


RESEARCH ARTICLE

Using demographic findings to compare wild and translocated populations of Florida goldenaster (*Chrysopsis floridana*) in west-central Florida, U.S.A.

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Evaluation of the success of rare plant introductions requires analysis of demographic success. We analyze the success of 10 wild and 8 introduced populations of Florida goldenaster (*Chrysopsis floridana*), a federally endangered forb endemic to west-central Florida, using demographic and stage-class data collected from 2017 to 2019. We also collected microhabitat data to characterize factors associated with this species' success. Introductions had higher annual survival rates and fecundity than wild populations; plants in scrub plots had higher survival than roadside plants, although fecundity was higher in roadside plants. Seedling recruitment was only higher for scrub plots in 1 year. *Chrysopsis floridana* occupancy was better predicted by lower soil nutrients and pH, but introduction success did not consistently vary according to soil conditions. Occupied plots had higher cover of bare sand, lichens, and forbs while unoccupied plots had higher cover of litter, shrub, and subcanopy. The presence of higher litter levels (>60%) appeared to significantly lower survival in 2018. Z-score site ranking suggested a slight disadvantage for wild populations overall, with the two highest ranked sites both being introductions. Conversely, stage-class data revealed that both wild and introduced populations had high counts across 3 years of sampling. Most of the healthiest populations had received recent fire, suggesting this may be crucial in providing conditions that promote recruitment and occupancy. More information is needed on aspects of fire and fire surrogates that are likely to affect the demography and distribution of this rare species.

Key words: *Chrysopsis floridana*, demographic, fire, introduction, microhabitat, population, translocation, wild

Implications for Practice

- Demographic analyses provide informative means of measuring rare plant population restoration efforts. Vital rates in multiple populations of *Chrysopsis floridana* indicate wild populations are often outperformed by introduced populations, suggesting the successful nature of translocation site-selection and diminishing habitat quality at wild populations.
- We suggest reimplementation of fire at poorly performing wild populations and continued fire maintenance at introduced populations; efforts may contribute to suitable microhabitat conditions (open sand, low litter, low shrub cover) required by *C. floridana*.
- We suggest further research efforts regarding rare plant population dynamics utilize demographic comparisons between translocations and reference (wild) populations to better inform species-based conservation measures.

Introduction

Rare species translocation success can be limited through a number of factors. Rare species translocation success is most often marked by population survival, first-generation establishment, vegetative growth, reproductive output, and recruitment of transplanted populations (Monks et al. 2012). In many cases,

thorough monitoring efforts, especially long term, are not implemented after rare plant translocation efforts due to funding deficiencies or other factors (Godefroid et al. 2011; Silcock et al. 2019). While initial short-term monitoring allows for analysis of population vital rates (e.g. survival, flowering, and recruitment rates; Menges 2008), these rates can decrease with time and many studies fail to properly categorize specific aspects of a species' biology or habitat requirements that may contribute to observed results (Godefroid et al. 2011). Monitoring of translocations can be administered in a variety of intensities, from lower intensity level-2 monitoring, in which counting of plants and classification of plant life stage (stage-class) can provide a rapid assessment of overall population densities, to level-3 monitoring, in which vital rates of individual plants are monitored

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over time (see Menges & Gordon 1996). More intensive modeling (Population Viability Analyses) can be performed on rare plant populations and help to inform long-term translocation trajectories, although the efficacy of these analyses may be limited in short-term studies (Crone et al. 2011). Ultimately, baseline monitoring efforts can provide biologists a general understanding of the success of their conservation efforts, where specific environmental and habitat factors can ideally help to explain translocation results (Godefroid et al. 2011; Halsey et al. 2017).

One strategy that has been more recently employed to assess translocation success (i.e. transplant survival and recruitment) has been to compare data available from introduced populations to reference wild populations. This method requires more intensive efforts as biologists need not only follow numerous introductions but also administer the same efforts for comparative wild populations. This method helps to further elucidate underlying causes to translocation results and can provide valuable demographic context between a variety of plant population types (Bell et al. 2003; Kirchner et al. 2006; Menges et al. 2016). Particularly, comparative demographic studies can help to place translocation results into proper context, especially if vital rates are low (Menges 2008). Specifically, low translocation survival or other vital rates can seem initially discouraging, but when compared to similar wild populations, rates may actually exceed what could be considered reasonable based on a species' biology (Maschinski et al. 2004).

Overall, while comparative demographic monitoring and classification of rare species habitat helps to inform translocation efforts, these methods are often either lacking or entirely missing from rare species recovery efforts. Owing to this, further gaps remain in our knowledge of comparative demography and how specific habitat characteristics (microhabitat) and disturbances (fire, mechanical disturbances) contribute to translocation results. As global habitat degradation continues to further threaten the persistence of rare plant species, it will become increasingly crucial to inform gaps in our knowledge of conservation dynamics and rare plant restoration efforts.

Study Species

More than 200 plant species occur in Florida and nowhere else globally (Wunderlin et al. 2021). One localized endemic, Florida goldenaster (*Chrysopsis floridana*), is a short-lived herbaceous perennial aster that occurs exclusively across five counties in west-central Florida, U.S.A. *Chrysopsis floridana* was initially listed as federally endangered in May 1986 due to habitat loss and degradation, a limited overall distribution, and lack of protection on public lands (USFWS 1999). Current extant populations of *C. floridana* are restricted to scrub and similar xeric habitats that historically may have experienced fire every 15–30 years (Menges 2007). Florida scrub is a xeromorphic habitat type, dominated by low-growing palm and shrub oak species with a low to moderate sand pine (*Pinus clausa*) canopy atop deep, nutrient-poor, xeric sands (Abrahamson et al. 1984; Menges 2007). Currently, more than 30 extant populations of *C. floridana* are known to occur, with 10 populations now occurring as introductions, and numerous populations occurring on private lands without permanent

protection. Outside of one introduction occurring as early as 1986 (Alafia River State Park [ARSP]), most translocations were implemented between 2008 and 2013 (Table 1). Translocations were all initially germinated at Bok Tower Gardens from seed collected at numerous wild populations and were outplanted primarily as small to large sized vegetative plants. Translocation densities initially varied from over 100 to approximately 1,000 individual plants per population (Table 1). It is believed that *C. floridana* has a relatively short life span (i.e. 3–5 years; USFWS 1999), thus in some cases, transplants can flower in situ shortly after their introductions.

Chrysopsis floridana populations occur within two primary habitats: scrub and firelanes (synonym: roads). Due to habitat fragmentation and fire-management precautions, Florida scrub habitats typically contain numerous sandy firelanes that are intentionally kept free of woody vegetation to provide fire breaks during prescribed burns. Limited research available suggests that *C. floridana* seedling recruitment is enhanced in open sandy habitats (Lambert & Menges 1996), which historically would have been maintained by fire or perhaps strong edaphic factors and which firelanes often mimic in fire-suppressed habitats. In fact, numerous populations of *C. floridana* now primarily occur along sandy firelanes, where fire suppression has failed to maintain open conditions in sandy gaps within shrub-dominated scrub interiors. No studies have thus far investigated whether population vital rates differ substantially between scrub and firelane populations of *C. floridana*, although similar research on *Hypericum cumulicola* has shown that plants occurring in firelanes often have diminished vital rates compared to scrub plants (Quintana-Ascencio et al. 2007). This major habitat comparison is crucial to understand in Florida scrub habitats due to the high prevalence of roads, but can be applied to other rare plant species occurring in similar conditions between intact and disturbed habitats in fragmented landscapes. Demographic comparisons between populations based on habitat type (e.g. anthropogenic vs. natural) provide a basis for understanding translocation results (Quintana-Ascencio et al. 2007), and in a larger sense, how human disturbances affect microhabitat conditions and subsequent rare plant restoration efforts (Weekley et al. 2008; Menges et al. 2016). Because both scrub and firelane populations are prone to frequent disturbances, it is crucial to understand how these conditions contribute to population vital rates in both wild and translocated populations.

