

SMALL POPULATIONS ON SMALL ISLANDS: WHAT CHANCE DOES AN ORCHID HAVE?

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Premise of research. Small populations on small islands are intrinsically more vulnerable to population decline and extinction. Nevertheless, small native populations that occur on multiple islands may have life-history characteristics that buffer impacts from novel disturbance regimes, and, rather than contracting, populations may be expanding. We monitored three populations of the orchid *Brassavola cucullata* from two Caribbean islands and asked what the likelihood of population persistence is.

Methodology. Over 3–4 yr, we recorded growth, fruit production, herbivory, recruitment, and mortality for all plants in each of our populations. We assessed persistence and predicted possible population changes using both population projection models (PPMs) and integral projection models (IPMs). Our results include a mixture of traditional indexes (λ and elasticities) and more recent indexes (transient dynamics and nonlinear sensitivities).

Pivotal results. Growth, reproduction, and predicted population persistence varied among years and islands. IPMs and PPMs gave similar results. The overall trend is toward a reduction in population growth rates, although population reactivity may buffer this pattern in the short term ($\lambda > 1$). Populations would be extremely vulnerable to reduction if small plants dominated, yet even with an abundance of large plants, substantial reductions in population density are possible. Medium and larger plants contribute more to the persistence of the population, yet the survival and growth of small individuals might have greater effects on λ if retrogression is observed. To attain population stability, effective recruitment rates must increase dramatically.

Conclusions. Populations of perennial plants on small islands can fluctuate substantially, suggesting a degree of vulnerability. While *B. cucullata* shows a general trajectory of decline, there are some signs of stability despite deforestation and herbivore activity. The outlook is precarious for the Saba population given the predominance of younger plants, and all three populations could decline if spasmodic recruitment fails to occur, which may happen if disturbance regimes change and the ongoing warming and drying trends persist.

Keywords: *Brassavola cucullata*, population dynamics, Lesser Antilles, transient dynamics, island conservation, Orchidaceae.

Online enhancements: supplementary appendix, tables, and figures.

Introduction

Under the best of conditions, long-term persistence of a species on a small island is not assured (Simberloff and Wilson 1969, 1970). Aside from the underlying stochastic-like phenomena of extinctions and immigrations, small islands have often suffered

from the activities of humans disproportionately more than larger islands or continental areas (Denslow 2003). Anthropogenic land use not only has been widespread on islands but also has changed drastically over time, substantially affecting ecosystem processes, community structure and composition, and species interactions (Lugo 2004; Prasad et al. 2010). Caribbean islands are no exception, as European colonization was often accompanied by a severe reduction in forest cover, to the extent that only 1%–5% of the original forest cover exists on some islands (Wadsworth 1950; Lugo 2004). While more recent socioeconomic changes have facilitated the recovery of ecological communities and ecosystems,

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the original forest structure, composition, and interactions have been modified largely because of the influx of alien taxa (e.g., Attena 1976; Hubbard 1996; Abelleira Martínez et al. 2010; Lugo et al. 2012).

Despite the radical ecological transformations that have occurred over the previous 500 yr, much of the Caribbean flora has been resilient or at least able to persist, contributing to the region's status as one of the world's biodiversity hot spots (Mittermeier et al. 2004). Current forest cover (old growth, secondary forests, and forestlike plantations) is variable across the Caribbean. At the extremes, Haiti may be the most depauperate, whereas the Bahamas are largely forested (84%). Most islands generally have about 20%–30% forest cover (FAO 2000; Acevedo-Rodríguez and Strong 2008). While widespread species, native or not, generally have excellent dispersal capabilities (Rojas-Sandoval and Acevedo-Rodríguez 2014), vagility is highly variable among taxa, ranging from high dispersibility to rare dispersal; their populations persist regardless of the ecological turmoil around them. Over time, disturbance regimes shift, and populations may have cycled, dependent on local refugia and/or dispersal, which occurs naturally in island systems (Thornton 1996).

The orchid family exhibits a broad spectrum of demographic dynamics and ecological amplitudes. Despite having wind-dispersed, dustlike seeds, presumably generating long-tailed dispersal kernels, many orchid species have restricted distributions. In the Lesser Antilles (lat. ca. 12°–18°N, long. ca. 59°–63°W), a Caribbean archipelago composed of relatively small islands—only Guadeloupe and Martinique exceed 1000 km²—some species have restricted distributions, often occupying higher elevations, whereas others are more widespread, often occupying lower elevations (Trejo-Torres and Ackerman 2000; Ackerman et al. 2007). This pattern is seen in continental areas as well as for other taxa (Ricklefs and Bermingham 2002; Kirby 2011; Steinbauer et al. 2012; Pérez-Escobar et al. 2017). Some species inhabit disturbed habitats, whereas others persist in relatively undisturbed regions on islands; however, the occupied areas are almost always very localized, regardless of protection regimes.

Are those species with small localized populations on small islands a sign of health and vitality, or are we witnessing their gradual demise? Herein we examine the population dynamics of one of those widespread orchids whose distributions give the appearance of persistent survival. We ask whether populations of *Brassavola cucullata* (L.) R. Br. in the Netherlands Antilles are stable or not and assess biotic and abiotic factors that may influence the population vitality of this orchid. To evaluate the likelihood of population persistence for this epiphytic and rupicolous species, we model the life history of the species using stage-based population projection models (PPMs). However, because population sizes are small, we calculate transition probabilities employing a Bayesian approach, the Dirichlet distribution (Frigyik et al. 2010), and explore the likelihood of population density changes in time using transient dynamics (Stott et al. 2011, 2012a, 2012b). Populations that are not at stable stage distribution (SSD) are expected to behave differently from those that are. While these methods mitigate the issues of small population sizes to a certain extent, interpretation of population growth rates may still suffer from bias and high variance. Consequently, we also assess the population status of *B. cucullata* using integral projection models (IPMs), a method that usually performs better when populations are small (Ramula et al. 2009). Finally, we seek

explanations for our demographic dynamics from the activities of pollinators and nonindigenous herbivores.

Methods

Study Species

Brassavola cucullata belongs to the subtribe Laeliinae and is an epiphytic and rupicolous species that can form large clusters of shoots. Each shoot is composed of a single stem 3.5–12.5 cm long and 1–3.5 mm in diameter and bears a single semiterete leaf 16–35 cm long and only slightly thicker than the stem. The terminal inflorescences are 3–30 mm long and are usually single flowered. The flowers are largely white, with the slender perianth parts often grading to pale yellow toward their apices. The lip is ovate acuminate and fimbriate around the column. The cuniculus extends into the inferior ovary and is nectarless. The deceitful flowers have a heavy, sweet nocturnal fragrance that may linger into the day. Fruit production is pollinator dependent. Capsules take several months to develop and are pedicellate and beaked (remnants of the column); the body of the capsule is 2–5 cm long and produces many thousands of dustlike seeds (Ackerman 2014).

