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Population dynamics and comparative demographics in sympatric populations of the round-leaved orchids *Platanthera macrophylla* and *P. orbiculata*

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Abstract

Orchids (Orchidaceae) are a family of flowering plants with a high proportion of threatened taxa making them an important focus of plant conservation. Orchid conservation efforts are most effective when informed by reliable demographic research. We utilized transition matrix models to examine the population dynamics and demography within sympatric populations of a species pair of terrestrial round-leaved orchids, *Platanthera macrophylla* and *P. orbiculata*. The models were parameterized from a large data set spanning 9 years from field observations of over 1,000 orchids. Life table response experiments (LTRE) were used to identify which life history transitions, and which vital rates within those transitions, most contributed to observed differences between the two species and most contributed to interannual variation within each species. Results from mean transition matrices projected finite rates of population growth that were not significantly different between the two species, with *P. macrophylla* near the replacement rate and *P. orbiculata* below it. LTRE revealed that the difference in population growth rates between the two species was mostly due to differences in fecundity (flowering adult to protocorm transition) driven by differences in fruit set and seed germination into protocorm, which were much greater for *P. macrophylla*. The two primary contributors to interannual variation in population growth rates for both orchids were adult survival and fruit set, respectively. These findings indicate that any environmental disturbances harming adult survival or fecundity will have a disproportionately negative effect on the orchid populations.

KEYWORDS

life table response experiment, orchid demography, plant population dynamics, *Platanthera macrophylla*, *Platanthera orbiculata*

1 | INTRODUCTION

Orchids (Orchidaceae) are an exceptionally diverse family of flowering plants that includes a very high proportion of threatened taxa making them an important focus of plant conservation (Swarts & Dixon, 2017). Orchids appear to be more sensitive than most plants to changes in their environment due to the complex and specialized interactions they must maintain with other species, both fungi belowground and pollinators aboveground (Bronstein, Armbruster, & Thompson, 2014; Fay & Chase, 2009; Fay, Pailler, & Dixon, 2015). For example,

orchids begin their life cycle dependent upon a mycorrhizal association with a fungal endophyte for seed germination and establishment, and many, if not most, terrestrial orchids also rely on mycorrhizal partners for part of their carbon gain into adulthood (Rasmussen, Dixon, Jersáková, & Těšitelová, 2015; Zelmer, Cuthbertson, & Currah, 1996). Within the genus *Platanthera*, *P. bifolia* has been confirmed as a partial mycoheterotroph receiving about 20% of its carbon from fungi in the adult stage (Schweiger, Bidartondo, & Gebauer, 2018). Several authors have proposed that fungal carbon supports belowground plant parts and orchid photosynthesis supports aboveground plant parts including fruit set (Gonneau et al., 2014; Lallemand et al., 2019). Because of their complex carbon balance and reliance on fungal partners in the soil, orchids are particularly vulnerable to changes in their environment including climate change and herbivore pressure. Climate change could impact both their fungal partners and pollinators, with mismatches in phenology becoming more likely (Robbirt, Roberts, Hutchings, & Davy, 2014). Increases in deer populations and wintering grounds (from changes in snowpack) could reduce reproduction and survival (Knapp & Wiegand, 2014). Demographic modeling provides an avenue to understand which aspects of the life cycle most impact population growth currently and which may be most vulnerable to future change.

We use the species pair of the round-leaved orchids, *Platanthera macrophylla* and *P. orbiculata*, to explore potential differences in their vulnerabilities to such looming environmental changes. Previous work on these orchids found critical thresholds for leaf area pertaining to both individual life stage transitions and survival (Cleavitt, Berry, Hautaniemi, & Fahey, 2016). Both species are forest dwelling, terrestrial orchids endemic to North America, and are variously listed as rare, threatened, endangered, or extirpated throughout parts of their range in Canada and the United States (NatureServe, 2015; USDA-NRCS, 2015). Within our study area in northeastern North America, the species are listed as rare in four of the six New England states (NatureServe, 2015; USDA-NRCS, 2015). Therefore, while our study populations are not of current conservation concern in New Hampshire, this work may inform conservation plans in nearby states. The co-occurrence of these two species has been noted as rare (Fernald, 1950; Reddoch & Reddoch, 1993) and our study populations therefore offer a unique opportunity for comparison of demography of the two species under similar habitat conditions.

One important question is: how big an impact does variation in key vital demographic rates, such as a loss of flowering adults or a reduction in juvenile recruitment, have on population dynamics of these species? Orchid capsules contain thousands of minute seeds such that a limited number of fruit set may be sufficient to maintain the population. However, given the very low rates of success for an individual seed to germinate, establish as a protocorm, and grow to an above ground stage, a large number of seeds produced by a substantial number of flowering adults may be required to sustain a population. Here we explore how such differences in vital rates contribute to population dynamics using matrix modeling and life table response experiments (LTRE).

Matrix models have proven to be one of the most popular and effective tools in plant conservation, in that they provide a way to translate the vital demographic rates experienced by individual plants to the population level for analysis (Caswell, 2001; Salguero-Gómez & De Kroon, 2010). To facilitate comparison between the two species, we extended the matrix analyses to include LTRE. LTRE analyses are used to decompose treatment effects on a dependent variable into contributions from differences in the parameters that are used to calculate that variable (Caswell, 2010). Such analyses are regularly used in demographic studies of plants to assess their conservation status or to compare among different populations, species, or years (e.g., Esparza-Olguín, Valverde, & Mandujano, 2005; Jacquemyn, Brys, & Jongejans, 2010; Jiménez-Sierra, Mandujano, & Eguiarte, 2007; Martínez, Medina, Golubov, Montana, & Mandujano, 2010; Raventós, González, Mújica, & Doak, 2015; Ureta & Martorell, 2009). For our comparative study, we utilized LTRE analysis to calculate the differences among the two species in population growth and decompose those differences into contributions from each of the two species' vital rates. Such analyses are crucial for identifying the specific demographic rates that are most responsible for observed differences between the two species. We also utilized LTRE analysis to examine the magnitude and causes of interannual variation within each species. This is important given that natural populations typically vary from year to year in their vital demographic rates.

The objectives of this study were to fit a population model to a 9-year set of demographic data, and to use the model to compare the population dynamics between the two *Platanthera* species in sympatric populations. Specifically, we assessed population fitness as to whether the orchid populations were projected to grow or to decline; we compared the population growth rates between the species; we examined interannual variation in population growth for each species; and lastly, we performed LTRE to identify which matrix entries, and which

vital rates within those matrix entries, most contributed to observed differences population growth between species and years. Given the observed recent increase in loss of flowering individuals to deer herbivory (2016 onward), we were particularly interested in how much impact loss of flowering individuals would have on the two species demographic rates. Cleavitt et al. (2016) reported *P. orbiculata* produced more flowers per spike and was more likely to flower consecutive years than *P. macrophylla*. Do these differences lead to more stable or growing populations for *P. orbiculata*? Cleavitt et al. (2016) additionally hypothesized that the understudied early stages, particularly belowground protocorms, may present a bottleneck for population growth in these two species. Here we include several years of new data on these early life stages, protocorm formation, and recruitment of one-leaf aboveground juveniles, to explore this hypothesis.

2 | MATERIALS AND METHODS

2.1 | Study site

The Hubbard Brook Experimental Forest (HBEF) is located in north-central New Hampshire, USA (43°56′N, 71°45′W; Figure 1). The forest is in a 3,160 ha valley with overstory vegetation dominated by northern hardwoods: sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britt.), which comprise over 90% of the forest basal area, with a higher proportion of spruce-fir-birch at the highest elevations (Van Doorn, Battles, Fahey, Siccama, & Schwarz, 2011). The valley covers an elevation range of 200 to 1,010 m and marked orchids occur from 215 to 750 m (Figure 1). The HBEF is mostly second-growth forest developed following horse logging in the late 19th and early 20th century resulting in a complex forest matrix having high structural heterogeneity. The climate is humid continental with short, cool summers and long, cold winters. Annual precipitation averages 140 cm; mean annual temperature is 5.5°C; and daily temperatures average from −8.5°C in January to 18.8°C in July (Bailey, 2003). The soils are mainly spodosols with a wide range of drainage characteristics (Bailey, Brousseau, Mcguire, & Ross, 2014).

2.2 | Species

The genus *Platanthera* is mainly north temperate and has 32 species in the flora of North America (Sheviak, 2003). The genus contains many pairs of closely related species including our study species, *P. orbiculata* (Pursh.) Lindl. and *P. macrophylla* (Goldie) P.M. Brown. These species are differentiated primarily based on flower morphology and density of flowers per raceme (Cleavitt et al., 2016; Reddoch & Reddoch, 1993; Reddoch & Reddoch, 1997). The nectar spur and pollinarium lengths have both been found to differ significantly between the species with *P. macrophylla* having the longer lengths for both floral parts (Reddoch & Reddoch, 1993).

