

ORIGINAL ARTICLE

Sheltered from the storm? Population viability analysis of a rare endemic under periodic catastrophe regimes

Benjamin J. Crain¹ | Raymond L. Tremblay^{1,2} | Jake M. Ferguson^{3,4}

¹Department of Biology, University of Puerto Rico-Río Piedras, San Juan, Puerto Rico

²Center for Applied Tropical Ecology and Conservation, Department of Biology, University of Puerto Rico-Río Piedras, San Juan, Puerto Rico

³NIMBioS, University of Tennessee-Knoxville, Knoxville, Tennessee

⁴Fisheries, Wildlife & Conservation Biology, University of Minnesota, St. Paul, Minnesota

Correspondence

Benjamin J. Crain, Department of Biology, University of Puerto Rico-Río Piedras, PO Box 23360, San Juan, PR 00936-3360.
Email: bcrainium@yahoo.com

Present address

Benjamin J. Crain, North American Orchid Conservation Center, Smithsonian Environmental Research Center, 647 Contees Wharf Rd., Edgewater, MD 21037.
Email: bcrainium@yahoo.com

Funding information

Decanato de Estudios Graduados e Investigación; Círculo de Amigos de Orquidistas de Puerto Rico

Abstract

Rare species are important targets for biodiversity conservation efforts because rarity often equates to small populations and increased endangerment. Rare species are prone to stochastic extinction events and may be particularly susceptible to catastrophes. Therefore, understanding how rare species respond to disturbances is critical for evaluating extinction risk and guiding conservation managers. Population viability analyses (PVAs) are essential for assessing rare species' status yet they seldom consider catastrophic events. Accordingly, we present a PVA of a rare tropical epiphyte, *Lepanthes caritensis* (Orchidaceae), under simulated disturbance regimes to evaluate its demographics and extinction risk. We aimed to test how demographic models incorporating catastrophes affect population viability estimates. Our goal was to better guide management of these orchids and other rare plants. Results revealed *L. caritensis* numbers have declined recently, but projected growth rates indicated that most subpopulations should increase in size if undisturbed. Still, projection models show that moderate catastrophes reduce growth rates, increase stochasticity in subpopulation sizes, and elevate extinction risk. Severe catastrophes had a more pronounced effect in simulations; growth rates fell below replacement level, there was greater variation in projected population sizes, and extinction risk was significantly higher. PVAs incorporating periodic catastrophes indicate that rare species may have greater extinction probabilities than standard models suggest. Thus, precautionary conservation measures should be taken in disturbance prone settings and we encourage careful monitoring after environmental catastrophes. Future rare plant PVAs should incorporate catastrophes and aim to determine if rescue and reintroduction efforts are necessary after disturbances to insure long-term population viability.

KEYWORDS

hurricane, *Lepanthes caritensis* (Orchidaceae), plant conservation, Puerto Rico, species extinction, tropical orchid

1 | INTRODUCTION

Rare and endangered species can be highly vulnerable to extinction because their restricted geographic distributions and limited population sizes can increase the risk of stochastic extinction and susceptibility to a number of threats including catastrophic environmental disturbances such as storms, floods, fires, volcanic eruptions, and anthropogenic

impacts (Gaston, 2003; Lawrence & Ripple, 2000; Mace & Lande, 1991; Matthies, Bräuer, Maibom, & Tschardtke, 2004; Morris & Doak, 2002; Nowacki & Abrams, 2008; O'Brien, Hayden, & Shugart, 1992; Raventós, González, Mújica, & Doak, 2015; Van Der Nat, Tockner, Edwards, Ward, & Gurnell, 2003). Still, some rare species have persisted as small populations for long periods of time and successfully adapted to dynamic environments (Coates, Lunt, &

Tremblay, 2006; Dennis, Munholland, & Scott, 1991; Glitzenstein, Platt, & Streng, 1995; Lande, 1993; Mace & Lande, 1991; Matthies et al., 2004; Menges, 1990; Pascarella, 1998). Thus, evaluating rare species' ability to persist in dynamic environments that are subjected to catastrophic events is an important task for ecologists and conservation biologists alike.

Population viability analyses are an effective analytical tool for quantifying extinction probabilities of rare and endangered species under various environmental scenarios (Caswell, 2001; Coates et al., 2006; Coates & Duncan, 2009; Dixon & Cook, 1989; Morris & Doak, 2002; Raventós, González, Mújica, & Doak, 2015; Schemske et al., 1994). These analyses, which are aimed at understanding and forecasting demographic dynamics through time, are critical for identifying appropriate conservation strategies to prevent population declines in rare species (Coates et al., 2006; Coates & Duncan, 2009; Jacquemyn, Brys, Hermy, & Willems, 2007; Sletvold, Øien, & Moen, 2010; Tremblay & Hutchings, 2002). At the same time, demographic transition data for rare species are often limited in availability due to costs and logistic constraints associated with long-term demographic studies (Doak, Gross, & Morris, 2005; Schödelbauerová, Tremblay, & Kindlmann, 2010). Furthermore, many population viability analyses of rare species do not incorporate the effects of catastrophic events in their models and thus they may over- or under-estimate extinction risks (Coulson, Mace, Hudson, & Possingham, 2001; Dennis et al., 1991; McClaran & Sundt, 1992; Newton, Massatti, Thorpe, & Kaye, 2010; Pascarella & Horvitz, 1998; Raventós, González, Mújica, & Doak, 2015). Fortunately, advances in matrix modeling techniques have made it easier to estimate demographic dynamics of rare species while incorporating the effects of catastrophic events (Lande, 1993; Morris, Bloch, Hudgens, Moyle, & Stinchcombe, 2002; Morris & Doak, 2002; Pascarella & Horvitz, 1998; Raventós, González, Mújica, & Doak, 2015; Stubben & Milligan, 2007; Tremblay & McCarthy, 2014).

The Caribbean Islands are among the planet's centers of threatened biodiversity and the region is regularly subjected to environmental catastrophes, namely hurricanes (Dale et al., 2001; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Scatena & Larsen, 1991; Walker, Voltzow, Ackerman, Fernandez, & Fetcher, 1992). Despite periodic hurricanes, the orchid flora of the Caribbean is particularly diverse (Ackerman, 1995, 2014), consisting of a variety of rare and endemic species that occur in dynamic habitats (Boose, Serrano, & Foster, 2004; Raventós, González, Mújica, & Doak, 2015; Rodríguez-Robles, Ackerman, & Meléndez, 1990; Tremblay, 2008). Although limited in number, some studies from the Caribbean show that hurricanes can have adverse effects on orchid populations (Mújica, Raventós, González, & Bonet, 2013; Raventós, González, Mújica, & Bonet, 2015; Raventós, González, Mújica, &

Doak, 2015; Tremblay, 2008; Wiegand, Raventós, Mújica, González, & Bonet, 2013) whereas others suggest that certain species can benefit from hurricane disturbances to varying degrees due to reduced competition and increased accessibility to resources for example (Ackerman & Moya, 1996; Pascarella, 1998; Pascarella & Horvitz, 1998; Wiegand et al., 2013). Accordingly, it is necessary to determine how hurricane disturbances might affect population growth and persistence of rare orchid species in the Caribbean to evaluate their conservation status.

For that reason, we investigated the potential effects of hurricane catastrophes on the population viability and extinction probability of *Lepanthes caritensis* Tremblay and Ackerman (Orchidaceae), a rare Puerto Rican endemic (Crain & Tremblay, 2012; Tremblay & Ackerman, 1993). Accordingly, we had two specific aims: (a) assess the current demographic attributes of *L. caritensis*, including stochastic growth rates (λ_s), stable stage distributions (w), reproductive values (v), elasticity measures, and transfer functions and (b) model this species' population trajectories while accounting for the stochastic effects of catastrophic hurricane events to quantify viability measures through time. These modeling efforts will be useful for gauging the significance of incorporating catastrophes into population viability analyses and they will help determine if rare orchid species such as *L. caritensis* are able to persist in disturbance prone environments. Ultimately, addressing these aims will help to evaluate and improve conservation strategies so that appropriate actions can be taken to ensure the long-term viability of this species.

2 | MATERIALS AND METHODS

2.1 | Study species

L. caritensis is a miniature epiphyte that occurs solely in the mountains of eastern Puerto Rico (Crain & Tremblay, 2012; Tremblay & Ackerman, 1993). Geographically, this species is restricted to only two sites on the island, one in Carite State Forest and the other in El Yunque National Forest (Crain & Tremblay, 2012). The limited distribution of this orchid may be due in part to the fact that it most often occurs on large individuals of Wild Balata, *Micropholis guyanensis* (A. DC.) Pierre, a tree species that was originally used extensively for furniture making and very few of which remain standing on the island (Little, Woodbury, & Wadsworth, 1974; Tremblay et al., 1998).

Previous assessments of *L. caritensis* suggest that the existing populations may be unsustainable based on their demographic trajectories (Crain & Tremblay, 2012; Tremblay, 1997). In addition, this species is subjected to a variety of potentially catastrophic processes, for example, storms, floods, and landslides that could significantly alter its demographics (Tremblay, 2000; Walker, 1991). For example,

tropical storms and hurricanes can thin canopies and increase exposure levels, leading to increased temperatures and light availability as well as decreased humidity levels (Pascarella & Horvitz, 1998; Rodríguez-Robles et al., 1990). These storms, as well as the floods and landslides that are often associated with them, can also lead to the direct loss of host trees beyond the natural mortality rate (Lugo, 2000; Walker, 1991; Walker et al., 1992). Moreover, an updated population viability analysis is warranted for *L. caritensis*, particularly since it has no official conservation status and there is currently no active management strategy for the species despite the fact that it occurs on only 15 trees distributed in two very small areas (Crain & Tremblay, 2012).

2.2 | Population surveys

We focused our surveys on *L. caritensis* subpopulations from the Carite State Forest since previous assessments demonstrated that it was the larger of the two known occurrences and because the second site of occurrence is in a very public area and appears to have been decimated by illegal collection (Crain & Tremblay, 2012). In Carite, we monitored six of the seven known subpopulations, which are defined as all individuals located on a single host tree (Crain & Tremblay, 2012; Rosa-Fuentes & Tremblay, 2007; Tremblay, 1997); one population was inaccessible due to its precarious position on the edge of a steep cliff.