The pollinators of *B. cucullata* are unknown on St. Eustatius, where we have two study populations, but on the nearby island of Saba, where we studied one population, Chipka (2009) reported that the pollinators are hawk moths (Sphingidae): *Manduca sexta* (L.) and *Protambulix strigilis* (L.). Larvae of the former feed primarily on Solanaceae, while the latter feed mostly on Anacardiaceae. These two plant families are abundant on Saba and St. Eustatius (Axelrod 2017). Both moth species are widespread not only in the Caribbean but also in continental regions of the Americas (Hodges 1971).

Brassavola cucullata is known from Mexico to Nicaragua, Colombia to Venezuela, Trinidad and Tobago, and then northward through many islands of the Lesser Antilles up to the US Virgin Islands (Ackerman 2012). Despite being widespread, populations are extremely localized. Herbarium records indicate that populations exist (or existed) on the Antillean islands of Grenada, St. Vincent, Martinique, Dominica, Marie Galante, La Désirade, Guadeloupe, Montserrat, Antigua, Nevis, St. Kitts, St. Eustatius, Saba, Barbuda, St. Barthélemy, St. Martin, and St. Thomas.

Study Sites

We monitored three populations. Two are on St. Eustatius, an island of 21 km²: the Boven population is primarily rupicolous (elevation ca. 235 m; lat. 17°37'16"N, long. 63°13'34"W), whereas the Quill population is entirely epiphytic (elevation ca. 200–300 m; lat. 17°28'20"N, long. 62°57'56"W). The third is on the nearby island of Saba, which is just 13 km², and the *B. cucullata* population there occurs mostly on trees between 135 and 325 m in elevation (lat. ca. 17°38'02"N, long. ca. 63°13'34"W). Voucher specimens are deposited at UPRRP.

Threats to population health vary. On Saba and St. Eustatius, the present primary threats are likely goats. We have seen evidence of goat herbivory on both islands. On Saba, where goat populations have become quite large, they may also be preventing the regeneration of a common phorophyte species, *Tabebuia heterophylla* (DC.) Britton. This may be ominous because some of the larger trees festooned with *B. cucullata* are dying. Occasionally,

the large, herbivorous native lizards, *Iguana iguana* L. on Saba and *Iguana delicatissima* (Laurenti) on St. Eustatius, may also eat plants, but these animals are far less abundant than goats and are not expected to be a significant factor. While the impact of goats on local vegetation (including orchids) is heatedly debated by local residents (Nielsen 2013), goats are known to eat other thick, tough-leaved Laeliinae in the Caribbean (Meléndez-Ackerman et al. 2008). Rats may also be a problem here as they are elsewhere in the region (Ackerman 1989). On a small island off the coast of Guadeloupe where goats have been eliminated, *B. cucullata* occasionally shows signs of herbivory, and black rats are the likely culprits (S. Rives and N. Barré, personal communication to R. L. Tremblay).

Data Collection

At each of the three populations, we tagged every plant of *B. cucullata* that we could find: Quill, 498; Boven, 535; and Saba, 834. We noted whether each plant was epiphytic or epilithic; measured the height aboveground; looked for evidence of leaf herbivory; measured the length of the longest leaf; and counted the number of leafy shoots, flowers, and fruits. Length of the longest leaf and number of leafy shoots are both measures of plant size. If flowers were present, we recorded whether they had been successfully visited by visually inspecting for pollinarium removal or pollinia on the stigma. These data were obtained once a year during the most active period of flowering. Our observations at the Quill population spanned 2009–2013, at Boven 2010–2013, and at Saba 2011–2014.

Determination of Categorical Groups for the PPM

To determine the categorical size groups for PPM analyses, we regressed plant survival rates against individual size (number of leaves). Survival parameters follow a binary variable (0 = dead, 1 = alive), which is a generalized linear regression, using the inverse logit function on the probability of survival (P_{surv}), $\text{logit}(P_{\text{surv}}) = \beta_0 + \beta_1 \times \text{size}$, where β_0 is the coefficient of the intercept and β_1 is the coefficient that relates the size variable to the probability of survival of the size of the plant (number of leaves). Analyses were performed using IPMPack (Merow et al. 2014; R Core Team 2018). Plant size ranged from 1 to 336 leaves. Observed and expected survival rates are lowest in the smallest plants (one or two leaves), rise as leaf number increases, and then stabilize when in the range of 20 leaves and more (fig. A1; figs. A1–A5 are available online). For the 95% confidence intervals (CIs) of probability of survival (binomial probabilities), we used the function `binconf` from the package `Hmisc` (Harrell 2018) following the Agresti and Coull (1998) suggestions for nonsymmetric distribution.

Analysis of Population Growth Rates Using PPMs

With a life-cycle diagram, we illustrate the hypothetical transitions between four developmental stages in successive census dates (fig. 1). Transition values represent the probability that individuals advance or regress from one developmental stage to another between consecutive census dates (i.e., from time t to time $t + 1$). In the case of *B. cucullata*, plants can leapfrog stages and regress to the smaller stages (i.e., fewer leaves). We did not incorporate the seed stage in these analyses because orchid seeds

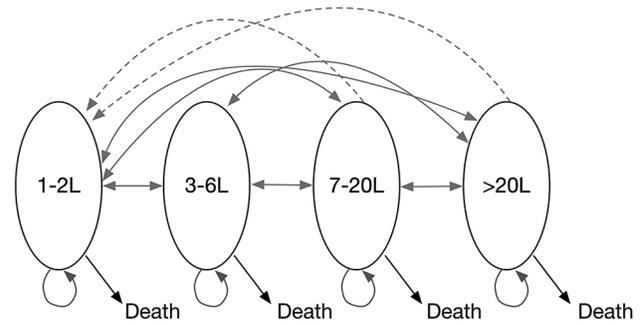


Fig. 1 Hypothetical life cycle of *Brassavola cucullata* used in analyses. The size categories represent the number of leaves (L): 1 or 2, 3–6, 7–20, and >20. The solid lines with arrows are the transitions from one stage to another or stasis (remaining in the same stage). The dashed lines represent reproduction.

are so small that quantification of production and recruitment from seeds to seedlings is exceptionally difficult (Swarts and Dixon 2017). We also did not use estimates based on results from other orchid taxa because such surrogates often give misleading results (Che-Castaldo et al. 2018). All of our transition probabilities and fecundities for *B. cucullata* are yearly transition estimates. Sample sizes at the beginning of each survey are noted in the supplementary material (table A1; tables A1 and A2 are available online).

