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Research Article

Long-term Monitoring and Management of American Chaffseed (*Schwalbea americana*) in the New Jersey Pine Barrens: Population Ecology of an Endangered Hemiparasite

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ABSTRACT

We studied the long-term demographic structure of the endangered hemiparasitic plant, *Schwalbea americana* (American chaffseed), in the New Jersey Pine Barrens from 1991 to 2020 in order to address important questions about its population biology, life history, and responses to management. These included the relative contributions of dormancy, recruitment, and other life stages to annual population changes, as well as its ecological responses to fire, mowing, and other factors over time. Following baseline surveys in 1991, we conducted annual censuses from 1993 to 2020 and individualistic plant monitoring from 1999 to 2020. The *Schwalbea* population initially exhibited positive growth, with major increases observed in the early 2000s, followed by steady, long-term declines. We used generalized linear models and mixed effects models to analyze the relationships between demographic and environmental variables at the population and individual levels, respectively. Dormant season prescribed burning and mowing yielded significant increases in flowering, stems, and survival, with apparent residual benefits in subsequent years following repeated treatments. Germination declined to 0% after 4 y in seed viability experiments, and recruitment was more strongly correlated with estimated seed bank sizes than with flowering alone. Dormant plants represented an average of 21% of the total population, with 20% of above-ground plants entering dormancy annually. Most dormancy events (92%) were 1–3 y in duration, indicating that mortality cannot be distinguished from dormancy for a minimum of 3 y after disappearance. Annual survivorship was high (mean = 88%), with 9% of individuals surviving 18 y on average, but differed significantly by cohort and increased with management. Significant differences were observed in size and flowering by age/stage class. However, size alone was insufficient to identify *Schwalbea* recruits from older plants, due to overlap of their lower size ranges. Long-term declines in survival and recruitment persisted despite suppression of woody succession by hand clipping and intermittent mowing and burning. Increased frequency of mowing or burning may be needed to sustain this population in the future. The relationships of growth and vital rates to other factors are provided, and the benefits of individualistic data for informing *Schwalbea* monitoring and management are discussed.

Index terms: dormancy; fire; individualistic studies; mowing; prescribed burning; rare plant conservation

INTRODUCTION

Monitoring the abundance of rare plant populations is one of the primary means of assessing their conservation status in the wild. Unfortunately, adequate biological knowledge of the target species is often insufficient to accurately interpret the results (Schemske et al. 1994). This is particularly problematic for species with life stages that are not conducive to casual observation, including those exhibiting prolonged winter dormancy, dormant seed banks, or other cryptic life stages (Norden and Kirkman 2004a; Kery et al. 2005; Hutchings 2010). Although not always feasible, individualistic population studies are best able to satisfy these needs (Menges and Gordon 1996); i.e., by allowing researchers to clearly discern the demographic structure of observed population changes and, with it, their biological and conservation significance.

With these concerns in mind, we studied the demography and population ecology of the globally imperiled hemiparasitic plant, *Schwalbea americana* L. (American chaffseed), in the New Jersey Pine Barrens. We used individualistic monitoring methods to help resolve a number of important, longstanding questions in the monitoring and management of this disjunct population, including (1) the relative contributions of different life stages to observed population changes over time, (2) the size and reproductive characteristics of different age and stage classes, and (3) the effects of management activities (fire and mowing) and other environmental variables on their survival and reproduction. By conducting individualistic demographic studies combined with field experiments on seed bank viability, we hoped to answer these questions about the life history and population ecology of *Schwalbea* in New Jersey, which are needed to better inform the monitoring and management of this endangered species in the future.

Schwalbea americana is a long-lived herbaceous perennial plant representing a monotypic genus in the broomrape family (Orobanchaceae). It is considered to be a generalist hemiparasite, capable of attaching to a wide range of host species but with evidence of host species preferences exhibited in different contexts (Helton et al. 2000; Kelly and Denhof 2022). *Schwalbea* occurs primarily on the sandy, acidic soils of the Atlantic coastal plain, with scattered populations from Texas to Massachusetts, USA, and is federally listed as endangered (USFWS 1995). Considerable research has been conducted on the ecology of *Schwalbea*, focusing on various aspects of its conservation, management, and recovery (Kirkman et al. 1998; Helton et al. 2000; Norden and Kirkman 2004a, 2004b; Kelly 2006; Kaeser and Kirkman 2012; Glitzenstein et al. 2016; Gustafson et al. 2017). However, long-term demographic studies of *Schwalbea* are currently lacking, and little information is available for the northern portions of its range, where populations have experienced significant declines (USFWS 1995; Obee and Cartica 1997; Kelly and Denhof 2022). Only two populations currently remain of more than 30 that historically occurred from Massachusetts to Virginia, and the protection and recovery of these isolated populations constitutes a major component of the federal recovery plan for the species (USFWS 1995). Of these, the *Schwalbea* population in the New Jersey Pine Barrens has been the longest studied, with monitoring, research, and management conducted by the New Jersey Department of Environmental Protection (NJDEP), Office of Natural Lands Management, since 1991 (Obee 1995).

In the early years of monitoring, researchers in New Jersey struggled to interpret the annual census data, especially the apparent lack of seedling recruitment occurring from 1993 to 1998 (Obee 1995; Yurlina 1998; Van Clef 1999). Although new plants regularly appeared in the population throughout this time period, they were attributed to emergence from dormancy rather than seedling recruitment, based on their large sizes compared to *Schwalbea* seedlings grown in the greenhouse at the time (Obee 1995; Yurlina 1998). The lack of survival and growth of these greenhouse-reared individuals (Obee and Cartica 1997; Yurlina 1998; Van Clef 2000), however, also suggested that they may not have been representative of the growth capabilities of *Schwalbea* seedlings in the wild (Kelly 2006). Although vegetative dormancy had been observed in southern populations (Kirkman et al. 1998), the morphological, demographic, and ecological dynamics of dormancy in *Schwalbea* have not yet been thoroughly described (Norden and Kirkman 2004a). To begin to answer these questions, we began placing permanent tags at the base of each plant in 1999 (Van Clef 2000). This allowed us to begin to be able to discern the age and stage structure of the population by 2001, after the minimum of three consecutive years needed to differentiate recruitment from emergence from dormancy (i.e., present-absent-present). With more than 20 y of individualistic data now available, abundant data exists to identify the morphological characteristics of these different age and stage classes as well as their relative contributions to annual population changes in *Schwalbea* in New Jersey.

A second motivation of this research was gauging the effects of ongoing management efforts (prescribed burning and mowing) on *Schwalbea* survival and reproduction. These activities are regularly implemented in the management of this species throughout its range, as they serve to maintain open canopy conditions and stimulate *Schwalbea* growth and flowering (USFWS 1995, 2017). Although experimental research has been conducted (Kirkman et al. 1998; Norden and Kirkman 2004b), questions remain about the relative effects of fire versus mowing on *Schwalbea*, as well as their optimal frequency and timing (USFWS 2017). Kirkman et al. (1998) found mowing during the growing season did not yield the same benefits as fire, for example, but subsequent studies by Norden and Kirkman (2004b) found dormant season mowing combined with raking yielded similar effects as fire. Although fire figures prominently in the literature of *Schwalbea* ecology and management (USFWS 1995, 2017), the New Jersey population was an exception, with no record of fire at the site until experimental prescribed burning was first used in 1998 (Cartica 1993; Van Clef 2000). Prior to that, habitat was maintained solely by intermittent mowing, with annual dormant season mowing taking place from 1986 to 1993 (Gordon 1986; Cartica 1993). Following the initiation of annual *Schwalbea* monitoring in 1993, mechanical mowing was replaced by selective hand clipping of vegetation; however, it was used again as a management tool in several later years. The intermittent use of both prescribed burning and dormant season mowing in New Jersey provided us with the opportunity to test the relative effects of these management activities on the survival and reproduction of *Schwalbea* compared to other years in which no management occurred.

A third research objective was explaining apparent time lags between flowering increases and recruitment, especially regarding the increased flowering that followed the first prescribed burning in 1998 and the first major recruitment event observed in 2001 (Kelly 2006). Staggered responses to environmental cues have been observed in other parasitic plants; e.g., to the development of favorable plant community or soil conditions that followed disturbance or other environmental events (Gawler et al. 1987). In the case of *Schwalbea*, it is possible that prescribed burning similarly increased the favorability of the host plant community or soils to seedling establishment, perhaps by increasing the abundance of preferred host species or the availability of host roots near the surface (Kelly 2006). It is also possible, however, that time lags observed in *Schwalbea* were instead related to seed dormancy and the cumulative quantities of seed accruing in the seed bank as a result of fire-stimulating flowering (Kaeser and Kirkman 2012) or, alternatively, the occurrence of temperature or precipitation conditions in those years that were more favorable to seed germination and/or seedling survival. We hoped to answer these questions by analyzing the relationships of recruitment events to variation in annual seed banks, based on field experiments on seed bank viability, as well to meteorological conditions over time.