At the same time, we also monitored potential host trees, that is, large individuals of *M. guyanensis* ≥ 20 cm dbh, (Tremblay et al., 1998) for the establishment of new subpopulations. Initially, we identified and tagged all potential host trees ($n = 4$) located within a 5 m radius of the six current host trees. Furthermore, we established 19 additional plots, each of which was 5 m in radius, that were centered on potential *M. guyanensis* host trees located between the current hosts. All potential hosts were less than 1 km from current hosts and most were within 100 m. Again, we monitored each potential host ($n = 36$) within the 5-m radius plots for recruitment of *L. caritensis*. Collectively, our potential host tree surveys included 40 individuals on 25 plots.

During the initial survey of *L. caritensis*, all individuals were tagged and assigned to one of four categorical life stages: (a) seedlings (S), which were minute plants without elongated stems or lepanthiform sheaths, (b) juveniles (J), which were small to full sized plants with at least one sheath surrounding the secondary stem, but with no evidence of reproductive structures, that is, active or persistent dried inflorescences, (c) reproductive adults (RA), that is, those plants with active inflorescences, and (d) nonreproductive adults (NA), which were mature plants with evidence of past reproduction, that is, old inflorescences. Since transitions between these life stages can occur within a very short period of time for *Lepanthes* spp. (Tremblay, Pomales-Hernández, & Mendez-Cintrón, 2006), we conducted surveys on a monthly basis for a period of 2 years. During each

successive survey, we reassessed the life stage of each individual, including fatalities, and tagged new recruits on all trees surveyed.

2.3 | Demographic analysis

We conducted a comprehensive demographic analysis of *L. caritensis* following established protocols (Caswell, 2001; Morris & Doak, 2002) while incorporating new estimation techniques geared toward analysis of rare species (Tremblay & McCarthy, 2014). Based on the life cycle of the species, we constructed life stage transition tables (Lefkovich, 1965) and calculated stasis probabilities (the proportion of individuals in each category remaining in the same category), transition probabilities (the proportion of individuals in each category moving into another), and fertility rates (the number of seedlings produced per flowering individual) for each time period to compile a series of projection matrices for each subpopulation (Figure 1).

Monthly projection matrices were constructed from vital rate models parameterized from the survey data. Because demographic transitions among some categories can be uncommon in rare species, resulting in small sample sizes, we used multilevel models to pool information across months following Tremblay and McCarthy (2014). Multilevel models allow parameters to arise from a common probability distribution. This serves to induce correlations among covariate levels (in this case month), in a manner that depends on the amount of uncertainty present in each level. Thus, the amount of partial pooling of information decreases as the amount and quality of data at each level increases (Gelman, 2006).

Matrix transitions (T) from stage m to stage n include survival (S), growth (G), retrogression (R), and death (Figure 1). These transitions were modeled as

$$\text{logit}(T_{n,m}^{i,j}) = \text{pop}_i + \text{month}_j$$

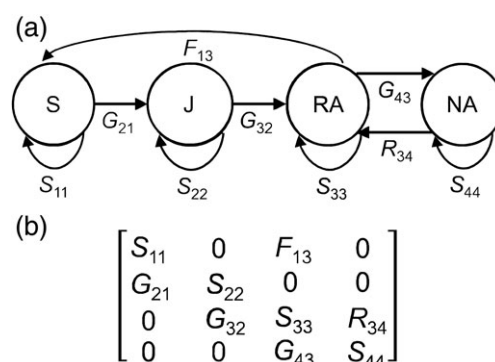


FIGURE 1 (a) Life cycle diagram for *Lepanthes caritensis*. Circles represent individual life stages: (S) seedlings, (J) juveniles, (RA) reproductive adults, (NA) nonreproductive adults. Arrows represent all possible transitions: (S_{nm}) survival, (G_{nm}) growth, (R_{nm}) retrogression, and (F_{nm}) fertility, between each of the four life stages, where m is the initial stage and n is the subsequent stage. (b) Generalized population projection matrix corresponding with the life cycle diagram in Figure 1(a)

where i indexes over the subpopulations, j over the months, and

$$\sum_{n=1}^4 T_{n,m}^{i,j} = 1$$

We assumed that all transitions were drawn from a multinomial distribution. The fixed effect pop_i accounts for differences among subpopulations and $month_j$ is a normally distributed random effect that accounts for monthly variability in the population. Fecundities (F) were similarly modeled as

$$\ln(F_{1,3}^{i,j}) = pop_i + month_j + \text{offset}(\ln(RA_{i,j}))$$

where seedlings are produced by reproductive adults (Figure 1). All fecundities were assumed to follow a Poisson distribution. We also included an offset term in this model to account for the monthly number of reproducing adults in each subpopulation for each month ($RA_{i,j}$). All model parameters were estimated using the Just Another Gibbs Sampler (JAGS) program version 4.3.0 (Plummer, 2003) and monthly projection matrices for each subpopulation were constructed using the mean of the posterior distribution of each estimated parameter (Supporting Information S1).

With each series of projection matrices, we calculated the stochastic growth rate (λ_s) and the log stochastic growth rate ($\ln \lambda_s$) of each subpopulation with Tuljapurkar's analytic approximation method (Tuljapurkar, 1982), which accounts for variation and covariation between matrix elements (Morris & Doak, 2002). We then generated mean matrices for each subpopulation (Figure 2), which were constructed by taking the averages of all stage-specific matrix elements (Morris & Doak, 2002; Zott & Schmidt, 2006). With the mean matrices for each subpopulation we calculated the stable stage distribution (w) and reproductive values of each life stage (v). Lastly, we calculated elasticity matrices and conducted a transfer function analysis on the mean matrices for each subpopulation to quantify the proportional change in the finite growth rates (λ) resulting from infinitesimal proportional changes and perturbations of different magnitudes

on matrix elements (de Kroon, Plaisier, van Groenendaal, & Caswell, 1986; Morris & Doak, 2002; Stott, Hodgson, & Townley, 2012a). Elasticity values can be used to identify the relative importance of individual transitions in terms of population growth. Demographic modeling and the transfer function analysis were performed with the popbio package (Stubben & Milligan, 2007) and the popdemo package (Stott et al., 2012a) for R version 3.0.1 statistical software (R Development Core Team, 2013; Supporting Information S2).

2.4 | Population dynamics and viability modeling

We used the series of monthly transition matrices to project the size of each subpopulation of *L. caritensis* in the Carite State forest over a period of 240 months (20 years). To accomplish this, we used the *stochastic_projection* function in the popbio package (Stubben & Milligan, 2007) and the stage vectors for each subpopulation from our final survey. Because there is a limited amount of space that *L. caritensis* can occupy on a given host tree (Tremblay & Ackerman, 1993; Tremblay et al., 1998), we set the maximum theoretical subpopulation size at 1,000 individuals with the *nmax* argument, given the average size of host trees and assuming that each individual would occupy a space of approximately 10 cm².

To incorporate the stochastic effects of large storms or hurricanes, that is, catastrophes, into the projection models, we created two hypothetical transition matrices for each subpopulation. The first matrix was created to simulate the effects of tropical storms or moderate strength hurricanes, for example, Saffir-Simpson Hurricane Category 1 (Schott et al., 2012). In these matrices, we used values from the mean matrices for each subpopulation but we reduced all transition probabilities (except fecundity) by 50% to simulate the lower survival and growth rates that have been observed in other *Lepanthes* spp. and other orchids when they are exposed to more open conditions as a result of canopy thinning (Boose et al., 2004; Mújica et al., 2013; Rodríguez-Robles et al., 1990; Tremblay, 2008; Tremblay & Salguero-Farías, 2001; Wiegand et al., 2013). Fecundity was not reduced because Tremblay and Salguero-Farías (2001)

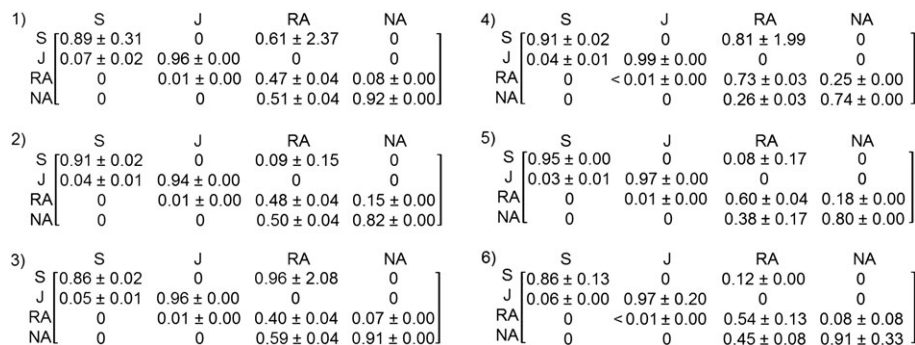


FIGURE 2 Mean transition probability matrices for six subpopulations of *Lepanthes caritensis* in the Carite state Forest calculated from modeled transitions. Data are means \pm SD calculated from the elements of 24 monthly transition matrices for each subpopulation. Life stages are as follows: (S) seedlings, (J) juveniles, (RA) reproductive adults, (NA) nonreproductive adults

documented similar reproductive effort by a closely related species in a forest edge near a clear cut and in an interior forest. Thus, if we assume that conditions after canopy thinning are comparable to those in a forest edge, there is some indication that plants could exhibit similar fecundity values after a disturbance.

The second hypothetical matrix for each subpopulation was created to simulate the effects of more severe hurricanes, for example, Saffir-Simpson Hurricane Categories 2–6 (Schott et al., 2012). In these matrices, we assumed extensive damage as a result of extreme winds, including the loss of host trees as has been observed in other studies (Boose et al., 2004; Lugo, 2000; Rodríguez-Robles et al., 1990; Tremblay, 2000; Walker, 1991), and we reduced all matrix entries except fecundity to zero to simulate conditions when a host tree is felled. Fecundity was not reduced because evidence from a closely related species indicates that individuals on the undersides of downed trees may survive long enough to disperse seeds (Tremblay, 2008). We used the *prob* argument in the *stoch.projection* function (Stubben & Milligan, 2007) to set the probability of selecting a hypothetical catastrophe matrix during projections to approximately one out of every 120 time steps, that is, once every 10 years, which is an approximate estimate of time between storm or hurricane landfalls for Puerto Rico (Boose et al., 2004; O'Brien et al., 1992). We then ran 100,000 population projections for each subpopulation using the monthly transition matrices along with one of the catastrophe matrices. To estimate the overall viability of each of the subpopulations, we used the population projections to quantify cumulative extinction probabilities. For this analysis, we quantified the cumulative proportion of 100,000 iterations in which a sub-population reached a quasi-extinction threshold of less than two individuals, since the species is known to be self-incompatible.