Outside of a few smaller populations in Hardee County, a majority of *C. floridana* populations occur primarily within the greater Tampa Bay area. From central Florida (near Orlando) southward, a subtropical, humid climate exists in which seasons are generally split between a hot wet season from June through September and a mild dry season from October through May (Noss 2018). Climate data available for two weather stations nearest to our monitoring sites (St. Petersburg, Wauchula) indicated an annual precipitation range from 108 to 130 cm (42.6–51.0 inches) in 2018 and 2019, and an average mean monthly temperature ranging from 14.8 to 29.1°C (58.6–84.4°F) with strong bimodality between wet and dry seasons (Florida Climate Center 2021). Peak flowering (and monitoring) time for *C. floridana* occurs between the months of October and December, as temperatures begin to

Table 1. Population name (and associated abbreviation) with population (pop.) type (introduction or wild), demography (demog.) type (level-3 demography or level-2 stage class), and county of occurrence. For introductions, available data are listed on initial year(s) of translocation (intro year), propagule type and number of plants introduced (initial intro size). Total population size describes the most recent precise population size, if available, and population estimates include population size class estimates conducted during 2018 Species Status Assessment (USFWS 2018). Year of last fire is listed for each population, where available. ^aTotal population size estimated from 2006 Florida Natural Areas Inventory survey. HHSP counts recorded during 2019 stage-class census. ^bIt is unclear if fire spread through opening in which plots occur. No woody vegetation occurs in clearing. ^cOnly half of monitoring plots were burned in 2016/2017 season. ^dPlots occur across multiple management units burned in different years. ^ePlots at Bullfrog Creek were treated mechanically (roller chopped) in 2018/2019. No management history was provided for sites managed by Hillsborough County Conservation and Environmental Lands Management Program.

Population	Abbreviation	Pop. Type	Demog. Type	County	Intro Year(s)	Propagule Type	Initial Intro Size	Population Size ^e (Estimate)	Year of Last Fire
Duette Preserve, north section	Duette North	Intro	Demography	Manatee	2013	Plants	147	Unknown (501–1,000)	2018
Duette Preserve, south section	Duette South	Intro	Demography	Manatee	2013	Plants	174	Unknown (501–1,000)	2019
Little Manatee River Southfork Tract, east section	LMRSF	Intro	Demography	Manatee	2008–2009	Plants	910	Unknown (>1,000)	2011
Paynes Creek Historic State Park	Paynes Creek	Intro	Demography	Hardee	2011	Plants	199	Unknown (>1,000)	2019 ^b
Weedon Island Preserve	Weedon Island	Intro	Demography	Pinellas	2012	Plants	922	Unknown (>1,000)	2013
Alafia River State Park	ARSP	Intro	Stage class	Hillsborough	1986–1987	Unknown	Unknown	Unknown (501–1,000)	Unknown
Boyd Hill Nature Preserve	Boyd Hill	Intro	Stage class	Pinellas	1986/1989	Seeds/plants	Unknown	Unknown (501–1,000)	Unknown
Little Manatee River Southfork Tract, west section (Cordell West)	Cordell West	Intro	Stage class	Manatee	2009	Plants	545	30 (<100)	2019
McKay Creek (FL Botanic Gardens)	McKay Creek	Intro	Stage class	Pinellas	2009	Plants	773	Unknown (>1,000)	2013
Alafia Scrub Preserve	Alafia Scrub	Wild	Demography	Hillsborough	NA	NA	NA	1781 (>1,000)	Unknown
Bell Creek Nature Preserve	Bell Creek	Wild	Demography	Hillsborough	NA	NA	NA	791 (501–1,000)	Unknown
Lake Manatee State Park	LMSP	Wild	Demography	Manatee	NA	NA	NA	100+ (>1,000)	2016/2019 ^c
Moody Branch Mitigation Area	Moody Branch	Wild	Demography	Manatee	NA	NA	NA	212 (>1,000)	2017 ^d
Rhodine Scrub Preserve	Rhodine Scrub	Wild	Demography	Hillsborough	NA	NA	NA	1,227 (>1,000)	Unknown
Balm Scrub Preserve	BSP	Wild	Stage class	Hillsborough	NA	NA	NA	712 (501–1,000)	Unknown
Bullfrog Creek Mitigation Area	Bullfrog Creek	Wild	Stage class	Hillsborough	NA	NA	NA	639 (100–500)	2015 ^e
Highlands Hammock State Park	HHSP	Wild	Stage class	Highlands	NA	NA	NA	861 (100–500)	2017
Little Manatee River State Park	LMRSP	Wild	Stage class	Hillsborough	NA	NA	NA	446 (>1,000)	2005

decrease at the onset of the dry season (mean T° : 17.6–27.4°C [63.7–81.3°F]) and precipitation levels fall: 0.05–0.33 cm (0.02–0.13 inches). High temperature/precipitation extremes are mostly experienced during summer months in the wet season (June–September).

Fire has been an integral disturbance throughout Florida, with wildfires most often occurring in the transition period between the dry and wet seasons (April–June), when fine fuels accumulated during the wet season dry and become subject to ignition via lightning strikes (Platt et al. 2015). Despite this historical context, complications from habitat fragmentation and wildland–urban interface have made prescribed fire more difficult for scrub habitats in which *C. floridana* grows. Given previous research indicating the often positive effect of fire on rare plant populations in Florida scrub and elsewhere (Yates & Broadhurst 2002; Bell et al. 2021; Nordstrom et al. 2021), it is also crucial to understand the implications of fire on *C. floridana* recovery.

In August 2021, the USFWS proposed the delisting of *C. floridana* from the Endangered Species Act (USFWS 2021), despite major gaps in our autecological knowledge of this species. Given these gaps, we were interested in assessing the overall demographic status of 10 wild and eight introduced populations in west-central Florida from 2017 to 2019. By utilizing demographic and habitat information from both population types, we were able to ask specific questions regarding the status of each monitored *C. floridana* population.

Specific questions addressed in this study included: (1) How did the demographic health, that is vital rates, compare between

population type (introductions vs. wild populations)? Such that, those with higher vital rates would equate to healthier populations. (2) How did demographic results compare between habitat type (road vs. scrub)? (3) Were microhabitat differences able to explain any potential differences in habitats in which *C. floridana* did and did not occur? (4) Was recent land management (e.g. fire) able to help explain population health?

Findings from this study provide major implications for the conservation and ecological understanding of *C. floridana*. In a larger sense; however, this research further contributes to our growing understanding of translocation dynamics using informative comparisons between introduced and wild reference populations, and specific microhabitat categorization to classify species occurrence. Strategizing the use of pertinent habitat and demographic data will best inform future rare plant population restoration in an era of increasing global change.

Methods

Monitoring

We collected 3 years of demographic (level-3 monitoring; see Menges & Gordon 1996) and stage-class data (level-2 monitoring; Menges & Gordon 1996) across 18 populations of *Chrysopsis floridana* (10 wild, 8 introduced; Fig. 1) across west-central Florida, U.S.A., each November and December from 2017 to 2019. Timing constraints did not allow us to sample all 18 populations using full demographic methods (level 3). This mixed

