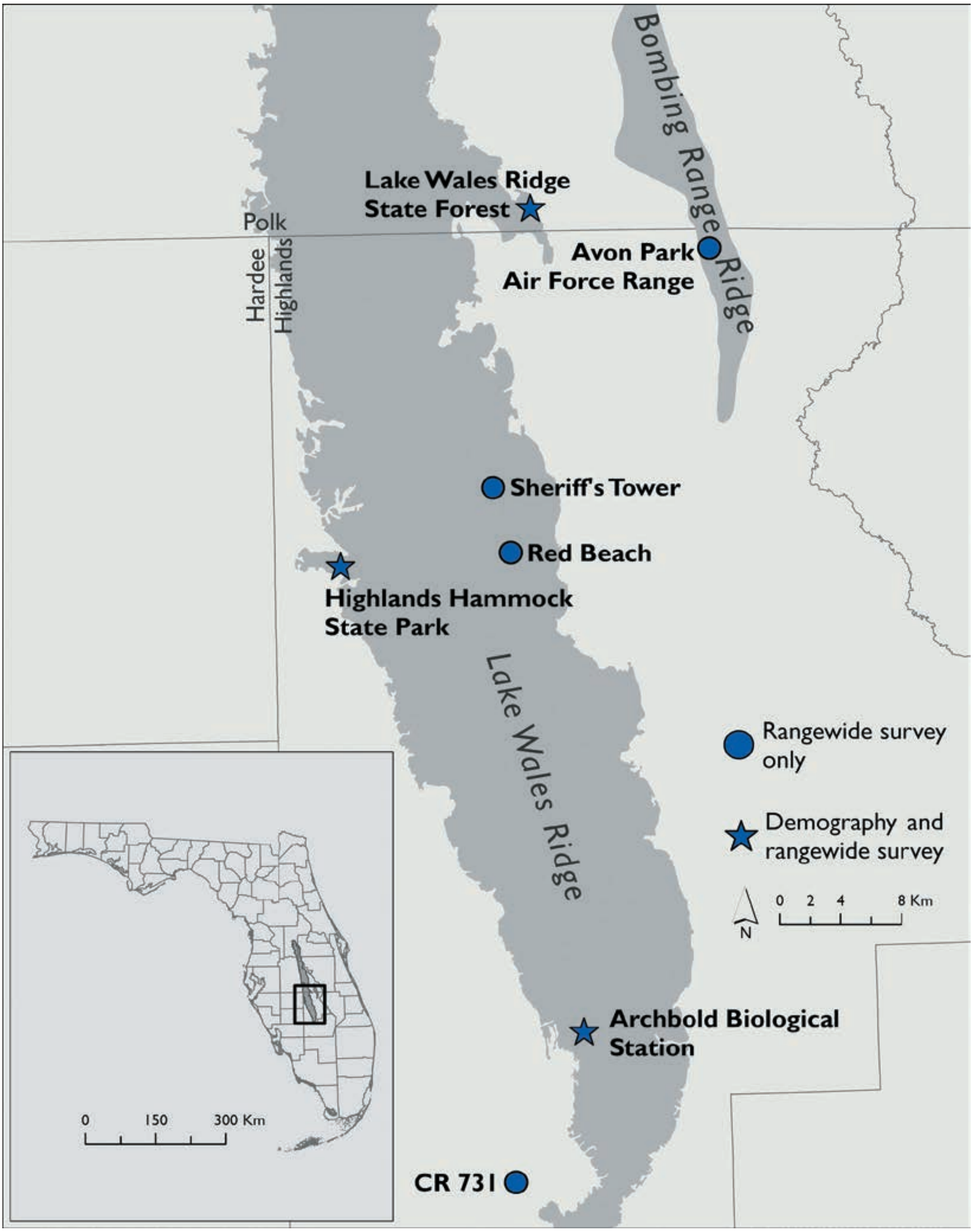

Figure 1. Map of *Chrysopsis highlandsensis* sites used for the demographic study (stars) and the rangewide survey (stars and circles). Inset shows location of the Lake Wales Ridge and Bombing Range Ridge in Florida, USA.

sand pine scrub, low oak scrub, rosemary scrub, and scrubby pinelands) dominated by clonal, resprouting oak, palm, and ericaceous shrubs and exposed sandy, xeric soils (Menges and Hawkes 1998). At many sites, plants persist in open sand gaps, or areas of exogenous soil disturbance such as firelanes, or sandy roadbeds and trails through Florida scrublands. Yet, little is known about the status of populations across its restricted range, including the general population trends and demography, and there is a critical need to better understand the ecology of the species to inform management and conservation.

In Florida's pyrogenic scrub habitats, understanding species' responses to fire is critical for managing populations. Fire is a naturally recurrent event throughout the southeastern United States (Noss 2018), and, within scrub habitat, is particularly important for reducing woody competition and creating sandy gaps where herbaceous plants persist (e.g., Menges and Quintana-Ascencio 2004; Menges et al. 2006). Populations of plant species in Florida scrub generally recover after fire by resprouting ('resprouters'), seed recruitment ('re-seeders'; typically recruiting from persistent seed banks), or a combination of both strategies (Menges and Kohfeldt 1995). Re-seeding endemic herbs will often experience a boom in seedling recruitment in the years immediately following fire (Menges and Quintana-Ascencio 2004; Menges et al. 2006; Quintana-Ascencio et al. 2018), after which the population declines until the next fire. In contrast, populations of resprouters are less affected by fire, but more sensitive to other factors such as light availability or herbivory (Tye et al. 2016; Menges et al. 2020). *Chrysopsis highlandsensis* is thought to be a post-fire re-seeder, and, consistent with this classification, smoke may increase germination rates (King and Menges 2018); however, in a survey of post-fire recovery strategies that classified plant species of scrub habitats as re-seeders or resprouters, *C. highlandsensis* was not assessed (Menges and Kohfeldt 1995), due to it being infrequently encountered.

Furthermore, an understanding of the species' ecology should shed light on the potential threats and guide future conservation efforts. First, external threats, particularly habitat destruction, threaten many plants of the Florida scrub and rare plants worldwide (Wilcove et al. 1998; Weekley et al. 2008a). Though roads fragment the landscape, many native species, including those in the Florida scrub, thrive in sandy unimproved roadbeds and along sandy firelanes (Quintana-Ascencio et al. 2007; Lazaro-Lobo and Ervin 2019; Wilson and David 2024), and the presence of such exogenous soil disturbances may similarly provide short-term benefits to *Chrysopsis highlandsensis* populations. Mechanical treatments such as roller chopping or disking are often used to manage scrub habitat in addition to or in place of fire, and the effects on individual species can vary widely (Menges and Gordon 2010). Second, natural ecological threats via negative species interactions may include high pressure from herbivores, including seed predators, that limit the plant's population growth. Similarly, understanding the species' microhabitat preferences can explain the conditions needed for seedling recruitment or growth (e.g., Ward et al. 2022; David et al. 2024), and, in some cases, these microhabitat conditions can be created by land managers (Whitehead et al. 2023). Third, demographic challenges such as slow growth, low seed production, or low seed germination (e.g., Menges et al. 2016) may reduce population growth. Investigating these potential threats can help direct resources towards the appropriate conservation activities.

Here, we provide the first detailed study of the population trends and demography of *Chrysopsis highlandsensis* in scrub and roadside habitat. We use a combination of field monitoring and experiments to investigate (1) population trends and vital rates in scrub and roadside populations using 24 years of demographic data, (2) the seed ecology of the species including viability, germination, and post-dispersal predation, and (3) rangewide trends across its narrow distribution conducted over a 15 years period.

METHODS AND MATERIALS

Demographic study

Study sites. From 1999-2022, we monitored *Chrysopsis highlandsensis* populations across nine sites at three properties: Archbold Biological Station (ABS; 27.183°N, 81.352°W), Highlands Hammock State Park (HHSP; 27.471°N, 81.531°W) and Lake Wales Ridge State Forest (LWRSF; 27.662°N, −81.394°W) (Table 1). Most sites experienced prescribed fire, some mechanical treatment (including exogenous soil disturbance or fuel reduction), or both during the study (Table 1). Within these sites, plots were established either within intact Florida scrub or along sandy roads used as firebreaks ('firelanes') between management units. Here, we use the term 'roadside' to refer to disturbed, sandy habitats including firelanes, sandy roads, and trails, and the term includes the area alongside the road as well as the road itself. 'Scrub' habitat refers to interior habitat that is unlikely to be affected by edges.