3 | RESULTS

3.1 | Population size

Over the course of our surveys, we monitored the fates of 527 individuals (Figure 3). The initial sum of all individuals from the subpopulations included 364 plants on six host trees with mean subpopulation sizes of 60.7 ($SD = 37.7$) individuals per host. The size of each subpopulation fluctuated throughout the survey period and the final sum of all individuals was 326 with a mean subpopulation size of 54.3 ($SD = 23.4$) individuals. We did not observe establishment of new subpopulations on any of the 40 potential host trees that we monitored.

3.2 | Demographic attributes

For each host tree monitored, we constructed projection matrices (Figure 1; Supporting Information S1) for each of the 24 monthly transitions from our monthly survey data and the mean of each vital rate's posterior distribution (Figure 2). Values of λ_s and $\ln \lambda_s$ were unique to each subpopulation and ranged between 0.9917 and 1.0179 (λ_s) or -0.0036 and 0.0024 ($\ln \lambda_s$), indicating that some subpopulations showed potential for growth, one for decline, and one for stability (Table 1). Overall, however, all values of λ_s were very close to one, suggesting that none of the subpopulations should experience substantial growth or decline in the near future under current stable conditions.

The stable stage distributions (w) obtained from the mean matrices also differed for each subpopulation (Table 2). The expected stable stage distributions in four subpopulations were skewed toward immature plants, that is, seedlings and juveniles, while two were skewed toward adults. Observed stage distributions fluctuated during the course of the study, but only half of the initial stage

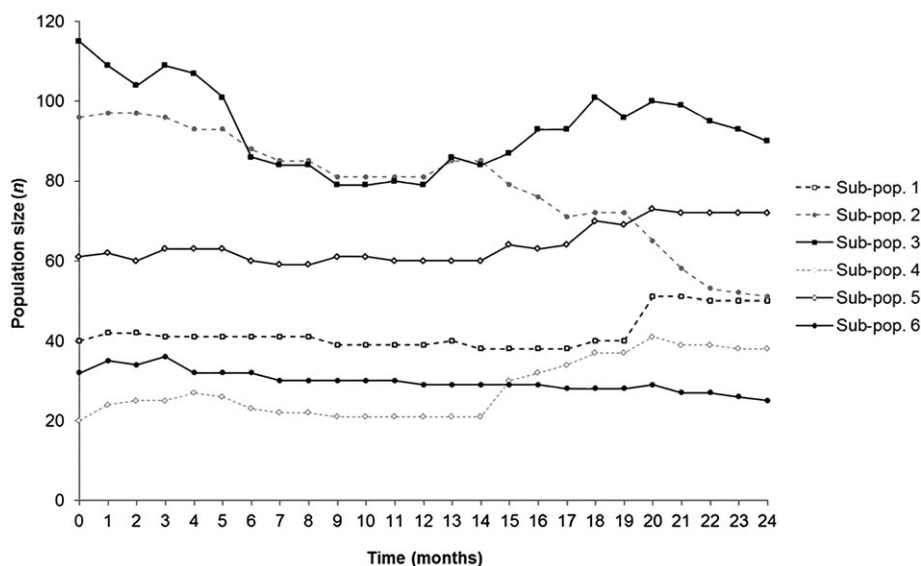


FIGURE 3 Observed sizes (n) of *Lepanthes caritensis* subpopulations in the Carite state Forest between October 2010 and October 2012. Subpopulations one, three, and six were also surveyed previously and correspond with populations one, three, and two, respectively, in Rosa-Fuentes and Tremblay (2007)

TABLE 1 Stochastic growth rates (λ_s , $\ln \lambda_s$) calculated using Tuljapurkar's analytic approximation method for subpopulations of *Lepanthes caritensis* under normal conditions, with moderate catastrophes, and with severe catastrophes. Numbers in parentheses are 95% credible intervals

Subpopulation	λ_s	$\ln \lambda_s$	λ_s (moderate catastrophes)	λ_s (severe catastrophes)
1	1.018 (1.017, 1.019)	0.008 (0.007, 0.008)	1.014 (1.012, 1.015)	1.000 (0.998, 1.001)
2	0.992 (0.991, 0.991)	-0.004 (-0.004, -0.004)	0.987 (0.986, 0.987)	0.971 (0.970, 0.973)
3	1.006 (1.005, 1.006)	0.003 (0.002, 0.003)	1.000 (0.999, 1.001)	0.984 (0.983, 0.986)
4	1.000 (1.000, 1.000)	0.000 (0.000, 0.000)	0.994 (0.994, 0.995)	0.928 (0.920, 0.935)
5	1.005 (1.004, 1.005)	0.002 (0.002, 0.002)	1.000 (1.000, 1.000)	0.991 (0.990, 0.992)
6	1.001 (1.000, 1.001)	0.000 (0.000, 0.000)	0.995 (0.994, 0.995)	0.969 (0.990, 0.971)

TABLE 2 Stable stage distributions (w) and initial observed stage distributions (in parenthesis) of individual subpopulations of *Lepanthes caritensis* in the Carite State Forest

Life stage	Subpopulation 1	Subpopulation 2	Subpopulation 3	Subpopulation 4	Subpopulation 5	Subpopulation 6
Seedlings	0.261 (0.150)	0.190 (0.448)	0.307 (0.374)	0.099 (0.600)	0.275 (0.213)	0.098 (0.375)
Juveniles	0.399 (0.525)	0.196 (0.354)	0.340 (0.374)	0.881 (0.200)	0.264 (0.262)	0.261 (0.313)
Reproductive adults	0.055 (0.050)	0.151 (0.073)	0.047 (0.043)	0.010 (0.100)	0.156 (0.295)	0.102 (0.063)
Nonreproductive adults	0.285 (0.275)	0.463 (0.125)	0.306 (0.209)	0.011 (0.100)	0.304 (0.230)	0.539 (0.250)

TABLE 3 Proportional reproductive values (v) of each life stage of *Lepanthes caritensis* for individual subpopulations in the Carite State Forest

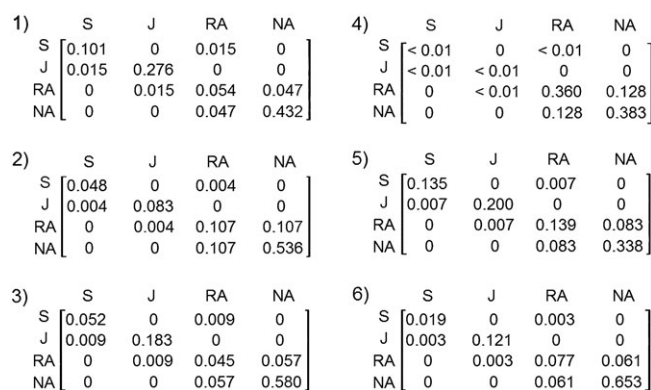
Life stage	Subpopulation 1	Subpopulation 2	Subpopulation 3	Subpopulation 4	Subpopulation 5	Subpopulation 6
Seedlings	0.089	0.076	0.038	<0.001	0.124	0.065
Juveniles	0.147	0.125	0.108	<0.001	0.189	0.140
Reproductive adults	0.423	0.408	0.455	>0.499	0.354	0.407
Non-reproductive adults	0.340	0.391	0.399	>0.499	0.333	0.389

distributions were in accord with the predicted stable stage distributions for each subpopulation. Three populations were skewed toward greater proportions of immature individuals as was predicted by the stable stage distributions. Conversely, the two populations that were predicted to have stable distributions skewed toward adults were initially skewed toward immature plants. Furthermore, one population that was predicted to have a stable distribution skewed toward immature plants was skewed toward adults. Overall, however, the observed distributions and the predicted stable stage distributions indicate that most subpopulations are likely to be dominated by immature plants.

The distribution of the reproductive values of each life stage (v) was somewhat consistent across subpopulations (Table 3). In all cases, the proportional reproductive values were largest for reproductive adults. This was followed closely by nonreproductive adults in each subpopulation. Seedlings had the lowest proportional reproductive value in all subpopulations.

Elasticity values derived from the mean matrices for each subpopulation were also rather consistent (Figure 4). In all cases, the matrix element for nonreproductive adult survival (S_{44}) was by far the highest elasticity value (Figure 4); however, the transfer function analysis also showed that seedling and juvenile survival are nearly as important and that all these survival rates respond much more strongly to positive perturbations than to negative

perturbations (Figure 5). The transitions from seedling to juvenile (G_{21}), from juvenile to reproductive adult (G_{32}), and the fecundity values (F_{13}) were the lowest elasticity values in all subpopulations. There were some differences, however, in elasticity values among subpopulations. In four instances, juvenile survival (S_{22}) had the second largest proportional change in λ , whereas the transitions between reproductive adults and nonreproductive adults (G_{43} and R_{34}) had the second largest value in one subpopulation, and survival of reproductive adults (S_{33}) had the second largest value in another.

**FIGURE 4** Mean elasticity matrices for six subpopulations of *Lepanthes caritensis* in the Carite State Forest. life stages are as follows: (S) seedlings, (J) juveniles, (RA) reproductive adults, (NA) nonreproductive adults

