


# The effects of hurricanes on the stochastic population growth of the endemic epiphytic orchid *Broughtonia cubensis* living in Cuba

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## Abstract

We carried out a posthurricane evaluation of *Broughtonia cubensis* (Lindl.) Cogn., an endemic Cuban epiphytic orchid, after Hurricane Ivan (2004). We studied the transient responses in the stochastic dynamics of the species at three different sites over 13 successive years (2006–2019), monitored plot inventories (464 individuals in 10 transects) and built stochastic population models. The deterministic stochastic growth rate values ( $\lambda$ ) did not significantly differ ( $F = 2.76$ ;  $p > 0.076$ ) among the three sites over the 2006–2019 period. The long-term stochastic growth rate was  $\lambda_s = 0.973$  [0.932, 1.034]. The matrix elements that had the largest effect on  $\lambda$  were the transition to and stasis within the largest size class. Transient responses explained an average of 86% of the variation in the observed population growth rates ( $R^2$  for  $r_{TD}$  vs.  $r_{obs}$ ), compared to 4% of the variation in the vital rates ( $R^2$  for  $r_{VR}$  vs.  $r_{obs}$ ). Because transient dynamics are dependent on the population size composition, we ran extinction risk analyses under two scenarios: a population composed mainly of juveniles and another composed mainly of adults. There was little risk of falling below the quasi-extinction threshold before 25 year for both juveniles and adults. However, the risk of quasi-extinction was almost certain for both size classes by 80 year. We also simulated the effect of increasing the hurricane occurrence probability over 80 year on the population. There was little risk of extinction before 20 year in the baseline model, but there was a significant risk of extinction within 5 year when 90% of the individuals were affected by a new hurricane event.

## KEYWORDS

elasticities analysis, hurricanes, management policies, quasi-extinction risk, sensitivity analysis

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## 1 | INTRODUCTION

In ecology in general, and particularly in population ecology, understanding variabilities in ecological processes has been a central issue over the last few decades (Bolker & Pacala, 1997; Inchausti & Halley, 2001; Krebs, 1972; Semmens, Ward, Moore, & Darimont, 2009; Wardwell & Allen, 2009). Ecologists have been using population projection models to derive management policies for more than 40 year (Crone et al., 2011; Crone et al., 2013). The usual emphasis of these matrix models has been on asymptotic behavior, but due to the formulation of some transient indices (Neubert & Caswell, 1997; Stott, Townley, & Hodgson, 2011), it has become possible to investigate short-term population dynamics that occur due to disturbances (Crain, Tremblay, & Ferguson, 2019).

Plants live and develop in variable environments, and this environmental variability could affect population dynamics over time, with plants exhibiting short-term dynamics that can differ strongly from their asymptotic behavior. An important point is that these short-term transient behaviors are strongly dependent on the initial conditions (i.e., the initial size of the population) (Stott et al., 2011). As indicated by Ellis (2013) and Williams, Ellis, Bricker, Brodie, and Parsons (2011), understanding transient responses is important for determining how initial conditions will influence a population's demographic trajectory. This understanding, in turn, could help researchers define appropriate conservation and management policies (Ezard et al., 2010).

Throughout the 20th century, the Caribbean Sea basin has been affected by more than 200 hurricanes, the dominant ecological disturbance in the region (Landsea, Pielke, Mestas-Nunez, & Knaff, 1999; <https://coast.noaa.gov/hurricanes>). Over the last 30 years, 27 hurricanes have affected the behavior and survival of epiphytic orchid populations in this region to various degrees (Tremblay, 2008). The increasing frequencies and intensities of hurricanes could change plant population dynamics, altering their survival, growth, and fitness (Crain et al., 2019; Tanner, Rodriguez-Sanchez, Healey, Holdaway, & Bellingham, 2014).

In these changing environments, matrix stochastic formulations seem to be an adequate approach to studying the population dynamics of these species (Tuljapurkar, 1982; Tuljapurkar, Gaillard, & Coulson, 2009; Tuljapurkar, Horvitz, & Pascarella, 2003); the usual focus of these models has previously been on asymptotic dynamics, and only recently has the role of short-term dynamics been explored using different transient indices (Caswell, 2007; Crain et al., 2019; Ellis, 2013; Ellis & Crone, 2013; Jelbert et al., 2019; McDonald, Gann, Jonson, & Dixon, 2016; Stott, 2016; Tremblay, Raventós, & Ackerman, 2015).

For the epiphytic orchid *Broughtonia cubensis* living in Guanahacabibes National Park (in western Cuba), recording the effects of disturbances on plant populations is particularly relevant since this endemic species is highly vulnerable to extinction (Albrecht, Guerrant, Maschinski, & Kennedy, 2011). In this paper, we analyze the post-Hurricane Ivan (2004) effects on *B. cubensis* (Lindl.) Cogn., from 2006 to 2019 using a stochastic population modeling approach. Since a population may be doomed to extinction even individuals are still alive, we calculated a quasi-extinction probability function (Gerber and González-Suárez, 2010). With this time series, our goals were (1) to estimate the deterministic ( $\lambda$ ) and stochastic population growth rate ( $\lambda_s$ ); (2) to decompose the variation in the observed population growth rates,  $r_{\text{obs}}$  into (a) the relative contributions of differences in the demographic rates alone ( $A_t$ ) and (b) the transient responses resulting from the differences between initial conditions ( $n_t$ ) and steady-state distributions (SSDs); (3) to determine the population size class that contributed the most to the dynamics of the population growth rate to propose effective conservation measures; and (4) to estimate the quasi-extinction probability function after manipulating two variables: (a) the starting life stage distribution (proportion of juveniles to adults) and (b) the frequency of disturbances (hurricanes).