ABS is located at the southern tip of the Lake Wales Ridge and represents the southern portion of the species' range (Figure 1). At ABS, *Chrysopsis highlandsensis* is found in xeric scrubby flatwoods and along sandy firelanes that are frequently used by 4×4 vehicles. In December 1999, we established three study sites, two roadside sites along sandy firelanes (Sites 1 and 2) and one scrub site within scrubby flatwoods (Site 3). Site 1 was a 40×1 m plot that ran parallel with a large firelane along the edge of the shrub line. Site 2 consisted of two 40×1 m plots along a firelane. Site 3 was two 30×1 m plots within scrubby flatwoods more than 10 m from a road edge. In 2002, a fourth study scrub site (Site 6) was established in scrubby flatwoods in a 50×20 m plot.

HHSP is located in central Highlands County and represents the center of the species range (Figure 1). At HHSP, *Chrysopsis highlandsensis* is found in scrubby flatwoods and roadsides, as well as transitional sand pine to oak scrub. In December 2002, we established two study populations (Site 4 and Site 5). Site 4 was a 40 m long base transect running parallel to a sandy road with eight 10×1 m plots running perpendicular every 5 m. The road was used as a hiking and biking trail by the public and as vehicle access roads for park staff. Plots ran from the road edge across a disturbed area and into the adjacent scrub. Meters 0.00–5.00 were classified as roadside habitat and meters 5.01–10.00 as scrub habitat. The scrub was best characterized as a mix of overgrown scrubby flatwoods habitat and sand pine scrub. Site 5 was five, 10×1 m plots under a developing canopy of sand pine trees. A third site (Site 10) was added in December 2014 consisting of seven 10×1 m long plots crossing a firelane and seven 1×2 m plots in scrub where *C. highlandsensis* was present. A large-scale, mechanical roller-chopping management treatment was conducted at Site 10 in 2019.

Lake Wales Ridge State Forest (LWRSF) in Polk County represents the northern extent of the range (Fig. 1). *Chrysopsis highlandsensis* here inhabits scrubby flatwoods, but most individuals are along the sandy firelanes and roads. Unlike at ABS and HHSP, the areas alongside LWRSF roads were not disturbed, and therefore our classification of 'scrub' habitat began at the edge of the road. In December 2002 we established two sites. Site 7 consisted of five, 10×1 m plots crossing a road into scrubby flatwoods. We classified these plots as half roadside (0.00–5.00m) and half scrub (5.01–10.00 m). Mechanical treatment (disking) occurred at Site 7 in 2018 and 2019. A sixth 1×2 m quadrat was considered entirely roadside habitat. Site 8 was established entirely in scrub habitat with five 10×1 m plots starting along the road edge and running perpendicularly into the scrub.

Demographic monitoring. Survival and recruitment were monitored quarterly (March, June, September, and December) with additional demographic measures recorded in December when plants were reproductive. We marked all plants within our study area with a numbered aluminum tag and colored pin flags and plastic toothpicks to identify individuals. New seedlings were differentiated from new adult plants by having a single vegetative rosette ≤ 5 cm in diameter.

In December, plants were assigned a stage of yearling (individuals that were observed as seedlings during the previous year), vegetative (non-reproductive individuals ≥1 year old), or reproductive (flowering individuals ≥1 year old). For seedling and vegetative stage plants, we measured rosette diameter (maximum distance spanning all of an individual's rosettes) to the nearest 0.1 cm. For reproductive plants, individuals produced flowering stems that emerged from the ground and often

Table 1. Nine study sites for *Chrysopsis highlandsensis* from 1999–2022 in two habitat types at three properties. The table shows the year monitoring began in December, the dominant habitat type (scrub or roadside) of each site and the area covered by each site. The years that fire took place during each site's study period are shown, and the estimated fire return interval for each site is calculated as the number of years studied divided by the number of fires. The years for mechanical treatments (if any) are also listed. The total number of plants for each site, the total number of seedlings observed during our study period, and the total number of plants whose full life (germination through death) was monitored is also recorded.

Property	Site	Year	Habitat	Area (m^2)	Fire	Est. fire-return interval	Mechanical treatment	# plants	# seedling	# full life
Archbold Biological Station (ABS)	1	1999	Roadside	40	2015	24	–	369	187	173
	2	1999	Roadside	80	2004, 2015, 2020	8	–	329	191	184
	3	1999	Scrub	60	1999,2004, 2020	8	–	805	569	520
	6	2002	Scrub	1000	2004, 2020	10.5	–	206	92	89
Highlands Hammock State Park (HHSP)	4	2001	Scrub	40	–	–	–	15	12	12
			Roadside	40	–	–	–	94	69	69
	5	2001	Scrub	50	–	–	–	483	281	281
	10	2014	Scrub	14	2017	9	2019	515	426	279
			Roadside	70	2017	9	2019	204	172	110
Lake Wales Ridge State Forest (LWRSF)	7a	2002	Scrub	25	2008	21	2018, 2019 (Disking)	417	365	355
	7b	2002	Roadside	29	2008	21	2018, 2019 (Disking)	2,688	2,577	2,437
	8	2002	Scrub	50	–		–	326	284	249

produced multiple branches off the same stem; therefore, we counted the number of branches (branching within 10 cm of the ground), maximum stem height, and number of flowering heads. Early demographic measures (1999–2001) used the number of stems that emerged at ground level to predict the number of flowering heads. In 2001, we collected both the number of stems and branches. We determined that branch number was a better predictor of total flowering heads (N=49; Pearson's r=0.76) compared to stem number (Pearson's r=0.22) and collected branch number for all remaining years.

To understand post-fire recovery, we assessed burn severity and survival. In the monitoring quarter following a fire, we recorded the burn severity of previously living plants. We assessed burn severity as unburned, scorched (leaves brown but with living plant material remaining), or consumed (charred with little to no living plant material remaining).

Seed production. We assessed seed production at ABS in 2003, 2006–2009, 2012, 2016, and 2017, and in 2003 at HHSP and at LWRSF. In 2003, we collected a single, undispersed flowering head with mature achenes into a coin envelope from 10 individuals at each site (Sites 1, 4, and 7). For the multiyear ABS collections, we collected between 11–75 heads per year across all populations depending on availability. In the laboratory, we quantified the total number of seeds and categorized viable seed by applying slight pressure to the achene to determine if the seed was intact or empty. We analyzed ABS data across years using analysis of variance to test the effects of the categorical predictor variables of habitat and year on the total viable seeds per head (natural log-transformed).

Data analysis. All data were analyzed using R v.4.3.2 (R Core Team 2023) and the packages lme4 (Bates et al. 2013), emmeans (Lenth 2021), car (Fox and Weisberg 2019), and mgcv (Wood 2011).

Demographic overview. We report basic statistics of the number of plants tracked during the study, lifespan (for those individuals documented from seedling until death), and general trends of each population in roadside and scrub habitat. We calculated quarterly seedling recruitment across all years.

Seedling recruitment. We calculated quarterly seedling recruitment across all years to determine seasonality of recruitment. To investigate the effect of fire and mechanical disturbances on seedling recruitment, we used a generalized additive model (GAM) to test for non-linear effects through time. The annual number of surviving seedling recruits was divided by the area to calculate seedling density, and natural log (x+0.005) transformed to achieve normality (0.005 corresponded to half the minimum non-zero value). We fit the GAM with the random effects of site and time-since-disturbance (k=3).