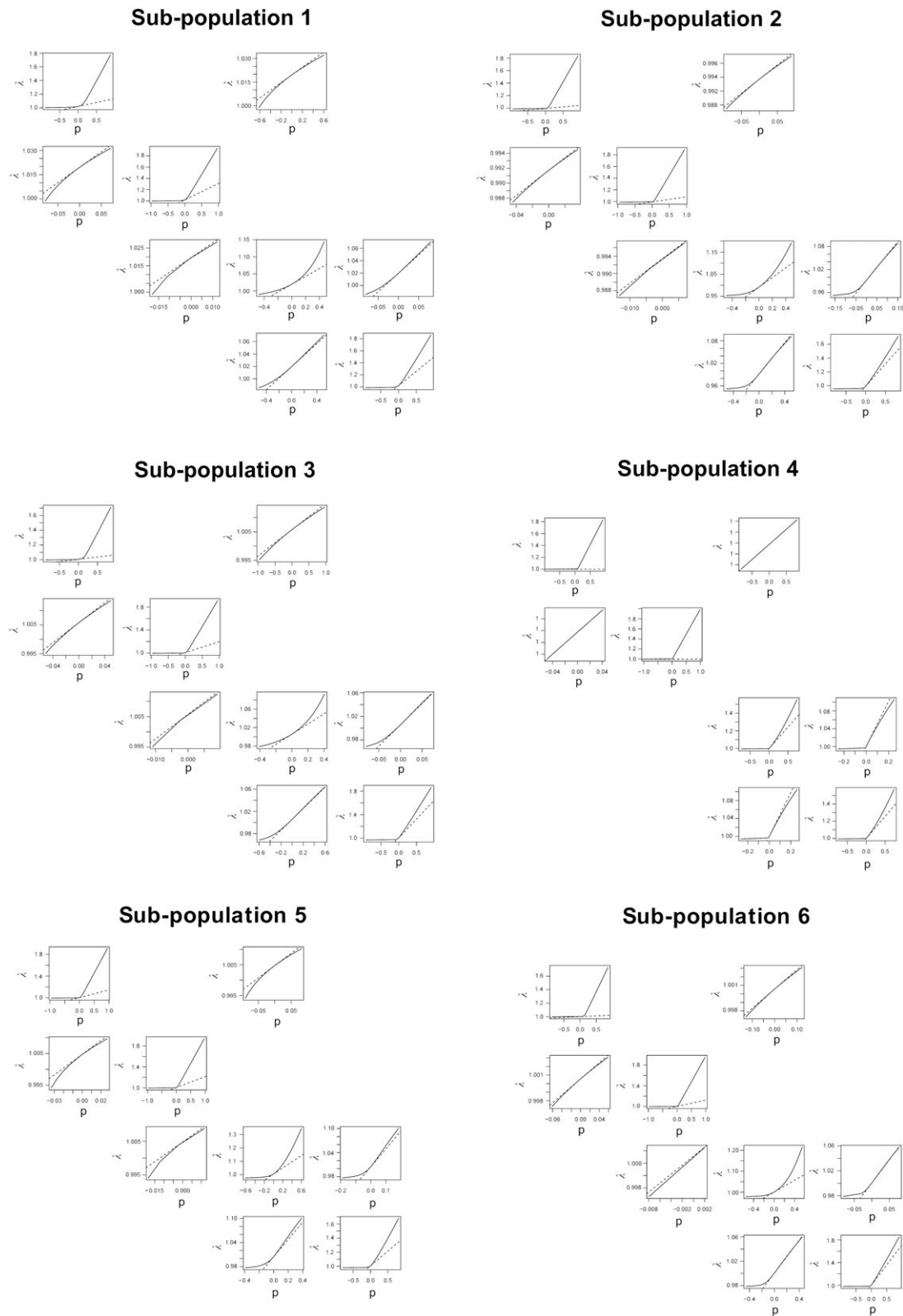


FIGURE 5 Graphical results of transfer function analyses showing the effects of perturbations of different magnitudes to each life stage transition (p) on lambda values (λ) for six subpopulations of *Lepanthes caritensis* in the Carite State Forest. The layout of each multi-plot corresponds with the layout of the population projection matrices. Solid lines are the transfer functions, dashed lines are the sensitivities

3.3 | Population dynamics and viability

The population projections for 240 months (20 years) primarily indicated that the majority of the individual

subpopulations were fairly robust over that time frame although the trajectories of each subpopulation varied from each other (Figure 6). In the projections simulating stable

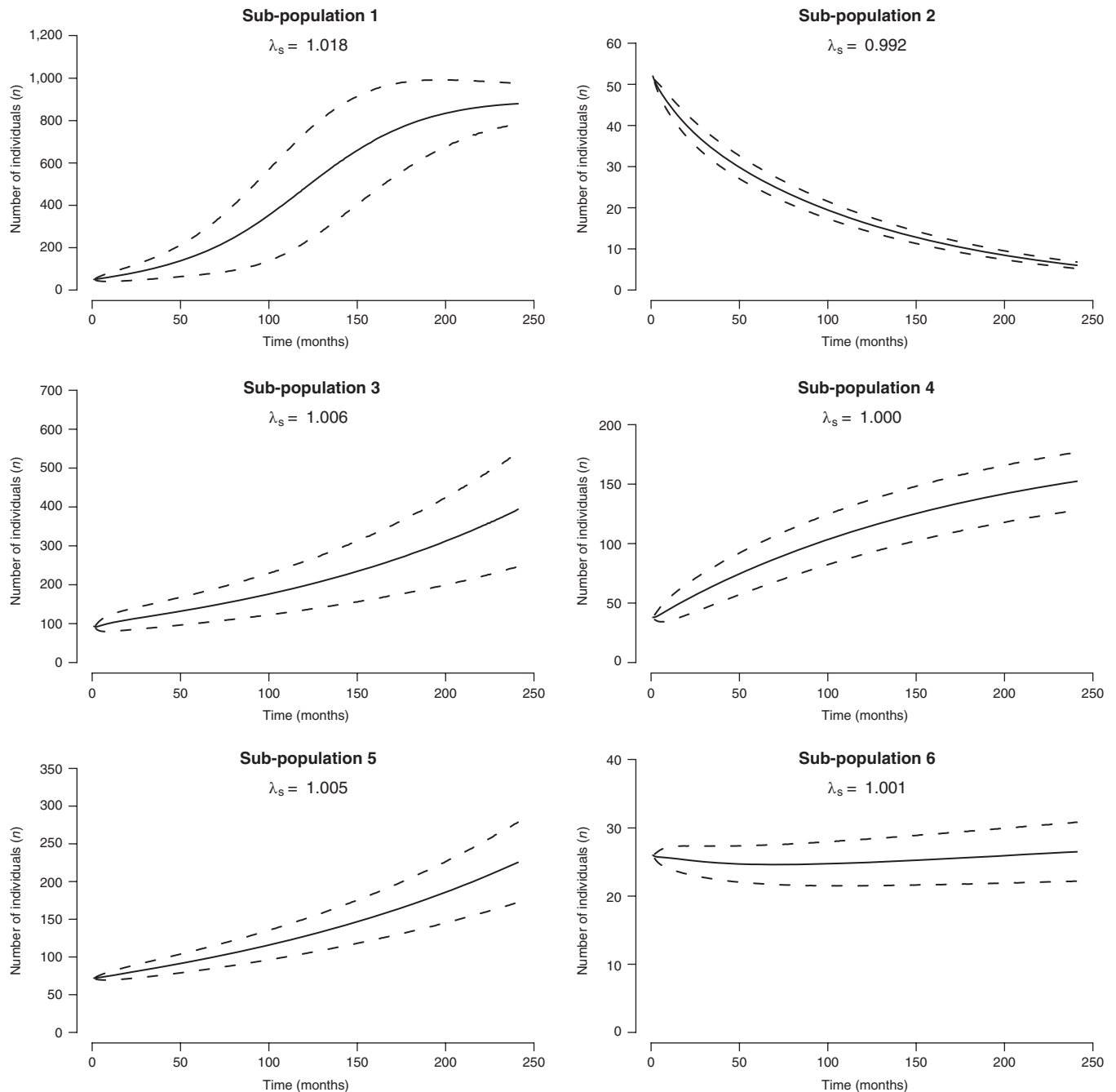


FIGURE 6 Stochastic population projection for subpopulations of *Lepanthes caritensis* in the Carite State Forest under stable conditions. Plotted values are mean subpopulation sizes (solid lines) \pm SDs (dashed lines). Also included are stochastic growth rates (λ_s) for each subpopulation. Note differences in scale bars on y-axis

conditions without catastrophes, four subpopulations were projected to increase in size over the next 20 years. Conversely, one population was projected to decrease in size over that same period. In the last subpopulation, the number of individuals remained virtually the same after 20 years. Collectively, with the exception of subpopulation two, the population trajectories represented growth rates (λ_s) that were greater than one in the stable conditions models (Figure 6; Table 1).

In the projections incorporating moderate strength catastrophes (Figure 7), four subpopulations were again expected

to increase in size over the next 20 years. Final population sizes, however, were substantially smaller for each of those subpopulations as compared to the final sizes observed in the catastrophe free models (Figure 6). Conversely, two subpopulations were projected to decrease in size over the 20-year projection period under moderate strength catastrophe scenarios. In addition, overall growth rates (λ_s) of the subpopulations were smaller than the original estimates when the moderate strength hurricane matrices were included (Table 1). Only two of the subpopulations had a λ_s value equal to or greater than one, indicating that the other