The ecological relationships of demographic events such as flowering and recruitment, dormancy and survival in *Schwalbea* thus remain important issues for research, and with persistent long-term declines observed in New Jersey and other populations, these questions are all the more pressing. Although our data were by necessity restricted to a single *Schwalbea* population, the wealth of data collected over 30 y of research captures significant variation over time and may be sufficient to illustrate general patterns in the species' life history, at least in this particular context. We used multivariate analyses to identify the relative significance of size, age/state, management activities, and other environmental conditions to *Schwalbea* vital rates and utilized mixed effects models to properly account for the dependency of repeated measurements collected from the same individuals over time (Zuur et al. 2009). In the end, we hope that these analyses will improve our understanding of the life history and population ecology of *Schwalbea* and will help advance the conservation and recovery of this species, especially in the northern portions of its range, and may further serve to illustrate the benefits of long-term, individualistic population monitoring for supporting rare plant species research in general.

METHODS

The New Jersey population of *Schwalbea americana* is located in Brendan T. Byrne State Forest, Burlington County, in an area known as the Pine Barrens, a national and state-designated protected area, and UNESCO International Biosphere Reserve (Figure 1). The population consists of several colonies scattered along approximately 500 m of a county highway, with the vast majority of plants occurring in an area referred to as the "Canal" colony. This area is 10–40 m from the road and is protected from vehicular and right-of-way impacts by a guardrail and ditch. The population exists in an open clearing surrounded by pitch pine lowlands (*Pinus rigida*; Figure 2) and is adjacent to a canal and reservoir that provide water to a large complex of active commercial cranberry (*Vaccinium macrocarpon*) bogs. Herbarium records of *Schwalbea* date to the 1920s in this vicinity. The water table averages 50–100 cm below the surface (never inundated; Kelly and Denhof 2022). Prescribed burning occurred in the dormant season prior to the 1998–2000, 2003, 2015, and 2018 censuses and mechanical mowing occurred in 1986–1993, 2009, and 2020 (Figure 3). There are no prior records of fire occurring at the site (Gordon 1991; Cartica 1993).

Consecutive annual censuses of the *Schwalbea* population were conducted in late June/early July each year in 1991 and 1993–2020. All individuals were systematically counted and measured using methods developed by the NJDEP Office of Natural Lands Management. Surveys were conducted by NJDEP staff, with occasional assistance from trained interns and volunteers. During each census, all open habitat in the vicinity was searched, and measurements were recorded for all *Schwalbea* plants, including the number of stems, maximum stem height (cm), and number of flowers per stem. Data were collected in consecutive meter-wide belt transects covering the entire area to ensure that no plants were missed (Figure 2). Great care was taken to avoid trampling any plants or compacting the soil, with only one observer moving through each transect, calling out measurements to be recorded by assistants on the periphery, and pivoting from fixed safe positions on tip-toe each 1–1.5 m. All individuals in the population were measured and mapped within their respective colonies since 1996 (Yurlina 1996), with the spatial coordinates of each plant recorded on a centimeter-scale grid system with permanent markers at the end of each transect (Kelly and Denhof 2022). Because of the high densities of *Schwalbea*, mapping alone proved inadequate to accurately track individuals over time (Van Clef 1999). To improve tracking, tags with a unique identification number were placed at the base of all plants in the Canal colony beginning in 1999 (Van Clef 2000) at a fixed distance and direction from *Schwalbea* individuals. To account for late season germination or emergence, the population was surveyed a second time each year in September from 2001 to 2020. Data for this study was restricted to the Canal colony, which comprised the vast majority of *Schwalbea* individuals (>95%) during the majority of the study period.

Seed dormancy experiments were initiated in December 1998, with 100 seeds placed in each of 15 nylon mesh bags (300 µm pore size) to allow for passage of water, nutrients, and microbes. The bags were buried in a 2 × 1 m area at a depth of 2 cm in suitable soils immediately adjacent to the Canal colony on 1 December 1998. The bags were arranged in 5 rows by 3 columns, with 50 cm between each bag, and rebar marking the four corners of the array. Three bags were randomly selected in March each year, beginning in 1999, to be exhumed and placed under controlled conditions in a germination chamber. These consisted of 12 hrs of light at 20 °C and 12 hrs of dark at 10 °C, in order to simulate spring conditions. Successful germination was defined as the extension of 1 mm of growth of the radicle and was recorded weekly. The procedure was repeated yearly for 5 y, or until germination dropped to zero.

Demographic data for each plant was entered into an MS Excel database each year and classified according to age/stage, including (1) seedling recruit vs. $\geq$2 y old, (2) flowering status, and (3) dormant vs. emergent the previous year. Each year was coded with associated environmental data, including habitat management (fire or mowing), total precipitation, and average maximum temperature. The latter two variables were measured as spring only (April through June), and the past year (April–June plus July–September the year before), including all growing season months since the last census. Precipitation and temperature data were collected by Rutgers University (D. Gray unpub. data 1993–2004) and USDA Forest Service (K. Clark unpub. data 2005–2020) at the Silas Little Experimental Forest, located approximately 10 km from the study site. Palmer Drought Severity Index measurements for southern New Jersey were also obtained, but preliminary analyses found no relationships for any *Schwalbea* variables tested, so they are not presented in order to simplify the presentation of results.

Population level data were analyzed in terms of the annual rates of recruitment, flowering, and mortality. Recruitment rates were measured in relation to the number of above ground adult plants the previous year. Mortality rates were measured in relation to the previous year's total above and below ground populations. The data for dormancy, survival, and mortality were truncated at 2017; plants absent in that year or prior years and which did not reappear by 2020 were identified as dead. For survivorship and longevity, plants last observed in 2017–2019 were censored to allow for the possibility that they were dormant rather than dead. Comparisons of survivorship curves were limited to 1999–2006 cohorts, which had a minimum of 15 y of survival data. Flowering rates were measured in relation to adult plants above ground the same year. Estimates of annual contributions of recruitment, dormancy, and mortality to the annual population were extrapolated backwards in time from 1996–2000 based on the annual rates observed from 2001–2020.

An index of the total seed bank each year was created by summing the number of flowers present in the three preceding years × the germination rate for each respective year from our seed bank viability experiment. Flowers are capable of self-

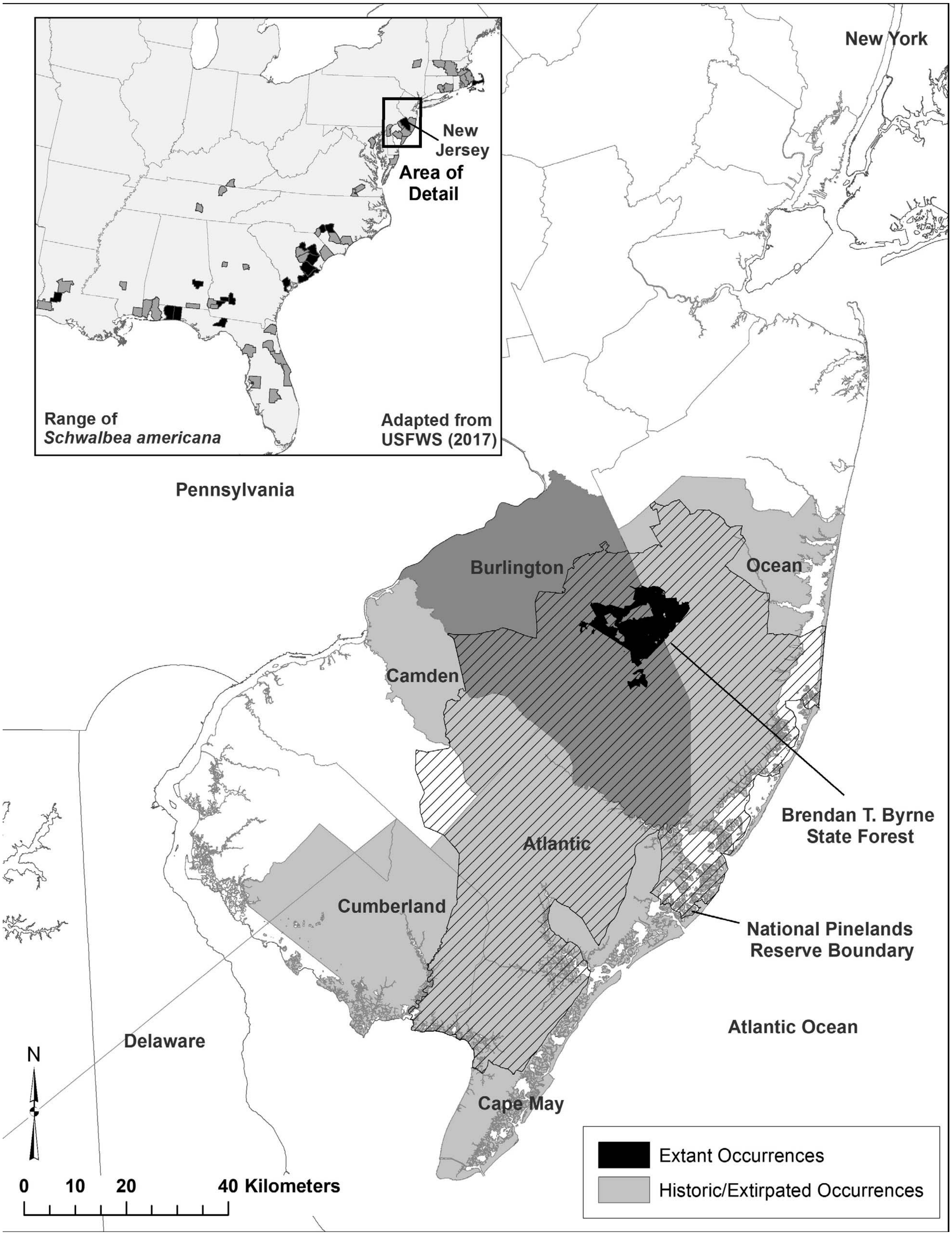

Figure 1.—Location of *Schwalbea americana* in the New Jersey Pine Barrens.