Yearling and vegetative survival and size. We analyzed size-specific survival of yearlings and vegetative plants. We constructed separate generalized linear mixed-effects models (GLMMs) for yearlings and vegetative individuals that tested the effects of rosette diameter, habitat, and their interaction on survival with the random effects of site and year. GLMMs were evaluated for significance using Analysis of Deviance, and Tukey's Honest Significant Differences were used to compare group means. We calculated relative growth rate (RGR) as natural log [rosette diameter of the current year/rosette diameter of the previous year]. We analyzed RGR between yearling-vegetative transitions and vegetative-vegetative transitions, using linear mixed-effects models (LMMs) similar to the GLMMs previously described. To analyze survival after fire, we combined data from the following quarter across all plants in a site that experienced fire, using data across five burns. We used a χ^2 test to analyze survival differences between the three burn ratings of unburned, scorched, and consumed. We conducted an additional χ^2 test to test whether burn rating affected the probability that an individual would eventually reach the reproductive stage.

Reproduction. We reported the median and quartile ages at first reproduction, and number of times individuals reproduced. Next, we calculated the survival of reproductive plants, and the probability of regressing to a vegetative stage. We analyzed the effect of habitat on survival of reproductive individuals using a GLMM fit with binomial error, the fixed effect of habitat, and the crossed random effects of year and site. The probability of flowering was modeled using a GLMM fit with binomial error with the fixed effects of rosette diameter, habitat, and their interaction, and the crossed random effects of year and site. Both GLMMs were evaluated for significance using analysis of deviance.

For reproductive individuals, the reproductive metrics of flowering heads, branch number, and height were analyzed by constructing LMMs with the random effects of plant nested within site and year, and the fixed effect of habitat. Response variables were natural-log transformed to meet model assumptions of normality. Models were evaluated for significance using analysis of deviance. Seeds per head were analyzed in two ways. First, we constructed a linear model in which the number of seeds per head was modeled as a function of habitat and year for the ABS collections. Second, using data from all three properties collected in 2003, the number of seeds per head was modeled with the predictor variable of property. In both models, the response variable was natural log-transformed, and the model was evaluated using analysis of variance (ANOVA). Finally, we estimated seed production (mean, maximum, and minimum expected per individual) as the product of flowering heads and seeds per head.

Seed Ecology

We conducted seven experiments that examine the seed ecology of *Chrysopsis highlandsensis* in laboratory and field conditions. For the field germination experiments specifically, our goals were to quantify germination percentages, seed bank longevity, and microhabitat requirements. All field germination experiments, except where indicated, used polyvinyl chloride (PVC) tubes 10 cm in diameter and height. Tubes were buried to ~2 cm above the soil surface in open sandy gaps, with no overhanging vegetation, at least 1 m apart. All seeds used in this study were encased within achenes, hereafter referred to simply as 'seeds.'

Laboratory viability experiment. This laboratory experiment compared seed viability by measuring germination percentages among four study sites (ABS Site 1, ABS Site 3, HHSP Sites 4–5, and LWRSF Sites 7–8) and between scrub and roadside populations. In December 2002–January 2003, we collected a single mature flowering head from 12–24 plants at each location. Seeds from each location were combined and categorized as intact (filled, robust achenes with substance and dark color), intermediate (visually questionable with seed present), or empty (achene not filled, straw colored). For intact seeds, we set up 10 replicate Petri dishes for each location with 30 seeds per dish for a total of 300 seeds per location and 1,200 seeds total. The same setup was used for intermediate and empty seeds but with only five replicate dishes, for a total of 600 intermediate and empty seeds respectively. All seeds were sown on filter paper and stored outside under a covered veranda with primarily indirect natural light and watered as needed. The experiment ran from January to March 2003.

We first analyzed differences in germination due to visual inspection of the achene using a generalized linear model (GLM) fit with binomial error. Second, we tested for differences between the four sites using a second GLM fit with binomial error.

Germination experiment 1. This experiment examined the effect of seed source and sowing location on field germination. In January 2002, we collected seeds from road and scrub ABS locations, transported them to the laboratory and sorted them to include only intact achenes. PVC tubes were buried in groups of three in ABS roadside (Site 1) or scrub (Site 3) locations with 15 replicate groups each. Each tube was randomly assigned 10 seeds sown from the road or scrub location or a control (no seeds) for a total of 300 seeds sown at each location. No supplemental water was provided. Germination was monitored monthly until May 2003, and quarterly through 2008. The effect of habitat on germination was analyzed using a Fisher's Exact Test.

Germination experiment 2. This experiment examined the effects of a recent burn and litter on seed germination. The burn was conducted in July 2003 in an ABS management unit south of the monitored *C. highlandsensis* populations in a similar habitat type. Seeds were collected from ABS Site 3 in December 2003, and sorted to use the fully intact seeds only, for a total of 520 seeds. In January 2004, PVC tubes were sown with 10 seeds each in 26 replicate pairs, one with and one without litter, at the burned site as well as an unburned site (Site 6). Tubes were checked monthly for germination and no supplemental water was provided from 2004–2009. Due to low germination (see Results), we were unable to statistically analyze the data.

Germination experiment 3. This experiment examined the factorial effects of supplemental water, disturbance, and seed source (scrub versus roadside) for a total of eight treatment combinations. Seeds were collected from ABS populations in December 2005 and January 2006. The experiment took place in a management unit at ABS with scrubby flatwoods habitat and without *Chrysopsis highlandsensis*. Ten replicates were assigned per treatment with 50 seeds per PVC tube in January 2006. Supplemental water was provided (50 mL) each week through June 2006, except on weeks when total weekly rainfall exceeded 50 mL. Disturbance was applied immediately before sowing seeds by running a small hand rake through the sand. Germination was monitored quarterly from 2006–2012. Data were analyzed using a binomial GLM model that fit the proportion of seeds germinated as a function of water, disturbance, and seed source, and all interactions. The model was evaluated for significance using analysis of deviance.

Germination experiment 4. In this experiment, we augmented the seed bank with the factorial combination of seed additions and litter removal. We conducted this experiment within Site 5 at HHSP, a population that went extinct in 2011, most likely due to a thick sand pine canopy (see Results). Using the five, 10×1 m demography plots, we divided each of these larger plots into four smaller, 2.5 m long plots for a total of 20 plots, each assigned a treatment. Litter was initially removed from all plots, down to the bare mineral soil. Seeds were sown into randomly assigned 2.5×1 m plots, 220 seeds per plot, and litter replaced in half of the plots. Seeds were collected from HHSP populations in December 2012 and sown into the appropriate plots in February 2013. A second litter removal event was conducted in February 2014 for the 10 seed addition plots such that the combined treatments across the two events were as follows: (1) control—control (three plots), (2) litter removal—litter removal (three plots), (3) control—litter removal (two plots), and 4) litter removal—control (two plots). Plots were monitored quarterly at the same time as the *Demographic Monitoring* until 2021.

Data were analyzed separately following each litter removal event. For the first litter removal event, the proportion of total germinants observed per plot through the end of 2013 was analyzed as a function of the litter removal treatment with a GLM fit with quasibinomial error to account for overdispersion. The model was evaluated for significance using analysis of deviance. For the second litter removal event, we calculated the number of germinants observed following the second event which included all data collected after March 2014, and we estimated the total seeds that would have been present as the initial number of seeds (220) minus the seeds that germinated in 2013. We analyzed the proportion of remaining seeds that germinated as a function of the two litter removal treatments using a GLM with quasibinomial error and analysis of deviance as above.

Germination experiment 5. This experiment examined the factorial effects of shade and soil disturbance. Using 40% polyethylene knitted shade cloth secured with ground staples over PVC tubes, we employed three levels of shade: full shade (two layers of cloth), partial shade (one layer of cloth), and no shade (1 cm^2 wire mesh cage). Disturbance was applied by breaking up sand soil crust with a hand rake prior to sowing. All PVC tubes were installed one week prior to the experiment to allow soils to settle. Seeds were collected in December 2013 from ABS Site 3. We sowed 50 intact seeds in each of 60 PVC tubes in scrub habitat (Site 6) in March 2014. Plots were monitored weekly from December 2014–February 2015, biweekly March–April 2015, and monthly May 2015–August 2016. We analyzed the effects of shade, soil disturbance, and their interaction on germination using a GLM with binomial error and evaluated the model for significance using analysis of deviance. Tukey's Honest Significant Differences were used to compare group means.