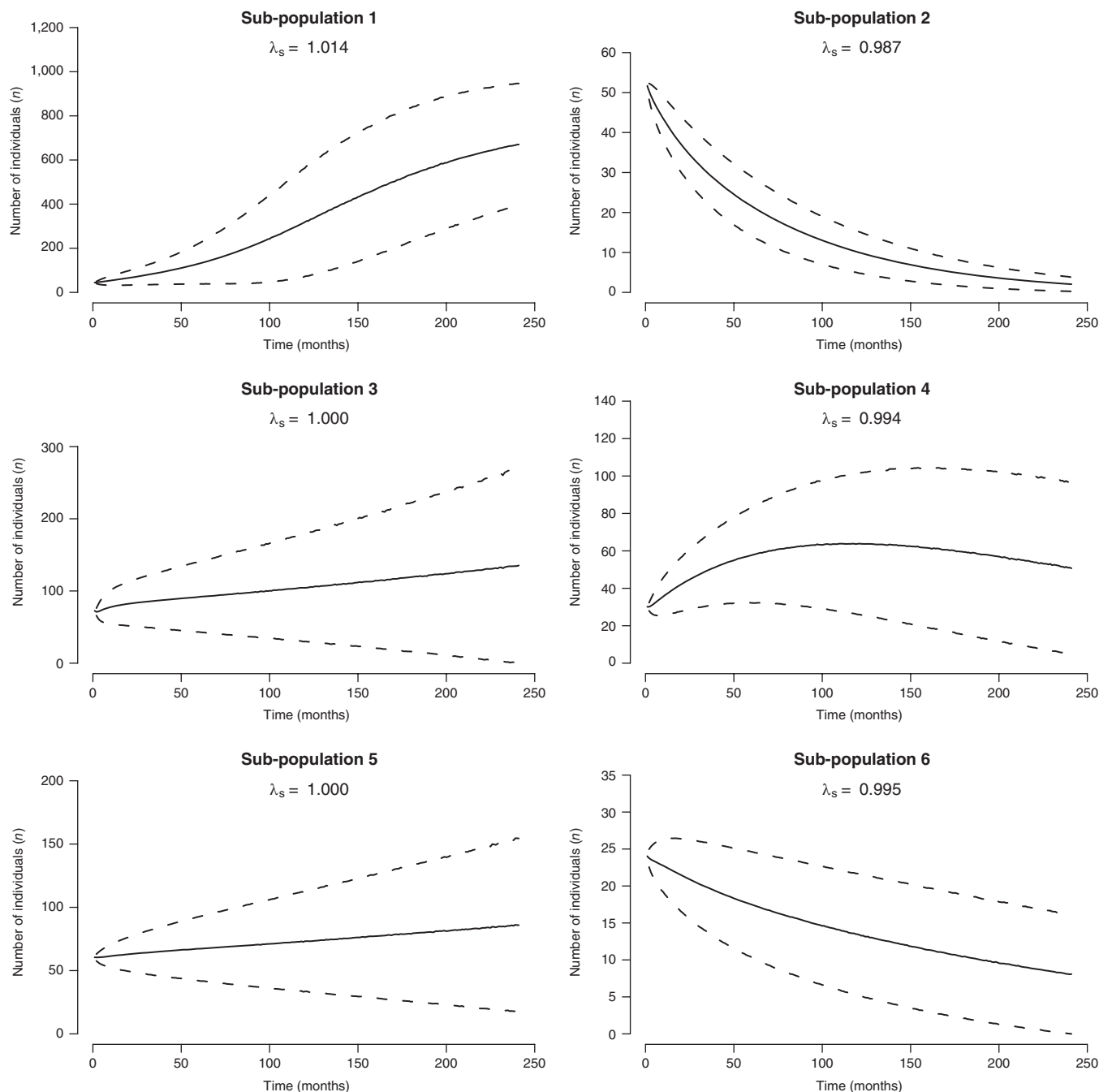


FIGURE 7 Stochastic population projection for subpopulations of *Lepanthes caritensis* in the Carite State Forest when exposed to moderate strength catastrophes such as storms or category 1 hurricanes at a simulated probability of once in 10 years. In these simulations, all mean survival, growth, and retrogression probabilities were reduced by 50% when a catastrophe occurred. Plotted values are mean subpopulation sizes (solid lines) \pm SDs (dashed lines). Also included are stochastic growth rates (λ_s) for each subpopulation under this scenario. Note differences in scale bars on y-axis

four subpopulations are likely to decline in size eventually, even if they exhibited signs of growth over the initial 20-year projection period. Moreover, increased stochasticity in these projections suggests that subpopulations are far more likely to be extirpated under this scenario (Figure 7).

In the projections incorporating severe catastrophes (Figure 8), differences in the final population sizes were even more pronounced than those from the moderate strength disturbances. In this scenario, five of the six subpopulations were projected to decrease in size over the next 20 years while only one (subpopulation one) was expected

to increase in size over that same period. Furthermore, for each subpopulation, the final projected mean population size was smaller than in either of the other two scenarios. Likewise, the overall growth rates (λ_s) when including the severe strength hurricane matrices were smaller than the original estimates as well as those from the moderate strength catastrophe scenario, and were less than one in all but a single instance (Table 1). Stochasticity in these projections was also greater than in the other scenarios suggesting that subpopulations face increased risk of extirpation when severe catastrophes are included in projection models (Figure 8).

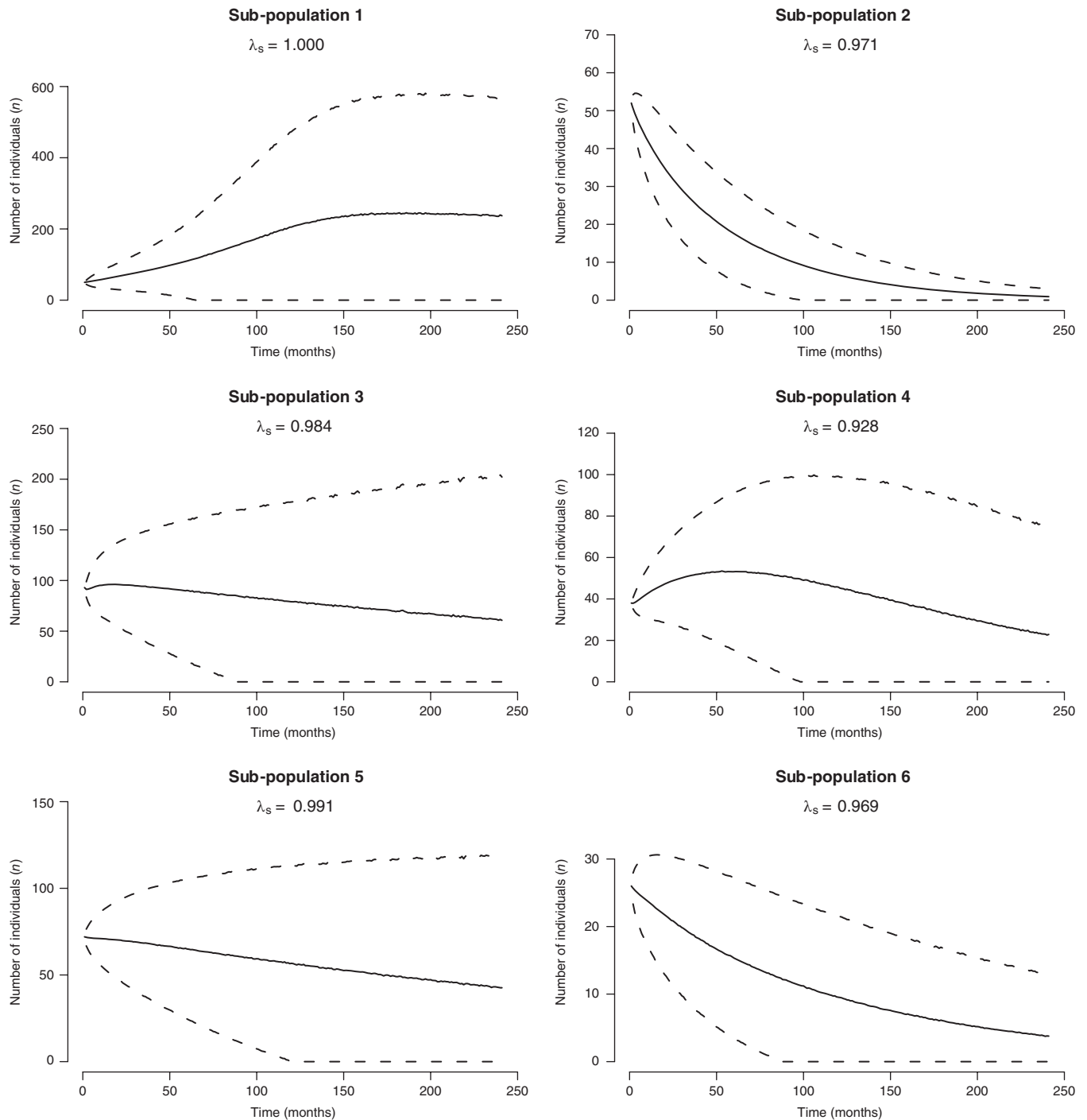


FIGURE 8 Stochastic population projection for subpopulations of *Lepanthes caritensis* in the Carite State Forest when exposed to severe strength catastrophes such as category 2–6 hurricanes at a simulated probability of once in 10 years. In these simulations, mortality was assumed to be 100% when a catastrophe occurred. Plotted values are mean subpopulation sizes (solid lines) \pm SDs (dashed lines). Also included are stochastic growth rates (λ_s) for each subpopulation under this scenario. Note differences in scale bars on y-axis

The frequency distributions of final subpopulation sizes produced by the 20-year projection models were highly variable (Figures 9–11). Under stable conditions, projected subpopulation sizes ranged between 3 and 1,000 individuals per host tree after 20 years (Table 4; Figure 9). There were large differences between the minimum, maximum, and modal sizes of each subpopulation. There were also marked differences in these values between subpopulations. In all cases, however, each sub-population

remained above the quasi extinction level ($n < 2$) in this scenario.

In the models that simulated the effects of moderate strength catastrophes, the frequency distributions of final subpopulation sizes showed that projected subpopulation sizes ranged between 0 and 1,000 individuals per host tree (Figure 10, Table 4). There were larger differences between the minimum, maximum, and modal sizes of each subpopulation than under stable conditions. Still, two subpopulations

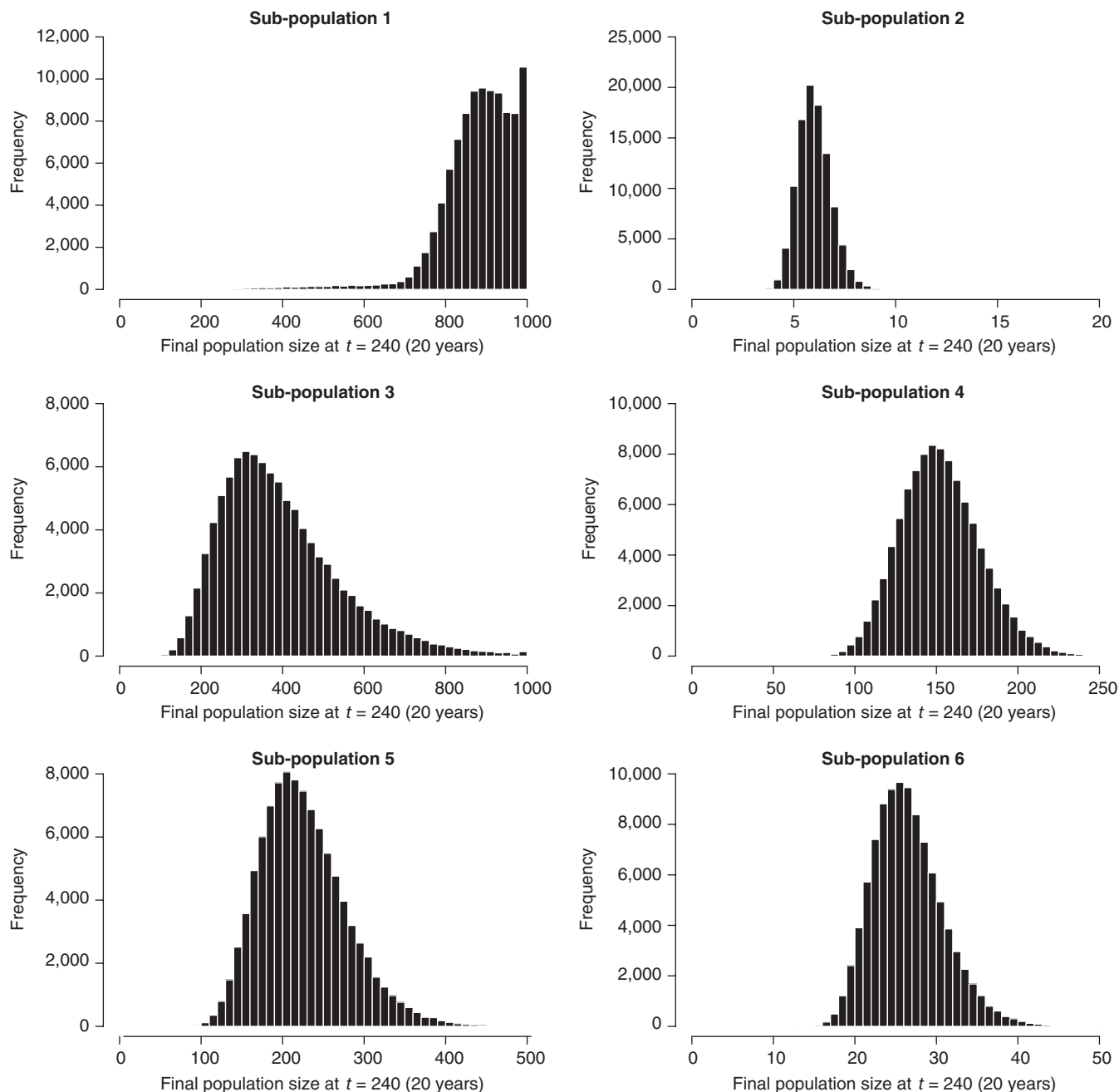


FIGURE 9 Frequency distributions of projected subpopulation sizes of *Lepanthes caritensis* sub-populations over 20 years under stable conditions. Note differences in scale bars on individual histograms