## 2 | METHODS

### 2.1 | Species and study site

*Broughtonia cubensis* is an endemic epiphytic orchid species from Cuba that is restricted to the western region of the island and is commonly found in the subcoastal xerophytic vegetation of the Guanahacabibes Peninsula (Pinar del Río province) and in the low-elevation regions of La Coca (Havana province). This species is endangered in Cuba due to its fragmented distribution, habitat destruction and overcollection of wild individuals (Vale, Rojas, Álvarez, & Navarro, 2013). Mature individuals have well-developed leaves and pseudobulbs, which function as storage organs and provide water and nutrients to affected plants after leaf damage occurs due to hurricanes. The plants are characterized by short inflorescences of a few small white flowers, with the labellum having purple stains and a yellow throat. The plants bloom between January and March (Mújica, Raventós, González, & Bonet, 2013). This species is prized and harvested for horticultural purposes and illegal orchid collections. Populations are often exposed to full sun and occupy different host tree species, although they are most

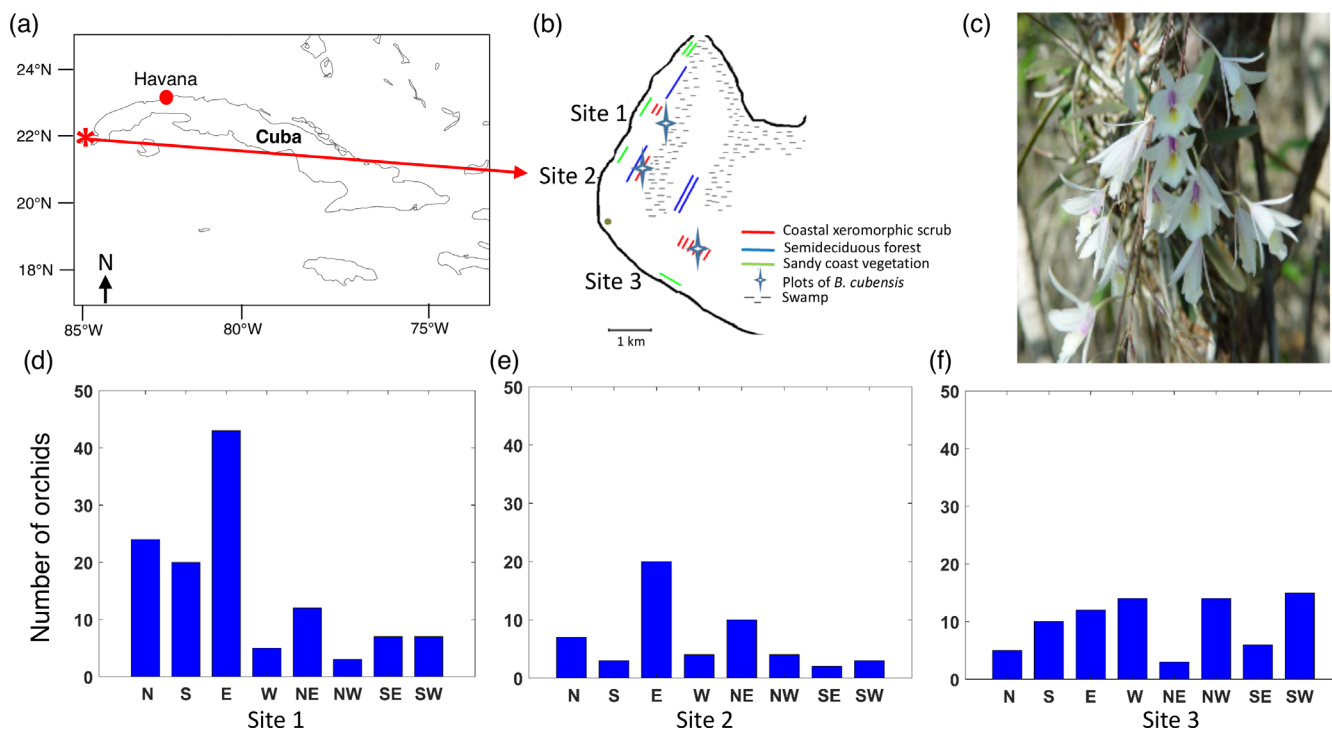
often found on *Plumeria tuberculata* Lodd, *Erythroxylum areolatum* Vell. and *Stigmaphyllon sagraeanum* A. Juss.