Seed predation experiment. A seed predation study was conducted to quantify post-dispersal seed removal by vertebrates in scrub and roadside habitats. This experiment was conducted across three trials in March 2022, April 2023, and May 2023. Seeds were collected from ABS in December of the previous year and sorted for viability based on their firmness. During each trial, 60 Petri dishes (10 cm diameter) were filled with sandy soil collected from a disturbed firelane away from *Chrysopsis highlandsensis* plants to avoid seeds in the soil, and each received five seeds (300 seeds total) which were pushed into the soil. Petri dishes were carefully transported to the field and arranged on the ground in sets of 10 in which a randomized set of five were caged with 20×20 cm hardware cloth (with 6×6 mm openings) to exclude vertebrate seed predators ('exclusion' treatment), and the other five were left without a cage ('open' treatment). Each trial ran for 48 hours and took place at three locations at ABS (locations were situated near Site 1, Site 3, and an additional, unmonitored *C. highlandsensis* population), with each location having one set in roadside and one set in nearby interior scrub habitat. The data were analyzed using a GLMM with binomial error, with habitat and treatment as fixed effects, and site and trial date as random effects. The model was evaluated for significance using analysis of deviance, and Tukey's Honest Significant Differences were used to compare group means.

Rangewide surveys

To document population trends across the species' range, we conducted rangewide surveys at all the known, extant sites with *Chrysopsis highlandsensis*. These were conducted at five-year intervals in 2005, 2010, 2015, and 2020. Seven populations were surveyed including four on protected property (ABS, Avon Park Air Force Range (APAFR), HHSP, and LWRSF) and three on unprotected property (CR731, Red Beach, and Sheriff's Tower). Within each population, we designated subpopulations as clusters of plants based on the following: barriers such as roads or firelanes, distinct habitats, or approximately 50 m separation. Within each subpopulation, all reproductive individuals were counted by a team of observers. In 2005, monitoring of 46 subpopulations was initiated, and new subpopulations were added to the surveys in 2010 (16), 2015 (7), and 2020 (8). Two populations on private property (Red Beach and Sheriff's Tower) were not surveyed in 2015 or 2020 due to access issues. Because we suspected these had been extirpated, we surveyed these populations in 2024 from a right-a-way from which we could assess the presence of reproductive individuals.

We estimated the percent change in reproductive individuals per year by constructing mixed-effects models. For each population, we modeled the number of adults (natural log-transformed +1) as a function of year, and included the subpopulation as a random effect to control for repeated measures. The model was evaluated for significance using analysis of deviance. This analysis allowed us to use the subpopulations that were initiated in 2005, 2010, and 2015. The subpopulations newly recorded in 2020 were not included in the analysis because we could not assess population trends over time, but were included in the estimated total counts from 2020, as this survey year represents the best estimate of the total species population size to date.

To understand habitat preferences, we also report the soil series and habitats that surveyed subpopulations occurred within. Soil series followed Menges (2007), and we also report the subsoil color (white, grey, or yellow). Habitat was classified as one of the following: disturbed habitat (including roadsides, sandy roads, firelanes, planted pine, canals, and ditches), oak scrub, sandhill, sand pine scrub, scrubby flatwoods, flatwoods, dry-mesic flatwoods/savannah, and mixed scrub. All data associated with this article have been archived using the Environmental Data Initiative (David et al. 2025).

RESULTS

Demographic study

Population trends. We followed 6,456 *Chrysopsis highlandsensis* plants from 1999–2022. Of these, 5,230 plants were tracked as seedling recruits, and 4,759 plants were tracked for their full life cycle from seedling to death. Across all individuals, the mean lifespan was 1.3 years (standard deviation=1.7), and ranged from 0.25–12 years. For individuals that reached the reproductive stage, the mean lifespan was 4.3 years (standard deviation=1.7) with an interquartile range of 3–5 years.

In general, populations declined during the 24 years of demographic monitoring (Figure 2). Of the four ABS populations (Sites 1–3, 6), all declined beginning in the first two years of monitoring. The HHSP populations at Sites 4 and 5 became extirpated by 2014, but the Site 10 population experienced a boom beginning in 2019 following a mechanical roller-chopping treatment. The LWRSF population, particularly the LWRSF Site 7 roadside population, remained mostly stable, while the scrub portion of Site 7 as well as Site 8 declined.

Seedling recruitment. Most seedling recruitment (53.4%) occurred during the winter dry season months December–March (Table 2). Subsequently, we observed relatively high mortality (49.8%) of new recruits in the following quarter (March–June), with only 29.2% of these winter recruits surviving an entire year to the following March. Recruitment was observed in lower numbers during the spring and summer (12.8% and 10.1%, respectively), and was intermediate during the fall (23.7%) with comparatively higher quarterly and one-year survival than in winter (Table 2).

Across 15 disturbance events (12 fires and three mechanical treatment events), we did not observe any significant relationship between seedling recruitment and the time-since-disturbance. Seedling recruitment was not associated with the time-since-disturbance (generalized additive model, p=0.588), although recruitment was significantly higher in the roadsides than the scrub (p<0.001).

Survival of yearlings and vegetative individuals. Yearling survival increased with rosette diameter (χ^2=177.5, d.f.=1, p<0.001) and was higher in scrub (back transformed mean 74.8±6.4% SE) than roadside habitat (68.4±7.6% SE; χ^2=6.3, d.f.=1, p=0.012) (Figure 3a). There was no significant habitat × diameter interaction term (χ^2=1.2, d.f.=1, p=0.265).

For the vegetative stage, large diameters (χ^2=198.3, d.f.=1, p<0.001) were associated with higher survival. Vegetative survival in the scrub (81.7±4.8% SE) was higher than road habitat (70.4±6.7% SE; χ^2=21.1, d.f.=1, p<0.001) (Figure 3a). We found no significant habitat × diameter interaction term (χ^2=0.007, d.f.=1, p=0.932).

Individuals frequently survived fire events. No seedling <1 year old survived fire damage (three scorched, five consumed), though 53 seedlings (86.9%) were unburned across all burns. For all plants that were non-yearlings (vegetative or reproductive), 38.7% of individuals that experienced fire (rated either as 'scorched' or 'consumed') survived to the next quarterly census, compared to 84.5% of unburned plants (Table 3, Figure 3b). In all but two burns, the proportion of surviving plants among unburned, scorched, and consumed plants significantly varied (Table 3). Across burns, unburned plant survival ranged from 73.9–100%, scorched survival ranged from 28.9–100%, and consumed plant survival ranged from 12.5–42.9% (Table 3). Probability of reaching the reproductive stage significantly decreased after surviving fire (χ^2=8.2, d.f.=2, p=0.017), with 40.8% of unburned (non-seedling) individuals eventually reproducing, compared with 28.6% of scorched individuals and 22.6% of consumed individuals.

Size of yearlings and vegetative individuals. Yearlings had a mean rosette diameter of 2.6±0.04 cm (median=1.9 cm) that ranged 0.2–18.3 cm. Yearling-vegetative RGR did not differ by habitat (χ^2=0.095, d.f.=1, p=0.758) and had a mean of 0.661±0.084 cm (Figure 3c).

Vegetative-vegetative stage growth was comparatively slower, and vegetative individuals had a mean of 8.2±0.1 cm. Vegetative individuals had higher RGR in road (0.210±0.037) than scrub habitat (0.154±0.0346; χ^2=5.09, d.f.=1, p=0.024) (Fig. 3c). Vegetative individuals that remained vegetative grew or remained the same in diameter in 76.3% of cases, and regressed in diameter in 23.7% of cases.

Vegetative diameter was a strong predictor of probability of reproduction the following year, and this effect differed by habitat as evidenced by the significant habitat × diameter interaction (χ^2=11.8, d.f.=1, p<0.001). Vegetative individuals in road habitat transitioned to reproductive individuals at a smaller diameter than those in scrub habitat (Figure 3d). In roadside habitat, a vegetative individual with a diameter of 16.6 cm had a 50% probability of transitioning to a reproductive individual, whereas in scrub habitat a 17.8 cm diameter was required for 50%.