Figure 2.—Photos of a *Schwalbea americana* individual (left) and habitat conditions during the population census in July 2019 (right). Plants have multiple stems that emerge from a central, stationary base, allowing for tracking individuals over time. Belt transects were used to ensure complete spatial coverage of suitable habitat during annual censuses. Vegetation structure in the foreground is suitable for *Schwalbea* and was maintained through the course of this study by prescribed burning, mowing, and manual hand clipping of woody vegetation. Adjacent pitch pine (*Pinus rigida*) lowlands in the background are outside the clearing where *Schwalbea* occurs and do not reflect suitable habitat conditions for the species. (Photo credits: left – J. Hafstad; right – P. Rivetti)

pollination (USFWS 1995), and few fail to develop seed capsules in New Jersey (JFK pers. obs.). Although herbivory of flowering stems is relatively common, the vast majority is caused prior to the July censuses by stem-boring insects (Kelly 2006). The number of flowers present in the annual census therefore provides a useful estimator of the number of seed capsules produced later each year. While the number of seeds vary by capsule, we have not observed variation to correspond with year, management, or other environmental variables, at least qualitatively.

Statistical Analyses

Nonparametric Wilcoxon ranks were generated for univariate analyses of annual *Schwalbea* responses to management, using Dunn tests for pairwise comparisons at 95% confidence intervals. Kaplan-Meier estimates were used to analyze survivorship and longevity of *Schwalbea* cohorts. Multivariate analyses of annual vital rates in the population were conducted using generalized linear models (GLM), and individual plant data were analyzed using mixed models (GLMM), accounting for the dependency of individual plant data over time by incorporating plant ID as a random effect (Zuur et al. 2009). Models were selected based on the types of response variables, including Gamma distributions (log link) for continuous data, Bernoulli (logit link) for binary, Negative Binomial (logit link) for counts, and Beta (logit link) for proportions. Data exploration, model formulation, and validation procedures followed Zuur and Ieno (2016) and Zuur et al. (2010). Factors from both the same and previous year ($t - 1$) were included in the analysis. Each analysis also tested for interaction effects of management × year. Continuous covariates were standardized by subtracting the mean and dividing by standard deviation, and year was analyzed as a continuous covariate scaled to begin at 1. For covariates that exhibited significant collinearity, only one was included in model formulation based on differences in respective AIC values, including (height, # stems, # flowers), precipitation (spring only vs. year), and reproduction (# flowers, estimated seed bank). Backwards model selection using information criteria (AIC) was applied using the drop1 function to optimize models. For each model, random effects were tested in terms of both intercept only and intercept and slope (correlated or not) in relation to year (Bates et al. 2015). Nonparametric univariate analyses were conducted in SAS-JMP 9.0, and all other analyses were conducted in R 4.0.3 (R Core Team 2020) and RStudio (2021) using the *glmmTMB* package.

RESULTS

Individualistic plant monitoring collected from 1999 to 2020 (Figure 3) resulted in measurements of 1002 *Schwalbea* individuals, including 8034 plant-year occurrences, 6402 of which comprised above ground, emergent plants. Vital rates measured from 2001 to 2020 included average annual mortality of 13% (max. 26% in 2012) relative to the previous year's total populations (above ground + dormant plants), dormancy of 20% (max. 31% in 2011), total emergence of 66%, and emergence from dormancy of 56%. Compared to the above ground population present in the same year, 29% additional plants were dormant on average (max. 57% in 2010), representing 21% of the total annual population size. From 1991 to 2020, flowering rates averaged 2.1 flowers per plant $\geq$2 y old (max. 9.7 in 1999), and 14% flowering (max. 73% in 1999). Seedling recruitment from 1997 to 2020 averaged 42% (median

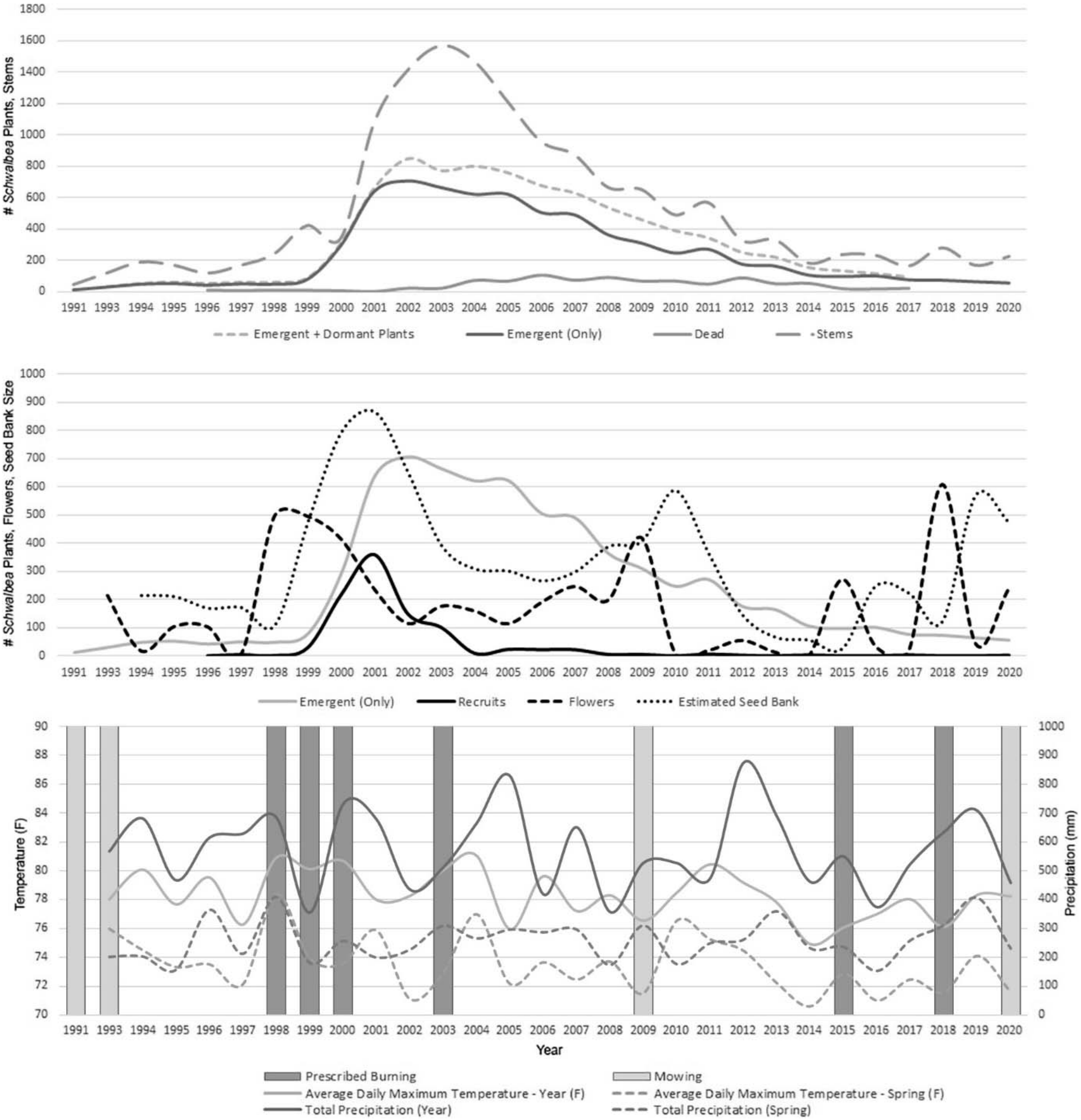

Figure 3.—Population trends of the main *Schwalbea americana* colony (top), reproduction (middle), and associated environmental variables (bottom) in New Jersey, 1991–2020. Bars indicate years in which prescribed burning or mowing occurred. Hand clipping occurred in all other years to prevent woody succession. See text for calculation of estimated seed bank and other details.

= 2.1%) relative to the previous year's adult population and 9.7% (median = 2.1%) of the annual total above-ground population.