To study the demography of this orchid, five plots were established in three different sites in Guanahacabibes National Park in Cabo San Antonio, which is located on the western point of Cuba in Pinar del Río Province. The plots were established in January 2004 before the impact of Hurricane Ivan (González, Raventós, Mújica, & Bonet, 2007). One plot was located at French Beach (coordinates 21.886°N, 84.943°W), two were located in Tumbadero (coordinates 21.911°N, 84.928°W) and two were located in Cemetery (coordinates 21.864°N, 84.950°W) (Figure 1). To evaluate the posthurricane effects on this orchid, in February 2005, we quantified the damage to host plants and orchids produced by Hurricane Ivan (the orchid population size and number of affected host trees). To increase the sample size, broaden our ability to document hurricane damage, and study the temporal dynamics in this species 14 months after Hurricane Ivan, we established 10 new transects (approximately 100-m long × 20-m wide, overlapping the five previous plots) to examine *B. cubensis* over 13 year (2006–2019). These 10 transects were located on the previous three sites: two transects were located on Plot 3 in French Beach; two transects were located on Plots 1 and 2 in Tumbadero, and six transects were on Plots

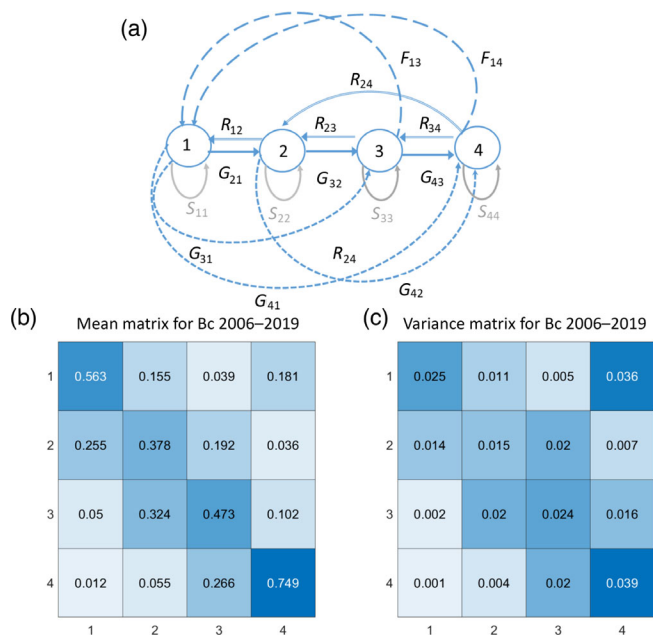
4 and 5 in Cemetery (Figure 1). All sites were within approximately 2 km, ensuring that they could be considered separate populations in subcoastal xerophytic vegetation growing over limestone outcrops.

## 2.2 | Population matrices

In previous studies (Raventós, González, Mújica, & Bonet, 2015), we defined four plant size categories based on the leaf area: 0.1–1.44 cm<sup>2</sup>, 1.45–3.45 cm<sup>2</sup>, 3.46–7.96 cm<sup>2</sup> and > 7.96 cm<sup>2</sup>. These size categories allowed more definition than categorizing by life stage (seedlings, juveniles, nonreproductive and reproductive adults) in population sampling (González et al., 2007). Moreover, the last two size categories included reproductive adult individuals. Other population studies on epiphytic orchids have chosen size as opposed to life stage to categorize plants (Zotz, 2007; Zotz & Schmidt, 2006). We marked a total of 464 individuals along the 10 transects at the three sites and monitored them during 13 successive years (2006–2019). We obtained a total of 39 population matrices (Text S1). The corresponding life cycle graph obtained from a time series of 13 irreducible and primitive 4 × 4 matrices (Caswell, 2001) shows all possible transitions among plant stages. Each matrix is



**FIGURE 1** (a) Map of Cuba with a red arrow indicating the Guanahacabibes National Park in the western part of Cuba (Pinar del Río province). (b) The five plots on the three sites in Guanahacabibes National Park with different types of vegetation. (c) Photo of *Broughtonia cubensis*, an endemic epiphytic orchid species. The abundance of this species prior to Hurricane Ivan on (d) Site 1 with one plot located at French Beach (coordinates 21.886°N, 84.943°W), (e) Site 2 with two plots located in Tumbadero (coordinates 21.911°N, 84.928°W) and (f) Site 3 with two plots located in cemetery (coordinates 21.864°N, 84.950°W) [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 2** (a) Life cycle graph showing the transitions between the four size classes (1: Seedling; 2: Vegetative adult; 3: Small flowering adult; and 4: Large flowering adult) between  $t$  and  $t + 1$  for *Broughtonia cubensis* (Bc). The arrows indicate transitions between size classes. (b) Mean matrix for Bc 2006–2019 period and (c) variance matrix for Bc. 2006–2019 period [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

composed of four vital rates: fecundity ( $F$ ), individuals encompassing the last two stages of adult size classes; stasis ( $S$ ), individuals who grow or decrease in size from  $t$  to  $t + 1$  but do not move up or down between size classes; growth ( $G$ ), individuals who move up a size class from  $t$  to  $t + 1$ ; and retrogression ( $R$ ), individuals who move down a size class in  $t + 1$  from the one they occupied in  $t$  (Figure 2a).

### 2.3 | Deterministic population growth

First, we calculated the deterministic growth rate from the mean matrix plus a matrix of the variability associated with this process for the 2006–2019 period. We assume that the environment is “iid” (independently and identically distributed) and that the deterministic growth rate is  $\log \mu$  (Caswell, 2001).