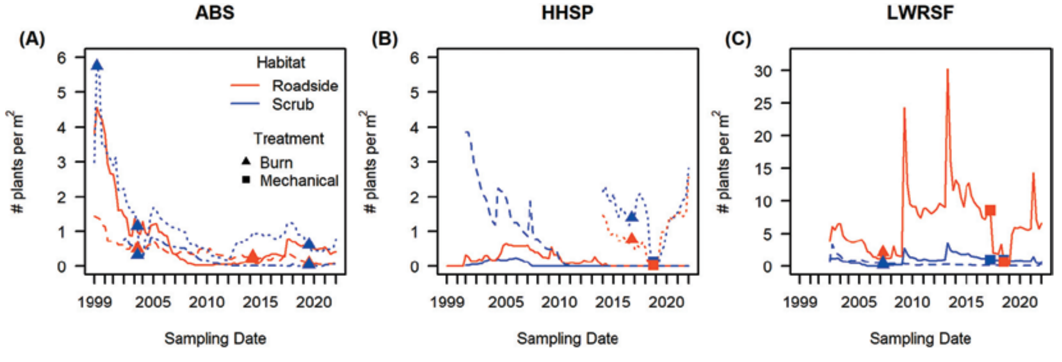

Figure 2. Population trends of *Chrysopsis highlandsensis* using quarterly censuses from the demographic monitoring study. Each line depicts a distinct population (Table 1) within a habitat (color-coded as roadside or scrub), with some populations spanning both habitats and therefore represented by two lines. Shapes indicate when burn or mechanical treatment events occurred. **(A)** Archbold Biological Station: solid=Site 1, dashed=Site 2, dotted=Site 3, dot-dash=Site 6. **(B)** Highlands Hammock State Park: solid=Site 4 (roadside and scrub habitat), dashed=Site 5, dotted=Site 10. (roadside and scrub habitat) **(C)** Lake Wales Ridge State Forest: solid=Site 7 (roadside and scrub habitat), dashed=Site 8.

Table 2. Recruitment and survival of *Chrysopsis highlandsensis* from 1999–2022 across nine sites. Data were collected quarterly every March, June, September, and December. Recruitment was the number of seedlings recorded during that census quarter. Quarterly survival of recruits was calculated as the percentage of new recruits that survived to the following census quarter. One-year survival was calculated as the percentage of new recruits that survived to that same census quarter of the following year.

Quarterly Census	Recruitment (% of annual total)	Survival of new recruits to next quarter	1-year survival of new recruits
March	2,794 (53.4%)	49.8%	29.2%
June	669 (12.8%)	81.2%	61.1%
September	527 (10.1%)	82.2%	54.5%
December	1,240 (23.7%)	83.4%	46.5%
Total or Mean	5,230 (100%)	64.4%	40.0%

Reproduction. Of the plants in which we documented the entire lifecycle, 17% reproduced at least once. The median age at first reproduction was three years with an interquartile range of 2–4 years (range 1–11 years). We documented 84 instances (15.7%) of 1-year-old plants reaching reproduction (second annual demographic census), and 85% of plants that reproduced did so for the first time by age 4. Only 15 plants (2.8%) reproduced for their first time at age 7 or older.

Of the individuals that reached the reproductive stage, most were only reproductive once (87%), indicative of a largely monocarpic life cycle. Importantly, we observed many instances of plants reproducing more than once—109 plants reproduced twice (10.8%), 19 reproduced three times (1.9%), and two reproduced four times (0.2%).

Across all years and sites, 19.2% of all reproductive individuals survived (80.8% mortality), of which 6.7% of all individuals regressed to the vegetative stage and 12.5% remained reproductive the next year. Survival of reproductive individuals was significantly higher in scrub compared to roadside (χ^2=4.0, d.f.=1, p=0.045; Figure 3a). Mortality was almost always preceded by reproduction regardless of whether the plant was monocarpic or polycarpicy. Of the plants that reached the reproductive stage, 95.5% of plants died the same year they flowered, while just 4.5% regressed to a vegetative stage in their final year.

The number of flowering heads across all flowering individuals was 63.4 (sd=71.7; range 1–525), and did not differ between habitats (χ^2=0.34, d.f.=1, p=0.558). The mean branch number was 3.0

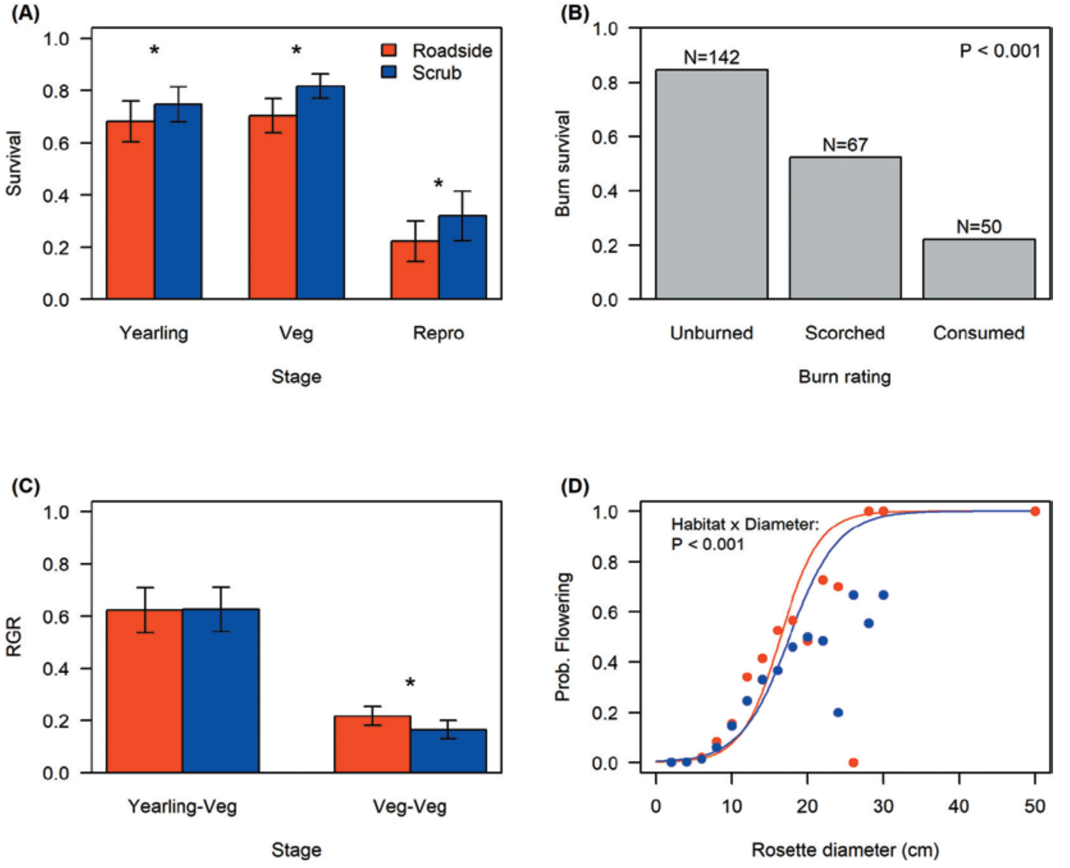

Figure 3. Population vital rates of *Chrysopsis highlandsensis* across all sites. **(A)** Stage-specific survival (yearling, vegetative, reproductive) for roadside and scrub populations with back transformed means and standard errors. Data were averaged across years. * denotes a significant difference between roadside and scrub populations. **(B)** Burn survival to the following quarterly census for plants scored as unburned, scorched, or consumed (vegetative and reproductive plants only). Number of plants within each category is shown above bars, and the P-value from χ^2 test is shown. **(C)** Relative growth rate (RGR) of rosette diameter for stage transitions with back transformed means and standard errors. * denotes a significant difference between roadside and scrub populations. **(D)** Size-specific probability of flowering. Points show the probability binned between each 2 cm of diameter, and lines show the binomial regression fit.

(sd=2.9; range 1–33) and similarly did not differ between habitats (χ^2=0.7, d.f.=1, p=0.395). Height of the tallest branch had a mean of 53.9 cm (21.8 sd; range 3.8–182.5) and was 9.1% greater in scrub compared to road habitat (χ^2=4.4, d.f.=1, p=0.035).