After the grouping of plants of different sizes was determined, the transition probabilities among the stages were estimated using the Dirichlet distribution, which is the multivariate generalization of the beta distribution (fig. A2). The parameters were estimated using a prior distribution with a Dirichlet distribution to obtain a posterior distribution of the parameters (Frigyik et al. 2010). We used the R package `MCMCpack` (function `MCmultinomialdirichlet`, ver. 1.4-4; Martin et al. 2011; R Core Team 2018) to calculate the mean transition probabilities, SDs, and medians. These parameters were visualized using posterior probability densities, which were graphed with the R package `ggplot2` (ver. 1.0.0; Wickham 2009). The prior distribution for the Dirichlet distribution was based on experience (a priori prior estimates from R. L. Tremblay) and corresponds to the expected transition of stasis, which is often dominant, and transitions to much smaller or larger stages (plus-minus two stages), which are rare (table A2). Prior distribution values have a low influence on parameter estimates if the observed sample sizes are large. To the best of our knowledge, the Dirichlet distribution has not been used to estimate transition probabilities for population studies.

We estimated intrinsic population growth rates for the individual transition periods (Caswell 2001) and calculated stochastic population growth rates and 95% CIs as described by Tuljapurkar (1982). The latter analyses were performed using the `popbio` package and the function `stoch.growth.rate` (Stubben and Milligan 2007).

Analysis of Population Growth Rates Using IPMs

The IPMs describe how the size distribution of individuals changes from one time step to another (Easterling et al. 2000; Metcalf et al. 2013; Merow et al. 2014). The kernel is the sum of

two functions. One describes the survival probability and growth (or shrinkage) of survivors (p kernel), and the second is the reproductive contribution of each individual and the size distribution of the new seedlings (f kernel). In *B. cucullata*, the p kernel was represented by the survival probability of individuals from a time step, $s(z)$, and the size (z) distribution of the survivors, $G(z|z)$. The f kernel included whether a plant was flowering or not (conditional to surviving, $P_{\text{flower}}[z]$), and if so, how many fruits were produced per plant ($F_{\text{fruits}}[z]$), the establishment probability (P_{estab} , a constant), and the size distribution of new seedlings ($F_{\text{recruit size}}[z]$). All of these vital rates are potentially a function of size in time t , and thus the entire kernel for *B. cucullata* was formulated as follows: $n_{t+1}(z') = \int_{\Omega} s(z) \times G(z'|z) + P_{\text{flower}}(z) \times F_{\text{fruits}}(z) \times P_{\text{estab}} \times F_{\text{recruit size}}(z')$, where z' is the plant size at time $t + 1$, and Ω represents the minimum and maximum plant sizes. See appendix text A1, available online, for some assumptions considered here to build IPMs for *B. cucullata*.

Even though the number of leaves was used to describe growth in the species and to build PPMs for *B. cucullata*, this trait cannot be used to parameterize IPMs because of its discrete condition. Nevertheless, the length of the largest leaf also describes the size dimensionality of the species, and it was significantly correlated with the number of leaves (fig. 2; Pearson's correlation coefficient, $r = 0.46$, $P < 0.01$). Therefore, the length of the largest leaf was used here as a growth variable for the development of the IPMs. Because some years' leaf length data were not recorded for the Saba population, we restricted our IPM analyses to the two populations on St. Eustatius. As in Ortiz-Rodríguez et al. (2019), we used generalized linear mixed models (GLMMs) with random-year effects to estimate the vital rates of the species and to parameterize each of the IPMs. We assessed the relationship of size with survival and the probability of reproduction (presence/absence of open flowers) using binomial error distribution, and fruit production (number of fruits per plant) was modeled with

Poisson error distribution, while growth was analyzed using Gaussian error distribution. To estimate the establishment probability, we divided the number of new recruitments observed in the field (11, according to J. D. Ackerman) by the maximum number of fruits (35 in total) reported over the study period. It was not possible to link the new seedlings with individual plants, so we used the mean and SD of the size distribution of the new seedlings for inclusion in the fecundity function, assuming a normal distribution. We fitted a series of polynomial models including different size combinations (linear, quadratic, and cubic), and the model with the lowest Akaike information criterion was chosen to build each of the IPMs using the year-specific statistical parameters (Ortiz-Rodríguez et al. 2019; fig. A3). Once the IPMs were created, we estimated the population growth rates and elasticity using the IPMpack (Metcalf et al. 2013). We also used the popbio R package (Stubben and Milligan 2007) to estimate stochastic population growth by adding each of the yearly IPMs developed for each locality. To assess transient population dynamics, we estimated each of the indexes proposed by Stott et al. (2010b, 2011) using the popdemo R package (Stott et al. 2012b; see "Population Dynamics Analysis and Transient Dynamics" for details on transient indexes). Nevertheless, and contrary to the PPMs, we lack both the size classes and the initial population size distribution (n_0) in each one of them. Therefore, n_0 was estimated as the relative density between each mesh point of the IPMs (Ortiz-Rodríguez et al. 2019).

Population Dynamics Analysis and Transient Dynamics

The traditional asymptotic analysis of PPMs focuses on long-term population dynamics to predict population trajectories and assumes SSD. SSDs (the predicted population structure when an asymptotic growth rate is attained) and elasticities (a measure of

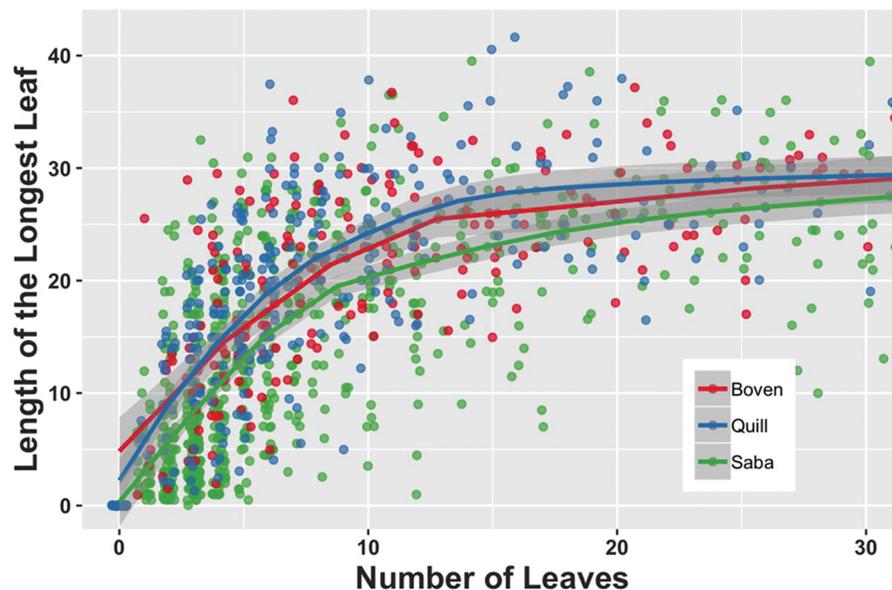


Fig. 2 Number of leaves and length of the longest leaf of *Brassavola cucullata* at three sites. Note that plants from Saba require more leaves to attain the same length than at the other two sites. Note that plants can have >330 leaves.