### 2.4 | Stochastic population growth

Following the approach of Ellis and Crone (2013), to perform replicate simulations of stochastic dynamics on these 39 population matrices, we simulated 1,000 population trajectories using equal probability selection at each step time step. As the first approach, we used equal numbers of individuals in each stage. We used a run-in period of 500 year on the

projected stochastic population growth to remove the effect of the arbitrary initial condition. We followed the method of Ellis and Crone (2013) to calculate the observed growth rate:  $r_{obs} = (\log(\lambda_{obs}))$ , as  $r_{obs} = \log(\sum(A_{500}n_{500})/\sum n_{500})$ , where  $A_{500}$  is the matrix and  $n_{500}$  is the vector of the population size structure at  $t = 500$ .

### 2.5 | Decomposing stochastic population growth

The observed growth rate could be decomposed into its two nonindependent contributors, the variation in vital rates,  $r_{vr} = \log(\lambda_{max})$ , at  $t = 500$ , which represents the population change due to differences in vital rates alone (demographic variations), and  $r_{TD} = \log\left(\frac{\sum A_{500}n_{500}}{\sum n_{500}}\right)$ , which represents the change in population size due to the transient response to  $n_{500}$ . In this case, we used the standardized matrix  $\left(\frac{A_{500}}{\lambda_{500}}\right)$  to remove the population trend from demographic rates, meaning that the population exhibited SSD. To calculate the proportion of the variance among  $r_{obs}$ ,  $r_{VR}$  and  $r_{TD}$ , we calculated the square of Pearson's correlation coefficient obtained from 1,000 simulations between  $r_{obs}, r_{VR}$  and  $r_{obs}, r_{TD}$ .

### 2.6 | Transient dynamics in stochastic population growth

Following Ellis and Crone (2013), we analyzed amplification and attenuation at  $t = 1$  (i.e., reactivity and first-step attenuation) as maximal and minimal column sums of the 10,000 simulations on the population mean matrix. We simulated only the amplification and attenuation transient bounds at  $t = 1$  (from  $t = 500$  to  $t = 501$ , that is, reactivity and first-step attenuation) because transient responses at different time steps have been found to be strongly correlated (Ellis, 2013; Ellis & Crone, 2013; Stott, Franco, Carslake, Townley, & Hodgson, 2010). Attenuation (ATT) is the short-term future density from  $t = 500$  to  $t = 501$  relative to a population at SSD for any  $no$  (initial conditions), and amplification (AMP) is the large future density from  $t = 500$  to  $t = 501$  relative to a population at SSD for any  $no$  (Stott et al., 2011).

### 2.7 | Deterministic and stochastic sensitivity and elasticity

To compare the results of the deterministic and stochastic analyses, we calculated the deterministic and stochastic sensitivity and elasticity values; then, a

correlation analysis was performed between the two approaches.

The deterministic sensitivity and elasticity were calculated from the right and left eigenvectors following the Caswell (2001) approach.

$$\frac{\partial \lambda_1}{\partial a_{ij}} = V_i * W_j \quad (1)$$

The sensitivity and elasticity of the stochastic growth rate to perturbations in the mean demographic projection matrix were calculated by performing 10,000 simulations using Rstudio version 1.2.1335 (popbio package; Stubben & Milligan, 2007).

## 2.8 | Quasi-extinction probability

We performed 10,000 simulations to estimate the quasi-extinction probability function after manipulating two variables: (a) the starting-life-stage distribution (proportions of juveniles to adults) and (b) the frequency of disturbances (hurricanes). All simulations were performed using the popbio package in Rstudio version 1.2.1335 (Stubben & Milligan, 2007).

### 2.8.1 | First variable

We simulated the dominance of nonreproductive versus reproductive individuals on the probability that the population will reach extinction. Given that in the last census, the population of *B. cubensis* was found to be composed of approximately 500 individuals, we assumed two cases: one case in which the population was composed mainly of juveniles (nonreproductive individuals) [200, 200, 50, 50], indicated by black lines on the plot; and another case in which the population was composed primarily of adults (reproductive individuals) [50, 50, 200, 200], indicated by red lines on the plot. In these two cases, we considered a range of minimum numbers of individuals (from 50 to 10) below which the population reached quasi-extinction.

### 2.8.2 | Second variable

We simulated the effects of increasing proportional damage caused by a perturbation (i.e., hurricane) on the quasi-extinction probability of *B. cubensis*. The 10 lines go from the actual baseline of the population (500 individuals) with 0% newly affected individuals (the lower right black line) to a progressive elimination

of 10% of the total individuals each time until 90% of affected individuals is reached (upper left black line). Each of these simulations was performed independently of the initial size distribution (juveniles and adults) of the population.

## 3 | RESULTS

### 3.1 | Deterministic population growth

A deterministic mean model constructed with the 39 matrices (Figure 2b) yielded the mean population growth:  $\lambda_{mean} = 0.9673$ . The variance matrix (Figure 2b) associated with these matrices showed that the variability was mainly associated with plants that remained in the largest size class and their reproductive outputs.