Across all samples, the mean number of seeds per head was 78.5 (sd=24.0, range: 3–291), and the number of intact seeds per head was 50.9 (s.d.=30.3, range 0–182), or 64.8% of seeds. Total seeds per head did not differ between scrub and road populations at ABS (F=0.68, d.f.=1, 213, p=0.412), but did vary among years (F=3.1, d.f.=7, 213, p=0.004) with means ranging from 67.8–84.6 seeds per head. In the cross-site analysis using data from 2003, ABS populations had significantly higher total seeds per head (94.7±12.1) than HHSP (60.0±7.7) or LWRSF (46.5±6.0) (F=7.9, d.f.=2, 27, p=0.002).

Using these estimates of flowering heads and seed production, we calculated that an individual reproductive plant produced, on average, 4,906 seeds of which 3,181 were intact. Using the

Table 3. Survival of *Chrysopsis highlandsensis* plants (yearlings excluded) following fire. Individual plants were rated as unburned, scorched (partially burned), or consumed (little to no green tissue remaining). χ^2 tests were used to assess the differences in survival rate across the burn rating and across all plants combined.

Burn	Property (Site ID)	# plants (non-yearlings)	Survival			χ^2	P
			Unburned	Scorched	Consumed		
2004	ABS (2,3,6)	96	83.3%	28.9%	12.5%	34.4	<0.001
2008	LWRSF (7,8)	32	96.6%	66.7%	–	0.61	0.438
2015	ABS (2)	9	100%	100%	42.9%	2.1	0.358
2017	HHSP (10)	77	73.9%	100%	22.2%	23.4	<0.001
2020	ABS (2,3,6)	45	91.7%	66.7%	22.2%	15.5	<0.001
Total		259	84.5%	52.2%	22.0%	68.3	<0.001

minimum and maximum estimates, we calculated that the seed production of an individual plant could range from as low as 3 seeds (0 viable) to as high as 152,775 seeds (95,813 intact).

Seed ecology

Laboratory viability experiment. Visual inspection and classification of seeds was highly predictive of germination (χ^2=92.8, d.f.=2, p<0.001). Fully intact seeds had a 19.8±0.1% SE germination percentage, compared with 2.7±0.1% for intermediate seeds and 0% for empty seeds. Considering that 64.8% of seeds are intact, we estimate that just 12.8% of the total seeds produced are viable.

Germination significantly varied by site (χ^2=83.7, d.f.=3, p<0.001), with HHSP seeds (30.3±2.7% SE) having significantly higher germination percentages than both ABS scrub (20.3±2.3% SE) and ABS roadside seeds (4.3±1.1% SE), and non-significantly higher rates than LWRSF seeds (24.0±2.5% SE).

Germination experiment 1. A total of 12 germinants (2%) were recorded in this study of seed source and sowing location (Table 4). Germination primarily occurred between December 2002 through March 2003 (11–14 months after sowing), and two germinants were observed in 2005. Eight germinants were observed in the roadside site, and four in the scrub site (p=0.383). The last germinant was observed in December 2005, nearly four years after sowing.

Germination experiment 2. From 2004–2009, only five germinants (1%) were recorded (Table 4). Of these, four germinants were in the *Litter* treatment and one in the *No Litter* treatment. One germinant was observed in the burned site, and the remaining four in the unburned site. One of the germinants was observed one month after sowing (February 2004), and all other germinants emerged on or after June 2005, with the last germinant emerging March 2008 (four years post-sowing).

Germination experiment 3. We observed 82 germinants out of 4,000 seeds during this experiment (2.1%) (Table 4). All germinants were observed after the watering treatment ended, with 89% of germinants first observed during the first three sampling times in September 2006 (25 germinants), December 2006 (9), and March 2007 (42). The last germinant was observed in December 2010, nearly 5-year post-sowing. We found a significant three-way interaction between disturbance × water × seed source (χ^2=5.07, d.f.=1, p=0.024), but Tukey HSD test did not reveal significant differences among any treatment groups (p-values ranged 0.144–0.999). Back transformed group means ranged from 0.8% (no disturbance, water, scrub seed source) to 3.4% (disturbance, no water, roadside seed source).

Germination experiment 4. From 2013–2016 we observed a total of 190 germinants, all of which were in the seed addition plots (8.6% germination; Table 4). All subsequent analyses therefore only considered the seed addition plots. Of these germinants, 113 germinated (59%) in September and

Table 4. Summary of results from five field germination experiments of *Chrysopsis highlandsensis*. The 'first year' encompasses the first full winter after sowing through March. The maximum seed bank duration refers to the latest germinant observed post-sowing (note that observations from December were considered part of the following year). Factors are bolded when significant (see main text for statistics), and the directionality of the factor is indicated with an up arrow (increased germination) or down arrow (decreased germination)

Experiment	Year seeds collected	Years actively monitored	Month initiated	Overall germ %	Proportion of germinants that emerged in first year	Max. seed bank duration	Factors
1	2001	2002-2008	Jan	2.0%	83%	4 yr	Habitat (scrub vs. road)
2	2003	2004-2009	Jan	1.0%	20%	4 yr	Fire Litter
3	2005 (includes early 2006)	2006-2012	Jan	2.1%	89%	5 yr	Soil disturbance Water addition Seed source
4	2012	2013-2020	Feb	8.6%	97%	5 yr	**Litter removal: ↑** **Seed addition: ↑**
5	2013	2014-2016	Mar	7.2%	92%	2 yr	**Shade: ↑** **Soil disturbance: ↓**

December 2013, and 72 germinated (38%) in spring 2014 following the second litter removal event. The last germinant was observed in June 2018 (5-year post-sowing). Plants continued to be monitored as part of the demographic study, and all plants within the study area died by 2020.

Following the first litter removal event, plots with litter removal had significantly higher germination percentage (back transformed mean±S.E: 9.4±2.7%) than control plots with no removal (0.8±0.8%, χ^2=10.2, d.f.=1, p=0.001). Following the second litter removal event in February 2014, there were no significant effects of the first removal (χ^2=0.04, d.f.=1, p=0.842), second removal (χ^2=1.7, d.f.=1, p=0.187), or their interaction (χ^2=0.51, d.f.=1, p=0.473), on germination percentage of the remaining seeds.

Germination experiment 5. A total of 217 seeds germinated during the experiment (7.2%; Table 4). The majority (75%) of these seeds germinated during the first month of monitoring, and 92% of these seeds germinated the first season from December 2014–April 2015. The last germinant was observed in July 2016 (2-year post-sowing). Shade significantly increased germination percentage (χ^2=119.5, d.f.=2, p<0.001), with partial shade (back transformed mean±S.E.: 11.6±0.01%) and full shade (8.8±0.01%) treatments leading to significantly higher germination percentage than the full sun treatment (0.01±0.003%, Figure 4a). Disturbance significantly decreased germination percentage (χ^2=18.0, d.f.=1, p<0.001) from 6.8±0.01% in undisturbed soil to 2.4±0.01% in disturbed soil. There was no significant shade × disturbance interaction (χ^2=3.6, d.f.=2, p=0.169, Figure 4a).

Seed predation experiment. The seed predation exclusion treatment had significantly higher percentages of seeds remaining after 48 hours than the open treatment (59% vs. 36%; p<0.001) and there were more seeds remaining in the scrub than the road (54% vs. 40%; p<0.001, Figure 4b). Exclusion treatment dishes had significantly higher proportions of seeds remaining compared to the open treatment within both the road habitat (49% vs. 32%; p=0.005) and scrub habitat (68% vs. 40%; p<0.001, Figure 4b).