Based on leaf morphology, size, and presence of an inflorescence, Cleavitt et al. (2016) structured the orchid's life cycle into six stages: seed, protocorm, juvenile (single linear leaf), immature (single round leaf), vegetative adult (two round leaves), and flowering adult (two rounded leaves and raceme) (Figure 2). The species are moderately long-lived perennials with a life expectancy

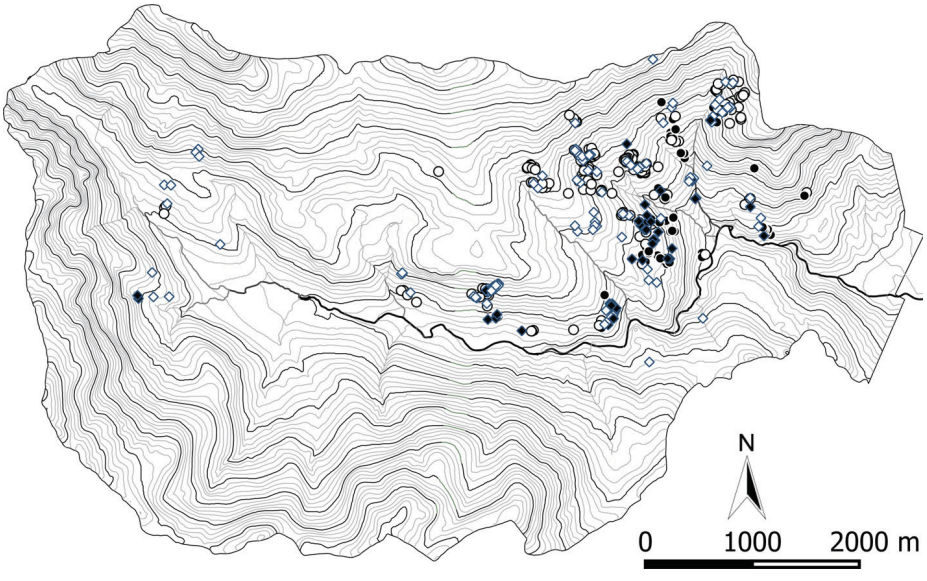

FIGURE 1 Marked orchids in the Hubbard Brook valley, Woodstock, NH, USA. Topographic contour lines are shown in 50 m elevation intervals. Orchids are differentiated by color: black for *Platanthera macrophylla*, white for *P. orbiculata*. Circles indicate orchids marked from 2011 to 2014 and diamonds indicate orchids marked from 2015 to 2019 [Color figure can be viewed at wileyonlinelibrary.com]

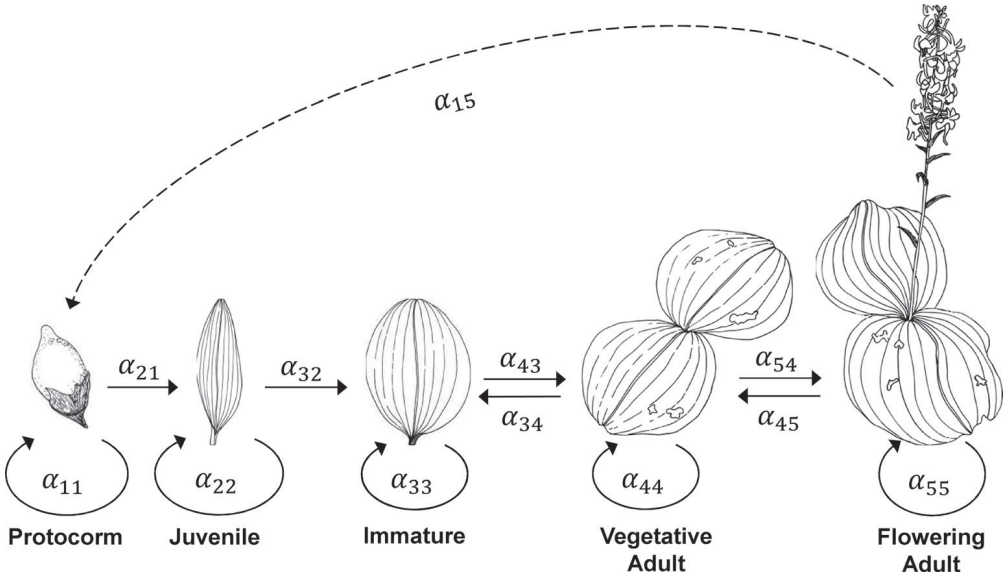

FIGURE 2 Life cycle graph for *Platanthera macrophylla* and *P. orbiculata*. Arrows indicate possible transitions between life-history stages and are labeled to show their corresponding matrix element from Equation (2a)

of 10–15 years for adults that survive through all the life stages (Cleavitt et al., 2016). Both species perennate during winter by setting their vegetative bud and initiating new roots for the following year by August of the current year (Cleavitt et al., 2016; Currah, Smreciu, & Hambleton, 1990). In our site with sympatric populations, *P. orbiculata* occurs over a wider elevation range than *P. macrophylla*, with the latter species occurring at lower elevations on average.

2.3 | Field demography

Since the summer of 2011, all individuals of the round-leaved orchids sighted in the HBEF have been individually marked and mapped using handheld Garmin GPSmap 62s (Figure 1). In cases where many orchids occur in close proximity, the location of groups was recorded with a GPS, and individual orchids are additionally mapped relative to each other within groups by compass and meter tape. From 2011 to 2019, all marked orchids were visited in May to assess their stage including orchids that were not visible for at least 5 years following their disappearance to check for the possible re-emergence after dormancy. In addition, starting in 2013, all flowering individuals were surveyed three times a season: (a) May for stage, (b) July for flower data (flower number, number healthy, damage notes for unhealthy, spike height, spur measurements, and flower density), and (c) late August–early September for capsule data (number formed, number viable, damage notes for non-viable). Three years of field incubated seed packets (2015–2017) with seed estimates per packet were also conducted and evaluated (2016–2018) to allow full parameterization of population models (Figure S1). Specific measurements are further detailed under the description of vital rates used in the model.

2.4 | Population projection matrix

The population model was constructed with the form

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \tag{1}$$

where $\mathbf{A}$ is a population projection matrix and $\mathbf{n}(t)$ is a vector with the number of individuals in each stage at time t. The projection interval is 1 year. The elements in matrix $\mathbf{A}$ include all the possible life-history stage transitions: stasis (α_{ii}), growth (α_{ji}), regression (α_{hi}), and reproduction (α_{15}).

$$\mathbf{A} = \begin{pmatrix} \alpha_{11} & 0 & 0 & 0 & \alpha_{15} \\ \alpha_{21} & \alpha_{22} & 0 & 0 & 0 \\ 0 & \alpha_{32} & \alpha_{33} & \alpha_{34} & 0 \\ 0 & 0 & \alpha_{43} & \alpha_{44} & \alpha_{45} \\ 0 & 0 & 0 & \alpha_{54} & \alpha_{55} \end{pmatrix}. \tag{2a}$$

The life history stage transition that corresponds with each matrix element is illustrated in the life cycle graph in Figure 2. Stages are defined as: (a) protocorm as a below-ground germinant, (b) juvenile with single linear leaf (at least 2:1 in length:width), (c) immature with single round leaf, (d) vegetative adult with two rounded leaves, and (e) flowering adult with two rounded leaves and a raceme. Given that life history transitions are calculated from different vital rates, matrix elements were written as a function of the appropriate vital rates as follows:

$$\mathbf{A}=\begin{pmatrix} \sigma_1(1-\gamma_{21}) & 0 & 0 & 0 & \varphi\upsilon\pi\varepsilon \\ \sigma_1\gamma_{21} & \sigma_2(1-\gamma_{32}) & 0 & 0 & 0 \\ 0 & \sigma_2\gamma_{32} & \sigma_3(1-\gamma_{43}) & \sigma_4\gamma_{34} & 0 \\ 0 & 0 & \sigma_3\gamma_{43} & \sigma_4(1-\gamma_{34}-\gamma_{54}) & \sigma_5\gamma_{45} \\ 0 & 0 & 0 & \sigma_4\gamma_{54} & \sigma_5(1-\gamma_{45}) \end{pmatrix}. \quad (2b)$$

We followed the mathematical notations for vital rates utilized by Jacquemyn et al. (2010) to model another orchid species, which are:

- σ Survival
- γ Growth
- ϕ Flowers per flowering adult
- υ Fruit set—proportion of flowers that set fruit capsules
- π Seed set—seeds per fruit
- ε Germination into protocorm

Writing the matrix transitions as vital rates shows that the growth transition ($\sigma_i\gamma_{ji}$) is conditional on survival, and the stasis transition ($\sigma_i\left(1-\gamma_{hi}-\gamma_{ji}\right)$) is calculated as the proportion of survivors that do not grow to another stage. Note that in our stage-classified model, "growth" means transitioning to another stage, which may be positive growth to a larger stage or negative regression to a smaller stage. Flowering adult reproduction is calculated as the product of flowers per flowering adult (ϕ), the proportion of those flowers that set fruit (υ), the number of seeds per fruit (π), and the germination rate of those seeds into protocorm (ε).