### 3.2 | Stochastic population growth

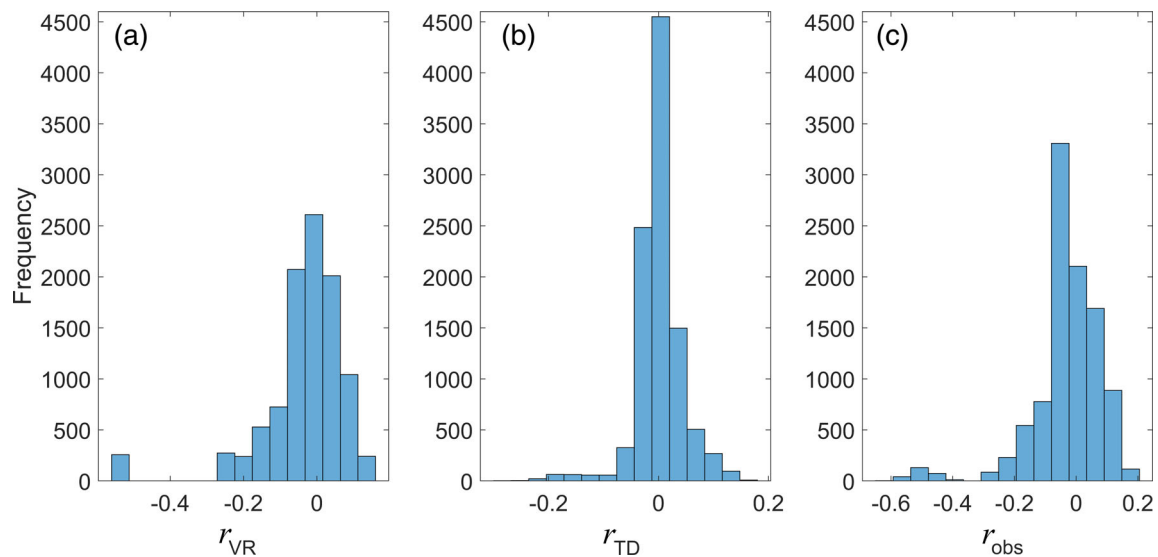
Assuming equal probabilities for the 13 annual transitions from 2006 to 2019, the long-term median-log stochastic growth rate was estimated as  $\lambda_S = -0.0012$  (75% percentile = 0.0369; 25% percentile = -0.043). This relative contribution of the growth rate can be attributed to transient and asymptotic dynamics, as the median log transient growth rate was estimated to be -0.0011 (75% percentile = 0.0184; 25% percentile = -0.0174) and the median log asymptotic growth rate was estimated to be -0.0252 (75% percentile = 0.0482; 25% percentile = -0.0531).

### 3.3 | Decomposing stochastic population growth

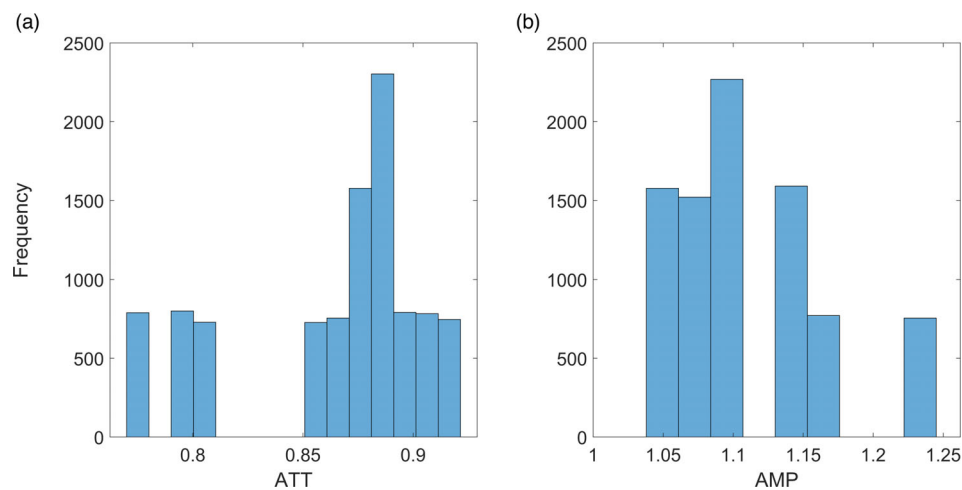
On average, transient responses explained 86% of the variation in the observed population growth rates ( $R^2$  for  $r_{TD}$  vs.  $r_{obs}$ ), compared to 4% of the variation in the vital rates ( $R^2$  for  $r_{VR}$  vs.  $r_{obs}$ ) (Figure 3).

### 3.4 | Transient dynamics

The overall tendency of *B. cubensis* boomed or busted in response to the temporally varying stable stage structure (Figure 4). The transient bounds calculated by simulating the dynamics of *B. cubensis* included a mean reactivity (AMP) ranging from a minimum value of 1.050 to a maximum value of 1.254 and a mean first-step attenuation (ATT) ranging from a minimum value of 0.763 to a maximum value of 0.943 at  $t = 500$  to  $t = 501$ .