evaluating the effect of the proportional change of a parameter on the growth rates) are calculated and are density-independent and time-invariant indexes (Caswell 2001). The assumptions behind the use of SSDs may be unwarranted, as a survey of the literature shows that few populations are at SSD (Williams et al. 2011; Ellis 2013). Initial demographic distribution often differs from the SSD because of biotic, abiotic, or anthropogenic disruptions; changing population structure; and vital rates. The difference between non-SSD initial structure and an SSD structured population may lead to either a temporary change in the rate of increase of population density (amplification) or a temporary decrease in density (attenuation). If no other perturbations or disturbances (e.g., hurricanes, flash floods, landslides, biotic invasions, anthropogenic modifications) occur, then the transient dynamics models are expected to settle to the SSD given enough time. The time that it takes to reach the stable stage is the transient period (Stott et al. 2011). Transient population dynamics are usually not evaluated in PPMs; however, indexes such as the damping ratio (Caswell 2001), Keyfitz's delta (Keyfitz 1971), and Cohen's cumulative distance metric (Cohen 1979) are sometimes considered indirect indexes of transient dynamics of populations, but they do have limitations (Stott et al. 2011).

We used the package *popdemo* in R (ver. 1.3-0; Stott et al. 2012b) to calculate the following indexes of transient dynamics and the bounds of the first time step (Stott et al. 2011): reactivity (maximum population growth in a single time step relative to the stable stage growth), first time attenuation (minimum population growth in a single time step relative to the stable stage growth), maximum amplification (the largest possible future population density relative to a stable growth rate and the same initial population structure), and maximum attenuation (the smallest possible future population density relative to a stable growth rate and the same initial population size). We also calculated two other indexes: amplified inertia (the largest long-term population density relative to a population with a stable growth rate and the same initial density) and attenuated inertia (the smallest long-term population density relative to a population with a stable growth rate and the same initial density). In other words, populations that have not achieved SSD are likely to achieve long-term population density at a fixed ratio below or above the expected SSD (Stott et al. 2011, 2012a). Thus, interpretation of transients represents the ratio of population densities that are not at SSD as compared with a population starting at SSD.

The response on λ to perturbations of demographic parameters was evaluated using transfer function and multiple perturbations of several demographic parameters (growth and stasis) on the basis that natural perturbations affect all the demographic parameters of the population to different degrees (Hodgson and Townley 2004; Hodgson et al. 2006). Transfer functions are commonly used in the analysis of nonlinear, time-invariant systems. They allow one to calculate the precise relationship between the asymptotic growth rate, λ , and the intensity of perturbation, δ . We need to define the position of the vital rate perturbed through two vectors, \mathbf{e} and \mathbf{d} , the intensity of the perturbation, with one scalar, δ , to obtain the new asymptotic growth rate as a consequence of the perturbed vital rate. The exact relationship between perturbation and growth rate was given by Hodgson and Townley (2004) as $\delta^{-1} = \mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-1}\mathbf{d}$, where \mathbf{I} is the identity matrix of the same dimension as \mathbf{A} .

Moreover, we investigate the expected effect of changes in parameter estimates on λ using a nonlinear function (Stott et al. 2012a). Nonlinear sensitivities are calculated (a modified *tfa_lambda* function from the *popdemo* package was used) to evaluate the change in λ to a change in a matrix element. The modified script is available in the appendix (app. script) and was graciously provided by Dave Hodgson, University of Exeter. This script limits the perturbation to a more reasonable range. Before all analyses mentioned above, we tested the assumptions of reducibility and ergodicity using the tests as described in Stott et al. (2010a), and all were met.

In addition, to evaluate the amount of recruitment needed in a population to attain a λ of 1, we increased the recruitment parameters (top right of each matrix), holding all other parameters in the matrix steady. This is an estimate of the mean recruitment per adult plant to hold the population at stasis. The assumptions are that recruitment is a function of only the fruit set of the previous year and that no migration and no seed bank are present.

Results

Plant Size Distribution and Survival

Leaf length varied little among individuals ($\mu \pm \text{SD}$: 18.1 \pm 0.29 cm). Once leaf number increases to about 20 leaves, leaf length becomes somewhat constant (fig. 2). However, the average length of the longest leaf was different among sites ($\mu \pm \text{SE}$: Quill, 20.5 \pm 0.55; Boven, 23.1 \pm 0.62; Saba, 15.2 \pm 0.36; one-way ANOVA, $F = 1517$, $df = 3, 1437$, $P < 0.0001$). Ultimately, plants at all sites attain the same mean leaf length, but it requires plants with more leaves to do so on Saba than on St. Eustatius. The number of leaves per plant was significantly different among sites, and Saba skewed toward having smaller plants (fig. 2; $\mu \pm \text{SE}$: Quill, 16.8 \pm 1.1; Boven, 27.3 \pm 2.4; Saba, 12.9 \pm 0.7; GLMM with Poisson [link = log], $df = 2, 1514$, null deviance = 38,130, residual deviance = 35,500; coefficients: Quill, 2.82; Boven, 3.31; Saba, 2.56). As expected, small plants with one or two leaves had a lower probability of survival from one year to the next (mean and 95% CI: 65.0% [56.3–72.9]) and a larger CI, and survival probabilities increase rapidly for larger plants, to more than 99% for the largest plants (mean and CI: 3–6 leaves, 95.2% [92.2–97.3]; 7–20 leaves, 97.7% [95.1–98.9]; >20 leaves, >99.1% [97.0–99.8]), with a decrease in the CI of the parameters as plants become larger.