Rangewide surveys

The rangewide surveys of seven populations conducted between 2005–2020 indicated that few populations were stable (Table 5, Figure 5). APAFR had by far the largest population (4,648 adults) and grew 7.0±1.9 % each year (χ^2=13.6, d.f.=1, p<0.001). LWRSF had roughly stable growth (−0.7±3.7

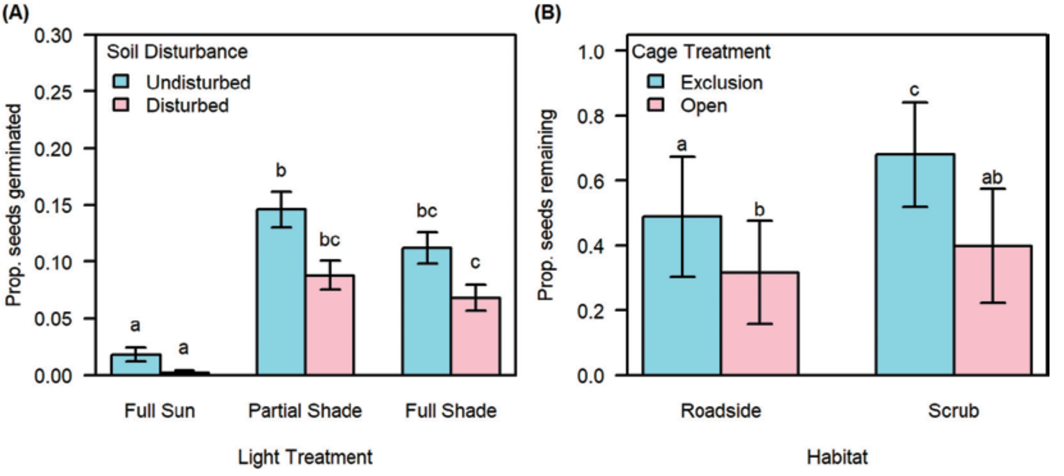

Figure 4. Seed ecology of *Chrysopsis highlandsensis*. **(A)** *Germination experiment 5* results show positive effects of shade and negative effects of disturbance on germination. **(B)** *Seed predation experiment* shows positive effects of cage exclusion on the proportion of seeds remaining in roadside and scrub habitats. Letters denote significant differences among groups using Tukey's Honest Significant Differences.

%; χ^2=0.038, d.f.=1, P=0.844). HHSP (−10.0 ±2.9 %; χ^2=13.5, d.f.=1, p<0.001), ABS (−6.9±3.5 %; χ^2=4.3, d.f.=1, P=0.038), and CR731 (−7.2±2.2 %; χ^2=11.9, d.f.=1, p<0.001) all showed significant declines. Two populations (Red Beach and Sheriff's Tower) had <10 reproductive individuals each during their most recent rangewide survey in 2010, and no reproductive plants were observed in 2024. A total of 7,444 reproductive individuals were counted as of the most recent survey in 2020, representing the best estimate of the total *Chrysopsis highlandsensis* population size.

On the Lake Wales Ridge alone, 77% of the subpopulations occurred on the white sand entisols Satellite and Archbold soil series. Rangewide, 63% of the plants occurred on Narcoossee soils series, a grey sand spodosol on the Bombing Ridge at APAFR. If soil preference is based upon the number of subpopulations, 49% of the sites occur on white entisols (Archbold and Satellite), followed by Narcoossee, which accounted for 19% of the subpopulations. Overall, more than 75% of the plants were located on grey color sands, followed by white sands, which comprised over 21% of the total. Additionally, non-xeric soils accounted for just over 3%, while xeric yellow entisols (Astatula soil series) represented less than 1% of the total distribution.

Habitat for 43% of subpopulations was classified as disturbed habitat. Scrubby flatwoods (25%) were the second most common habitat type, followed by sandhill (11%), oak scrub (7%), dry-mesic flatwoods/savannah (5%), and flatwoods (5%). Sand pine scrub and mixed scrub habitats each contained only a single site.

DISCUSSION

In this study we provided the first description of the life history and demography of *Chrysopsis highlandsensis*. First, our study revealed key life history characteristics of the species, including timing of germination, stage-specific survival and transitions, and lifespan. Notably, we report that the species is mostly monocarpic, and only 13% of individuals survive their first reproductive event. Second, we report low field germination, likely due in part to low seed viability and high post-dispersal seed predation, but a capacity to maintain persistent seed banks up to five years. Third, we report population declines across most of the range from 2005–2020, with stable and/or growing populations occurring in the northern populations. Together, these findings provide critical information relevant to the management and conservation of the species.

Table 5. *Chrysopsis highlandsensis* rangewide survey sites and counts of reproductive plants. Surveys were conducted at four time points (2005, 2010, 2015, and 2020). The statistical analyses tested whether the number of reproductive individuals within each population significantly changed through time (see main text for details), and the slope estimate, standard error, χ^2 test statistic, and P-value from these analyses are shown. For soil color: G=grey, W=white, Y=yellow.

Population	Soil series present (color)	# reproductive individuals (# sampling plots surveyed)				Slope estimate (SE)	χ^2	P
		2005	2010	2015	2020			
CR731	Pomello (W)	92 (2)	29 (2)	35 (2)	29 (2)	–0.072 (0.022)	11.85	0.001
ABS	Satellite (W), Satellite/Basinger (W), Basinger (W)	254 (7)	251 (9)	155 (9)	84 (11)	–0.069 (0.035)	4.31	0.038
APAFR	Pomello (W), Zolfo (G), Narcoossee (G), Satellite (W)	844 (23)	1854 (27)	2627 (33)	4648 (37)	0.070 (0.019)	13.60	<0.001
HHSP	Archbold (W), Smyrna (G), Myakka (G), Archbold/Myakka (W), Archbold (W)	4314 (7)	2854) (17)	3220 (18)	1373 (20)	–0.100 (0.029)	13.45	<0.001
LWRSF	Archbold (W), Satellite (W)	841 (5)	703 (5)	1481 (5)	1310 (5)	–0.007 (0.037)	0.04	0.844
Red Beach	Astatula (Y)	32 (1)	6 (1)	–	0 (1)*	–	–	–
Sheriff's Tower	Satellite (W)	7 (1)	4 (1)	–	0 (1)*	–	–	–

*Survey conducted in 2024

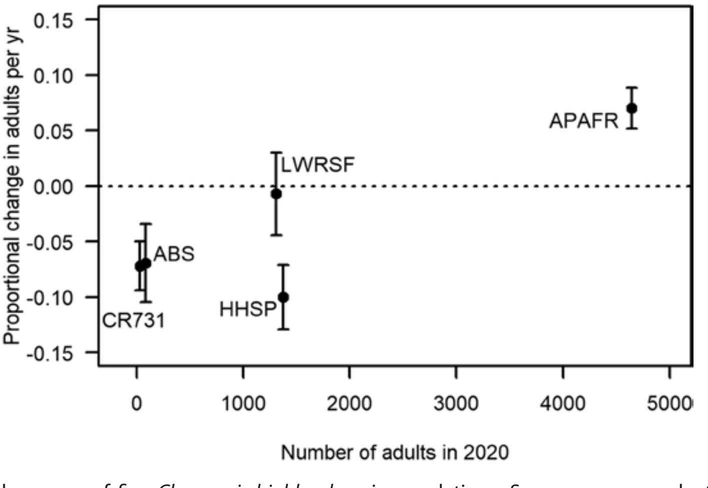

Figure 5. Rangewide survey of five *Chrysopsis highlandsensis* populations. Surveys were conducted in 2005, 2010, 2015, and 2020. Y-axis shows the proportional change in reproductive individuals per year with standard error as calculated using linear mixed-effects models. Note that two populations (Red Beach and Sheriff's Tower) are not shown and no reproductive plants were observed in the most recent survey (2024). Refer to main text for property abbreviations.

Life history

Our study revealed several previously unknown aspects of the life history of *Chrysopsis highlandsensis*. The species is a short-lived herb that, when reaching the reproductive stage, averages 4.3 years but may live as long as 12 years. Most of the seeds produced are either not intact or otherwise not viable, though it is possible that our approach could have underestimated seed viability if any cues are required to break dormancy. Germination occurs year-round, though over half of all germinants emerge in the winter dry season (Dec–Mar). Rarely, seeds may enter a persistent seed bank and remain viable for up to five years before germinating. Once germinated, plants typically spend 1–3 years in the vegetative stage before producing flowering branches. Only 13% of reproductive individuals survive to flower again, and the maximum number of flowering years we recorded for any individual was four.