were projected to reach a maximum size of 1,000 individuals, which was the set carrying capacity, in at least one model iteration. The modal population sizes, that is, the most frequent outcomes, were variable between subpopulations in this model and ranged from 1 to 1,000 individuals, however five of the subpopulations had values of less than 40 individuals (Figure 10, Table 4). Furthermore, all subpopulations reached a minimum size below the quasi-extinction level within 20 years in several model iterations.

In the projection models that simulated the effects of severe catastrophes, the frequency distributions of final subpopulation sizes showed that final subpopulation sizes again ranged between 0 and 1,000 individuals per host tree

(Figure 11, Table 4). There were also larger differences between the minimum, maximum, and modal sizes of each subpopulation than in the previous scenarios. In terms of maximum sizes, two subpopulations were projected to reach carrying capacity in at least one iteration. The modal values in this scenario were far less variable than the values from the stable model or from the moderate strength catastrophe model; however, this was because the most frequent outcome was zero individuals for each of the subpopulations. Thus, every subpopulation reached a minimum final size below the quasi-extinction level in a large percentage of the model iterations (Figure 11, Table 4). In fact, each subpopulation reached the quasi-

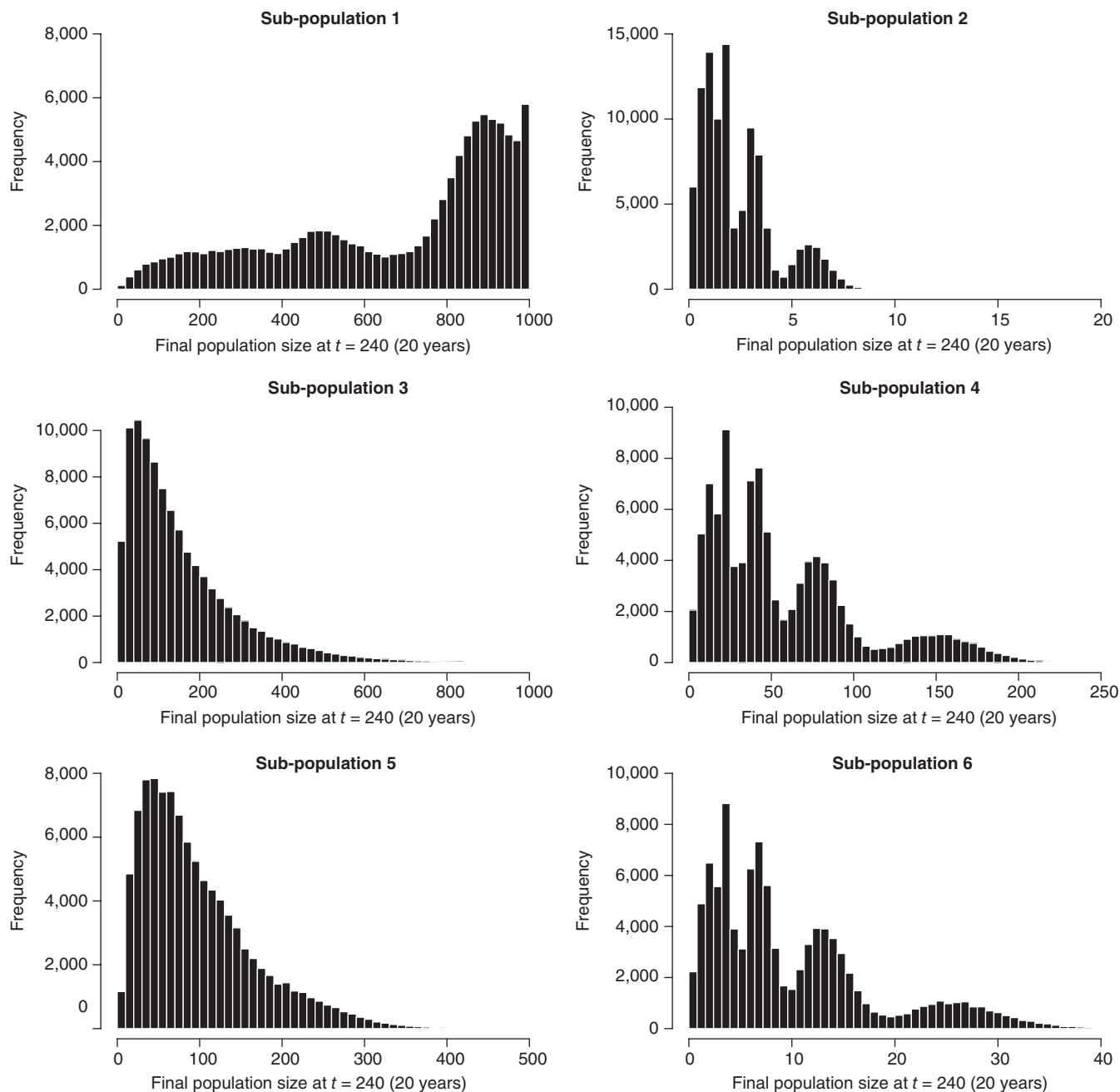


FIGURE 10 Frequency distributions of projected subpopulation sizes of *Lepanthes caritensis* subpopulations over 20 years when exposed to moderate strength catastrophe regimes, for example, storms or category 1 hurricanes. In these simulations, all mean survival, growth, and retrogression probabilities were reduced by 50% when a catastrophe occurred. Note differences in scale bars on individual histograms

extinction threshold in at least one simulation within the first 10 years.

Cumulative extinction probabilities over the next 20 years varied between subpopulations and over time (Figure 12a). In the projections incorporating effects of moderate catastrophes, the cumulative extinction probabilities for the majority of subpopulations remained less than 1% over the next 20 years. Alternatively, extinction probabilities for two subpopulations (two and six), stayed below 1% for approximately 5 years, but increased steadily after that time. While the final extinction probability for subpopulation six remained below 20% after 20 years, it

increased to close to 60% for subpopulation two (Figure 12a).

In the model incorporating effects of severe catastrophes, cumulative extinction probabilities were substantially higher over the 20-year projection period (Figure 12b). Extinction probabilities were above 1% for all subpopulations within the first few years and were above 15% after 5 years. Furthermore, each subpopulation had an extinction probability greater than 50% after 20 years. In some cases, the final cumulative extinction probabilities were well over 80%. In all cases, the probability of extinction was much greater for each subpopulation under the severe catastrophe scenario (Figure 12).

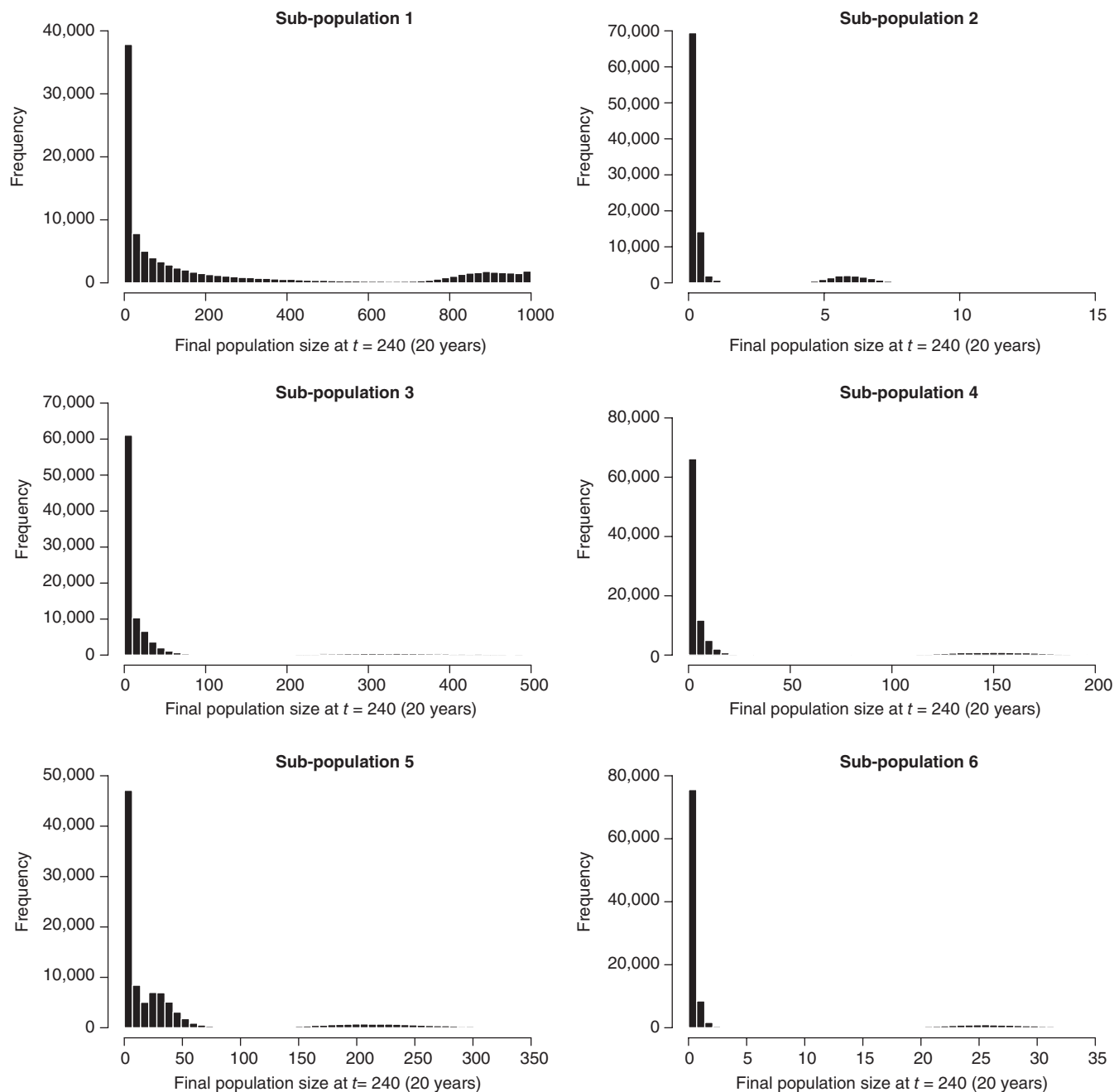


FIGURE 11 Frequency distributions of projected subpopulation sizes of *Lepanthes caritensis* sub-populations over 20 years when exposed to severe catastrophe regimes, for example, category 2–6 hurricanes. In these simulations, mortality was assumed to be 100% when a catastrophe occurred. Note differences in scale bars on individual histograms