Schwalbea morphological variables were strongly correlated (Figure 4), with taller plants having more stems ($R^2 = 0.537$) and more flowers ($R^2 = 0.518$), and plants with more stems having more flowers ($R^2 = 0.475$). Because height was most closely related to the other two variables, it was included as the primary morphological covariate for multivariate model formulation. Flowering was limited to individuals ≥2 y old, and seedling

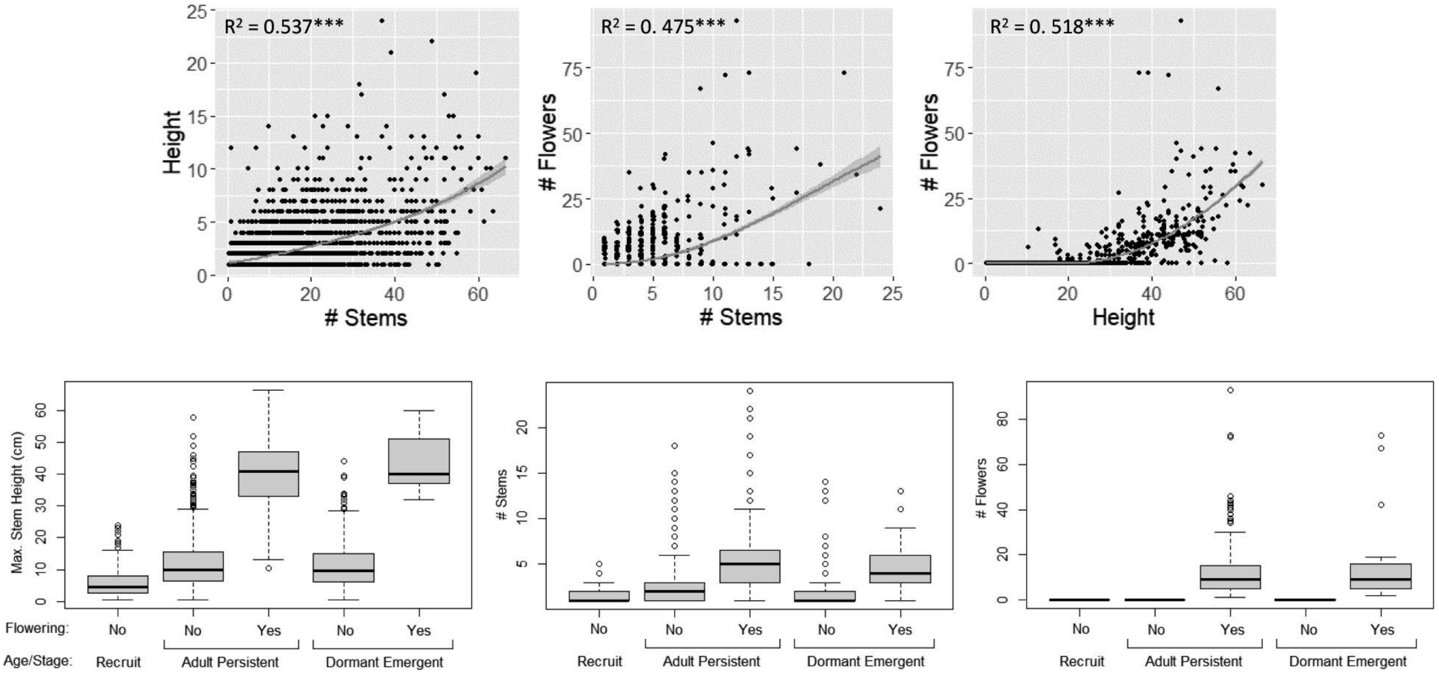

Figure 4.—Relationships of *Schwalbea* size, flowering, and age/stage classes. Morphometric (top) and age/stage class (bottom) relationships from pooled data (2000–2020). Lines are fitted with loess method and R^2 values from linear regression. Box plots include upper and lower quartiles to either side of the median, with whiskers extending an additional 1.5*interquartile range, or the min/max points if shorter.

recruits were significantly smaller compared to older plants ($P <$ 0.0001; Figure 4, Table 1). However, four outliers were removed from the seedling recruit category (<1% of data set), including one with three flowers in 2004, and three plants with heights ≥33 cm in 2008 and 2020. These outliers were attributed to late-season germination (after the July census the year before) and/or observer error. No significant differences in height or flowering status were found between plants emerging from dormancy compared to persistent emergent plants, but the former had fewer stems on average when non-flowering ($P < 0.0001$). Despite the differences in mean values for each size class, the ranges of sizes exhibited by non-flowering plants ≥2 y old overlapped entirely with first-year plants. Significant differences in size were observed according to flowering status ($P < 0.0001$), with 90% of flowering stems being ≥27 cm tall, and 90% of non-flowering plants being ≤22 cm tall.

Schwalbea responded positively to mowing and prescribed burning, with 47% greater height ($\chi^2 = 7.72$, df = 1, $P = 0.0054$), 51% more stems ($\chi^2 = 10.32$, df = 1, $P = 0.0013$), 11× more flowers per plant ($\chi^2 = 13.07$, df = 1, $P = 0.0003$), and 9× greater proportions of plants flowering ($\chi^2 = 14.86$, df = 1, $P = 0.0001$) compared to years when neither occurred (Figure 5, Table 2). No differences were detected between *Schwalbea* responses to fire and mowing ($P = 0.544$–0.931). These were consequently lumped together as "management" in subsequent multivariate model formulation, which was further confirmed by model selection using AIC. There also appeared to be some evidence of residual effects from repeated mowing and burning to varying degrees, as indicated by both the higher *Schwalbea* responses in pre-1998 control years (following eight consecutive years of mowing) and the increased response for some variables in several years after burning. This was especially the case for 2001, after three consecutive years of burning, which was an outlier among the post-1998 control years for several variables (Figure 5). When treatment types were compared to pre- and post-1998 control groups (when prescribed fire was first used), there were significant differences between fire and post-1998 for all variables ($P < 0.001$) but none for pre-1998 controls ($P = 0.128$–0.671). Mowing differed from post-1998 controls for all variables ($P = 0.019$–0.002) except height ($Z = 1.88$, $P = 0.060$),

Table 1.—Relationships of individual *Schwalbea* morphology to age/classes from 2000 to 2020. Letters (superscript) for mean values indicate pairwise Dunn tests, with different letters indicating significant differences at 95% confidence intervals.

			Means (± SE)			Range (Min–Max)		
Age	Treatment	N	# Flowers	Height	# Stems	# Flowers	Height	# Stems
1 year	Seedling Recruit	504–522	0 ^{A}	5.7 ± 0.2 ^{A}	1.4 ± 0.03 ^{A}	0	0.5–24	1–5
≥2 years	Persistent Non-Flowering	3663–3964	0 ^{A}	11.8 ± 0.1 ^{B}	2.1 ± 0.03 ^{C}	0	0.5–58	1–18
≥2 years	Persistent Flowering	227–236	12.4 ± 0.8 ^{B}	40.0 ± 0.7 ^{C}	5.4 ± 0.3 ^{D}	1–93	6–66.5	1–24
≥2 years	Dormant$_{(t-1)}$ Non-Flowering	894–946	0 ^{A}	11.2 ± 0.2 ^{B}	1.7 ± 0.04 ^{B}	0	0.5–44	1–14
≥2 years	Dormant$_{(t-1)}$ Flowering	29	14.7 ± 3.2 ^{B}	42.9 ± 1.5 ^{C}	5.2 ± 0.6 ^{D}	2–73	32–60	1–13