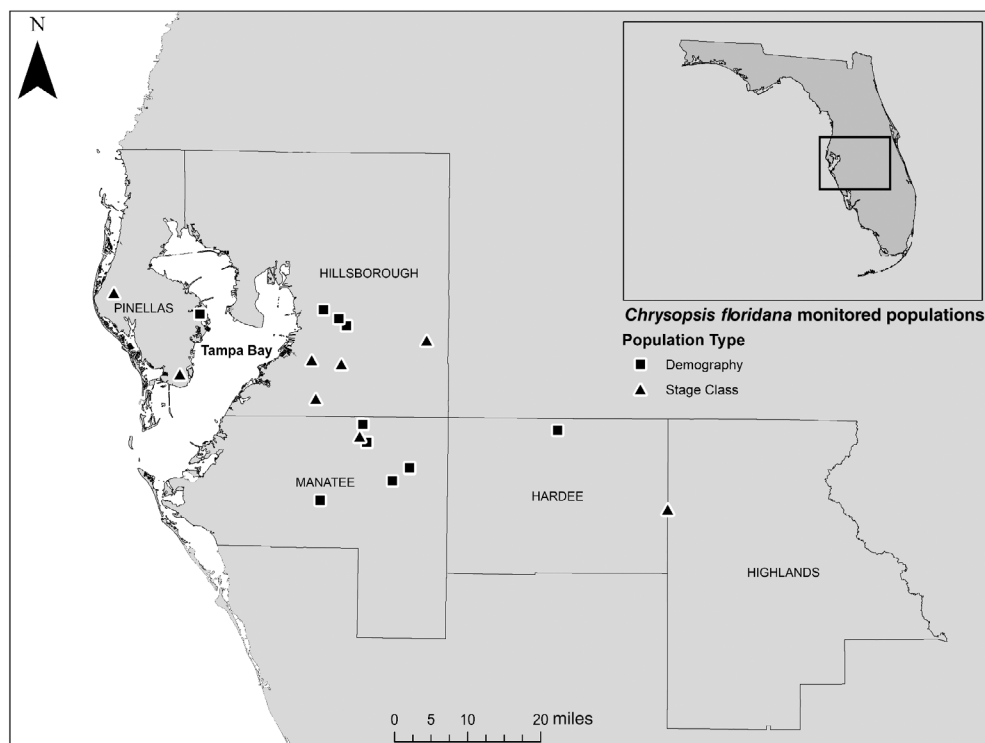


Figure 1. Introduced and wild populations of *Chrysopsis floridana* in west-central Florida sampled from 2017 to 2019 including populations with demographic (squares) and stage-class (triangles) monitoring protocols. Borders are indicated for the five counties (labeled) in which *C. floridana* occurs. Overview map is provided in top right corner.

approach allowed us to sample a greater number of populations as stage-class sampling is often a more time-sensitive monitoring approach in that it relies on annual count data in predetermined plots. Conversely, demographic sampling requires that thousands of individual plants are relocated annually and measured for vital rates. Although the implications of stage-class data are limited, these data can still provide a basis for understanding inner-annual population count fluctuations and allow for a great number of populations to be sampled overall in any monitoring efforts. Stage-class and demographic populations were divided between introduced and wild populations, but were assigned randomly. For each study population, we established at least 10 randomly chosen plots in 2017 that contained live plants of *C. floridana*.

For demographic populations, we established ten 2-m² plots throughout each population's extent. Within plots, we tagged individual plants and followed the survival and measured growth variables of each plant from 2017 to 2019. Plants were categorized as seedlings (nonreproductive plants with basal rosettes <5 cm wide), vegetative adults (nonreproductive plants with basal rosettes ≥5 cm wide), or reproductive adults (plants with at least one reproductive stem present). Basal rosette size was measured for vegetative plants, while reproductive plants were measured for rosette size, longest length of reproductive stems, total number of reproductive stems, and total number of flowering heads per plant (the last on a subset of approximately 20% of reproductive plants present). Each year, we recorded the survival status of each previously marked plant, tagged new plants present within plots, and categorized these new plants as either new seedlings or adults.

For stage-class populations, we established 10 circular 4-m diameter plots per population at seven populations. One site, Highlands Hammock State Park (Highlands County), had a total stage-class census recorded due to the overall smaller size of the population. In each plot, we recorded the total count of all *C. floridana* plants present each year from 2017 to 2019. All plants were counted and categorized as either small vegetative (one or two rosettes), large vegetative (more than two rosettes), or reproductive.

Microhabitat Variable Collection

We aimed to quantify a diverse suite of plot characteristics as subtle microhabitat differences have been shown to play critical roles in translocation results (Guerrant & Kaye 2007). In 2018, multiple microhabitat variables were measured across 204 total plots across all 10 level-3 demography populations. All 100 demography plots had microhabitat variables recorded, and additionally, 10–14 random plots (established regardless of *C. floridana* presence) were analyzed for microhabitat variables and *C. floridana* occupancy in 2018. Thus, we had a mix of microhabitat data from occupied and nearby unoccupied plots that would help to explain possible factors related to occupancy. Although previous research has shown *C. floridana* germination to increase in open sandy areas (Lambert & Menges 1996), there still exist major gaps in our knowledge of *C. floridana* habitat preference. Thus, we aimed to thoroughly classify the dominant vegetation type surrounding plots with and without *C. floridana*

present. We quantified the overall percent cover of ground lichen, litter, forbs, graminoids, shrubs (woody species <1 m tall), and subcanopy (woody species 1–3 m tall) within a 50-cm diameter subplot surrounding each plot center. Previous research has indicated the importance of surrounding species composition, particularly growth form, in determining rare species translocation success (Dunwiddie & Martin 2016). For each cover category, we distinguished between a true absence (i.e. 0%) and “trace” (i.e. <10%). Percent cover values were converted into 10% bins for analyses (0–10, 10–20, and so on), such that trace covers equated to 10% cover. We also recorded the line intercept cover of all woody individuals at least 1 m in height for 50 cm in all four cardinal directions such that total percent shrub cover was calculated out of 200 cm. We recorded the percent canopy cover using a densiometer placed in four cardinal directions above the central plot location. Within the entire 50-cm diameter microhabitat subplot, we then noted the dominant species overall, regardless of growth type (e.g. woody, forb, graminoid), and measured the distance of plot center to the nearest woody plant of any size, and recorded the height and species identity of this individual. Because bare sand has been shown to influence *C. floridana* germination, we quantified bare sand cover in plots, and if litter was present, we classified litter cover based on dominant type (forb, graminoid, oak, pine, palm, and so on).

In addition to microhabitat classification, we also successfully collected soil samples from 195 of the 204 occupancy plots. Soil samples were sent to the University of Florida IFAS Extension Soil Testing Laboratory and analyzed for pH and soil nutrients phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca), copper (Cu), manganese (Mn), and zinc (Zn). We classified the habitat type for each demographic and stage-class plot by analyzing if its location was greater than or less than 5 m from an artificial road or firelane for all 204 plots. Plots greater than 5 m from an anthropologically disturbed area were classified as scrub plots. These classifications were made using ArcGIS (10.3) and plot location data were collected with a Trimble Geo7x. Lastly, we were able to obtain management information for a majority of *C. floridana* populations regarding the most recent year of mechanical treatment and/or prescribed fire, although this information was not available at the plot level. We were unable to obtain recent fire histories for four Hillsborough county populations (Table 1).

Vital Rates, Reproductive, and Microhabitat Analyses

For each plot within a population, we calculated the following vital rates: annual percent survival, seedling annual percent survival, relative growth rate, total number of flowering heads, total number of seedlings per square meter, and total number of reproductive stems. Relative growth rate was calculated for two time periods (2017–2018 and 2018–2019), and was calculated as the difference in the natural log of stem length for surviving reproductive plants between time 2 and time 1 (2019 vs. 2018 and 2018 vs. 2017) divided by time (1 year for each time period difference). Annual survival and seedling annual survival were calculated for two time periods (from 2017 to 2018 and 2018 to 2019). To analyze for differences in each vital

rate between introduced versus wild populations and road versus scrub plots, we performed t tests on either natural-log-transformed count/growth data (heads, stems, relative growth rate) or angular-transformed proportion data (annual survival, seedling annual survival). While debates have occurred over appropriate transformations for data types and both contain limitations, both transformation types have demonstrated benefits for count (log) and proportion (angular) data types (Ahrens et al. 1990; Lin & Xu 2020).