Transition Probabilities

The transition probabilities are shown as a posterior probability density in addition to the mean, SD, and median for Quill, Boven, and Saba (figs. 2, A2) and the individual-year transitions for Quill (2009–2010, 2010–2011, 2011–2012, 2012–2013), Boven (2010–2011, 2011–2012, 2012–2013), and Saba (2011–2012, 2012–2013, 2013–2014). The precision of our estimates can be viewed in the density distribution for every transition probability for every year and site (fig. A2). In general, the central tendencies of the probability distribution tend to be encompassed within a small credible interval, except for the plants in the smallest stage (one or two leaves). The steeper the probability distribution, the more confidence we have in that specific transition probability (smaller SDs). As a consequence of small sample sizes

Table 1

Transition Probabilities and Elasticities for *Brassavola cucullata*

Quill, 2009–2010								
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.5181	.1622	0	.0456	.0163	.0110	0	.0018
3–6 L	.0705	.7063	.1043	.0921	.0094	.2021	.0379	.0155
7–20 L	.0149	.1298	.7954	.0503	.0027	.0517	.4039	.0118
>20 L	.0036	.0002	.0514	.8115	.0007	.0001	.0283	.2068
Quill, 2010–2011								
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.3195	.1231	0	.0002	.0137	.0289	0	0
3–6 L	.4013	.6060	.1227	.0514	.0170	.1399	.0638	.0081
7–20 L	.1304	.2399	.7963	.2552	.0060	.0600	.4478	.0435
>20 L	.1266	.0002	.0799	.6927	.0059	0	.0456	.1198
Quill, 2011–2012								
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.2586	.1675	0	.0456	.0144	.0314	0	.0059
3–6 L	.5358	.5442	.1043	.0921	.0364	.1242	.0366	.0145
7–20 L	.0074	.1661	.7954	.0503	.0007	.0559	.4118	.0117
>20 L	.0018	.0002	.0514	.8116	.0002	.0001	.0317	.2245
Quill, 2012–2013								
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.5110	.0741	0	.0002	.0101	.0077	0	0
3–6 L	.0423	.7881	.4351	.0429	.0055	.5385	.0703	.0034
7–20 L	.0089	.0720	.4892	.2127	.0017	.0709	.1139	.0239
>20 L	.0022	.0003	.0742	.7439	.0006	.0005	.0262	.1269
Boven, 2010–2011								
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.2770	.0081	0	.0002	.0004	.0010	0	.0001
3–6 L	.1055	.5916	.0742	.0540	.0001	.0578	.0148	.0231
7–20 L	.5231	.2240	.8559	.0056	.0009	.0306	.2390	.0034
>20 L	.0056	.0438	.0674	.9395	0	.0064	.0201	.6023
Boven, 2011–2012								
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.2777	.1819	0	.0001	.0039	.0099	0	0
3–6 L	.6057	.4612	.1402	.0210	.0094	.0278	.0108	.0113
7–20 L	.0221	.2676	.6135	.0226	.0004	.0174	.0512	.0132
>20 L	.0055	.0438	.1643	.9562	.0001	.0042	.0202	.8202
Boven, 2012–2013								
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.6388	.0698	0	.0001	.0052	.0027	0	0
3–6 L	.0526	.5067	.1996	.0294	.0020	.0902	.0692	.0102
7–20 L	.0111	.3616	.6030	.1744	.0005	.0787	.2556	.0739
>20 L	.0028	.0003	.1961	.7673	.0001	.0001	.0838	.3278

Table 1 (Continued)

	Saba, 2011–2012							
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.6130	.2516	0	.0001	.1463	.0738	0	0
3–6 L	.2301	.5801	.1964	.0007	.0727	.2255	.0603	0
7–20 L	.0016	.1179	.7667	.0818	.0007	.0591	.3039	.0019
>20 L	.0004	0	.0014	.8909	.0004	.0001	.0014	.0538
	Saba, 2012–2013							
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.8473	.2999	0	.0001	.0301	.0032	0	0
3–6 L	.0132	.6273	.2754	.0014	.0014	.0195	.0082	.0001
7–20 L	.0028	.0716	.6946	.0752	.0008	.0064	.0594	.0136
>20 L	.0007	.0001	.0291	.9230	.0010	.0001	.0126	.8438
	Saba, 2013–2014							
	Transition probability				Elasticity			
	1–2 L	3–6 L	7–20 L	>20 L	1–2 L	3–6 L	7–20 L	>20 L
1–2 L	.5021	.1483	0	.0001	.0060	.0056	0	0
3–6 L	.2300	.7031	.1061	.0029	.0039	.0373	.0097	.0006
7–20 L	.0757	.1186	.7903	.0408	.0017	.0085	.0980	.0121
>20 L	.0004	.0001	.0360	.9555	0	0	.0127	.8038

Note. We estimated transition probabilities using the Dirichlet multinomial function, and elasticities were generated by population projection models. Stages were defined by number of leaves (L).

within any year and site, many transitions were not observed so that the traditional method of calculating the transition probabilities would have rendered a 0, which would have resulted in many matrices that would have been nonergodic, reducible, or biologically nonsensical.

The transitions among stages (table 1) showed that, in almost all cases, sites, and years, the probability of staying in the same stage was higher than that of transitioning to a different stage. Thereafter, transitions to the next-largest stage were the most common. However, this pattern was not consistent for the smallest stage (one or two leaves). For all sites and time periods, the probability of death within 1 yr was highest for the smallest-size class, whereas it was negligible (<1%) for the largest plants, even in stressful years when they lost leaves but rarely died.

The PPM for all years was calculated using the sum of all the data of all years, not the mean of the individual PPMs. When all data are used (all years and sites; fig. 3), the probability density is steeper, having smaller SDs. The single exception was for the smallest-plant stage, whose SDs remained large. The probability densities for stasis and growth tend to be almost flat (e.g., stage with one or two leaves at Boven, sum of all years), suggesting low confidence in these parameter estimates. For the other life-history stages, stasis and growth estimates have a much more condensed distribution. The relative size of the credible intervals (and the coefficient of variation, not shown) is smallest for the stasis stage, in part because the frequencies of these stases/transitions are more common.

The Boven population revealed striking differences in transition probabilities and stasis (fig. 3). For example, the probability

of the smallest plants (one or two leaves) remaining small in the next time period varied from 27% (2010–2011 and 2011–2012) to a high of 64% (2012–2013). Growth to the next stage (three to six leaves) was most frequent in 2011–2012. Death rate in the smallest plants was highest (29%) in 2012–2013. Usually, in a year when the smallest plants suffered high mortality, the other size classes suffered as well but to a lesser degree. In the first two transition periods, the largest plants remained in the same size class (>93%), while in 2012–2013, only 77% remained among the largest plants. Net leaf loss of large plants (transitioning to a smaller stage) was just <6% in 2010–2011 but jumped to >20% in 2012–2013.