As noted in the species description, Cleavitt et al. (2016) referenced six life-history stages, including a seed stage that was distinct from the flowering adult stage. For this model, we incorporated the seed stage as a component in flowering adult reproduction because keeping the seed stage as distinct would have produced an unwanted 1-year delay in reproduction. Leaving seeds in the life cycle for the model would imply that flowering plants in year t produce seeds in year $t+1$, which may germinate into a protocorm in year $t+2$. However, for these species, flowering plants produce seeds in year t that may germinate into a protocorm in year $t+1$. Removing the seeds stage from the life cycle more accurately reflects the timing of those life cycle transitions. Seed dormancy appears to be absent or very rare for these species (Cleavitt et al., 2016), and therefore a seed bank was not included in the model.

2.5 | Matrix parameter estimation

2.5.1 | Vital rates for above ground stages

Vital rate estimates for above-ground stages were based on annual (post-breeding) census data of tagged individuals as described above. Flowering orchids were visited multiple times per growing season between 2011 and 2019 to record information on mortality, growth (or regression), flowers per flowering adult, and fruit set (fruits per flower). Survival rates for the above ground stages ($\sigma_{2\ldots5}$) were calculated from counts of individuals that survived from the previous year's census to the current year. Growth rates for above ground stages included both positive transitions to a larger stage class (γ_{32}, $_{43}$, and $_{54}$) and negative transitions to a smaller stage class ($\gamma_{34\text{ and }45}$). These rates were calculated based on observed changes in individual plant's stage class from the previous year's census to the current. Adult plants were classified as flowering or vegetative (non-flowering), and for flowering adults the number of flowers per plant (ϕ) was recorded. Flowering adult plants were re-censused for the proportion of flowers that set fruit (υ), which was calculated as the number of fruits divided by the number of flowers.

The number of above ground individuals per stage class per transition year is summarized in Table S1. Juvenile plants were much less abundant than the other stage classes, and for the years in which there were less than 10 individuals monitored, demographic estimates (σ_2 and γ_{32}) were based on pooled data (all years combined) for that species. Some of the demographic results from 2011 to 2015 in this data set were reported in Cleavitt et al. (2016). This paper incorporates those data into the population modeling and expands the data set of above ground vital rates for the two orchid species with four additional years of annual census data (2016–2019). Vital rates used to construct matrix models for both species and each year are listed in Table S2.

TABLE 1 Fecundity metrics for two *Platanthera* species using measurements from 2013 to 2018 (combined $n = 1{,}048$ flowering individual measures)

	P. macrophylla		*P. orbiculata*	
Metric	***n***	**Mean (1 *SE*)**	***n***	**Mean (1 *SE*)**
Spike height (cm)	192	38.3 (0.59)	473	34.9 (0.36)
ϕ—Flowers (#/spike)	273	13.5 (0.31)	611	18.9 (0.31)
Pollination (% of flowers)	167	44.9 (2.7)	387	33.5 (1.5)
υ—Fruit set (capsules/flower)	269	0.141 (0.015)	680	0.063 (0.005)
Viable capsules (#/spike)	182	3.7 (0.4)	392	2.5 (0.2)
Capsule predation (% of capsules)	115	46.5 (3.8)	241	60.5 (2.4)
π—Seeds (#/capsule)	9	2,408 (381)	14	2,061 (251)
ε—Germination to protocorm (% of seed)	10	2.32 (1.19)	20	0.96 (0.43)

Note: Seed counts are from capsules collected for seed packet experiments, 2015–2017. Protocorm data are from seed packets incubated in the field. All metrics are significantly different between the two species at $p < 0.05$ or lower.

2.5.2 | Seed counts and germination rates

Platanthera orchids produce large quantities of minute seeds per capsule, making field estimates during the annual census impractical. Data on the number of seeds per capsule (π) were generated from select capsule sampling methods as described in Cleavitt et al. (2016) over 3 years, 2015–2017, using capsules collected for germination experiments (Figure S1). In total, seed counts from 9 *P. macrophylla* and 14 *P. orbiculata* capsules were estimated (Table 1). These data were used as a fixed rate for all of the years. Rates of seed germination into protocorm (ε) were based on germination trials using plankton netting seeds packets (Figure S1) and more fully described in Cleavitt et al. (2016) conducted from 2015 to 2018 that included 10 replicate packets for *P. macrophylla* and 20 for *P. orbiculata*.

2.5.3 | Protocorm survival and growth

Estimates of protocorm survival (σ_1) and growth rate into juveniles (γ_{21}) were inferred based on field observations of timing between adult seed production and the emergence of juveniles. For this analysis, we only examined data from fruiting adults that were sufficiently distant from other adults that fruited during the time we monitored (and up to a few years before) to ensure that emerging juveniles could be reasonably matched with specific adults. These inferences of parentage are reliable given that seeds tend to disperse in the highest densities near the parent (Clark, Silman, Kern, Macklin, & Hillerislambers, 1999). Our data set included 47 seedlings from 25 known parents for *P. macrophylla*, and 120 seedlings from 52 known parents for *P. orbiculata*.

To estimate protocorm survival, we first estimated the number of protocorms produced by each fruiting adult. For this, we calculated total seed number as the product of the number of flowers per flowering adult (ϕ), mean fruit set (υ), and mean seed set per capsule (π). Total number of seeds was then multiplied by the mean germination rate (ε) from the trials described above. This provided the number of protocorms produced, and from that we then inferred the percentage of protocorms surviving over the observed number of years by examining juvenile emergence as described above. This value of protocorm survival was converted to an annual rate that was used as the estimate for protocorm survival (σ_1).

The final parameter for this life stage, protocorm growth, was estimated using a geometric distribution method, which assumes that the probability of growth is a constant and is independent of time spent in that stage (Caswell, 2001). Using the notation described in matrix **A** (Equation (2b)), protocorm growth was estimated as $\gamma_{21} = \overline{T}_{21}^{-1}$, where $\overline{T}_{21}$ is the mean duration of the protocorm stage, which we observed was 2.8 years. The resulting parameter estimate of 0.355 was a fixed value that was used as the protocorm growth rate (γ_{21}) in the models for both species.

2.6 | Matrix analyses

For each model, the asymptotic rate of population growth (λ) was calculated as the dominant eigenvalue of matrix **A**. The stable stage structure and reproductive value was calculated as the right and left eigenvectors associated with λ, respectively. These eigenvectors were used to calculate the sensitivities and elasticities (proportional sensitivities) of λ to changes in matrix elements (a_{ij}) of **A** as described in Caswell (2001).

The 95% confidence intervals for λ were obtained by a bootstrap procedure that resampled the original data set in the same manner that the data were collected (Scheiner & Gurevitch, 1993). This analysis involved creating 3,000 resampled matrices for each species and year and then calculating λ for each matrix. Non-overlapping confidence intervals with $\lambda = 1.0$ indicate populations that were significantly ($p \leq 0.05$) either growing ($\lambda > 1$) or declining ($\lambda < 1$).

Statistically significant ($p \leq 0.05$) differences in population growth between the two species, λ_{mac} and λ_{orb}, were evaluated using permutation tests, which are also called randomization tests (Caswell, 2001). These tests utilize a null hypothesis that the life history rates for individuals are independent of which species they belong to. By examining all possible permutations of individuals between the two species and calculating the variance (V) in λ for each permutation, a distribution of $V(\lambda_{\text{perm}})$ under the null hypothesis is generated. If the fraction of permutations in which $V(\lambda_{\text{perm}})$ exceeds the observed differences between the species is small, then the null hypothesis that life history rates are independent of which species individuals belong to is rejected. We had no reason to believe that one species was growing faster than the other and therefore chose the two-tailed test statistic $\theta = \left(\overline{\lambda}_{\text{mac}} - \overline{\lambda}_{\text{orb}}\right)^2$, and computed significance as

$$P_r[\theta \geq \theta_{\text{obs}} | H_0] = \frac{\#\left\{\theta^{(i)} \geq \theta_{\text{obs}}\right\} + 1}{N_{\text{p}} + 1}, \tag{3}$$

where P_r is the probability that randomly generated values of θ are larger than the observed value of θ, and # is the number of observations for which $\theta^{(i)} \geq \theta_{\text{obs}}$. N_{p} is the number of permutations. Because the total number of permutations for our data set was large, we estimated the significance level from a random sample of 3,000 permutations of the data.