To analyze the effect of microhabitat and soil variables on *C. floridana* reproductive output, we used general linear models (GLMs) for each year of demographic data in years 2018 and 2019. Four dependent variables were chosen for each year (annual survival, seedling annual survival, total reproductive [total reproductive plants per plot], and total seedling output). Only plots with five or more plants were included within GLM's analyzing total reproductive and seedling output. Five total microhabitat variables were chosen as predictor variables for these models: litter, shrub, and graminoid covers, and two soil variables (principal component analyses [PCAs] explained below). Litter, shrub, and graminoid covers were converted into three equal cover categories for each variable (0–33%, 34–67%, 68–100%). Soil principal components were calculated by converting all soil nutrient data into two final variables (axes) from PCAs. Two axes were calculated based on variable extraction that accounted for 56.8% of the cumulative variance in soil data. PCA1 (Soil PCA1) corresponded to greater loadings in pH, P, Ca, Cu, and Zn, while PCA2 (Soil PCA2) corresponded to greater loadings in K, Mg, and Mn. Differences in microhabitat variables between occupied and unoccupied plots were tested using t tests, whereas Mann–Whitney U tests were performed on soil samples. Microhabitat and soil variable differences were compared between population type (wild vs. introduction) and plot type (road vs. scrub).

Population Standardization

Using all final calculated vital rates, we then performed a Z-score standardization for all demography sites ($n = 10$). Each separate vital rate percentage or value within each population was converted into an initial standardized Z-score. Each converted vital rate was then combined into one composite Z-score by taking the average of all Z-scores for each population. Thus, each demographic population received a final Z-score representing a cumulative average of all vital rate Z-scores calculated. These final values provided a robust method of population comparison, such that sites with overall relativized values above zero (mean value) represented above average population health. This method of standardization has been employed in ecological studies relating covers of different biological populations (Guest et al. 2018) and has been shown to be useful in a variety of biological analyses (Wang & Chen 2012). Furthermore, translocation success often combines short-term survival with both reproductive (flower, seed production) and recruitment of subsequent generations (Monks et al. 2012), thus our combined Z-score at each population represents a combination of vital rates most indicative of overall population health. All analyses were performed in SPSS version 22 (SPSS Inc., IBM, Chicago, IL, U.S.A.).

Results

Vital Rates

Overall, plants of *Chrysopsis floridana* within introduced populations had 11–11.4% greater annual percent survival rates and 18.4–21.9% greater seedling annual percent survival rates than wild populations across both years (Fig. 2). Scrub plots had 10.0–20.3% greater annual survival rates and 21.6–22.9% greater seedling annual survival rates compared to road plots across both years (Fig. 2). Introduced populations consistently had significantly higher rates of annual survival in 2019: $t(1,914) = -5.613$, $p < 0.001$ and 2018: $t(1,788) = -5.439$, $p < 0.001$, as well as seedling annual survival in 2019: $t(1,929) = -5.026$, $p < 0.001$ and 2018: $t(1,758) = -5.803$, $p < 0.001$ (Fig. 2). Similarly, scrub plots had significantly higher rates of annual survival compared to road plots in 2019: $t(1,914) = -4.765$, $p < 0.001$ and 2018: $t(1,788) = -5.045$, $p < 0.001$. Seedling annual survival was significantly higher in scrub plots compared to road plots in 2019: $t(1,469) = -4.296$, $p < 0.001$ and 2018: $t(1,444) = -4.826$, $p < 0.001$.

While survival and seedling survival rates were consistent across introduction status and habitat type, vital rates related to growth, fecundity, and seedling recruitment showed less consistent patterns. For instance, relative growth rate was significantly greater for scrub plots compared to road plots only in 2018: $t(1,315) = -4.847$, $p < 0.001$. There was no significant difference in relative growth rate between introduction statuses for both years. Fecundity showed mixed patterns as well, with the total number of flowering heads found to be significantly higher in road plots compared to scrub plots in 2017: $t(230) = 2.91$, $p = 0.004$ and 2019: $t(363) = 2.526$, $p = 0.012$, but not 2018 (Fig. 2). Stems showed similar patterns, with significantly higher amounts of flowering stems across all 3 years in road plots compared to scrub plots—2017: $t(631) = 2.694$, $p = 0.007$; 2018: $t(784) = 3.626$, $p < 0.001$; 2019: $t(682) = 2.145$, $p = 0.032$. Fecundity analyses indicated that plants in introductions had significantly more heads than wild populations in 2018: $t(321) = -2.341$, $p = 0.02$ and 2019: $t(363) = -2.476$, $p = 0.014$. Introductions also had significantly more stems in 2018: $t(555) = -5.195$, $p < 0.001$ and 2019: $t(502) = -5.312$, $p < 0.001$. Lastly, seedling recruitment was not significantly different between introductions and wild populations and was only significantly higher in scrub plots for 1 year, 2017: $t(87) = -1.79$, $p = 0.04$ (Fig. 2). Thus, while we found no significant differences in seedling recruitment based on introduction status and habitat type, road plots and introductions tended to have plants with higher overall fecundity compared to scrub plots and wild populations.

Soil and Microhabitat Results

Chrysopsis floridana occupancy was better predicted by soils with lower nutrient availability but higher pH levels. Among all plots, pH values ranged from 3.8 to 7.6, with 75% of plot pH values falling within a range of 4.4–5.1, and only 3% of plots containing a pH greater than 7. Unoccupied plots had significantly higher levels of potassium (median = 11.05,