**FIGURE 3** (a) Proportion of the variation in the observed population growth rate ( $r_{obs}$ ) due to the variation in demographic rate ( $r_{VR}$ ), (b) due to transient behavior ( $r_{TD}$ ); (c) variation in the observed population growth rate ( $r_{obs}$ ) based on 10,000 simulation values [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



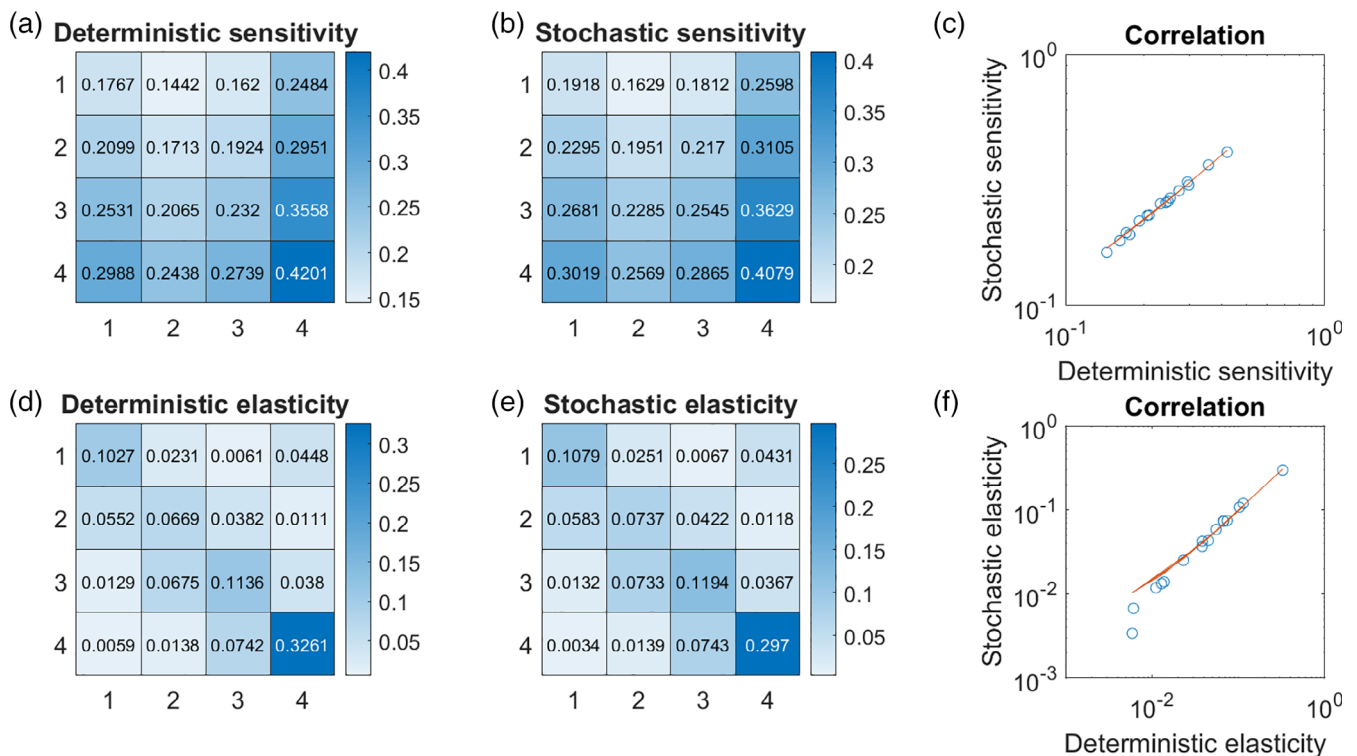
**FIGURE 4** (a) The maximum attenuation (ATT) as the smallest future density relative to an SSD (steady stage distribution) population for any *no* (initial conditions) and (b) the maximum amplification (AMP) as the largest future density relative to an SSD population for any *no* (Stott et al., 2011). Following Ellis and Crone (2013), we analyzed amplification and attenuation at  $t = 1$  (i.e., reactivity and first-step attenuation as maximal and minimal column sums of the 10,000 simulations on the population mean matrix) [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 3.5 | Deterministic and stochastic sensitivity and elasticity

A high correlation was observed between the deterministic and stochastic sensitivities and elasticities of  $\lambda_s$ . For the deterministic and stochastic approaches and for both single and proportional changes, the key matrix element that contributed most to  $\lambda$  was reaching and maintaining status in the larger size class (Figure 5).

### 3.6 | Quasi-extinction risk

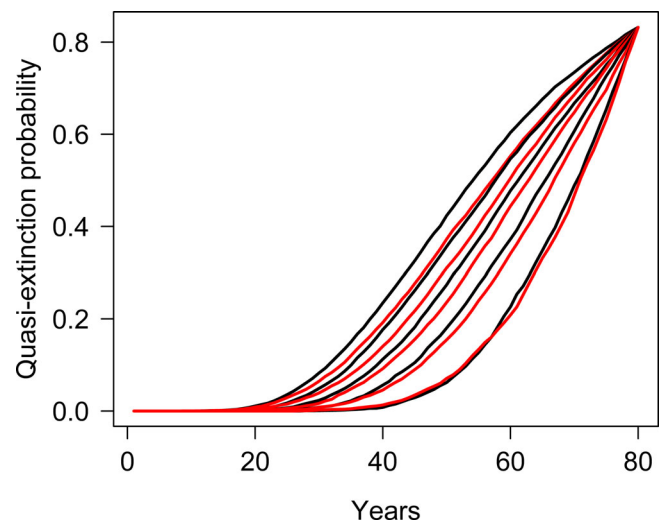
Because the transient dynamics are dependent on the initial size composition of the population, we ran extinction risk analyses under two scenarios: a population composed mainly of juveniles and another population composed mainly of adults. In these two scenarios, following Dulić et al. (2020), who argued that terrestrial orchid populations are close to extinction when the declining number of plants reaches