In general, we observed the same patterns at Quill as at Boven; however, the probability densities tended to be steeper for the small plants (one or two leaves) at Quill (fig. A2). Stasis of small plants varied from 26% (2011–2012) to a high of 50% (2009–2010 and 2012–2013). Death rates for the smallest stage were higher at Quill than at Boven, ranging from 2% in 2010–2011 to 43% in 2012–2013. Meanwhile, the probability of death for plants with three to six leaves varied among years (3% in 2009–2010 to 12% in 2011–2012), which is similar to the pattern found at Boven (table 1).

Compared with populations on St. Eustatius, the smallest plants on Saba showed less variation in stasis and mortality among years (50%–85% and 13%–19%, respectively). Mortality of small plants ranged from 13% to 19%. However, for the other stages, the probability of death in general was lower than for the sites on St. Eustatius. Large plants on Saba tend to stay large (89%–96%; table 1; fig. A2).

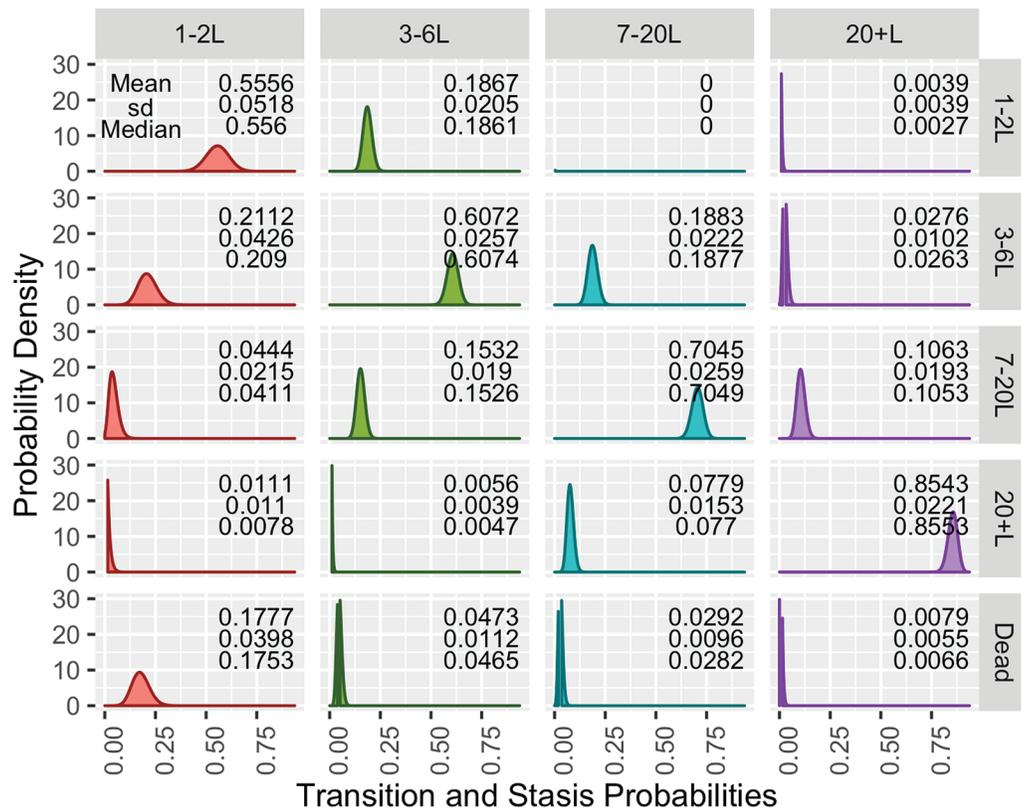


Fig. 3 Posterior probability distributions for transitions between size classes of *Brassavola cucullata* at Boven, St. Eustatius, Netherlands Antilles, for all sites and all time periods. The mean, SD, and median of the posterior distribution are identified in the figure. L = leaves.

Population Growth Rates Using PPMs

Observation of recruitment in the field was rare; only a few plants across the years were clearly recruits, and these were observed on one boulder at Boven. The 11 plants that were likely recruits were composed of individuals with fewer than eight short leaves; five plants died, and only two plants increased their number of leaves (from 4 to 7 leaves and from 1 to 22 leaves across the survey period). Consequently, we expected all estimates of intrinsic population growth (λ) to be below 1, and indeed they were (table 2). Growth rates varied among sites and times. The Quill population was stable in 2010–2011, while in

2012–2013, it decreased by 10%. The Boven population dropped 2%–3.5% per year, while the Saba population fell 3%–8% per year. However, no significant difference in population growth rates was noted among the three sites (GLMM; log likelihood, 2.26; $\chi^2 = 4.52$, $df = 2, 7$, $P = 0.104$).

Transient Dynamics and Sensitivities Using PPMs

Large differences in demographic behavior are predicted among sites and time periods (fig. 4). In general, population density at the first time step (reactivity), as compared with that of a population

Table 2

Intrinsic Population Growth Rates for Populations of *Brassavola cucullata* by Transition Period Using Population Projection Models (PPMs) and Integral Projection Models (IPMs)

Transition period	Quill		Boven		Saba
	PPM	IPM	PPM	IPM	PPM
2009–2010	.926	.979			
2010–2011	.991	1.019	.981	1.021	
2011–2012	.927	.770	.985	.879	.922
2012–2013	.904	.648	.964	.821	.938
2013–2014					.971
Stochastic growth rate with 95% confidence interval	.9357 (.9354–.9359)	.879 (.87–.881)	.9715 (.9714–.9715)	.909 (.909–.9112)	.9460 (.9458–.946)

Note. Individual PPMs were given equal weight in the stochastic model. Saba was not analyzed using IPMs because of inconsistency within the data set.