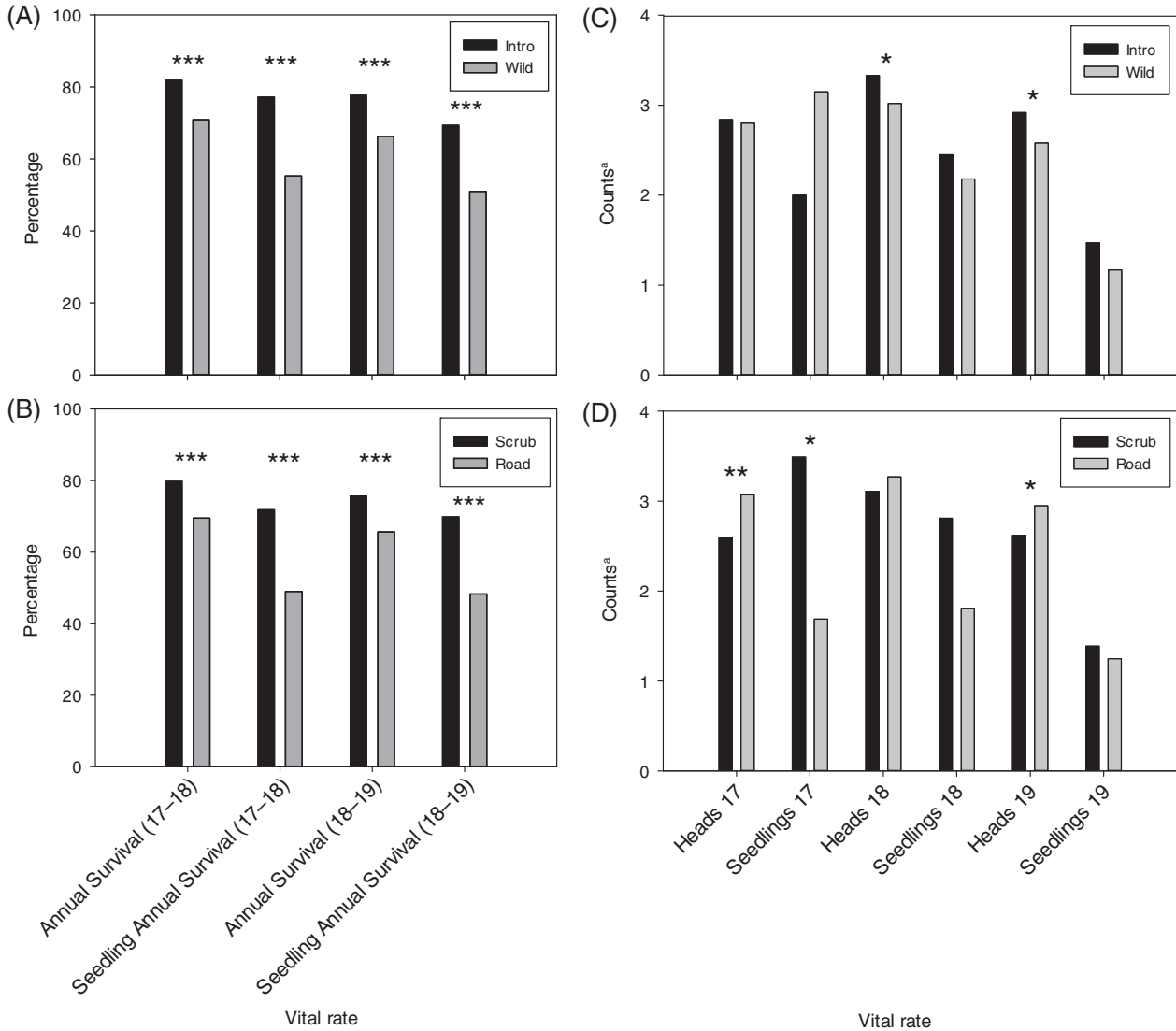


Figure 2. Vital rates for *Chrysopsis floridana* demography plots ($n = 100$) across two population types: introduced (intro) versus wild and two habitat types: scrub versus road from 2017 to 2019. Graphs A and B indicate annual survival percentages and seedling annual survival percentages from 2017 to 2018 and 2018 to 2019 for introduced (black) versus wild (gray) populations and scrub (black) versus road habitats. x-Axis labels for (B) also apply to (A); x-axis labels for (D) apply to (B). Asterisks above bar pairs denote significant differences between groups (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$), such that the taller bar represents the significantly greater value in each pair. Graphs (C) and (D) indicate counts for reproductive heads and seedling output rates for introduced (black) versus wild (gray) populations and scrub (black) versus road (gray) habitats in 2017, 2018, and 2019. ^aCount units are different for heads versus seedling counts in graphs (C) and (D) such that heads equate to log-transformed total flowering heads in each year and seedlings equate to number of seedlings per square meter in each year.

$U = 3,827.5$, $p = 0.019$) and magnesium (median = 15.27, $U = 3,863$, $p = 0.025$), while pH levels were significantly greater in occupied plots (median = 4.91, $U = 3,469$, $p = 0.001$; Fig. 3). Certain soil nutrients varied between introduction status and habitat type, with the tendency for introduction nutrient levels to exceed wild populations and mixed patterns between scrub and road plots. Introductions had significantly higher pH levels compared to wild populations (median: 4.98, $U = 2,361.5$, $p < 0.001$), in addition to significantly higher levels of phosphorus (median: 5.88, $U = 3,571$, $p = 0.003$), calcium (median: 134.5, $U = 3,775$, $p = 0.014$), copper (median: 0.20, $U = 3,296.5$, $p < 0.001$), and manganese (median: 2.37,

$U = 2,164$, $p < 0.001$; Fig. 3). Scrub plots had significantly higher levels of magnesium (median: 15.5, $U = 3,090.5$, $p < 0.001$), calcium (median: 132.33, $U = 2,780.5$, $p < 0.001$), and manganese (median: 1.86, $U = 3,591.5$, $p = 0.01$) compared to road plots, while road plots had significantly higher phosphorus levels (median: 6.67, $U = 2,738.5$, $p < 0.001$; Fig. 3).

Results from microhabitat variables across plot occupancy type suggest that *C. floridana* is generally associated with areas with significantly higher cover of bare sand: $t(202) = -2.437$, $p = 0.016$; lichens: $t(202) = -2.83$, $p = 0.005$; and forbs: $t(202) = -5.19$, $p < 0.001$ (Fig. 4). Results from unoccupied

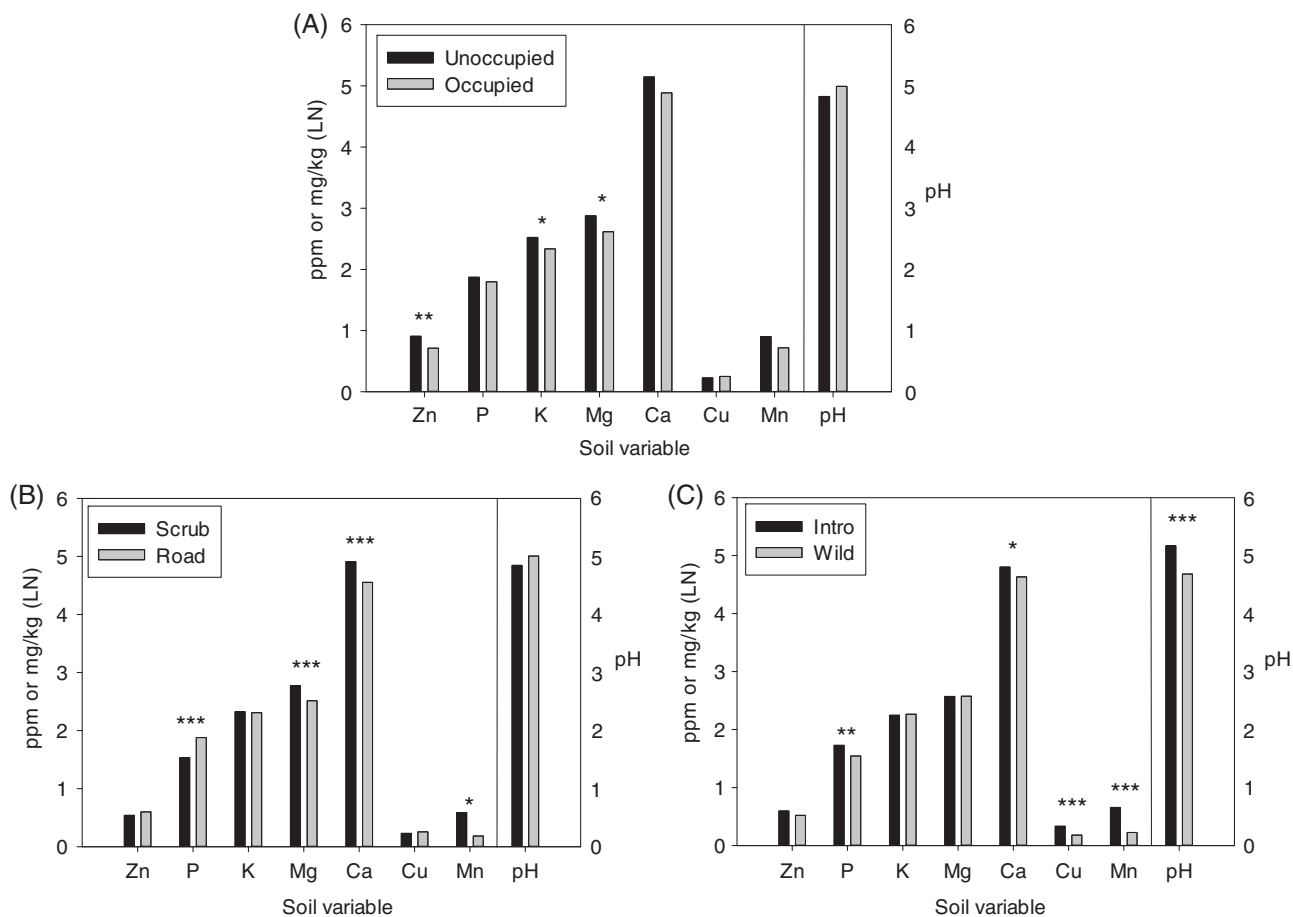


Figure 3. Mean soil nutrient and pH values for population, habitat, and occupancy types across *Chrysopsis floridana* plots ($n = 195$). Zn, zinc; P, phosphorus; K, potassium; Mg, magnesium; Ca, calcium; Cu, copper; Mn, manganese. Soil nutrient values correspond to left axis in each graph (A–C) and represent natural log (LN) transformed ppm or mg/kg values except for copper which represents initial value. P, K, Mg, and Ca correspond to ppm, Zn, Cu, and Mn correspond to mg/kg. Soil pH values correspond to the right axis of each graph and represent original values; one vertical line in each graph separates nutrients from pH values. Graph (A) indicates differences in soil variables between unoccupied (*C. floridana* not present; black) and occupied (*C. floridana* present; gray) plots. Graph (B) indicates soil nutrient and pH differences between scrub (black) and road (gray) plots. Graph (C) indicates soil nutrient and pH differences between introduced (intro; black) versus wild (gray) populations. Nonparametric tests (Mann–Whitney U) were performed on original values for all three datasets (A–C). Asterisks above bar pairs denote significant differences between groups ($*p < 0.05$, $**p < 0.01$, and $***p < 0.001$) such that taller bars represent significantly greater values.

plots suggest that occupancy is less likely in areas with significantly higher covers of litter: $t(202) = 3.201$, $p = 0.002$; shrub: $t(202) = 6.476$, $p < 0.001$; and subcanopy: $t(202) = 4.402$, $p < 0.001$ (Fig. 4). Thus, plots supporting *C. floridana* tended to have higher cover of bare sand, lichens, and forbs and lower cover of litter, shrub, and subcanopy (Fig. 4).