Several aspects of *Chrysopsis highlandsensis*' life history differ substantially from the ecologically and morphologically similar congener *Chrysopsis floridana* Small, a Florida state-listed species that was recently delisted from the federal list (USFWS 2024). *Chrysopsis floridana* is a similarly short-lived perennial herb but regularly exhibits a polycarpic life history (Ward et al. 2022). Our data suggests that *C. highlandsensis* better capitalizes on roadsides and other disturbed habitats than scrub (survival, seedling recruitment) compared to *C. floridana* which better performed in scrub habitats (Ward et al. 2022). While the germination of both species was reduced with leaf litter (Lambert and Menges 1996), the seed ecology of *C. highlandsensis* differed from *C. floridana* in several ways. In contrast to *C. highlandsensis*, *C. floridana* seeds tended to germinate slightly later in the year (early spring) and were unaffected by light (Lambert and Menges 1996). Interestingly, soil disturbance increased germination of *C. floridana* (Lambert and Menges 1996), but not *C. highlandsensis*, which is contrary to the relative demographic success of both species in disturbed roadside habitat.

A remaining question is the role of the seed bank for maintaining *Chrysopsis highlandsensis* population persistence. While we have documented that *C. highlandsensis* seeds can germinate up to five years after sowing, these instances were infrequent. Many rare herbs of the Florida scrub have persistent seed banks (e.g., Menges and Quintana-Ascencio 2004; David et al. 2024), though other scrub endemic asters lack persistent seed banks (e.g., *Liatris ohlingerae* (S.F.Blake) B.L. Rob., Weekley et al. 2008b). Based on our results, the role of the seed bank in persistence is uncertain over the long-term and requires additional study, especially as to how it might relate to climate factors and changes to El Niño–Southern Oscillation cycles (Slocum and Orzell 2013).

The mostly monocarpic life cycle of *Chrysopsis highlandsensis* is unusual for perennial herbaceous scrub species. Monocarpic plants typically wait until conditions are optimized for reproduction, including avoiding herbivores that may damage the flowering branches (Metcalf et al. 2003). We rarely if ever observed herbivory on the flowering branches of *C. highlandsensis* (A.S. David, pers. obs.), though granivorous insects such as ants have been observed carrying seeds (A.S. David, unpublished data). Further work with *C. highlandsensis* is needed to understand the ecological consequences of partial monocarpy on maintaining population persistence.

Fire ecology

Unlike many endemic herbs of the Florida scrub, we found little evidence that *Chrysopsis highlandsensis* exhibits population booms following fire. In contrast, several species that occur in rosemary scrub (Menges and Quintana-Ascencio 2004; Quintana-Ascencio et al. 2018), yellow sand oak hickory scrub (Menges et al. 2006), as well as the congener *C. floridana* (Bowen et al. 2025) exhibit high seedling recruitment pulses in the years immediately following fire with gradual population decline as the shrub canopy closes over time. *Chrysopsis highlandsensis* habitats such as scrubby flatwoods are presumed to burn every 6–19 years, which is more frequent than upland scrub habitats like rosemary scrub or oak hickory scrub where other endemic herbs are frequently encountered (Main and Menges 1997), and this difference in habitat might account for the species' distinct post-fire strategy. Germination of *C. highlandsensis* appears to require the relatively open canopy and low litter the fires provide but does not similarly capitalize on the post-fire environment.

We suggest that three aspects of the species' life history explain this surprising lack of response to fire. First, as mentioned above, it is not clear what the role of a persistent seed bank plays for *Chrysopsis highlandsensis*, given that so few seeds enter this seed bank. Our seed ecology experiments demonstrated that post-dispersal seed predation likely reduces seed numbers substantially, and, once in the soil, the vast majority of seeds that germinate do so in the first year. Second, the predominantly monocarpic life cycle suggests that reproduction is relatively rare in the population. While individual plants can produce thousands of seeds, the extended vegetative stage and high likelihood of mortality following reproduction suggest that populations may occasionally be seed-limited. Third, the ability of individuals to survive fire, particularly low intensity fire resulting in scorching, is likely an important mechanism by which the species persists in a pyrogenic habitat.

In contrast, our rangewide surveys lend additional insight into the fire regime in which *Chrysopsis highlandsensis* evolved. At APAFR, Landsat Burned Area Imagery from 1978–2018 at 15 sites with >50 individuals of *C. highlandsensis* revealed a range in fire frequency of 2.0–10 years, with the lowest fire return interval being 4.1 years for scrubby flatwoods, followed by 4.3 years for scrub, and 10 years for sand pine scrub (S. Orzell, unpublished data). These APAFR sites, which were generally burned more frequently than our demographic sites (Table 1) were primarily scrubby flatwoods and to a lesser extent low oak scrubs. Time-since-fire is critical for maintaining sandy gaps in scrubby flatwoods, with more frequent fire needed in comparison to other Florida scrub communities making scrubby flatwoods particularly vulnerable to fire suppression (Young and Menges 1999; Dee and Menges 2014). The fire history at APAFR and its increasing population size may suggest a shorter fire-return-interval than 6–19 years is required to sustain populations, and sites with naturally lower fire frequencies such as rosemary scrub and sand pine scrub may at best be marginal habitat for *C. highlandsensis*. A similar finding that the required fire frequency was underestimated was recently demonstrated for the congener *C. floridana* (Bowen et al. 2025). Additional work is still needed to determine what constitutes proper fire management for the species.

Microhabitat conditions

Our study suggests that a restrictive microhabitat could be one factor that limits populations of *Chrysopsis highlandsensis*, particularly seedling recruitment. Germination benefited from low litter levels with some canopy, yet dense litter, particularly in long unburned sand pine scrub strongly reduced germination, and populations generally performed better in roadside habitats where shrub canopy was relatively open. The microhabitat of *C. highlandsensis* is similar to that of the congener *C. floridana*, particularly with respect to litter cover (Ward et al. 2022). Furthermore, our analysis of site preference from the rangewide survey indicated that grey and white sand soils are preferred, with the high density APAFR sites accounting for most of the grey soils and the declining Lake Wales Ridge sites accounting for many of the white sand soils. This finding could suggest that grey soils are better suited for *C. highlandsensis* growth, and that white sand soils are less preferable, though further research is needed. Importantly, disturbed habitat, including roadsides, appears to boost *C. highlandsensis* populations rangewide, and this habitat time may provide the restrictive microhabitat the species needs.

The high post-dispersal seed predation we observed suggests that there are top-down controls on the population. Importantly, the caged plots in our seed predation experiment also showed substantial seed loss; this loss was most likely due to invertebrate seed predation by ants (A.S. David, unpublished data), but the limitations on our experimental design mean that we cannot rule out the effect of wind blowing seeds away or other factors. Regardless, the fact that so many seeds in caged plots were gone suggests that many of the seeds produced in a population will similarly be removed, and such high seed predation could potentially account for declining populations.

Conservation

Our study documents substantial declines of *Chrysopsis highlandsensis*, both within demographic monitoring sites and across most of the range. The external threats the species faces include continued habitat destruction or extirpation on unmanaged, unprotected lands. Within habitats, there are numerous ecological challenges to maintaining populations including the monocarpic life history of the species, low overall fecundity, low seed viability (20%), high seed predation, and low potential for seed banking. Consistent and frequent application of fire to habitat containing *C. highlandsensis* is also likely key for population persistence. Further research is needed to understand the causes for these ecological challenges, including quantifying pollinator visitation, genetic diversity, and pre-dispersal seed predation.

Action is likely needed to bolster existing populations and add new populations of *Chrysopsis highlandsensis*. Seed addition is likely insufficient to introduce or augment populations. None of our germination experiments resulted in persistent populations, suggesting that either higher numbers of seeds are needed or that the introduced habitat does not provide a conducive microhabitat. Transplanting plants propagated from seed could be a more efficient alternative than seeding, as has been found in most translocations (Albrecht and Maschinski 2012). Eight introductions of *C. floridana* used vegetative plants, and roughly half of these populations are stable (Bowen et al. 2025). Additional work is needed to identify potential recipient sites on protected land within *C. highlandsensis*' restricted range and to conduct introductions likely needed to secure the species' persistence.

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