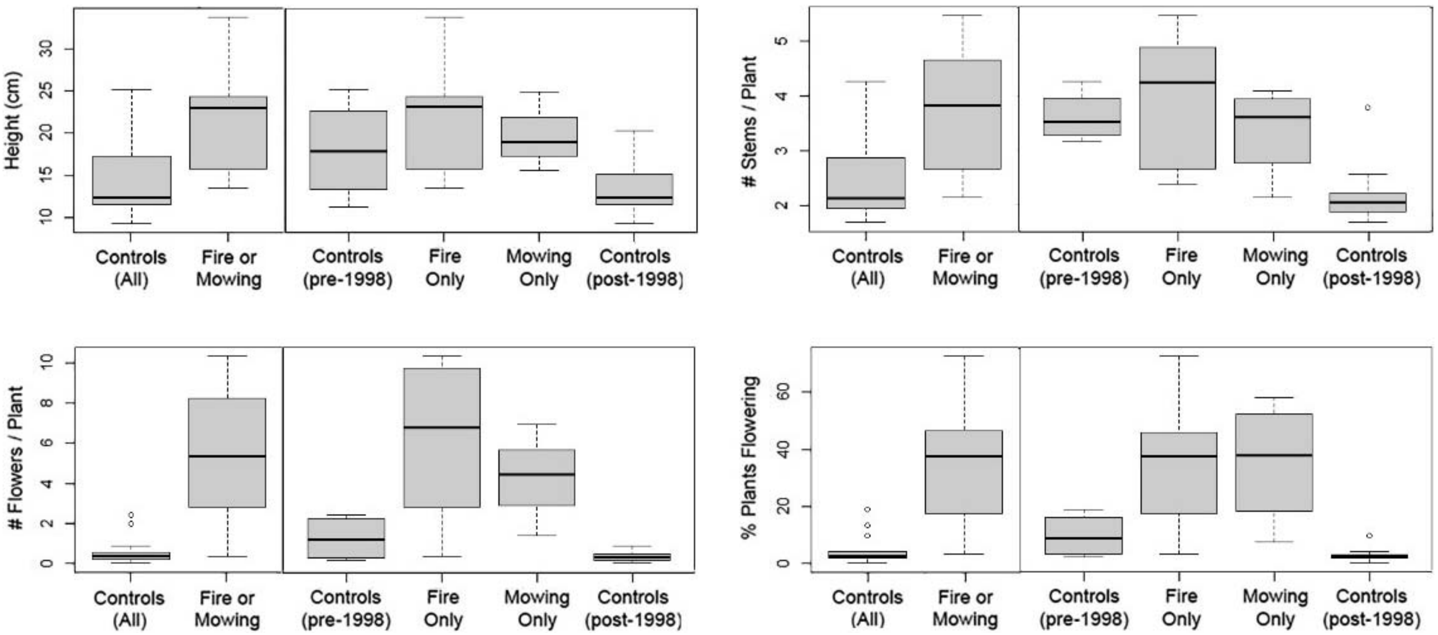

Figure 5.—Responses of *Schwalbea* to fire and mowing from 1991 to 2020. Average *Schwalbea* size and flowering rates in years with fire or mowing compared to years without (controls). First-year plants were excluded from the analyses except for 1991–1995, when age class data were unavailable. Data for those years therefore represents underestimates of size and flowering compared to other years. Outliers appearing in the post-1998 control group are from 2001.

and there was no difference with pre-1998 controls ($P = 0.227$–0.868). The two control groups differed only for # stems ($Z = 2.56$, $P = 0.010$. The *Schwalbea* data prior to 1996 also represented underestimates for each variable, as they were measured against total # plants (rather than the smaller number of adult plants ($\geq$2 y) used as a denominator in later years), since age class data was not available and prior data was insufficient to estimate.

The 1161 plant-year observations of prolonged winter (vegetative) dormancy included 987 continuous dormancy episodes averaging 1.6 ± 0.04 y in duration (Figure 6). The vast majority of dormancy events (92%) were 1–3 y in length, including 69% for 1 y, 16% for 2 y, and 8% for 3 y dormant. Although 11 instances were greater than 6 y (including one case of 10 y max.), these represented only 1% of the data and may have resulted from observer error. Results of the field experiment on seed dormancy found germination rates of 89.7% the first year (1999), 70.7% after 2 y (2000), and 0% after 4 y (2002) (Figure 7). Germination trials did not occur in the third year (2001) but rates were estimated at 29.3% based on an apparent doubling of seed mortality in each prior year. Of the 300 seeds exhumed in 2002, an empty seed coat was all that remained of all but seven and none of those successfully germinated. There was a strong relationship between seed bank viability and time ($R^2 = 0.975$; Figure 7). Based on these germination rates, the available seed bank each year was estimated (Figure 3), showing a major peak from 1999 to 2002 closely associated with peak years of recruitment in 2000–2003, and with smaller spikes following later flowering events.

Multivariate analyses (Tables 3 and 4, Figure 8) confirmed the relative significance of management to *Schwalbea* flowering and other vital rates compared to other environmental factors, with age/stage classes having the greatest effect for several responses as well. Although significant responses to precipitation and temperature were exhibited to varying degrees, the estimated slopes for these factors were far lower than for management or age/stage class with each variable. When random effects of individuals were incorporated into the model, age class and flowering status proved to be more strongly associated with plant height than management (Table 3). There was a strong positive association between mortality and dormancy at both the population and individual levels (Tables 3 and 4), and between

Table 2.—Response of *Schwalbea* to fire and mowing from 1991 to 2020. See Figure 5 for details. Letters (superscript) indicate results of pairwise Dunn tests, indicating significant differences at 95% confidence intervals. Variation around the mean is presented in SE.

Treatment	Height (cm)	# Stems / Plant	# Flowers / Plant	% Plants Flowering
Controls (All)	14.6 ± 1.0 ^{A}	2.5 ± 0.2 ^{A}	0.5 ± 0.1 ^{A}	4.0 ± 1.1 ^{A}
Fire or Mowing	21.5 ± 2.1 ^{B}	3.7 ± 0.3 ^{B}	5.5 ± 1.2 ^{B}	35.4 ± 7.0 ^{B}
Controls (Pre-1998)	18.0 ± 3.0 ^{AB}	3.6 ± 0.2 ^{B}	1.2 ± 0.6 ^{AB}	9.5 ± 3.9 ^{AB}
Fire Only	22.3 ± 2.9 ^{B}	4.0 ± 0.5 ^{B}	6.1 ± 1.6 ^{B}	35.6 ± 9.8 ^{B}
Mowing Only	19.8 ± 2.7 ^{AB}	3.4 ± 0.4 ^{B}	4.2 ± 1.6 ^{B}	35.1 ± 11.0 ^{B}
Controls (Post-1998)	13.7 ± 0.9 ^{A}	2.2 ± 0.1 ^{A}	0.3 ± 0.1 ^{A}	2.5 ± 0.6 ^{A}

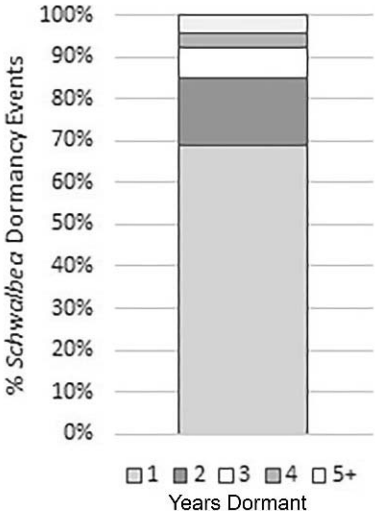

Figure 6.—Length of vegetative dormancy events ($n = 1161$) in years for *Schwalbea* individuals from 2001 to 2020.

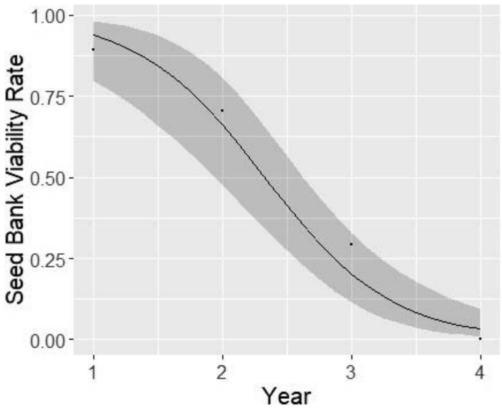

Figure 7.—Results of field experiments on *Schwalbea* seed bank viability from 1998 to 2002. Data in the third year of the study was estimated based on seed mortality in the first two years.

dormancy plant height and past state of emergence. Model selection found optimal results with correlated random intercepts and slopes of individual plant ID by year, except for probability of survival and dormancy, which had uncorrelated random slopes and intercepts.

Observations of seedling recruitment from 2000 to 2020 averaged 28% relative to the # adult plants in the prior year, with major decreases in recruitment over time. Recruitment rates were 18–462% (mean = 240%) from 2000 to 2003, compared to 5% or less (mean = 2%) from 2004 to 2020. Recruitment rates were more strongly associated with estimated seed bank sizes ($Z = 4.65$, df = 13, $P < 0.0001$) than with flowering output the previous year alone ($Z = 1.67$, df = 13, $P = 0.0952$). Late-season germination after the July census was observed only in 2001 and included 38% of the total 573 first-year plants observed in that year.

Annual survival rates of *Schwalbea* individuals ($n = 955$) from the 1999–2006 cohorts were relatively consistent over time

Table 3.—Results of generalized linear mixed effects models for size and vital rates of *Schwalbea* individuals in relation to demographic and environmental variables. Vital rates include probabilities of survival, dormancy, emergence from dormancy, and flowering. Dashes ("–") indicate factors dropped through backwards model selection using AIC. Temperature and precipitation are abbreviated for spring (SPR = April–June) and year (YR = April–June, July–September) prior to survey. Data from previous year indicated by "(t–1)". R^2 (marginal) indicates fit for fixed effects only. R^2 (conditional) includes random effects when possible.