Survival rates of *C. floridana* from 2017 to 2018 tended to decrease as litter cover increased (Fig. 5). Average annual survival rates were typically 80% or higher when litter cover was 60% or lower, and annual survival rates tended to decrease substantially as litter cover increased from 60 to 90%. Interestingly, annual survival rates appeared to increase for a small number of plots with 100% cover of litter (Fig. 5). Five of the 10 demographic plots with 100% litter cover occurred in roadside plots at Rhodine Scrub, a wild population, in which survival rates were 60–100%. Mean annual survival rates were 59.8, 47.8, and 45.2% for 70, 80, and 90%

litter covers, respectively, and mean annual survival rates increased to 78.7% for 100% litter covers. Wild populations tended to have a higher mean cover of litter (60.4%) compared to introductions (31.9%).

Only litter had a significant effect on annual survival and seedling annual survival in 2017–2018 and 2018–2019, while graminoid cover was only marginally significant (Table S1). Litter had a highly significant effect on annual survival in 2017–2018 but no effect in 2018–2019 and only had a significant effect on seedling annual survival in 2019. A Tukey's post hoc test revealed that annual survival rates from 2017 to 2018 were significantly lower for the highest litter cover group (61.6 ± 29.2) compared to the middle cover group (78.1 ± 22.1 , $p = 0.025$), and the lowest litter cover group (85.3 ± 21.1 , $p < 0.001$). There was no significant difference in 2018–2019 survival based on litter cover. No microhabitat variables helped to predict variation in reproductive and seedling output (Table S2).

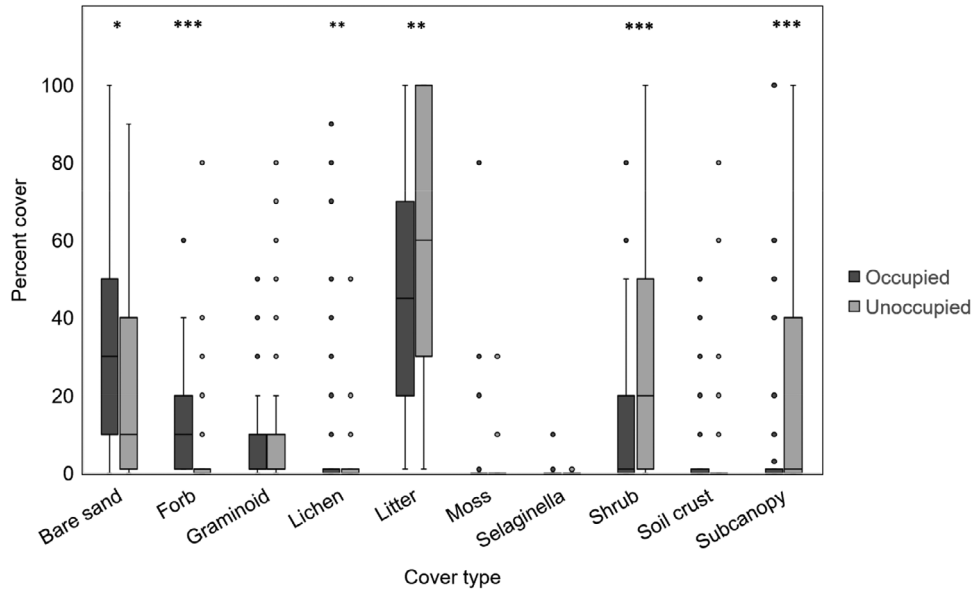


Figure 4. Percent cover of microhabitat variables in plots with *Chrysopsis floridana* (occupied; dark gray) and without *C. floridana* (unoccupied; light gray) across 204 plots at 10 demographic populations in 2018. Midlines indicate group medians, boxes indicate the interquartile range, whiskers indicate 1.5 times the interquartile range, and points indicate outliers. Asterisks above bar pairs denote significant differences between occupied and unoccupied plots (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$) such that taller bars represent significantly greater values.

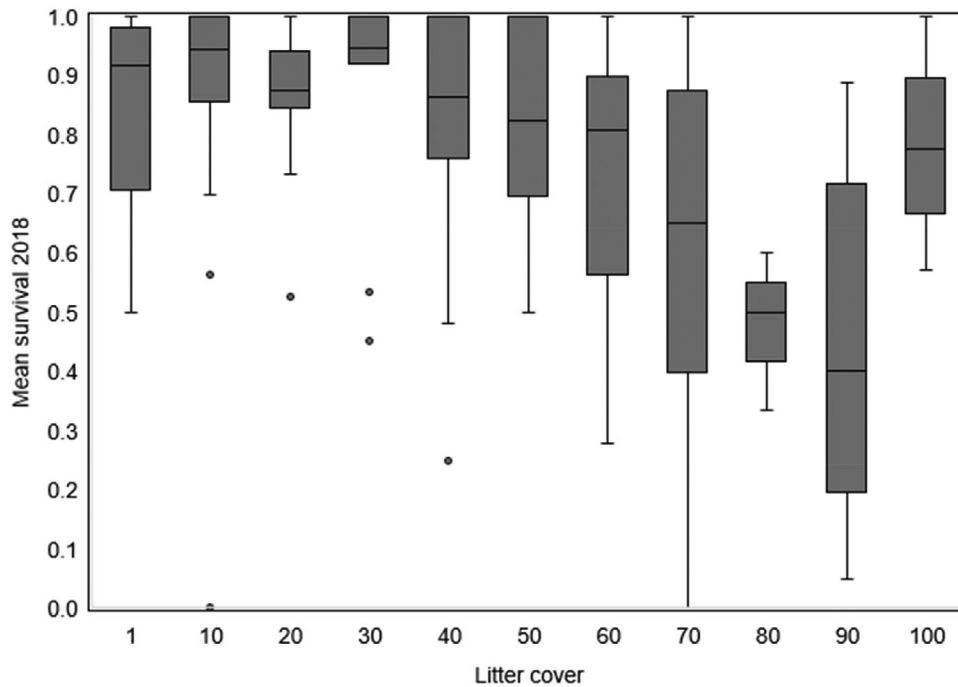


Figure 5. Mean survival rates (proportion) of *Chrysopsis floridana* demographic plots ($n = 100$) in 2018 by litter cover. Boxplot midlines represent median survival rates of each litter cover category, whiskers 1.5 times the interquartile range, and points represent outliers within cover categories.