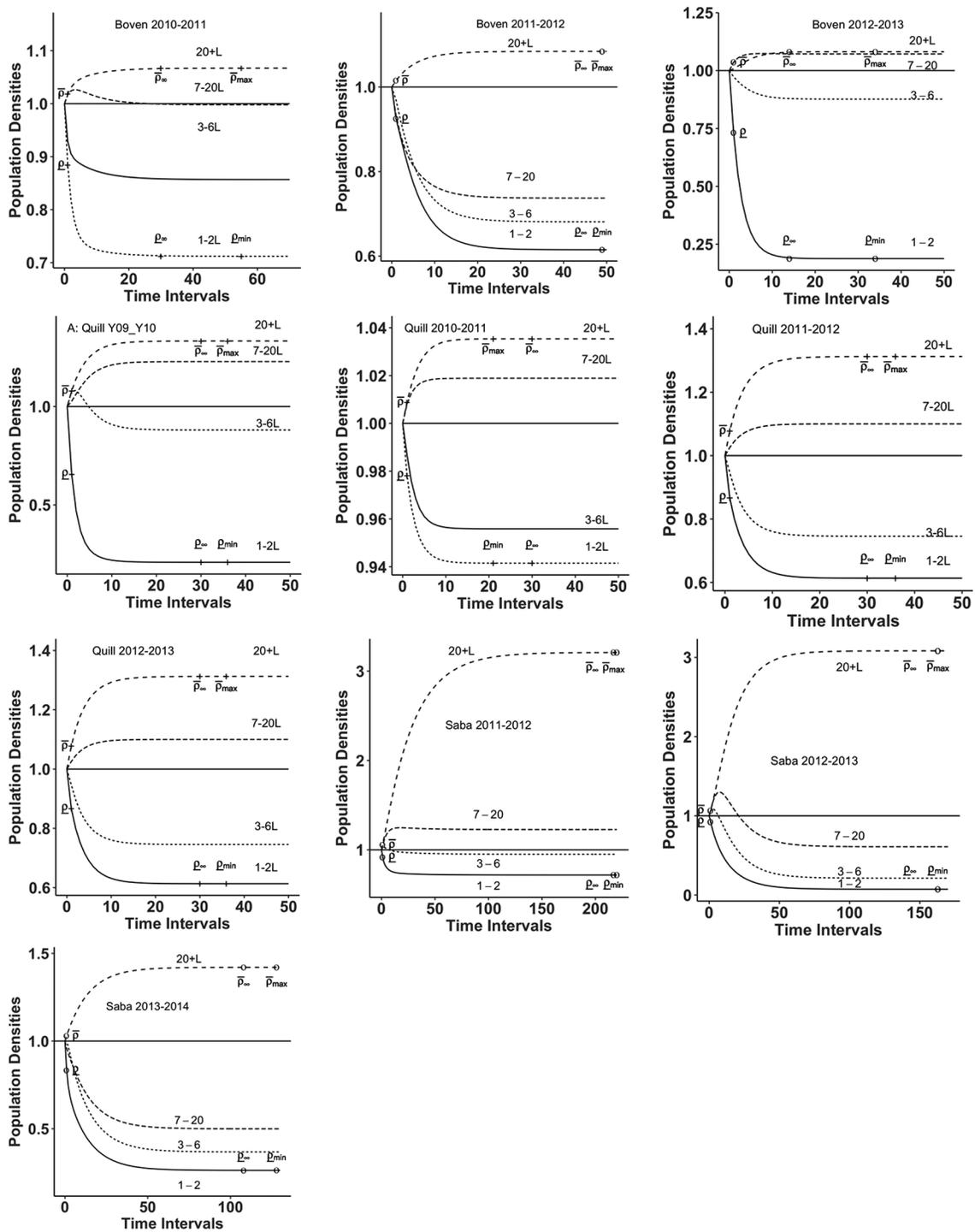


Fig. 4 Transient dynamics for each population for each year. Reactivity = $\bar{\rho}$ (maximum population growth in a single time step relative to the stable stage growth), first-time attenuation = ρ (minimum population growth in a single time step relative to a population at stable stage distribution [SSD]), maximum amplification = $\bar{\rho}_{\max}$ (the largest possible future population density relative to a population at SSD), and maximum attenuation = ρ_{\min} (the smallest possible future population density relative to a population at SSD). We also calculated two other indexes: amplified inertia = $\bar{\rho}_{\infty}$ (the largest long-term population density relative to a population at SSD) and attenuated inertia = ρ_{∞} (the smallest long-term population density relative to a population at SSD). L = leaves.

at SSD, is expected to be small, from less than 1% to 8%. However, if populations are dominated by the smallest stage, then the first time-step attenuation suggests that a drop in population density of 62% is possible (Quill, 2012–2013). Maximum amplification varies significantly among sites; it may be three times greater in the Saba population than in the St. Eustatius populations (GLMM; log likelihood, 4.440; $\chi^2 = 8.881$, $df = 2, 7$, $P = 0.012$). Times to maximum amplification and attenuation also significantly varied among sites, from a low of 21 yr for Quill to 217 yr for Saba, and Saba's times to amplification and attenuation are significantly different from those of St. Eustatius (GLMM; log likelihood, 197.9; $\chi^2 = 8395.9$, $df = 2, 7$, $P < 0.001$). The upper and lower inertias were exactly equal to the maximum amplification and maximum attenuation (data not shown).

Elasticities (proportional change in λ as a function of the proportional change in the matrix elements) varied considerably among years, but the transition stage with the highest elasticities was more or less consistent within a site (table 1). At Quill, plants with 7–20 leaves had the highest elasticities for 3 of 4 yr, whereas at Boven, the largest-size class always had the highest elasticities. On Saba, elasticities of the largest-size class were the highest in 2 of 3 yr.

Nonlinear Sensitivities: Transfer Function

We performed transfer function analyses for all three sites and all time periods by evaluating the sensitivities for each element on λ . The 2011–2012 analyses for all three sites are shown in figure A3. The expected influences of change on population growth rate as a function of parameter estimates are generally not linear. Nonlinearity in sensitivities was most clearly noted for stasis, while transitions tended to have more linear relationships between perturbation and λ . In general, transfer function analysis demonstrates that stasis parameters tend to have a larger impact on population growth rates than transition parameters (increase or decrease in leaf number). The rate of change (steepness of the curve) in λ as a consequence of the amount of perturbation showed a consistent pattern for almost all populations and sites at the different time periods; the largest changes in nonlinear sensitivities were noted in plants from Saba with >20 leaves and infrequently in plants with 3–6 leaves, 7–20 leaves, and the transition from 7 to 20 leaves. For example, small changes in plants with >20 leaves at Saba in 2012–2013 would result in a large change in population growth rates. We also noted a nonlinear increase in population growth rate when plants grew to the next stage, but the pattern of change tended to be more linear. Transfer functions for every site and time period suggest that very large changes in population growth rate could be attained if plants grew two stages or more in 1 yr, but these are rare events.

Vital Rates as a Function of Size Using IPMs

Survival probability had a significant association with plant size regardless of location and time period (all $P < 0.001$; fig. A5). Larger individuals were most likely to survive, while smaller plants had a lower probability of survival. However, regardless of location, survival probability in smaller plants was higher in the first 2-yr period, and this vital rate decreases in the last census. Altogether, plants <4 cm in length had a lower probability of survival

(<66%). Plant size at time $t + 1$ was significantly related to the size at time t (fig. A5). Changes in size were similar in both localities. In Boven, an increase in plant size was observed in the first-year period, while a shrinkage in size was observed in the last two censuses. Quill had a similar pattern: an increase in size in the first two censuses and a decrease in the others. The probability of plants having open flowers was significantly related to plant size (all $P < 0.001$; fig. A5). Overall, larger plants have a higher probability of reproduction regardless of the site. The number of fruits was related to plant size at Boven but not at Quill (fig. A5). Plants producing fruits at Boven occurred in larger individuals, while at Quill, no such relationship was observed.