4 | DISCUSSION

4.1 | Population size

Over the course of this study, the collective population size of *L. caritensis* in the Carite State Forest has slightly declined. Nevertheless, even slight declines in overall population size can be problematic for rare species because it increases the probability that stochastic events could lead to extinction (Gaston, 2003; Morris & Doak, 2002) as well as the possibility of succumbing to other rarity associated problems such as pollen limitation or Allee effects (Courchamp et al., 2006; Kearns, Inouye, & Waser, 1998).

Despite the overall population decline, however, three of the individual subpopulations increased in size. This finding suggests that the dynamics of specific subpopulations are independent and not necessarily predictive of others. It also suggests that the overall population is potentially stable and fluctuating around equilibrium. Many epiphyte populations, including those of some *Lepanthes* spp. (Tremblay, Meléndez-Ackerman, & Kapan, 2006), are thought to behave more as metapopulations than as populations, with some subpopulations acting as sources and others as sinks. Thus, the overall long-term growth rate of the population may be different from each individual subpopulation. Consequently, it will be

TABLE 4 Projected minimum, maximum, and modal values for subpopulation sizes (*n*) of *Lepanthes caritensis* after 20 years under stable conditions and when exposed to moderate and severe strength hurricane regimes

		Subpopulation 1	Subpopulation 2	Subpopulation 3	Subpopulation 4	Subpopulation 5	Subpopulation 6
Conditions	Population size						
Stable	Minimum (<i>n</i>)	155	3	97	85	92	15
	Mode (<i>n</i>)	1,000	5	296	150	214	25
	Maximum (<i>n</i>)	1,000	9	1,000	255	526	45
Moderate hurricane	Minimum (<i>n</i>)	1	0	0	0	0	0
	Mode (<i>n</i>)	1,000	1	39	18	26	3
	Maximum (<i>n</i>)	1,000	10	1,000	276	552	52
Severe hurricane	Minimum (<i>n</i>)	0	0	0	0	0	0
	Mode (<i>n</i>)	0	0	0	0	0	0
	Maximum (<i>n</i>)	1,000	10	1,000	269	568	57

particularly important to protect source populations after disturbances to sustain colonization of new sites.

Still, we observed no establishment of new subpopulations in 2 years of surveys, suggesting that the potential for population growth may ultimately be limited by the availability of suitable microhabitats (Batty, Dixon, Brundrett, & Sivasithamparam, 2001; Jersáková & Malinová, 2007; McCormick & Jacquemyn, 2013) or by seed dispersal among suitable sites (Ackerman, Sabat, & Zimmerman, 1996; Jersáková & Malinová, 2007; Machon et al., 2003; Murren & Ellison, 1998). Additional studies should be useful for determining which habitat characteristics, for example, presence of mycorrhizal fungi and bryophytes or microclimatic conditions (Bayman, Gonzalez, Fumero, & Tremblay, 2002; Crain, 2012; Crain & Tremblay, 2017; Tremblay & Salguero-Farías, 2001), are responsible for the success of the species at certain sites but not at others, as well as for the apparent lack of colonization to new sites. The differences between subpopulation dynamics and the apparent limitations to dispersal and colonization emphasize the importance of monitoring the unique attributes of individual subpopulations and their habitats, as well as meta-population dynamics when evaluating the conservation status of rare species.

4.2 | Demographic attributes

The stochastic growth rates (λ_s) exhibited by each of the subpopulations of *L. caritensis* in the Carite State Forest were very close to one, indicating that the overall population should be stable or growing, albeit slowly, over time. Still, one of the largest subpopulations (subpopulation 2) exhibited a growth rate below one over the course of our study and appears to be in decline. The 95% credible intervals associated with the lambda values were very small (Table 1), suggesting that they were good estimates of the current growth rates. The monthly sample sizes in some subpopulations tended to be small, however, and the use of multilevel

models of vital rates allowed us to better estimate months with low sample sizes by borrowing information from the distribution of the other monthly vital rates. We note that the credible intervals of the stochastic growth rates incorporated variability of the mean vital rates through time, as is common practice in PVA (Morris & Doak, 2002). An alternative is to use the full predictive posterior distribution of the stochastic growth rate, which includes uncertainty in the parameter estimates in addition to this annual variation. Using the predictive posterior interval would lead to broader intervals than the standard interval that incorporates only the mean vital rates.

Collectively, the growth rate values in this analysis were in close accord with, but slightly higher than, earlier estimates of λ_s calculated from a subset of the individuals we monitored in this study (Tremblay, 1997). Considering the general fluctuations we observed in the subpopulation sizes, with each of them increasing in some months but decreasing in others, the small inconsistencies between the estimated growth rates in these studies are likely the result of temporal variation in environmental conditions. Increased variability in monthly growth rates can reduce the ability to forecast future population sizes and a recent study on several plant species (Crone et al., 2012) demonstrated that while matrix projection models were effective at characterizing current conditions, and therefore, for making across sites comparisons, they were rather poor at forecasting future population dynamics. The study also showed that forecast error was significantly associated with environmental differences. These factors are important to consider because variation in monthly growth rates can make the population grow more slowly than a population occurring in more stable environmental conditions (Morris & Doak, 2002). Thus, the combined effects of temporal variability and differences in growth rates among subpopulations likely explain the slight decline in the overall population size that we observed despite the fact that most of the λ_s values were greater than one. These results again highlight the importance of

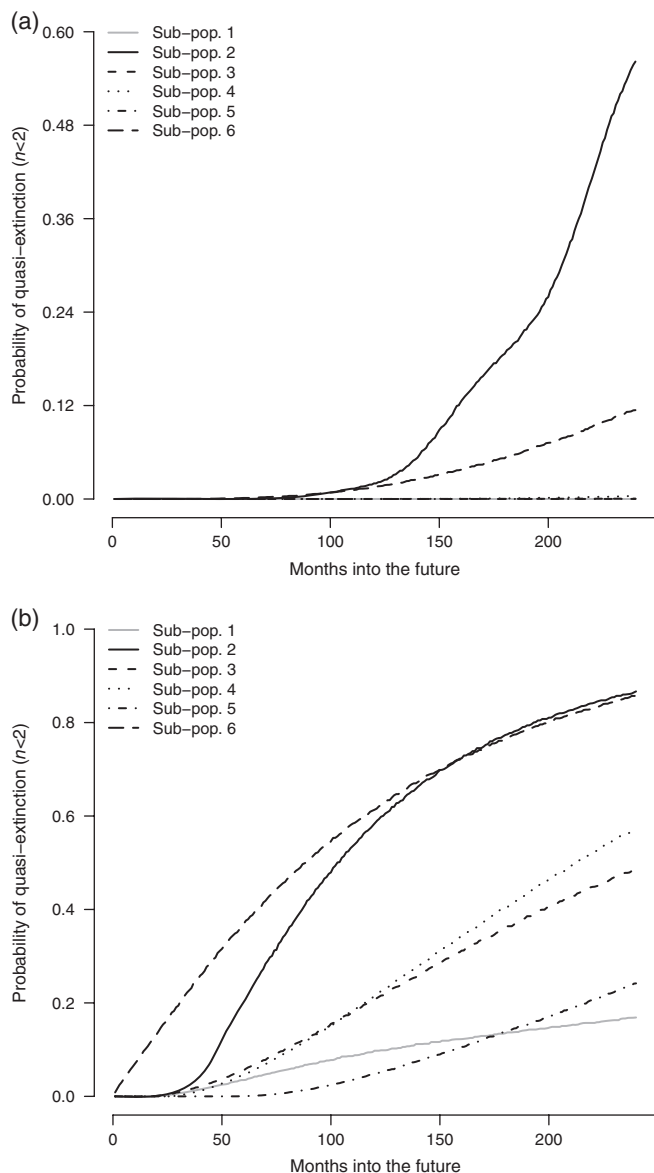


FIGURE 12 Cumulative probabilities of six subpopulations of *Lepanthes caritensis* reaching quasi-extinction ($n < 2$) over the next 20 years when exposed to: (a) moderate strength hurricane regimes, and (b) severe strength hurricane regimes. Ultimate probabilities of extinction $\pm 95\%$ credible intervals were as follows: (a) subpopulations 1, 3–5: $<1.0\% \pm 0.2$, subpopulation 2: $59.2\% \pm 0.9$, subpopulation 6: $13.2\% \pm 0.6$, (b) subpopulation 1: $55.8\% \pm 0.9$, subpopulation 2: $86.6\% \pm 0.6$, subpopulation 3: $61.2\% \pm 0.9$, subpopulation 4: $86.7\% \pm 0.6$, subpopulation 5: $80.2\% \pm 0.7$, subpopulation 6: $86.3\% \pm 0.6$

monitoring the unique attributes of individual subpopulations when evaluating the overall conservation status of rare species.

In terms of stable stage distributions, immature individuals dominated the majority of subpopulations (Table 2), while adults dominated the remaining two. The results were inconsistent with earlier assessments of *L. caritensis* suggesting that the population should be skewed toward a composition of adults (Tremblay, 1997). The observed stage distributions, however, were not always in accord with estimated stable stage distributions (w). One possible

explanation for this pattern is that higher levels of reproductive success observed over the course of this study contributed disproportionately to the smaller life stages in the population. Further studies are also needed to determine the cause of the apparent increase in reproductive success.