Stage-Class and Standardization Results

Stage-class results indicated that four of the eight populations: Balm Scrub Preserve (BSP), Lake Manatee River State Park (LMRSP), ARSP, and McKay Creek had consistently high and stable counts of plants across all 3 years of sampling

(Fig. 6). Of these four sites, two (BSP and LMRSP) were wild populations. Sites with consistently low counts included Bullfrog Creek (except in 2017), Boyd Hill, and Cordell West (Fig. 6), of which only Bullfrog Creek represents a wild population. Total census counts at Highlands Hammock State Park

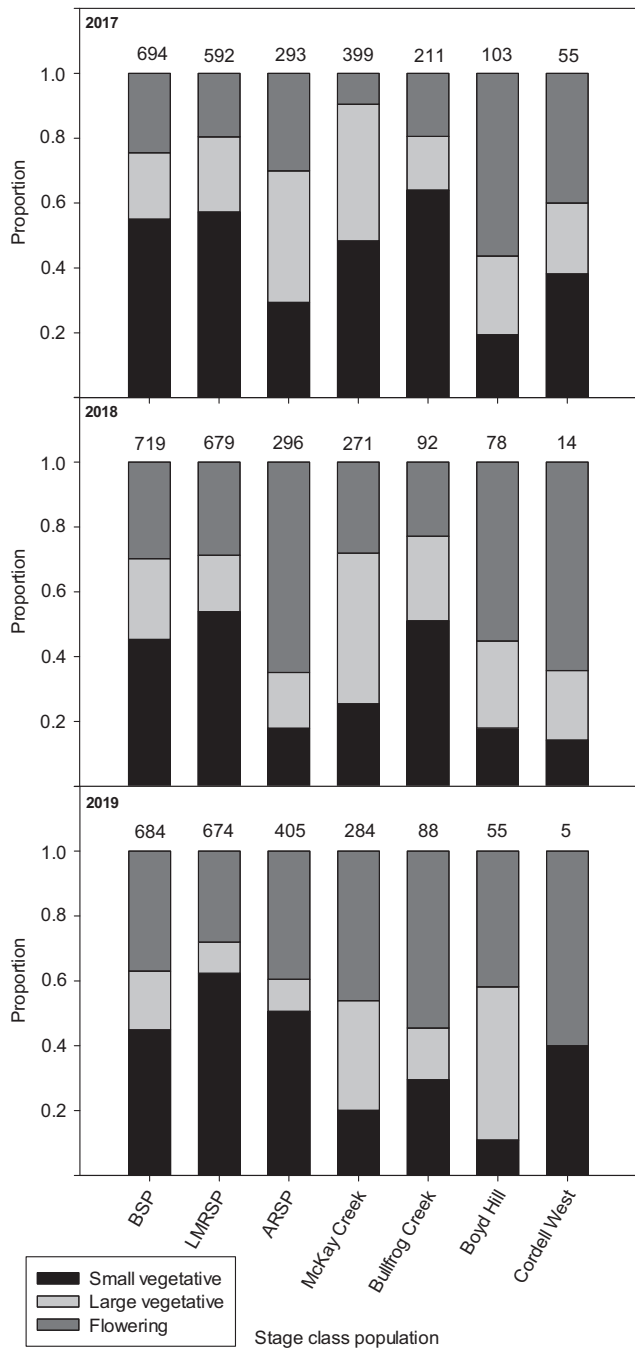


Figure 6. Stage-class results for seven sites supporting *Chrysopsis floridana* in west-central Florida across 3 years (2017–2019). Each year is denoted in the top left corner of each panel. Colored proportions in bars represent the total proportion of life stages of all plants present within 10 monitoring plots at each site within each year. Life stages are defined as small vegetative plants (black), large vegetative plants (light gray), and flowering plants (dark gray). Numbers above each bar indicate the total number of plants counted at each site per year. Sites are listed from highest total counts from left to right for each year except for 2019 in which McKay Creek counts exceeded those for Alafia River State Park. ARSP, Alafia River State Park (Hillsborough County); BSP, Balm Scrub Preserve (Hillsborough County); LMRSP, Lake Manatee River State Park (Manatee County).

(HHSP; wild) were relatively high each year (2017: 452 plants; 2018: 1,469 plants; and 2019: 861 plants). Overall, the two populations with the highest counts in each year were wild populations, although two introductions also had high counts.

Proportions of each stage-class type in each population tended to vary across years. For instance, ARSP initially had high proportions of small and large vegetative plants in 2017; however, this proportion decreased dramatically in 2018 and then marginally increased in 2019. It is possible that greater proportions of flowering individuals at ARSP in 2018 led to increased numbers of small and large vegetative individuals in 2019. Other sites saw a gradual decrease in both total count and flowering proportion throughout the entire sample period, such as Bullfrog Creek, while sites such as LMRSP saw an initial increase in total count from 2017 to 2018 but remained stable in both total counts and life-stage proportion into 2018 and 2019.

Z-score relativizations of demographic sites indicated that the two highest ranked sites were introductions, yet both population types ranked both above and below average (Fig. 7). Duette North (introduction) was the most demographically robust within demography sites and Bell Creek (wild) was the least

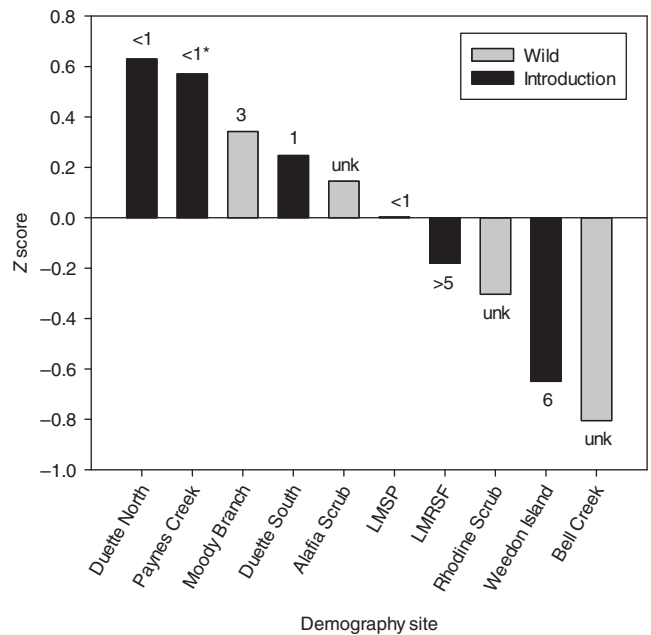


Figure 7. Overall population health of 10 *Chrysopsis floridana* demography sites (five introductions and five wild populations) in west-central Florida. Population health was calculated as a standardized Z-score based on combined vital rate data calculated for each site. Z-scores range from -1 to 1, such that positive scores correspond to populations with greater than average population health scores, negative scores correspond to populations with lower than average health, and scores close to zero correspond to sites with average health. Numbers above and below bars represent the number of years between last fire and the final year of sampling (2019) such that <1 represents populations that received fire in 2019. Unk: fire management information not available. *Paynes Creek plants occur within an open sandy area in which plants are not likely affected by prescribed fire. LMRSF, Little Manatee River South Fork; LMSP, Lake Manatee State Park (LMSP is a wild population).

demographically robust. The average overall Z-score for introductions was greater at 0.12 compared to an average Z-score of 0.05 for wild populations.

Discussion

Population Type and Translocation Success

Our study provides the first in-depth demographic analysis using multiple populations of *Chrysopsis floridana* to compare introduced, translocated populations with reference wild populations. Comparative studies such as this help to place demographic results into context, as wild populations tended to have slightly lower vital rates overall. Especially low vital rates at two populations, Rhodine Scrub and Bell Creek, likely contributed to the lower overall rates of wild populations, while conversely, only one introduction (Weedon Island) had distinctly low population health. Furthermore, only one wild population, Moody Branch, was found to have relatively high overall vital rates, while two introductions, Paynes Creek and Duette North, had the highest vital rates of all demographic (level 3) populations, which contributed to the higher overall health ranking of introductions. It is unknown if the high-ranking introductions have the demographic inertia to maintain their vital rates over longer time periods, as a majority of translocation research relies on short-term data and demographic data are subject to fluctuations over time (Maschinski et al. 2012). Numerous early translocation efforts using primarily seeds had failed to successfully establish *C. floridana* at multiple sites in Hillsborough and Pinellas counties (e.g. Lithia Springs, Alderman's Ford Park, Anderson Park, Magnolia Falls) (Campbell 2008). Conversely, translocations from plants cultivated prior to translocation (Boyd Hill) had better establishment rates, suggesting translocations from plants appeared to have better success rates compared to seeds. Interestingly, in this study, a lower number of propagules were originally introduced at Duette North, Duette South, and Paynes Creek compared to LMRSF and Weedon Island, yet the latter two had lower overall vital rates. This suggests that propagule density did not necessarily always translate to higher translocation success. This contrasts general trends among rare species translocations, in which although there are examples of successful translocations using low numbers of initial transplants, smaller translocations have been shown to be more prone to extinction (Albrecht & Maschinski 2012). Furthermore, habitat differences and differing disturbance regimes were also shown to often be more important in determining the success of equally sized translocations (Albrecht & Maschinski 2012). We discuss these other factors in relation to *C. floridana* demographics in further detail below.