	Height			Probability of dormancy			Probability of emergence			Probability of survival			Probability of flowering		
	Intercept	SE	Pr(>|z|)	Intercept	SE	Pr(>|z|)	Intercept	SE	Pr(>|z|)	Intercept	SE	Pr(>|z|)	Intercept	SE	Pr(>|z|)
	1.73	0.03	<0.001	3.405	0.2	<0.001	−1.68	0.16	<0.001	3.46	0.22	<0.001	−6.57	1.73	<0.001
Covariates	Slope	SE	Pr(>|z|)	Slope	SE	Pr(>|z|)	Slope	SE	Pr(>|z|)	Slope	SE	Pr(>|z|)	Slope	SE	Pr(>|z|)
Age	0.47	0.03	<0.001	–	–	–	–	–	–	0.36	0.17	0.032	–	–	–
Flowering	0.80	0.04	<0.001	–	–	–	–	–	–	–	–	–	–	–	–
Dormant^{t-1}	–	–	–	−0.88	0.10	<0.001	–	–	–	−0.99	0.10	<0.001	–	–	–
Dormant$^{t\geq 2}$	–	–	–	–	–	–	−1.42	0.13	<0.001	–	–	–	–	–	–
Height	–	–	–	0.83	0.07	<0.001	–	–	–	0.83	0.07	<0.001	3.86	1.09	<0.001
# Stems	0.16	0.01	<0.001	–	–	–	–	–	–	–	–	–	–	–	–
Temperature^{SPR}	−0.03	0.01	<0.001	–	–	–	−0.29	0.06	<0.001	–	–	–	–	–	–
Precipitation^{SPR}	0.04	0.01	<0.001	−0.18	0.05	<0.001	–	–	–	−0.23	0.05	<0.001	–	–	–
Precipitation^{YR}	–	–	–	–	–	–	0.19	0.05	<0.001	–	–	–	–	–	–
Management$_{(t-1)}$	–	–	–	–	–	–	–	–	–	0.39	0.13	0.003	–	–	–
Management	0.06	0.04	0.088	−0.51	0.23	0.029	1.56	0.29	<0.001	−0.61	0.25	0.013	−3.00	1.09	0.006
Year	0.01	0.003	0.005	−0.21	0.02	<0.001	0.26	0.02	<0.001	−0.23	0.03	<0.001	−0.32	0.17	0.054
Management:Year	−0.01	0.003	0.0018	0.06	0.02	0.008	−0.18	0.03	<0.001	0.068	0.03	0.013	0.50	0.17	0.003
Random Effects	Variance	SD	Correlation	Variance	SD	Correlation	Variance	SD	Correlation	Variance	SD	Correlation	Variance	SD	Correlation
ID	0.28	0.54	–	<0.001	0.00	–	<0.001	0.00	–	<0.001	0.00	–	6.91	2.62	–
Year	0.001	0.04	−0.73	0.005	0.07	–	0.009	0.10	–	0.006	0.08	–	0.08	0.29	−0.69
Observations (n)	–	5313	–	–	5131	–	–	2405	–	–	5054	–	–	5315	–
Individuals (i)	–	976	–	–	974	–	–	926	–	–	972	–	–	976	–
R^2 (marginal)	–	0.22	–	–	0.30	–	–	0.39	–	–	0.33	–	–	0.65	–
R^2 (conditional)	–	0.54	–	–	–	–	–	–	–	–	–	–	–	0.87	–

Table 4.—Results of generalized linear models for population-level vital rates of *Schwalbea*. See Table 3 for details.

	Mortality rate			Recruitment rate			Flowering rate			Dormancy rate		
	Intercept	SE	Pr(>|z|)	Intercept	SE	Pr(>|z|)	Intercept	SE	Pr(>|z|)	Intercept	SE	Pr(>|z|)
	−3.93	0.45	<0.001	−1.71	0.4	<0.001	−0.86	0.25	<0.001	−1.69	0.14	<0.001
Covariates	Slope	SE	Pr(>|z|)	Slope	SE	Pr(>|z|)	Slope	SE	Pr(>|z|)	Slope	SE	Pr(>|z|)
Dormancy Rate	4.64	1.34	<0.001	–	–	–	–	–	–	–	–	–
Mortality Rate	–	–	–	–	–	–	–	–	–	2.61	0.97	<0.007
Seed Bank	–	–	–	1.36	0.19	<0.001				–	–	–
Management	–	–	–	–	–	–	2.46	0.49	<0.001	–	–	–
Year	0.05	0.02	0.018	−0.07	0.03	0.029	–	–	–	–	–	–
R^2	0.47			0.98			0.81			0.26		

(Figure 9), with an average of 87.8% survival each year. Kaplan-Meier estimates showed 9.3% of plants surviving 18 y on average, and projections indicated 1% survival to 45 y or more. Significant differences existed between cohorts ($\chi^2 = 85.6$, df = 7, $P < 0.0001$), with the mixed-age cohorts from 1999 and 2000 exhibiting higher survival rates than others. The 1999 cohort, for example, survived 12.2 y on average, with a total of 24.7% of plants surviving 18 y. The 2002–2006 cohorts, in comparison, averaged 4.3–6.2 y with 8.7% surviving to the end of the study period (13–18 y). Annual survival rates were highest at the beginning (92.7% in 2000–2003) and end of the study period (93.2% in the last three years) when more frequent management occurred, compared to 84.7% survival in 2004–2014, when management occurred only once (2009).

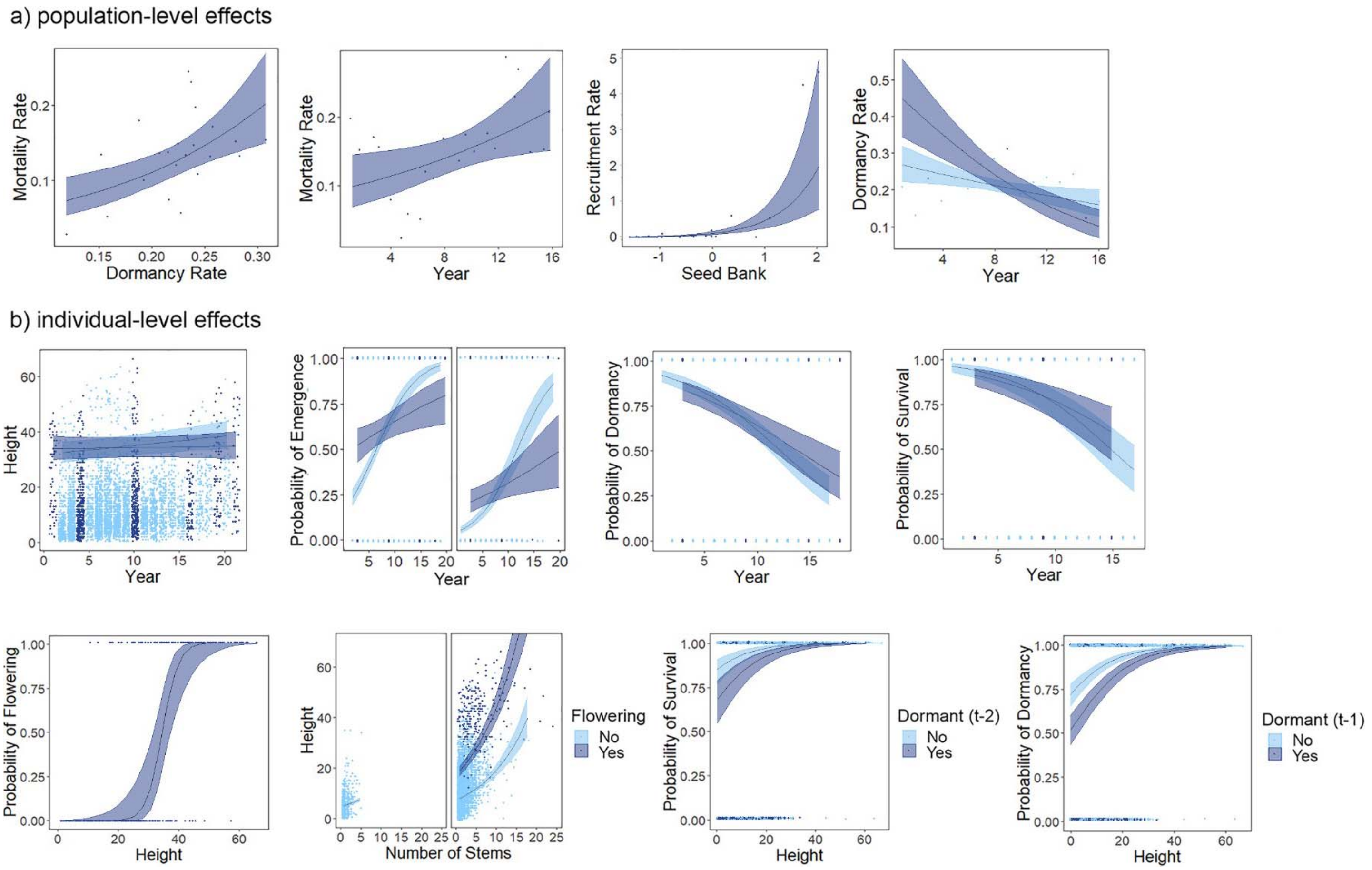

Figure 8.—Relationships of *Schwalbea* to demographic and environmental factors at the (a) population and (b) individual levels. Model visualization for the most significant fixed effects for respective response variables, with other variables held constant (average). Points depict observed values. Lines indicate predicted values from model with 95% confidence intervals (ribbons). Unless otherwise indicated, dark shaded ribbons = management, light shaded = no management; dark only = all data. Seed bank values presented are standardized and calculated as a function of # flowers × seed viability rate/year (see Methods for details).