Additional studies are also needed to determine how the current stage distribution might affect growth rate and elasticity estimates (Stott, Franco, Carslake, Townley, & Hodgson, 2010). Variation in number of recruits/seedlings across time periods is expected to be large, as hundreds of seeds can be produced in a single fruit of *L. caritensis*. Therefore, a single effective fruiting event can result in large changes in population size and stage distributions. Stage distributions where immature plants are overrepresented, as we observed in multiple populations, could mean that projected lambda values are not representative of what is expected in the short term. Differences between observed and projected stable stage distributions can lead to attenuation of the population and increased extinction probabilities (Stott et al., 2012a; Stott, Hodgson, & Townley, 2012b). These issues may explain why we witnessed declines in some populations with lambda values greater than one as well as discrepancies between earlier estimates of λ_s (Tremblay, 1997) and those presented here. Transient events need further scrutiny to determine how they may influence long-term persistence and appropriate management decisions (Stott et al., 2010).

The reproductive values (v) obtained from this analysis (Table 3) matched closely with those obtained from previous surveys of *L. caritensis* (Tremblay, 1997). In both cases, it is clear that nonreproductive adults and reproductive adults are expected to make the greatest contributions to future population growth. Considering that the stage structure of the population is skewed toward smaller size classes, insuring the preservation of adult classes is critical from a conservation standpoint, since the smaller classes contribute very little to future population growth. Conservation practitioners' responses to catastrophic events should therefore emphasize recovery of adult individuals, as they offer the greatest potential for population recovery after these disturbances.

Relocation is a delicate process, however, as research on a closely related species demonstrated that while transferring orchids from felled trees to standing trees as a management tool after hurricane disturbances had a positive effect on survival, plants on nonfelled trees exhibited greater survival rates (Tremblay, 2008). Accordingly, managers should relocate orchids to standing host trees as soon as possible after a hurricane to maximize individual survivorship. Transferring plants causes stress, however, and managers should refrain from doing so if it is not completely necessary, for example, if the base of the trunk where orchids are growing remains standing. If transfer is necessary, managers should also take care to keep as much of the orchids' original substrate intact when relocating individuals.

Elasticity values also matched closely with those obtained from previous surveys of *L. caritensis* (Tremblay, 1997) and showed that among all projection matrix elements nonreproductive adult survival rates (S_{44}) have the greatest relative impact on λ_s for a given proportional change. This underscores the importance of maintaining adult individuals in the population, a factor that has been recognized in conservation efforts for several orchid species (Gregg & Kéry, 2006; Nicolè, Brzosko, & Till-Bottraud, 2005). In some subpopulations, elasticity values for juvenile survival (S_{22}) and transitions between nonreproductive and reproductive adults (R_{34} , G_{43}) were also high, and thus, maintenance of juvenile individuals and improving reproduction in adults may be potential avenues for increasing the overall size of the population. It is important to note that the magnitude of perturbations to vital rates can affect their impact on population growth rates (Stott et al., 2010, 2012a, 2012b) and our transfer function analysis confirmed the significance of nonreproductive adult survival rates (S_{44}) but also showed that seedling (S_{11}) and juvenile survival (S_{22}) are nearly as important depending on perturbation strength. Thus, specific management decisions for the species should consider elasticity values as well as transfer functions before they are implemented.

4.3 | Population dynamics and viability

The results of our projections indicate that the population of *L. caritensis* in Carite State Forest is not in any immediate danger if conditions remain stable and catastrophes are averted (Figure 6). This result was somewhat surprising because previous surveys revealed evidence indicating that the species was in decline (Crain & Tremblay, 2012; Tremblay, 1997), but there are several possible explanations for the differences in the findings of these surveys. Temporal variation in population trends could account for the somewhat small differences observed in the studies, particularly since growth rates (λ_s) in all surveys were close to one, albeit on different sides of it. For example, Tremblay's (1997) survey period included a rare dry spell which resulted in high mortality of seedlings and juveniles. In addition, mean population matrices were used across all time periods for the population projections in Tremblay's (1997) analysis, thus masking temporal effects. Crain and Tremblay's (2012) survey included populations that occurred in Carite as well as in the El Yunque National Forest where evidence of human disturbances (i.e., illegal collection) was documented, a factor that likely decreased estimated growth rates and projected population sizes. A last consideration is that a greater number of individuals and subpopulations were included in the models for this survey; Tremblay (1997) monitored two of the subpopulations in Carite, whereas Crain and Tremblay (2012) focused only on the adult individuals. Because of differences in growth rates between individuals and

subpopulations, one would expect potentially divergent results from each of these surveys.

Consequently, it appears that *L. caritensis* might be capable of persisting as a small population and that the majority of the subpopulations should continue to grow if left undisturbed. Seemingly, the historic frequency of hurricanes has been low enough to allow the population to recover after catastrophic disturbances. This is in accord with other studies suggesting that very small plant populations can persist for long periods and even develop into large populations in time (Matthies et al., 2004). The expected lifespan for *L. caritensis* individuals is rather long and adults can survive for more than 10 years (Tremblay, 2000). Thus, under noncatastrophic environmental conditions *L. caritensis* adults may persist for a long period. If this is indeed the case, managers of the species should take a "hands off" approach and focus on protecting the existing populations and their surrounding environment unless large catastrophes occur.

Still, the growth rates estimated for many of the subpopulations in both moderate and severe catastrophe scenarios were less than one (Figures 6 and 7, Table 1) and indicate that the population of *L. caritensis* could decline over the long run (> 20 years) if exposed to recurring disturbances such as storms or hurricanes. Additionally, subpopulations reached quasi-extinction on numerous occasions when catastrophe regimes were incorporated into the projection models (Figures 9 and 10). These results are in close accord with observations from previous assessments of *L. caritensis* in Carite State Forest after large disturbances, where more than 90% of the known population was eliminated (Tremblay, 2000). The recent impacts of Hurricanes Irma and Maria in Puerto Rico should offer an ideal opportunity to reevaluate the effects of disturbances on these orchids once accessibility to the populations is improved. Since many studies suggest that these types of disturbances are likely to increase in frequency and intensity in the future (Lugo, 2000; O'Brien et al., 1992), catastrophes may have an increasingly negative impact on the species over time. The most recent hurricane season in Puerto Rico, with hurricanes Irma and Maria hitting the island within weeks of each other, suggests that this may be a realistic scenario. Furthermore, our models were only run to simulate the patterns of catastrophic storm events, and if we were to incorporate additional disturbances associated with these catastrophes, such as floods or landslides (Larsen & Torres-Sánchez, 1992, 1998; Lugo, 2000; Scatena & Larsen, 1991; Tremblay, 2000), the probability of extirpation events would certainly increase. Likewise, our models do not include any enduring effects of hurricane disturbances, that is, reduced growth or reproduction in the months following a hurricane disturbance, and such effects could increase adverse outcomes of these disturbances. Therefore, the results of our projections should be interpreted carefully.

For species as rare as *L. caritensis*, the loss of even a single subpopulation could have lasting effects on future population growth and viability (Schemske et al., 1994), particularly if recruitment to new host trees remains so elusive. Considering these issues, conservation managers should continue to monitor *L. caritensis*, especially after storms or other catastrophic events. In particular, managers should work to rescue and transplant the species in the event that host trees are lost and also explore the possibility of establishing new populations on unoccupied potential host trees.

L. caritensis' potential vulnerability to extinction also begs the question as to how the species has persisted up to this point under conditions that include regular disturbances. One possibility is that the demographic response of *L. caritensis* populations is positive after the direct impacts of catastrophes occur. This hypothesis needs testing, however, since studies on other species of *Lepanthes* in Puerto Rico have documented increased flower production following disturbances in some settings, but they have also noted increased mortality, loss of leaves, and reduced flowering in other instances (Tremblay, 2008; Tremblay & Salguero-Far a, 2001). Again, our models do not incorporate potential lasting effects of hurricane disturbances on growth or reproduction and if there is a positive effect, it could explain how these populations persist through such events. Thus, additional research is needed to evaluate how populations of *L. caritensis* respond to altered conditions, for example, increased temperatures, exposure to wind, and exposure to photosynthetically active or ultraviolet radiation, after catastrophes to determine if there are increases in reproduction and recruitment that counterbalance increases in mortality and allow the species to persist. These possibilities should also be considered when interpreting our model results.

Changes in colonization after catastrophes occur may also help explain how *L. caritensis* has endured. *L. caritensis* is currently found only on large trees, which are more susceptible to snapping or uprooting during large storms (Walker, 1991; Wiegand et al., 2013). If the open conditions that are created after a host tree is broken or uprooted results in a positive demographic response in terms of reproduction and seedling survival, it may also be the case that recruitment to new host trees is limited until disturbances occur. Consequently, catastrophes may be necessary for *L. caritensis* to colonize and establish populations on new, and perhaps smaller or more exposed, host trees. This hypothesis may explain why populations have been stable on current hosts, but colonization to new host trees has yet to be observed. Still, the known populations occur in dense forests, albeit close to openings from streams, and additional studies are needed to test for increases in colonization success after catastrophes open new gaps where *L. caritensis* occurs.

5 | CONCLUSIONS

Although the population of *L. caritensis* in Carite State Forest has experienced recent declines, it is projected to grow over the near future and consequently, this orchid may represent an example of a species that is rare, but not necessarily endangered, as it appears historically capable of persisting in a habitat that is subject to intermittent disturbances. Still, when the effects of catastrophic events are incorporated into a viability analysis of this species, it suggests that extinction risk will increase dramatically. This finding highlights the importance of including sources of variability, such as catastrophes, into population viability analyses, particularly if they are expected to increase in frequency and intensity as many climate models predict. By incorporating catastrophes into viability analyses, conservation managers will have a better understanding of the potential fates of target species' populations under different scenarios, and accordingly, they will be able to make more informed decisions that will help increase the effectiveness of rare species conservation efforts.

ACKNOWLEDGEMENTS

We genuinely thank our families and friends for their ongoing support. Special thanks to A. S nchez-Cuervo for continual backing and assistance with fieldwork. Additional thanks to A. Hern ndez for help with coding. We also recognize D. Pompei, R. Kent, Y. Ferrer, P. Bracho, J. Gonzalez, and many others for aiding with fieldwork. Lastly, we sincerely thank the C rculo de Amigos de Orquidistas de Puerto Rico and the Decanato de Estudios Graduados e Investigaci n for providing financial support.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

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

How to cite this article: Crain BJ, Tremblay RL, Ferguson JM. Sheltered from the storm? Population viability analysis of a rare endemic under periodic catastrophe regimes. *Popul. Ecol.* 2018;1–19. <https://doi.org/10.1002/1438-390X.1002>