2.7 | Life-table response experiments

LTRE were used to examine the contribution of matrix entries and their constituent vital rates to the observed variation in λ between the two species. Variance in population growth rate between the two species $V(\lambda_{\text{sp}})$ was evaluated as a random-effects LTRE based on the mean matrix $\mathbf{A}^{(\cdot)}$ of eight annual transitions for each species ($\mathbf{A}^{(\cdot)}_{\text{mac}}$ and $\mathbf{A}^{(\cdot)}_{\text{orb}}$). For these analyses, we followed Caswell (2001) and constructed a contribution matrix derived from observed variation between the two species' matrix entries combined with their sensitivities using the following formula:

$$V\left(\lambda_{\text{sp}}\right) \approx \sum_{ij}\sum_{kl} C(ij,kl) s_{ij} s_{kl}. \tag{4}$$

$C(ij,kl)$ is the covariance of $\alpha^{(\text{mac})}_{ij}$ and $\alpha^{(\text{orb})}_{kl}$. Sensitivities $s^{(\text{mac})}_{ij}$ and $s^{(\text{orb})}_{kl}$ were evaluated at the mean matrix of the two species calculated as $\mathbf{A}^{(\cdot)}_{\text{sp}} = \left(\mathbf{A}^{(\cdot)}_{\text{mac}} + \mathbf{A}^{(\cdot)}_{\text{orb}}\right)/2$. To examine the effect of specific vital rates on variation in λ, we decomposed the contributions to $V(\lambda_{\text{sp}})$ into the lower-level parameters that constitute each matrix entry (defined in Equation (2b)). This is written as

$$V\left(\lambda_{\text{sp}}\right) \approx \sum_{ij} \text{Cov}\left(p_i, p_j\right) \frac{\partial \lambda}{\partial p_i} \frac{\partial \lambda}{\partial p_j}, \tag{5}$$

where $\mathbf{p}$ is a parameter vector that includes all stage-specific rates for growth probabilities γ_i, survival probabilities σ_i, and reproductive outputs.

$$\mathbf{p} = (\sigma_1, \sigma_2, \sigma_3, \sigma_4, \sigma_5, \gamma_1, \gamma_2, \gamma_3, \gamma_4, \gamma_5, \phi, \upsilon, \pi, \varepsilon). \tag{6}$$

Sensitivities were evaluated by applying the chain rule (equation 9.38 in Caswell, 2001) to the mean matrix of the two species.

Similar analyses were conducted to examine the effect of matrix entries and vital rates on interannual variance in population growth rate $V\left(\lambda_{\text{yr}}\right)$ within each species. Interannual variance $V\left(\lambda_{\text{yr}}\right)$ was evaluated as a random-effects LTRE based on the observed year-to-year variation from 8 years of matrix data ($\mathbf{A}_{\text{yr1}} \ldots \mathbf{A}_{\text{yr8}}$) for each species. Similar calculations using Equation (4) for matrix entries and Equation (5) for lower level vital rates were utilized for these analyses, with appropriate changes to analyze the interannual variance within each species rather than the variance between the two species. Namely, covariance was calculated from the different years of data for each species ($\alpha^{(\text{yr1})}_{ij} \ldots \alpha^{(\text{yr8})}_{kl}$) and sensitivities were evaluated based on a mean matrix calculated from the different years ($N = 8$) for each species, using $\mathbf{A}^{(\cdot)}_{\text{yr}} = \frac{1}{N}\sum_i \mathbf{A}^{(i)}$.

3 | RESULTS

Over the nine study years (2011–2019), we have marked and followed 1,168 individual orchids varying between 226 and 656 individuals in a given year (Table S1). *P. orbiculata* appears to be more frequent in the Hubbard Brook valley than *P. macrophylla*, hovering around a 2:1 ratio throughout the study (Table S1). Dormancy in adults was extremely rare and only happened for 1 year. No adult has returned after 2 years without an aboveground presence (Table S3). For both species, the years of

TABLE 2 Mean population projection matrices ($n = 8$ transition years), with their corresponding finite rates of growth (λ) and elasticity matrices

Stage	Protocorm	Juvenile	Immature	Veg adult	Flw adult
Platanthera macrophylla					
Average matrix ($\lambda = 0.98$, 95% CI = 0.92–1.04)					
Protocorm	0.011	0	0	0	129.394
Juvenile	0.006	0.311	0	0	0
Immature	0	0.400	0.520	0.059	0
Veg adult	0	0	0.283	0.526	0.536
Flw adult	0	0	0	0.312	0.349
Elasticity					
Protocorm	0.001	0	0	0	0.064
Juvenile	0.064	0.029	0	0	0
Immature	0	0.064	0.089	0.015	0
Veg adult	0	0	0.078	**0.218**	0.110
Flw adult	0	0	0	**0.173**	0.096
P. orbiculata					
Average matrix ($\lambda = 0.94$, 95% CI = 0.92–0.97)					
Protocorm	0.014	0	0	0	24.245
Juvenile	0.008	0.307	0	0	0
Immature	0	0.417	0.575	0.043	0
Veg adult	0	0	0.233	0.480	0.481
Flw adult	0	0	0	0.382	0.446
Elasticity					
Protocorm	0.000	0	0	0	0.030
Juvenile	0.030	0.015	0	0	0
Immature	0	0.030	0.067	0.013	0
Veg adult	0	0	0.043	**0.221**	**0.170**
Flw adult	0	0	0	**0.200**	**0.180**

Note: Matrix entries producing the largest elasticity of λ are indicated in bold.
Abbreviations: Flw, flowering; Veg, vegetative.

highest mortality were 2012 (71 individuals), 2018 (94 individuals), and 2019 (120 individuals).

Fecundity metrics varied significantly between the two orchid species (Table 1). Although *P. orbiculata* produced more flowers per spike (ϕ), *P. macrophylla*'s higher rates of pollination, fruit set (υ), seeds per capsule (π), and seed germination (ε), as well as, lower rates of capsule damage, all contribute to higher fecundity in *P. macrophylla* at Hubbard Brook. The four specific parameters used to model flowering adult reproduction in the population matrices—ϕ, υ, π, ε—yielded notably higher reproductive rates (α_{15}) for *P. macrophylla* (Table 2).

3.1 | Matrix analyses

The mean finite rate of increase (λ) for *P. macrophylla* did not differ significantly from the replacement rate of $\lambda = 1.0$, meaning that the population is projected to be stable (Table 2). Populations of *P. orbiculata* were projected to decline based on its mean matrix that produced λ significantly less than 1.0. However, permutation tests indicate that the difference in population growth rate $V(\lambda_{\text{perm}})$ based on the mean matrix for the two species was not statistically significant ($p = 0.34$).

Most of the life-history transitions within the mean matrices of the two species had very similar rates, but there were a few exceptions (Table 2). *P. orbiculata* had higher transition rates from vegetative to flowering adults and higher rates of flowering adults that remained flowering the next year, while *P. macrophylla* had much higher fecundity rates per flowering adult. Elasticity analyses of the mean matrices indicated survival and growth transitions between the vegetative and flowering adults contributed most to the projected population growth rate. Collectively, the adult growth and stasis transitions contributed 60% to *P. macrophylla* and 77% to *P. orbiculata* (Table 2).

TABLE 3 Stable stage distributions (SSD) and observed frequencies of above-ground stages for each species

	Platanthera macrophylla				*P. orbiculata*			
Stage	**SSD**	**Observed**	G^2	p	**SSD**	**Observed**	G^2	p
Juvenile	0.224	0.073	16.55	<0.005	0.103	0.099	0.02	0.900
Immature	0.240	0.186	1.72	0.189	0.165	0.148	0.23	0.635
Vegetative adult	0.359	0.464	4.61	0.032	0.414	0.396	0.13	0.720
Flowering adult	0.177	0.278	6.12	0.013	0.318	0.357	0.68	0.409
Overall			22.78	<0.005			0.74	0.865

Note: Shown are the overall test statistic based on likelihood-ratio G^2 test and results of post hoc exact binomial tests for each stage (Bonferroni correction $p = 0.05/4 = 0.0125$).

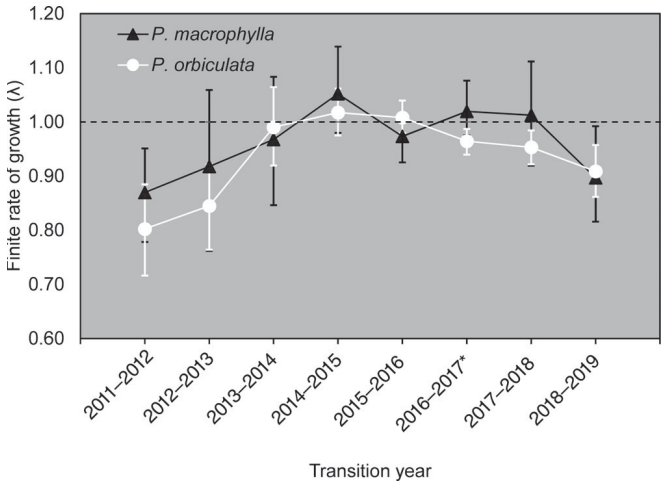

FIGURE 3 Finite rates of population growth (λ) and 95% confidence intervals over 8 years in *Platanthera macrophylla* and *P. orbiculata*. Values are mean rates from bootstrapping analysis ($n = 3{,}000$). Asterisks (*) indicate years in which population growth differed significantly ($p \leq 0.05$) between the two species based on permutation tests. Non-overlapping confidence intervals with the horizontal dashed line for either species indicates significant difference from $\lambda = 1.0$ (replacement rate of growth)