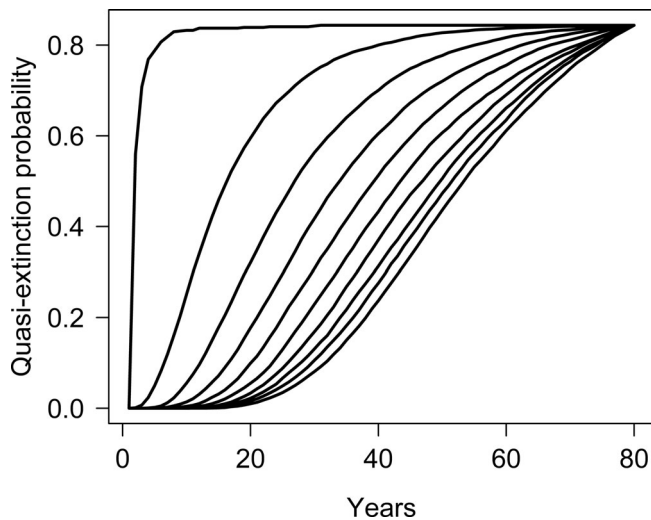
**FIGURE 5** Left column (a): Sensitivity ( $\frac{\partial \log \lambda_1}{\partial a_y}$ ) and (d) elasticity ( $\frac{\partial \log \lambda_1}{\partial \log a_y}$ ) of *Broughtonia cubensis* based on the mean matrix deterministic model. Middle column: (b) sensitivity ( $\frac{\partial \log \lambda_s}{\partial a_y}$ ) and (e) elasticity ( $\frac{\partial \log \lambda_s}{\partial \log a_y}$ ) obtained from the stochastic model. Right column: (c) correlation between stochastic sensitivity and deterministic sensitivity and between (f) stochastic elasticity and deterministic elasticity. The intensity of the sensitivity or elasticity values are indicated by different intensities of the blue color on the background and the black and white color on their values [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

10 and that less than 1% of protocorms reach advanced stages (Jersáková and Malinová, 2007), we evaluated different thresholds to reach quasi-extinction from 50 to 10 individuals. While little risk of falling below the quasi-extinction threshold was found for the first 25 year following a hurricane, an 85% risk of falling below this threshold is calculated by 80 year for the two hypothetical scenarios (Figure 6). Notably, in all scenarios and thresholds, the population composed mostly of juveniles had a higher probability of reaching quasi-extinction than the population composed mostly of adults.

Finally, we simulated the effect of increasing the number of affected individuals due to the hurricane occurrence probability on the quasi-extinction probability over 80 year. These simulations ran from the absence of new hurricane events (0% affected individuals, our baseline curve) to a progressive increasing elimination of 10% of individuals on each curve until the elimination of 90% of the actual individuals was reached (only 50 individuals remained). While there was little risk of falling below the quasi-extinction threshold before 20 year without a new hurricane event, this probability decreased to 5 year if 90% of individuals were affected by a new hurricane event (Figure 7).



**FIGURE 6** We simulated the time taken to reach quasi-extinction thresholds ranging from 50 to 10 individuals under two different scenarios given the actual population size of ca. 500 individuals. Scenario 1: The population was dominated by adults (red lines), with and initial condition,  $n_0 = [50, 50, 200, 200]$ ; Scenario 2: The population was dominated by juveniles, (black lines),  $n_0 = [200, 200, 50, 50]$ . In the two scenarios, the simulation goes from 0% occurrence of hurricanes (lower line) to 90% occurrence of hurricanes (upper line). The number of replications in each simulation was 10,000 [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 7** The effect of increasing the percentage of the total population size affected by the occurrence of a hurricane. The quasi-extinction probability was fixed at  $N_x = 50$  individuals, and the number of replications in each simulation was 10,000. The different black lines range from 0% hurricane occurrence (right low line) to a 90% probability of being affected by a hurricane (left upper line)

## 4 | DISCUSSION

Many orchids are threatened by random disturbances (i.e., hurricanes) and habitat changes (Crain et al., 2019; Crain & Tremblay, 2014; Crain & Tremblay, 2017; Fay, 2018; Swarts & Dixon, 2009).

The epiphytic orchids living in the Caribbean Sea basin in Guanahacabibes National Park (West Cuba) are exposed to random temporal occurrences of hurricanes, which disturb their demography (Landsea et al., 1999). Hurricane Ivan was particularly strong and seriously affected the coastal vegetation of the Guanahacabibes Peninsula in September 2004, causing considerable damage to local epiphytic orchids (Raventós, González, Mújica, & Bonet, 2015; Raventós, González, Mújica, & Doak, 2015). In the epiphytic orchid *B. cubensis*, Hurricane Ivan killed 242 individuals in the four size classes ( $S_1 = 51$ ,  $S_2 = 58$ ,  $S_3 = 93$  and  $S_4 = 40$ ), representing 34% of the original population. The effects of the hurricane on tree communities varied according to the type of vegetation. Coastal xeromorphic vegetation was less affected: 3.7% of its trees were completely lost, while semideciduous forest and sandy coastal vegetation were more affected, with 8.8% and 22.6% losses, respectively (Mújica, 2007).