Interestingly, compared to our level-3 demographic results, our level-2 stage-class results indicated that annual densities were highest and most consistent from year-to-year for two wild populations: BSP and Little Manatee River State Park (LMRSP). Two introduced populations, ARSP and McKay Creek, also had consistent densities in each year of monitoring, but slightly lower densities compared to BSP and LMRSP. Both stage-class and demography results revealed that there are both healthy and poorly performing populations of *C. floridana* across wild and introduced

sites; however, level-3 demography data were able to reveal the overall underlying vital rates of translocations and point to the possible role of underlying habitat conditions in demographic performance.

Habitat Type

In addition to patterns related to population type, we found that *C. floridana* plants growing within interior scrub habitats had consistently higher annual survival, seedling annual survival, and seedling recruitment in all 3 years of monitoring compared to firelane (road) plants. Conversely, fecundity and seedling recruitment results indicated that while plants in road plots may have had higher rates of fecundity, this did not translate to higher seedling recruitment compared to scrub plots. Our research supports, in part, a limited but growing body of evidence suggesting that disturbed habitats such as roads or firelanes, and the microhabitats in which they are found, promote a shorter-lived, often weedier life strategy for rare scrub plants (Quintana-Ascencio et al. 2007). This has been demonstrated similarly for *Hypericum cumulicola*, in which life spans tended to vary much more drastically, and tended to be shorter, for plants growing in roads compared to scrub plants (Quintana-Ascencio et al. 2007). Other scrub herbs (e.g. *Liatris ohlingerae*), however, have not shown differing vital rates based on habitat type (Weekley et al. 2008), suggesting that different species of scrub herbs vary substantially in their response to differing habitat.

While we were unable to calculate life span data in our study due to time constraints, our survivorship and recruitment results appear to align with these previous findings on *H. cumulicola*. Roadside habitats may encourage a weedier growth form for scrub specialists, and such habitats may act as ecological traps or sinks (Schlaepfer et al. 2002; Quintana-Ascencio et al. 2007). Conversely, roadside populations could also potentially act as seed sources to recently burned, adjacent scrub with lower propagule densities (Quintana-Ascencio et al. 2007). Numerous wild populations of *C. floridana* are now primarily relegated to roadside habitats that support some aspects of suitable microhabitat conditions, but are often more prone to anthropogenic disturbances used during periodic firelane maintenance. Major pulses in seedling recruitment after mechanical disturbances have been observed in roadside populations of a Florida endemic congener, *C. highlandsensis*, a species that has also shown higher seedling recruitment in road plots compared to scrub plots (Menges et al. 2020). An additional congener, *Chrysopsis delaneyi*, has shown low recruitment rates but high annual survival rates after fire (Ward et al. 2020). Given that previous research has shown *C. floridana* germination is enhanced in open sandy areas (Lambert & Menges 1996), but ex situ germination rates are as low as 29.8% (Peterson 2013), more research is needed on the dynamic relationship between habitat type, disturbances, and germination dynamics in *C. floridana*.

Microhabitat and Soils

In comparing plants in road and scrub plots, microhabitat differences also helped to explain observed differences in vital rates.

Microhabitat analyses indicated that occupied sites and introductions contained significantly higher bare sand cover, and lower litter, shrub, and subcanopy cover. Microhabitats with low litter, shrub, and subcanopy cover are often a reflection of time-since-fire as these types of biomass are consumed during fire but reaccumulate rapidly postfire (Abrahamson 1984; Menges 2007). Previous research on the interactions between fire, microhabitat, and rare plant demographics suggest that numerous herbaceous species endemic to Florida scrub habitats peak in abundance and other vital rates soon after fire (Menges & Hawkes 1998). Mechanical surrogates of fire have also been shown to reduce woody plant cover (Menges & Gordon 2010); however, this form of management fails to reduce litter cover as fuels are not consumed and can also lead to an increase in weedy species and rapid resprouting of dominant woody species (Menges & Gordon 2010), which would thereby diminish future microhabitat conditions for *C. floridana*. Further microhabitat analyses indicated the importance of litter cover on annual survival and seedling survival rates given that this cover was consistently shown to negatively affect both *C. floridana* occupancy and vital rates. Specifically, plots with greater than 60% litter cover appear to limit survival rates and thereby offer unsuitable microhabitat conditions for *C. floridana*. This parallels previous research showing the importance of open sands in promoting *C. floridana* germination (Lambert & Menges 1996). Interestingly, another Florida scrub gap specialist, *Dicerandra christmanii*, has been shown to prefer sites with canopy covers below 60% (Menges et al. 1999), suggesting a possible microhabitat limitation for certain rare scrub herbs. Interestingly, other scrub herbs (e.g. *Asclepias curtissii*) may benefit from some level of shrub facilitation within early life stages (Mondo et al. 2010), though others seem to also prefer open microhabitats (e.g. *Euphorbia rosescens*, see Jones et al. 2017), thus the interaction between management, microhabitat, and life histories may vary substantially between rare scrub herbs. Soil analyses suggest that the greater vital rates of introductions may in part be due to their overall elevated soil nutrient availability and pH levels. Given the overall acidic and nutrient poor nature of Florida scrub (Abrahamson et al. 1984), it is possible that even slightly elevated nutrient differences across habitat types (road vs. scrub) can affect vital rates.

Fire Implications

While there were limitations to analyzing relationships between population vital rates and fire during this study, it cannot be ignored that three of the highest ranking demographic populations had received recent fire (Paynes Creek, Duette North, Duette South), and multiple sites with a longer fire return interval had lower demographic rankings (Weedon Island, McKay, LMRSF). This suggests that translocations and wild populations of *C. floridana* may benefit from fire, as it consumes shrub and litter covers which were shown to limit the occupancy of *C. floridana* in this study. While we had incomplete fire data for other poorly ranking sites (Rhodine Scrub, Bell Creek), these sites had an overall severely overgrown vegetation structure, a likely result of fire exclusion, which will likely offer less ideal habitat over time and thus not encourage occupancy and higher

vital rates in *C. floridana* populations. Interestingly, some translocations (e.g. LMRSF, Weedon Island) increased in population densities substantially after initial translocation efforts (Peterson 2014) but have since reduced dramatically (C. Peterson, personal communication; 2020), an occurrence potentially due to lack of fire and increased shrub growth; however, other dynamics may have contributed to this steady decline over time. Specifically, translocations are subject to demographic stochasticity, inbreeding depression, Allee effects, and other unforeseen environmental characteristics that can cause populations to decline shortly after introduction (Albrecht & Maschinski 2012), although these were not directly analyzed in this study. We suggest future research that directly analyzes fire effects and mechanical disturbances on *C. floridana* populations. Overall, this study helped to illustrate the relative success of various *C. floridana* translocations using demographic comparisons to reference wild populations, although the short-term nature of this study warrants further monitoring to properly assess the recovery of this species. By classifying microhabitat and soil conditions, and comparing between major habitat types, we have helped to illustrate habitat conditions that may promote higher vital rates and occupancy in *C. floridana* populations. While this study has shown that some populations appear demographically robust, a number of populations have much lower vital rates that may be connected to land management. Nonetheless, the successful nature of some introductions shows promise for possible future conservation efforts of this rare herb.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. General linear model results for annual survival and annual seedling survival.

Table S2. General linear model results for total number of reproductive plants per plot and total number of seedlings.

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