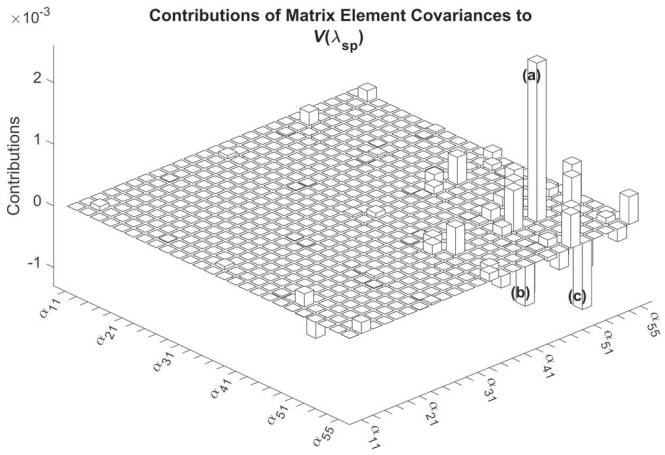

FIGURE 4 The contributions of covariances in matrix elements to $V(\lambda_{sp})$ between *Platanthera macrophylla* and *P. orbiculata*. Values in the diagonal are variances and values in the off-diagonal are covariances. Letters identify the most prominent contribution values: (a) = variance in flowering adult reproduction (α_{51}), (b) = covariance between flowering adult reproduction and vegetative adult growth (α_{45}), and (c) = covariance between flowering adult reproduction and flowering adult stasis (α_{55})

Model-generated stable stage distributions (SSD) from the mean transition matrices were significantly different from the observed distributions of above ground stages for *P. macrophylla*, but were very similar for *P. orbiculata* (Table 3). Post hoc analyses revealed that the differences in *P. macrophylla* stage distributions were driven mostly by the juvenile and flowering adult stages. Specifically, the model for *P. macrophylla* predicted a SSD with proportionally fewer flowering adults and more juveniles than were observed in our field data.

3.2 | Interannual population dynamics

Year-to-year variation in population growth ranged from 0.80 to 1.05 and was generally synchronous for the two species (Figure 3). The finite rate of population growth for *P. orbiculata* was significantly below the replacement rate of $\lambda = 1.0$ during five of the eight transition years, whereas *P. macrophylla* differed from the replacement rate only twice. While rates for *P. orbiculata* were almost always lower than for *P. macrophylla* (just one exception), permutation tests examining variation between the two species ($V(\lambda_{perm})$) revealed that population growth was significantly different during only one of the years.

3.3 | LTRE—Species comparison

Results from the LTRE examining the contribution of each life stage transition's variance to the overall variance in population growth rate between the two species revealed that much of $V(\lambda_{sp})$ was due to variance associated

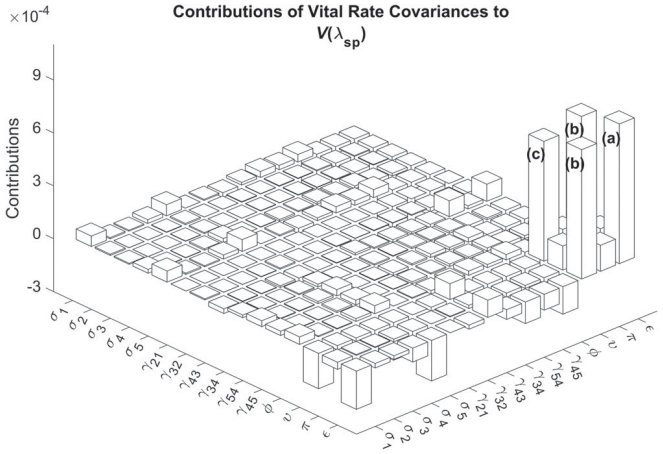

FIGURE 5 The contributions of covariances in lower level vital rates to $V(\lambda_{sp})$ between *Platanthera macrophylla* and *P. orbiculata*. Values in the diagonal are variances and values in the off-diagonal are covariances. Letters identify the most prominent contribution values: (a) = variance in germination into protocorm (ε), (b) = covariance between germination into protocorm and proportion of flowers that set fruit (υ), and (c) = variance in proportion of flowers that set fruit

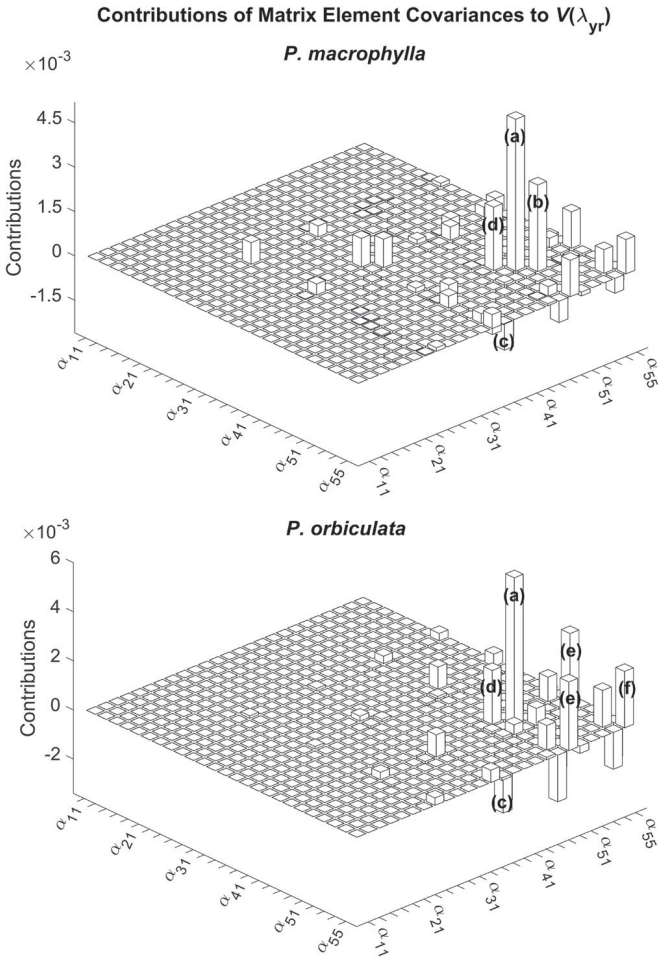

FIGURE 6 The contributions of interannual covariances in matrix elements to $V(\lambda_{year})$ for *Platanthera macrophylla* (top) and *P. orbiculata* (bottom). Values in the diagonal are variances and values in the off-diagonal are covariances. Letters identify the most prominent contribution values: (a) = variance in vegetative adult growth (α_{45}), (b) = variance in flowering adult reproduction (α_{51}), (c) = covariance between vegetative adult stasis (α_{44}) and growth, (d) = variance in vegetative adult stasis, (e) = covariance between vegetative adult growth and flowering adult stasis (α_{55}), (f) = variance in flowering adult stasis

with the flowering adult reproduction stage (Figure 4). Variance in this stage produced the largest single contribution. A negative covariance between flowering adult reproduction with both vegetative adult growth and flowering adult stasis produced the next two largest contributions.

Decomposition of the differences in population growth rate between the two species into contributions by lower-level vital rates revealed that, within the flowering adult reproduction stage, differences in the specific vital rates of fruit set and seed germination contributed most to $V(\lambda_{sp})$ (Figure 5). Just those three contribution values alone—the variances in the two vital rates along with the positive covariance between the two rates—contributed to the majority of variance in λ_{sp}.

3.4 | LTRE—Interannual population dynamics

For both species, the transition of vegetative adult growth into flowering adults contributed the most to their respective interannual variation in population growth rates (Figure 6). Other important contributions to $V(\lambda_{yr})$ for *P. macrophylla* were variances in flowering adult reproduction and vegetative adult stasis, and a negative covariance between vegetative adult stasis and growth. Flowering adult reproduction contributed much less to $V(\lambda_{yr})$ for *P. orbiculata*, but the species experienced a similar trade-off as *P. macrophylla* between vegetative adult stasis and growth. For *P. orbiculata*, interannual differences in flowering adult stasis, and the positive covariance between flowering adult stasis and vegetative adult growth, were more important than for *P. macrophylla*.

Several differences between the two orchids were observed in the contributions of the lower-level vital rates that compose each stage transition to the interannual variation in population growth rates for each species (Figure 7). Variance in the reproductive measure fruit set contributed by far the most to $V(\lambda_{yr})$ for *P. macrophylla*, but much less for *P. orbiculata*. Negative covariances between fruit set and both juvenile survival and vegetative adult survival were also notable for *P. macrophylla*, but not *P. orbiculata*. For *P. orbiculata* it was interannual