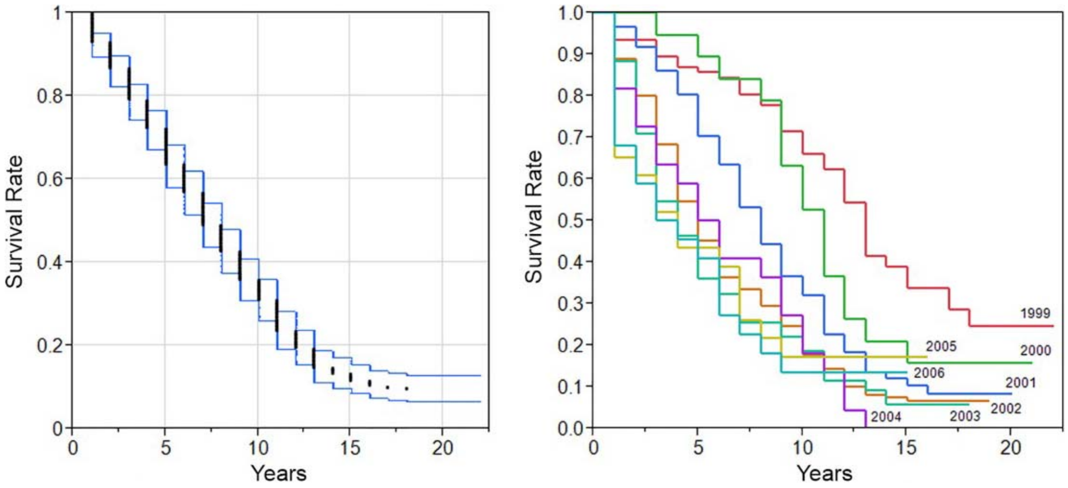

Figure 9.—Average (left) and cohort-specific (right) survivorship of *Schwalbea* for 1999–2006 cohorts. Error bars (left) indicate 95% confidence intervals. Individuals absent after 2017 were censored to allow for up to 3 y of dormancy.

DISCUSSION

Long-term demographic studies can provide valuable insights for the ecology and conservation of rare plant species (Hutchings 2010), and our 30 y study represents the first of this kind for *Schwalbea*. Prior population studies occurred over shorter time scales and in experimental contexts (Kirkman et al. 1998; Norden and Kirkman 2004a; Glitzenstein et al. 2016) or consisted of long-term *Schwalbea* census results without demographic or environmental data to explain observed trends or relationships (Glitzenstein et al. 2001; USFWS 2016, 2017). While not always feasible (Menges and Gordon 1996), the value of long-term individualistic monitoring was made clear to us by the clarity it provided for understanding observed population changes in New Jersey compared to previous years in which such methods were not used (Obee 1995; Yurlina 1998; Van Clef 1999). For the first time we were able to identify the relative significance of seedling recruitment, dormancy, survival, and mortality for explaining annual population changes, and to better understand the relationships of management and other environmental factors to them. While numerous questions remain, this research yielded important insights for the conservation and recovery of *Schwalbea* in New Jersey, and far less would have been learned had these individualistic methods not been adopted.

In retrospect, the absence of individualistic data in the early days of *Schwalbea* monitoring in New Jersey contributed greatly to the uncertainty and ultimately the misinterpretation of census results. Researchers were especially concerned with the apparent lack of seedling recruitment in the population, attributing observed increases instead to emergence from dormancy. However, while these presumptions were based on the larger sizes of new plants observed compared to seedlings being grown in the greenhouse at the time (Obee 1995; Yurlina 1996), we found that the age/stage classes of *Schwalbea* individuals were not in fact recognizable based on size alone, at least for smaller individuals. Although first-year recruits were significantly smaller on average, their range of sizes overlapped fully with those of plants emerging from dormancy and other persistent plants $\geq$2 y old. Seedlings were also capable of attaining much greater sizes ($\leq$24 cm tall, $\leq$5 stems) than those observed in the greenhouse at the time, suggesting the smaller relative sizes were the result of suboptimal greenhouse conditions rather than limitations intrinsic to the seedling age class per se. Based on the sizes of plants recorded, and the continual rates of population growth observed, from 13 plants observed in 1991 (Gordon 1991) to 49 in 1997 (Yurlina 1998), it seems highly likely that recruitment was indeed taking place in the population but was simply not recognized as such.

Our timing in implementing these individualistic methods was also serendipitous, as it allowed us to clearly discern the causes of the much larger population increase observed in 2001, which would otherwise have been less certain. With individual plants labeled since 1999 (Van Clef 2000), we were able to document emergence from dormancy for the first time in 2001, and the results indicated that only a small proportion of the 2001 increase was composed of plants from this life stage. Maps of all individuals in the population further indicated that much of the increase took place in an area where few to no plants had previously occurred, at least as far back as 1996 (Yurlina 1996; Kelly and Denhof 2022). With fewer than 1% of dormancy events from 2001 to 2020 being being 6–10 y in length, and seed dormancy capabilities limited to 3–4 y on average (Kaesar and Kirkman 2012), a sudden mass emergence from much longer periods of dormancy also seemed highly implausible, especially since prior surveys dating to the 1970s found only 5–20 plants in this area in any given year (Gordon 1986, 1991). Observed dormancy rates from 2001 to 2020 combined with past population numbers in fact suggested that only 11 plants were likely emergent from two or more years of dormancy in 2001. All the evidence therefore pointed to seedling recruitment as the primary cause of the increase rather than the emergence of dormant *Schwalbea* individuals.

Having discerned the demographic causes of the population increase, it was then possible to investigate the causal relationships of environmental conditions to them. Spatial analyses of the microhabitat conditions associated with the population increase, for example, identified correlations with a variety of soil, hydrological, and plant community conditions (Kelly and Denhof 2022), and greenhouse experiments confirmed the biological significance of several of these factors for *Schwalbea* germination and establishment. These new insights about *Schwalbea* microhabitat preferences led to the first successful propagation and reintroduction efforts conducted in New Jersey (Kelly 2006; Glitzenstein et al. 2016; Kelly and Denhof 2022). However, the temporal dimensions of this major recruitment event, including its apparent time lag with the elevated flowering that followed the first prescribed burn in 1998, remains largely unexplained (Kelly 2006). Our study suggested that the timing of recruitment was likely related to increases in seed abundance, through accumulating seed banks, resulting from continual increases in flowering from prescribed burning in 1998–2000 combined with persistent seed viability for 3–4 y after flowering (Figure 3). Seedling recruitment itself was more strongly related to estimates of accumulated seed banks from the previous three years of flowering than with flowering output from the previous year alone.

We also identified important sources of past observer error related to the timing of the population increase and its relation to management. Earlier analyses (Kelly 2006), for example, did not account for a prescribed burning event that occurred in 2000 as there was no record of it in prior reports (Van Clef 2000, 2001). However, we since found written records of this event in unpublished timelines of management activities at the site, which were confirmed by photographs of the prescribed burning that year with time stamps on the image files. Other errors were also discovered, including reports that "mowing" had occurred in 2001–2002 (Kelly and Cartica 2002). Later interviews with the land managers who carried out these activities found that they consisted merely of mechanical trimming of woody stems with a brush blade, which is little different than the hand-clipping that took place in other years. Improper attribution of any of these respective management events to our demographic data would have created significant sources of error in our analyses, attesting to the importance of careful recordkeeping not only of the study population, but the activities taken to manage it.

Other errors may have resulted from incongruities in the timing of *Schwalbea* monitoring relative to the life stage events in question. Specifically, we failed to account for the possibility of late-season germination or emergence until 2001, when late-season (September) surveys were first initiated. In that year, no less than 38% of the total 573 "first-year" plants observed germinated after the main July census. Had we not conducted a late season survey, these individuals would have mistakenly been identified as first-year plants in 2002. The exceptional large sizes and flowering status of several of the "first-year" plants observed in the July 2001 census itself indicated that many of them had also likely germinated in the fall of the previous year, and were themselves actually second-year plants. Based on the dormancy and survival rates observed from 2001 to 2020, we estimated that as many as 198 additional plants had likely germinated in the fall of 2000. Although these observations of late-season germination were novel for New Jersey, similar observations were made in studies of *Schwalbea* in Georgia (Kirkman et al. 1998) and other species (Shefferson et al. 2001). These observations suggest that the apparent time lag between flowering and recruitment was not as significant as previously thought and demonstrate the importance of accounting for the phenology of important life stage events in the design of plant monitoring regimes in order to avoid possible observer error in describing population changes or attributing causation to them.

Our results for *Schwalbea* flowering responses and seed viability generally confirm prior research of southern populations. Flowering was positively associated with both prescribed burning (Kirkman et al. 1998; Norden and Kirkman 2004b) and mowing (Norden and Kirkman 2004b) in the dormant season, with regular and often dramatic increases in the number of flowers occurring in years when either of these activities took place. Our seed viability rates differed slightly from those of Kaeser and Kirkman (2012), who found substantially lower average germination rates of Schwalbea in the first two years after burial (45–49%), but higher rates in the fourth year (28%). These differences may be partially due to the smaller sample sizes in our own study; however, the magnitude of the variation between them suggests that seed viability and germination rates may be responsive to local soil types or other conditions as well.