Preliminary posthurricane assessments suggested that microhabitat conditions and species morphology were the determining factors affecting the fate of populations in the short-term and medium-term (Mújica et al., 2013;

Raventós, Mujica, Wiegand, & Bonet, 2011; Wiegand, He, & Hubbell, 2013).

Tremblay (1997), working on *Lepanthes caritensis* (Orchidaceae), found that among all projection matrix elements, nonreproductive adult survival rates ( $S_{44}$ , the probability of remaining a nonreproductive adult from  $t$  to  $t + 1$ ) have the greatest relative impact on  $\lambda$  for a given proportional change. Furthermore, Crain et al. (2019) reanalyzed this rare orchid species using transfer function analyses and confirmed the significance of nonreproductive adult survival rates ( $S_{44}$ ) but also showed that seedling survival ( $S_{11}$ , the probability of remaining a seedling from  $t$  to  $t + 1$ ) and juvenile survival ( $S_{22}$ , the probability of remaining a juvenile  $t$  to  $t + 1$ ) were nearly as important depending on the perturbation strength. In our case, in *B. cubensis* orchids, deterministic and stochastic elasticity analyses showed that the reproductive adult survival rates ( $S_{44}$ ) and seedling survival ( $S_{11}$ ) had the greatest relative impacts on  $\lambda$  for a given proportional change.

We found a high correlation between deterministic and stochastic sensitivities and elasticities. The same results were found by Caswell (2001) when analyzing a population of threatened desert tortoise (*Gopherus agassizii*) (Doak, Kareiva, & Klepetka, 1994) and when reanalyzing the impact of the presence/absence of fire on the neotropical savanna grass *Andropogon semiberbis* (Silva, Raventos, Caswell, & Trevisan, 1991); the same comparison of deterministic and stochastic sensitivities and elasticities was made by Dixon, Friday, Ang, Heppell, and Kshatriya (1997), who applied three population management goals, conservation, harvest and control, depending on the species analyzed.

Caswell (2001) synthesized these results, indicating that in general, it seems that the sensitivity and elasticity obtained from a deterministic environment could be used as predictors for the corresponding results of stochastic models except when the variability becomes very large (Benton & Grant, 1996). Furthermore, the addition of environmental stochasticity to these models is robust in relation to which part of the life cycle would have the greatest impact on growth (Caswell, 2001). In our case, this part of the life cycle represented the largest size class.

Raventós, González, Mújica, and Doak (2015) conducted a 5-year study of the demography of a rare ghost orchid, *Dendrophylax lindenii*, in Guanahacabibes National Park to assess the stability of a protected population of this species in Cuba. Using both stochastic and deterministic integral projection models, we found that the mean annual population growth rates were negative ( $\lambda = 0.975$ ). However, we found that both the population growth rate and extinction risk were highly sensitive to survival rates and reproduction, which are difficult-to-quantify for many



orchids, including our study species. Hurricanes, which are predicted to increase in frequency as a result of climate change, dramatically increase adult mortality in orchids. Simulations of these effects indicate that hurricanes and similar disturbances could result in near-certain extinctions in short time horizons (25 year) if their annual probability of occurrence exceeds 14%.

Management strategies should be applied to aid in the recovery of declining *B. cubensis* populations (Fay, 2018; Vale et al., 2013). Feasible strategies to ensure the survival of local populations could integrate in situ conservation practices and ex situ propagation (Swarts & Dixon, 2009). Our results indicate a high probability of quasi-extinction risk related to a habitat that is frequently affected by hurricanes when the population is composed mainly of juveniles. Sensibility and stability analysis showed that the adult class survival rates ( $S_{44}$ ) and seedling survival rates ( $S_{11}$ ) contributed most to the population growth rate. Manipulating the initial class sizes and increasing the adult and seedling class sizes by introducing reproductive adult and juvenile individuals could modify the quasi-extinction risk of *B. cubensis* in Guanahacabibes National Park.

Management strategies must lead to the rapid recovery and restoration of populations after a disturbance occurs, including transfer of orchids from felled trees to standing trees (Crain et al., 2019; Tremblay, 2008). Additionally, the translocation of a reservoir of adult individuals cultivated and preserved in orchid nurseries and botanic gardens could be considered; this would provide both seed and in vitro cultivation to ensure a sufficient individual stock (Gale, Fischer, Cribb, & Fay, 2018; Pedersen, Find, Petersen, & Seberg, 2018). Successful artificial reintroduction of a small epiphytic endemic orchid obtained through in vitro cultivation in southern México, *Barkeria whartonia* (C. Schweinf.) Soto Arenas, was reported by Segovia-Rivas, Meave, González, and Pérez-García (2018). Complementary strategies to restore populations could include the relocation of reproductive individuals from trees affected by hurricane events to suitable host trees to minimize the impact of the perturbation on the population size. Alternatively, we could increase the population by reintroducing individuals from populations safe from hurricanes, such as those maintained in the Orquideario of Soroa Botanical Garden (Artemisa, Cuba). Relocation conservation practices are common for epiphytic orchids. High survival rates during the first year after population restoration were obtained by Tremblay (2008) when examining the relocation of the protected orchid *Lepanthes eltoroensis* Stimson from host trees affected by hurricane Georges to unaffected trees.

In summary, while our modeling approach represents a way to envision different scenarios depending on the

structure of the population, it is nevertheless a projection, and the long-term dynamics of the population may or may not follow these projected dynamics.

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