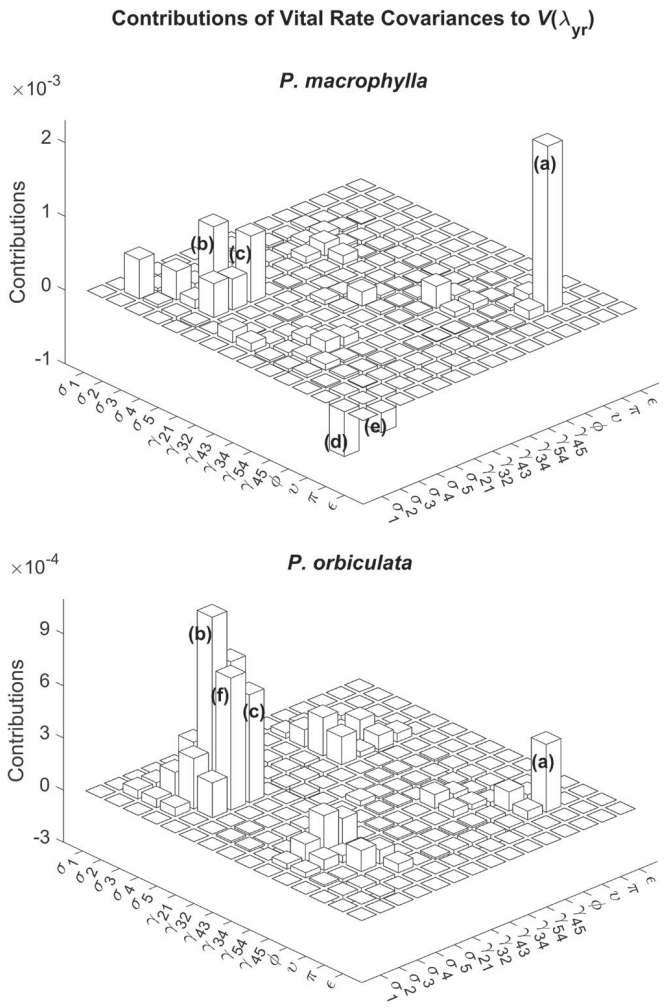

FIGURE 7 The contributions of interannual covariances in vital rates to $V(\lambda_{year})$ for *Platanthera macrophylla* (top) and *P. orbiculata* (bottom). Values in the diagonal are variances and values in the off-diagonal are covariances. Letters identify the most prominent contribution values: (a) = variance in fruit set (π), (b) = variance in vegetative adult survival (σ_4), (c) = variance in flowering adult survival (σ_5), (d) = covariance in fruit set and juvenile survival (σ_2), (e) = covariance in fruit set and vegetative adult survival, (f) = covariance between vegetative and flowering adult survival

differences in survival rates of the two adult stages, and the positive covariance between those two rates, that contributed most to $V(\lambda_{yr})$.

4 | DISCUSSION

Understanding the demographic limitations of co-occurring orchid species where they are common can aid in their conservation in areas of the range where they are in decline (Brundrett, 2019). We hypothesized a key difference between the study species would be the greater flowering of *P. orbiculata*, which we expected to result in a more stable or growing population for this species. To our surprise, the higher fecundity of *P. macrophylla* due to higher rates of fruit set, seed set, and germination appeared to more than compensate for the potential reproductive benefits of higher transition rates between vegetative and flowering adults and greater number of adults that remain flowering in *P. orbiculata*. Instead of an obvious advantage, the differences between the species may highlight different reproductive strategies. This suggests a focus area for future research efforts.

The evolving picture of the two species is one of more specialization in habitat and perhaps pollination for *P. macrophylla* and more generalization for both aspects in *P. orbiculata*. This would agree with previous work in the genus showing that species with longer spurs, *P. macrophylla* in this case, have many fewer and usually one large moth pollinator (Catling & Catling, 1991). Differences in their pollination biology have been little explored, with sphinx moths as suggested pollinators for *P. macrophylla* and looper moths as pollinators for *P. orbiculata* (Argue, 2011). At Hubbard Brook, *P. orbiculata* was visited by a range of generalist pollinators including daytime documentation of ruby-throated hummingbird, lesser carpenter bee, and geranium plume moth (Bergum, Cleavitt, & Matthews, 2018). However, the effectiveness of these pollinators in pollen transfer is unknown. The reproductive differences documented here may be related to specialist (and more efficient) pollination in *P. macrophylla* versus generalist pollination in *P. orbiculata*. The idea that *P. macrophylla* could have a more specialist pollinator relationship is supported by two results here: higher pollination efficiency producing increased fruit set and greater interannual variability. Specialist pollinator relationships have trade-offs of more efficient pollen transfer, but greater susceptibility to any factors impacting the specialist insect creating good pollination years when insect and plant phenology and abundance aligns and bad years when they do not (Brundrett, 2019; Harder & Johnson, 2008).

Our second hypothesis pertained to limitation of the orchids during the initial belowground stage as protocorms as a suspected bottleneck to population growth. This hypothesis also appeared more complicated with greater application to *P. macrophylla* than *P. orbiculata*. The elasticity analyses indicated that the population growth rate for both orchids was most sensitive to changes in adult life history transitions and least sensitive to changes in fecundity and recruitment of protocorms and juveniles. However, a notable difference from the elasticity results above was the finding that *P. macrophylla* fecundity transition (flowering adult to protocorm) had the second-largest LTRE contribution value after the vegetative to flowering adult transition. To

explain this difference, in which LTRE analysis ranked the contribution of the fecundity transition more highly than in the elasticity analysis, it is necessary to keep in mind the distinction between elasticity and LTRE analyses. Elasticity is a type of perturbation analysis that examines how much population growth *would change* if matrix entries were changed, whereas LTRE analysis examines how much λ *did change* based on the observed variation in the matrix entries (Caswell, 2001; Esparza-Olguín et al., 2005; Horvitz, Schemske, & Caswell, 1997; Jongejans & De Kroon, 2005). What this means for our analyses is that although the fecundity transition from seed to protocorm had a low elasticity, the year-to-year variation in that rate for *P. macrophylla* was sufficiently large as to contribute substantially to the interannual variation in population growth rate. This makes sense mathematically given that contribution values are calculated as a function of both a given transition element's sensitivity and its covariance (Caswell, 2001). Even with a relatively small sensitivity, the fecundity transition may produce a large contribution value so long as its variance were sufficiently large, which is the case for *P. macrophylla*. Therefore, a bottleneck in the recruitment into the underground protocorm stage seems most possible for *P. macrophylla*.

4.1 | Population projections

Projected population growth rates did not differ significantly between the two species, both of which had finite rates of increase just below the replacement rate of 1. Our finding of growth rates near stasis, or slightly below, for these two *Platanthera* orchids appears to be typical for terrestrial orchids based on a recent review by Shefferson, Jacquemyn, Kull, and Hutchings (2020) that reported a mean population growth rate of 0.983 from a data set of 180 populations of 73 species. Although we found no significant difference between the two species, the average projected rate of growth for *P. orbiculata* was sufficiently lower than for *P. macrophylla* so as to be significantly less than the replacement rate ($\lambda = 1$). The average projection of approximately a 6% annual population decline for *P. orbiculata* was reflected in a pattern of interannual variation where most years were in population decline, a few were at stasis, and none were positively growing (i.e., λ significantly greater than 1). Although the population status of *P. macrophylla* appeared somewhat more optimistic, in that its pattern of interannual variation showed a population at stasis for most years, it was notable that even the species best years failed to produce growth that was significantly greater than the replacement rate. Such a pattern suggests that *P. macrophylla* may persist so long as conditions remain the same; however, the species may be unable to recover from disturbances by significantly increasing population growth.

Our elasticity analysis indicates that both species would be very sensitive to changes in adult transition rates, but especially *P. orbiculata* in which adult transitions contributed to over three-quarters of the total elasticity. These results are consistent with Silvertown, Franco, Pisanty, and Mendoza (1993) that observed that population growth in iteroparous forest herbs was characterized by a notably low fecundity elasticity. They also support the observation that long-lived perennial plants are generally more sensitive to survival than reproductive rates (Burns et al., 2010; Franco & Silvertown, 2004).

As with all models, these projections come with the caveat that they are not necessarily forecasts of what will happen, but rather projections of what would happen if current conditions are maintained. Nevertheless, there are good reasons to trust the reliability of these models. The transition matrices were parameterized with a robust set of data that spanned nearly a decade and were based on a very large sample of over 1,000 orchids. The accuracy of projections for *P. orbiculata* was also supported by the fact that the observed population structure very closely matched the model's projected SSD. As reviewed by Williams, Ellis, Bricker, Brodie, and Parsons (2011), one can expect a population to behave more similarly to its asymptotic dynamics if it is close to its asymptotic SSD. SSD for *P. macrophylla* less closely matched observed stage distributions, which may mean that near-term transient dynamics will be different from the asymptotic population projections and should be interpreted with caution (Caswell, 2007; Williams et al., 2011). In addition, the under-representation of *P. macrophylla* juveniles in our database suggests we are either missing more individuals and/or that they have higher mortality than for *P. orbiculata*. In particular, the plankton netting of the seed packets may protect the protocorms from mortality that they experience normally. Another possibility given the slightly higher tendency for *P. macrophylla* to skip life stages (Table S3), would be that some individuals first appear as stage 2 with one-round leaf and skip the juvenile (one linear leaf) stage all together. Further investigation of protocorm and juvenile stage transitions for *P. macrophylla* will be a future research priority.

4.2 | LTRE—Species comparison

Life-table response experiments comparing the mean transition matrices for the two orchids reveal that

differences in fecundity (flowering adult to protocorm transition) most contributed to the difference in population growth between the two species. The importance of this stage transition is consistent with the fact that the fecundity transition for *P. macrophylla* was more than five times greater than for *P. orbiculata*. More specifically, this difference in fecundity was driven almost entirely by variation between the two orchids in the vital rates of fruit set and seed germination into protocorm (and the positive covariance between those). To underscore this difference, the greater fecundity of *P. macrophylla* is apparent in a number of other metrics summarized in the fecundity results (Table 1): taller flowering spikes, greater fruit set that develops into more viable capsules, lower capsule predation, and most significantly, much greater rates of seed germination into protocorms.