We also observed strong positive relationships between flowering and plant size and age/stage, which may suggest importance of light or other nutrients in limiting *Schwalbea* flowering (Norden and Kirkman 2004b). Of the hundreds of flowering *Schwalbea* observed in two decades of individualistic monitoring, nearly all were greater than 24 cm tall and two or more years old. *Schwalbea* flowering was associated with larger size classes based on leaf length in past studies as well (Obee 1995; USFWS 1995). Such size thresholds indicate that there may be high energetic costs associated with flowering in *Schwalbea* as with other species (Primack and Stacy 1998; Nishikawa et al. 2005). Although individuals consistently flowered from year to year in Georgia (Kirkman et al. 1998), they often fluctuated in New Jersey from flowering to non-flowering status with associated changes in height (Kelly 2006), perhaps related to lower ambient light levels from the partial shade of adjacent forest canopies (Figure 2). The specific height and age thresholds observed for flowering in New Jersey are therefore not necessarily categorical for *Schwalbea*, but may be driven instead by the conditions present in this particular context. Comparisons with other populations are needed to determine the degree to which these flowering rates and size/age relationships are responsive to environmental variation (Gawler et al. 1987; Wesseslingh et al. 1997).

Although it was not a significant contributor to the 2001 *Schwalbea* population increase, emergence from dormancy played an important role in the annual population from 2001 to 2020, with an average of 20% (31% max.) of plants entering into dormancy each year. Dormant plants numbered 29% (57% max.) of the above-ground *Schwalbea* present in each census, or 21% of the total population on average. Similar lengths and proportions of dormancy have been observed in other species (Shefferson et al. 2001; Hutchings 2010), although long-term studies are lacking for most (Lesica and Steele 1994). The patterns of dormancy observed for *Schwalbea* illustrate the importance of taking this life stage into account in population monitoring of this species. Although a minimum of 3 y of consecutive data are needed to detect dormancy in general, longer-term data sets appear to be warranted for *Schwalbea*, given the regular occurrences of dormancy events lasting 2–4 y. That being the case, it may not be possible to effectively distinguish between dormancy, recruitment, and mortality of individuals in driving population changes for at least as many years after they were initially observed. This presents obvious challenges for land managers wishing to respond to observed population changes in an informed manner on shorter time scales.

On the other hand, the high annual survival rates of 88% (74% min.) and long lifespans observed in *Schwalbea* appear to offer some assurance that populations are less vulnerable to extirpation in the short term. An average of 9% of *Schwalbea* survived 18 y, and several plants present in 2020 could be traced back to the maps of the population first drawn in 1996 (Yurlina 1996). Projections based on survivorship curves, moreover, indicated that small numbers of individuals could be expected to survive 45 y or more. Longevity is thought to have evolved to buffer species from short-term demographic fluctuations and environmental change (Garcia et al. 2008; Morris et al. 2008), with greater persistence of perennial hemiparasite populations in grasslands compared to annuals, for example (Ameloot et al. 2006; Borowicz et al. 2019). Such benefits may be vital for the ecological dynamics of *Schwalbea*, allowing the species to withstand lengthy periods of less hospitable conditions until more favorable conditions are restored by wildfires or other stochastic events.

The differences in survivorship observed between cohorts also suggested the possibility that even greater lifespans may result from exposure to favorable management regimes or other environmental conditions. No less than 24.7% of the plants first tagged in 1999 survived to 18 y, for example, and higher survival rates occurred in general in the earlier and later years of study when more regular burning and mowing was taking place. However, studies in Georgia showed 10–17% survival of *Schwalbea* individuals to 10 y (Norden and Kirkman 2004a), despite more frequent fire regimes than those that took place in New Jersey, suggesting that other factors may also be relevant to determining the lifespan of individuals or populations. Although no demographic data was provided, similar population-level persistence was documented in four occurrences in Francis Marion National Forest (Glitzenstein et al. 2001; USFWS 2016). Increases followed fire in 1992–1994 (Glitzenstein et al. 2001), and all populations persisted for 9 y or more despite small initial population sizes. Subsequent reports indicated that the two populations subjected to subsequent burns in 1996 and/or 1998 appeared to persist for more than 20 y (USFWS 2016).

Such knowledge of *Schwalbea* longevity and survival rates may serve to inform expectations about the length of time that populations are likely to persist and deciding which actions must ultimately be taken to avoid extirpation. Similarly, the limited amounts of longer-term vegetative dormancy (>5 y) observed and the total loss of seed bank viability after 3–7 y (Kaeser and Kirkman 2012) enhance our ability to confirm population extirpation. Based on these rates of dormancy and seed bank viability, for example, we can infer that the absence of individuals in a local population for 5–8 consecutive years has a high probability of representing actual extirpation. Given the lack of any major positive response of emergence from dormancy to fire or mowing, moreover, such activities unfortunately do not seem to offer much potential to revive populations after they are gone.

While previous research focused on explaining the causes of observed increases in the New Jersey population (Kelly 2006; Kelly and Denhof 2022), equally important are the reasons for its subsequent declines. With the heightened clarity of demographic changes brought by individualistic monitoring, the dwindling numbers of *Schwalbea* individuals, flowering plants and seedlings in New Jersey present significant concerns for the future viability of this last wild population in the state and cause to consider adopting alternative management regimes to counter these trends. Although selective hand cutting of young tree growth and occasional mowing and prescribed burning succeeded in maintaining open habitat structure for this species at the site (Figure 2), the continual declines observed suggest that these efforts were insufficient for sustaining *Schwalbea*.

The USFWS (2017) recently recommended implementing prescribed burning treatments on 1- to 2-year cycles for maintaining *Schwalbea* based on the increased stability of *Schwalbea* populations in Francis Marion National Forest subjected to 2-year burn cycles. The positive trends exhibited from 1986 to 2003 in New Jersey, when the *Schwalbea* population was subjected to mowing and burning at much greater frequencies, appears to confirm the benefits of more frequent management. In all, dormant season mowing or burning occurred in 12 out of 18 y during this period, with positive population growth occurring in all but three. There also appeared to be some evidence of positive residual effects after repeated management, as witnessed by the increased response of *Schwalbea* in the 4 y after annual dormant season mowing (Figure 5, Table 2), as well as in the year after several prescribed burns. In contrast, mowing or burning occurred in only 4 of the next 17 y (2004–2020), with declines occurring in all but 2.

Interestingly, if such high frequencies of disturbance are necessary for maintaining *Schwalbea,* the 8- to 12-year return intervals predicted for fire throughout the range of *Schwalbea* in New Jersey (Guyette et al. 2012) suggest that fire alone may not have sustained natural populations in this region in the past. At this particular site, no record of fire existed at least as far back as the 1970s (Cartica 1993) with habitat conditions throughout the population instead created by mowing for roadside right-of-way maintenance, cranberry farming operations, and *Schwalbea* management (Gordon 1986). As a management tool, mowing serves as partial substitute for grazing, and although nothing is known about the historical grazing regimes of the large native herbivores that are now extinct from eastern forests and grasslands of North America, the positive response of *Schwalbea* to both mowing and frequencies of disturbance above the natural fire regime suggests that grazing may have played an important role in maintaining habitat for this species in addition to fire. In either case, the monitoring history of this population indicates that regular dormant season mowing and/or burning are likely to be more supportive of *Schwalbea* populations in New Jersey than current management regimes involving less frequent burning and mowing.

Although isolated fire and mowing events generated positive flowering and growth responses, the lack of subsequent seedling recruitment suggests that other factors may be constraining it besides reproductive output. Variable population responses to management were also documented by Glitzenstein et al. (2001), with major increases correlated to fire in some populations but not others. Further research is therefore needed to identify the particular conditions that are conducive to germination and establishment of plants from seed in the wild, such as microsite disturbances, bare ground, host root availability, relative humidity, or other factors (Kirkman et al. 1998; Van Clef 2000; Norden and Kirkman 2004b; Kelly 2006). Future quantitative research on the population dynamics of *Schwalbea* should also be conducted, using transition matrix models (Shefferson et al. 2001) to further delve into the general significance of different life stages and environmental events driving population outcomes in New Jersey and elsewhere. Lastly, increased propagation and recovery efforts aimed at establishing additional populations at historical and/or other appropriate sites are needed (Glitzenstein et al. 2016; Gustafson et al. 2017), so that the New Jersey *Schwalbea* population will not be lost should these efforts at sustaining this last wild population ultimately fail.

Author Credits

J. Kelly: data collection, research and planning, statistical analyses and report writing (2001–2020); R. Cartica: administration and oversight of *Schwalbea* monitoring and management (1991–2020) and assistance with field data collection in 2001; M. Van Clef: data collection (1998–2001), research and planning, design and implementation of seed dormancy experiment (1998–2000), initiation of individual tagging system in 1999.

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