This finding that *P. macrophylla*'s greater fecundity is most responsible for the species improved population growth rate is interesting given that, at first glance, *P. orbiculata* appeared to have the key demographic advantages in terms of greater rates of vegetative adults growing to flowering adults and lower rates of flowering adults regressing to vegetative adults. This difference manifests in the contributions as negative covariances between the two vegetative-flowering adult transitions (growth and regression) and fecundity. And while these differences did contribute to variation in the population growth rates between the two orchids, the effect was many times smaller than the impact of fecundity values. In other words, the population growth rate of *P. orbiculata* is lower because its modest benefit of having improved adult transition rates is dwarfed by the much greater demographic advantage of *P. macrophylla* in terms of fecundity. This again supports the observations discussed above that fecundity measures have been undervalued relative to adult transitions in driving the population dynamics of long-lived perennial plants (Clark, Poulsen, Levey, & Osenberg, 2007; Jacquemyn et al., 2010; Poulsen, Osenberg, Clark, Levey, & Bolker, 2007) and the relative importance of these measures may correspond to real differences in reproduction strategies.

4.3 | LTRE—Interannual variation

Population projections for transition years from 2011 to 2019 reveal a dynamic pattern of interannual variation that is generally synchronous for the two species. This raises the question as to what is driving the observed year-to-year variation in these orchids. Consistent with elasticity results showing the importance of adult life-stage transitions, contributions of matrix elements to interannual variation in population growth for both species were largely driven by year-to-year variation in adult transition rates, particularly with respect to flowering and reproduction. The highest contributions to interannual variation all came from matrix elements associated with either flowering or reproduction: vegetative to flowering adult growth (both species), flowering adult fecundity (*P. macrophylla*), and flowering adult stasis and its positive covariance with vegetative adult growth (*P. orbiculata*). Two observed events contributed to the interannual variation: (a) an extreme mortality event seemingly related to a fungal pathogen in early spring of 2012, and (b) increased loss of adults, particularly flowering adults to herbivory by white-tailed deer in 2016 to the present. The middle years of the study (2014–2016) appear to represent the most stable period after recovery from the 2012 mortality and prior to increased mortality from deer herbivory (Figure 3).

Extending the LTRE analysis of both orchids by decomposing the life history transitions into contribution values for each vital rate provided more precision as to what was driving the observed interannual variation. For both orchids it was adult survival, more so than growth (or regression), that contributed most to interannual variation in population growth rates. Within the fecundity transition it was variation in fruit set rather than flower number that contributed the most. Variation in fruit set appears to be a particularly important determinant of population growth for *P. macrophylla*, as fruit set had the highest contribution value of any of the vital rates. Interestingly for *P. macrophylla*, we observed a negative covariance between fruit set and survival rates for juveniles and vegetative adults, suggesting that years with environmental conditions that are most favorable for pollination and fruit set are difficult for those other stages in the life cycle. More years of demographic data will help resolve whether this relationship is spurious or meaningful. The two lowest years of fruit set, 2012 and 2017, for *P. macrophylla* were associated with the increased mortality by fungal pathogen in 2012 and by deer herbivory in 2017, but how these events might relate to juvenile and vegetative adult survival is not clear.

As mentioned above, identifying that the survival of adults most impacts the interannual population dynamics of these orchids was perhaps to be expected, given that they are relatively long-lived iteroparous forest herbs. What was unexpected was the relative importance of fecundity, namely fruit set, in driving the population dynamics of these two orchids. Despite the clear importance of the adult stages of perennial plants, evidence is accumulating that seed production and seedling recruitment play a more important role than previous thought in these plant populations. Meta-analyses by Clark

et al. (2007) and Poulsen et al. (2007) documented that most plant populations, including long-lived perennials, are seed limited by showing that seedling recruitment nearly always increases with a supplemental addition of seeds. An example most similar to our study was documented in Jacquemyn et al. (2010) that showed seed limitation restricting population growth in the terrestrial woodland orchid *Orchis pupurea*. Our finding of the relative importance of fruit set in driving year-to-year population dynamics in *P. macrophylla* and *P. orbiculata* is consistent with these seed limitation studies, and it provides a warning of the negative population impacts that could come from disturbances to the orchid's flowering and fruiting stages (e.g., deer herbivory on flowering spikes discussed in Section 4.4).

4.4 | Conservation implications and future research

Based on an initial examination of elasticities and contribution values from LTRE analyses, it would appear that conservation efforts should focus on the survival of adult orchids. While an increase in adult survival would help ensure population persistence by keeping growth near the replacement rate of $\lambda = 1$, there are reasons why this stage transition might not be the most important focus for conservation. First, the mortality of adult stages is already quite low for both species (mean matrices range = 7–12%), leaving little room for potential improvement in those rates. Second, annual adult mortality rates are mostly consistent from year-to-year, which suggests that they are fairly insensitive to environmental changes, and presumably would be insensitive to conservation efforts to improve those rates. This recommendation is not to suggest that adult survival is unimportant; a reduction in those rates would certainly have a significant negative impact on population growth. Rather, it is a recognition that those rates are currently healthy and stable, and not a likely conservation priority.

Adult fecundity parameters appear to be a more useful stage to focus attention. Although the elasticity values for fecundity were relatively low, the very large variation observed in fecundity values resulted in contribution values that accounted for a large portion of the variance in population growth rates. This was particularly the case where variation in fruit set was a lead driver of interannual variation for *P. macrophylla*, and seed germination was a lead driver of variation between the two orchid species.

This observation that a life-history stage transition with low elasticity could still be an important driver of population dynamics illustrates the need to take care when interpreting elasticities for conservation applications. Elasticities indicate the relative sensitivity of population growth to small changes in a particular life history transition, but they do not indicate how sensitive a life history transition is to environmental perturbation (Silvertown, Franco, & Menges, 1996). Therefore, a life history transition that has a small elasticity, but has a very large amount of variation, may have a greater potential effect on population growth than a life history transition with a large elasticity, but a relatively small range of variation. This appears to be the current dynamic with these orchids, where the larger magnitude of variation in the fecundity parameters produced a bigger impact on population growth than the more consistent adult survival, which had a much larger elasticity.

Given the important role of fecundity in the population dynamics of these orchids, any environmental changes or disturbances that impact seed production or seedling recruitment will inordinately impact their populations. Predicted decreases in winter snowpack could be a double-edged sword by extending the winter range and seasonal foraging range of white-tailed deer and by potentially decreasing the survival of seedlings in the organic layer of the soil which would freeze more often (Groffman et al., 2012). Seedling recruitment remains a difficult and understudied aspect of orchid biology (Rasmussen & Whigham, 1998; Shefferson et al., 2020). Although seed packets can provide germination rates, we are still struggling for a method that allows the germinants to develop fully to above ground individuals in the field, a process that we estimate takes 3–4 years in these round-leaved orchids. Future research will focus on the impact of white-tailed deer herbivory in our populations with some caging of flowering adults and snowpack manipulation over seed packets. Given the significant inverse relationship between deer abundance and orchid numbers documented in a decades-long study by Knapp and Wiegand (2014), we anticipate significant negative effects of the increased deer activity on the orchids at HBEF. We also seek to explore the pollination biology of these orchids to test the hypothesis put forth here that *P. macrophylla* is more specialized than *P. orbiculata*, which would make the former species more vulnerable to pollinator disruption from climate change. The risk of climate-induced asynchrony between flowering and pollinator flight phenology is greater for specialist orchids in that they attract a much more narrow range of pollinators (e.g., Robbirt et al., 2014).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

REFERENCES

Argue, C. L. (2011). *The pollination biology of North American orchids: Volume 1: North of Florida and Mexico*. Berlin, Germany: Springer Science & Business Media.

Bailey, A. S. (2003). *Hydrometeorological database for Hubbard Brook Experimental Forest, 1955–2000*. Newtown Square, PA: US Department of Agriculture, Forest Service, Northeastern Research Station.

Bailey, S. W., Brousseau, P. A., Mcguire, K. J., & Ross, D. S. (2014). Influence of landscape position and transient water table on soil development and carbon distribution in a steep, headwater catchment. *Geoderma*, *226*, 279–289.

Bergum, M., Cleavitt, N., & Matthews, D. (2018). An unexpected visitor. *Frontiers in Ecology and the Environment*, *16*, 502–502. https://doi.org/10.1002/fee.1968

Bronstein, J. L., Armbruster, W. S., & Thompson, J. N. (2014). Understanding evolution and the complexity of species interactions using orchids as a model system. *New Phytologist*, *202*, 373–375.

Brundrett, M. C. (2019). A comprehensive study of orchid seed production relative to pollination traits, plant density and climate in an urban reserve in Western Australia. *Diversity*, *11*, 123.

Burns, J. H., Blomberg, S. P., Crone, E. E., Ehrlen, J., Knight, T. M., Pichancourt, J. B., ... Buckley, Y. M. (2010). Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. *Journal of Ecology*, *98*, 334–344.

Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation*. Sunderland, MA: Sinauer Associates.

Caswell, H. (2007). Sensitivity analysis of transient population dynamics. *Ecology Letters*, *10*, 1–15.

Caswell, H. (2010). Life table response experiment analysis of the stochastic growth rate. *Journal of Ecology*, *98*, 324–333.

Catling, P. M., & Catling, V. R. (1991). A synopsis of breeding systems and pollination in North American orchids. *Lindleyana*, *6*, 187–210.

Clark, C., Poulsen, J., Levey, D., & Osenberg, C. (2007). Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist*, *170*, 128–142.

Clark, J. S., Silman, M., Kern, R., Macklin, E., & Hillerislambers, J. (1999). Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology*, *80*, 1475–1494.

Cleavitt, N. L., Berry, E. J., Hautaniemi, J., & Fahey, T. J. (2016). Life stages, demographic rates, and leaf damage for the round-leaved orchids, *Platanthera orbiculata* (Pursh.) Lindley and *P. macrophylla* (Goldie) P.M. Brown in a northern hardwood forest in New Hampshire, USA. *Botany*, *95*, 61–71. https://doi.org/10.1139/cjb-2016-0164

Currah, R., Smreciu, E., & Hambleton, S. (1990). Mycorrhizae and mycorrhizal fungi of boreal species of *Platanthera* and *Coeloglossum* (Orchidaceae). *Canadian Journal of Botany*, *68*, 1171–1181.

Esparza-Olguín, L., Valverde, T., & Mandujano, M. C. (2005). Comparative demographic analysis of three *Neobuxbaumia* species (Cactaceae) with differing degree of rarity. *Population Ecology*, *47*, 229–245.

Fay, M. F., & Chase, M. W. (2009). Orchid biology: From Linnaeus via Darwin to the 21st century. *Annals of Botany*, *104*, 359–364. https://doi.org/10.1093/aob/mcp190

Fay, M. F., Pailler, T., & Dixon, K. W. (2015). Orchid conservation: Making the links. *Annals of Botany*, *116*, 377–379. https://doi.org/10.1093/aob/mcv142

Fernald, M. L. (1950). *Gray's manual of botany*, (corrected printing, 1970) (Vol. 1632, p. 1.0). New York, NY: Van Nostrand Company.

Franco, M., & Silvertown, J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology*, *85*, 531–538.

Gonneau, C., Jersáková, J., De Tredern, E., Till-Bottraud, I., Saarinen, K., Sauve, M., ... Selosse, M. A. (2014). Photosynthesis in perennial mixotrophic *Epipactis* spp.(Orchidaceae) contributes more to shoot and fruit biomass than to hypogeous survival. *Journal of Ecology*, *102*, 1183–1194.

Groffman, P. M., Rustad, L. E., Templer, P. H., Campbell, J. L., Christenson, L. M., Lany, N. K., ... Wilson, G. F. (2012). Long-term integrated studies show complex and surprising effects of climate change in the northern hardwood forest. *Bioscience*, *62*, 1056–1066.

Harder, L. D., & Johnson, S. D. (2008). Function and evolution of aggregated pollen in angiosperms. *International Journal of Plant Sciences*, *169*, 59–78.

Horvitz, C., Schemske, D. W., & Caswell, H. (1997). The relative "importance" of life-history stages to population growth: Prospective and retrospective analyses. In *Structured-population models in marine, terrestrial, and freshwater systems* (pp. 247–271). Boston, MA: Springer.

Jacquemyn, H., Brys, R., & Jongejans, E. (2010). Seed limitation restricts population growth in shaded populations of a perennial woodland orchid. *Ecology*, *91*, 119–129.

Jiménez-Sierra, C., Mandujano, M. C., & Eguiarte, L. E. (2007). Are populations of the candy barrel cactus (*Echinocactus platyacanthus*) in the desert of Tehuacán, Mexico at risk? Population projection matrix and life table response analysis. *Biological Conservation*, *135*, 278–292.

Jongejans, E., & De Kroon, H. (2005). Space versus time variation in the population dynamics of three co-occurring perennial herbs. *Journal of Ecology*, *93*, 681–692.

Knapp, W. M., & Wiegand, R. (2014). Orchid (Orchidaceae) decline in the Catoctin Mountains, Frederick County, Maryland as documented by a long-term dataset. *Biodiversity and Conservation*, *23*, 1965–1976. https://doi.org/10.1007/s10531-014-0698-2

Lallemand, F., Logacheva, M., Le Clainche, I., Bérard, A., Zheleznaia, E., May, M., ... Selosse, M.-A. (2019). Thirteen new

plastid genomes from mixotrophic and autotrophic species provide insights into heterotrophy evolution in Neottieae orchids. *Genome Biology and Evolution*, *11*, 2457–2467.

Martínez, A. F., Medina, G. I. M., Golubov, J., Montana, C., & Mandujano, M. C. (2010). Demography of an endangered endemic rupicolous cactus. *Plant Ecology*, *210*, 53–66.

NatureServe (2015). *NatureServe Explorer: An online encyclopedia of life*. (Version 7.1). Retrieved from http://explorer.natureserve.org

Poulsen, J., Osenberg, C., Clark, C., Levey, D., & Bolker, B. (2007). Plants as reef fish: Fitting the functional form of seedling recruitment. *The American Naturalist*, *170*, 167–183.

Rasmussen, H. N., Dixon, K. W., Jersáková, J., & Těšitelová, T. (2015). Germination and seedling establishment in orchids: A complex of requirements. *Annals of Botany*, *116*, 391–402. https://doi.org/10.1093/aob/mcv087

Rasmussen, H. N., & Whigham, D. F. (1998). The underground phase: A special challenge in studies of terrestrial orchid populations. *Botanical Journal of the Linnean Society*, *126*, 49–64.

Raventós, J., González, E., Mújica, E., & Doak, D. F. (2015). Population viability analysis of the epiphytic ghost orchid (*Dendrophylax lindenii*) in Cuba. *Biotropica*, *47*, 179–189.

Reddoch, A. H., & Reddoch, J. M. (1993). The species pair *Platanthera orbiculata* and *P. macrophylla* (Orchidaceae): Taxonomy, morphology, distributions and habitats. *Lindleyana*, *8*, 171–187.

Reddoch, J. M., & Reddoch, A. H. (1997). The orchids in the Ottawa District: Floristics, phytogeography, population studies and historical review. *Canadian Field-Naturalist*, *111*, 1–185.

Robbirt, K. M., Roberts, D. L., Hutchings, M. J., & Davy, A. J. (2014). Potential disruption of pollination in a sexually deceptive orchid by climatic change. *Current Biology*, *24*, 2845–2849.

Salguero-Gómez, R., & De Kroon, H. (2010). Matrix projection models meet variation in the real world. *Journal of Ecology*, *98*, 250–254.

Scheiner, S. M., & Gurevitch, J. C. (1993). *Design and analysis of ecological experiments*. New York, NY: Chapman and Hall.

Schweiger, J. M. I., Bidartondo, M. I., & Gebauer, G. (2018). Stable isotope signatures of underground seedlings reveal the organic matter gained by adult orchids from mycorrhizal fungi. *Functional Ecology*, *32*, 870–881.

Shefferson, R. P., Jacquemyn, H., Kull, T., & Hutchings, M. J. (2020). The demography of terrestrial orchids: Life history, population dynamics and conservation. *Botanical Journal of the Linnean Society*, *192*, 315–332.

Sheviak, C. J. (2003). *Platanthera. In Flora of North America North of Mexico*. (Eds. 1993+). Retrieved from http://beta.floranorthamerica.org/Platanthera

Silvertown, J., Franco, M., & Menges, E. (1996). Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology*, *10*, 591–597.

Silvertown, J., Franco, M., Pisanty, I., & Mendoza, A. (1993). Comparative plant demography—Relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology*, *81*, 465–476. https://doi.org/10.2307/2261525

Swarts, N., & Dixon, K. W. (2017). *Conservation methods for terrestrial orchids*. Plantation, FL: J. Ross Publishing.

Ureta, C., & Martorell, C. (2009). Identifying the impacts of chronic anthropogenic disturbance on two threatened cacti to provide guidelines for population-dynamics restoration. *Biological Conservation*, *142*, 1992–2001.

USDA-NRCS. (2015). *The PLANTS Database*. Retrieved from http://plants.usda.gov

Van Doorn, N. S., Battles, J. J., Fahey, T. J., Siccama, T. G., & Schwarz, P. A. (2011). Links between biomass and tree demography in a northern hardwood forest: A decade of stability and change in Hubbard Brook Valley, New Hampshire. *Canadian Journal of Forest Research*, *41*, 1369–1379.

Williams, J. L., Ellis, M. M., Bricker, M. C., Brodie, J. F., & Parsons, E. W. (2011). Distance to stable stage distribution in plant populations and implications for near-term population projections. *Journal of Ecology*, *99*, 1171–1178.

Zelmer, C. D., Cuthbertson, L., & Currah, R. S. (1996). Fungi associated with terrestrial orchid mycorrhizas, seeds and protocorms. *Mycoscience*, *37*, 439–448.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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