Population Growth Rates and Transient Dynamics Using IPMs

Each of the λ values estimated from the IPMs at Boven (fig. 5) suggests that population was increasing during the first-year period ($\lambda = 1.0208$; 2010–2011) and decreased 12% and 18% in the second and third censuses, respectively (table 2). Of the IPMs for Quill (fig. 6), only one from the four studied year periods had $\lambda > 1$ ($\lambda = 1.0186$; 2010–2011), while the rest show a declining pattern (λ ranged from 0.6479 to 0.9789). The estimated stochastic λ was 0.9091 for Boven and 0.8787 for Quill; these values suggest that populations decreased in both sites when non-stable environmental conditions were assumed. Nevertheless, transient indexes suggest an overall increase in the population when the long-term λ values are below the stable population growth rate (table 2). For example, an amplification was observed when $\lambda < 1$ and an attenuation when $\lambda > 1$. The time to reach the maximum amplification/attenuation varied between the two sites; the Boven population might last up to 17 yr, whereas the Quill population may persist up to 30 yr (table 3).

Elasticities Using IPMs

Elasticity analyses from IPMs suggest that proportional changes in the survival and growth components of the IPMs had a greater impact on λ than fecundity (>0.97 for both sites). In the first census at Boven, the survival and growth of larger plants (>20 cm) had a greater influence on λ , while in the subsequent censuses, the medium-size plants (about 15–30 cm in length) had no such effect (fig. 7). At Quill, the survival of medium-size plants (about 15–30 cm in length) and their growth to larger individuals (>30 cm) had the greater effect on λ for the first- and second-year periods, respectively, while the survival and growth of smaller plants (<20 cm) had more influence on λ in the last 2 yr (fig. 8).

Climate Patterns

The Caribbean climate trend for the previous 30 yr shows an increase in near-surface air temperature, as has been shown globally. For the northeastern region of the Caribbean, where St. Eustatius and Saba are, there will be a continuing warming and drying trend for the foreseeable future (Taylor et al. 2018). Over a 60-yr period for which we have monthly St. Eustatius rain data (January 2010–December 2014), precipitation was frequently irregular, with more than half of the months being significantly different from the average. Eighteen of them were significantly drier, and

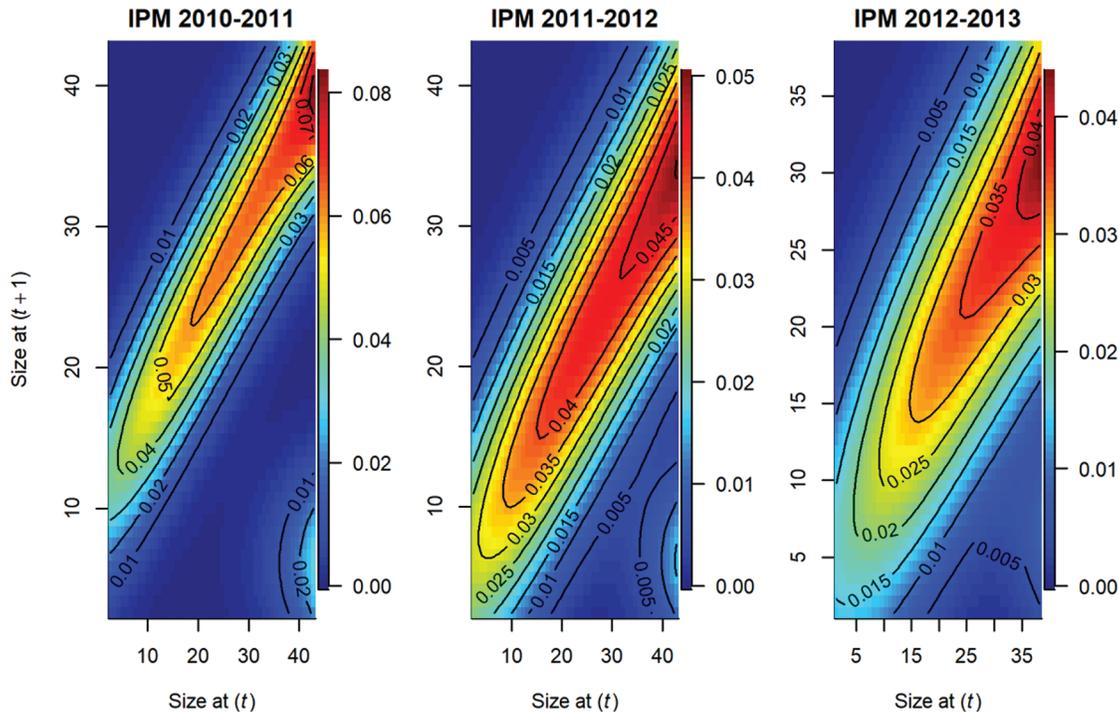


Fig. 5 Integral projection models (IPMs) describing survival/growth (diagonal lines) and fecundity of *Brassavola cucullata* at Boven over a 3-yr period. Red represents the greatest likelihood of transition in each plot. $t =$ time.

15 were significantly wetter (St. Eustatius Animal Welfare Foundation 2019; fig. A4). The first 2 yr of our study were unusually wet years, whereas the last 3 yr were progressively drier.

Flowering and Fruiting Activity

While plants can be seen in flower at any time of the year (Boeken 2014), we visited the three populations during the peak flowering period (April–August). Nevertheless, not many flowers were open at one time (table 4). Using Poisson regressions, we found that the differences in the numbers of flowers among sites were significant, with Boven (coefficient, -3.54) having fewer flowers, Quill (coefficient, 0.22) having the highest number, and Saba (coefficient, 0.06) having intermediate flower production. In addition, variation in flower production was dependent on the year of survey, with 2010 (coefficient, 2.12) and 2014 (coefficient, 2.24) having the highest production and the other years having lower flower production (2011: coefficient, 1.46 ; 2012: coefficient, 1.45 ; 2013: coefficient, 1.60).

The number of flowers that could be inspected for the presence of pollinarium was limited by their inspection accessibility; 89 flowers were verified, with 58 at Quill and 31 at Boven (none were examined at Saba). The pollinarium removal rate was 0.097 at Boven and 0.12 at Quill, and if we assume that we sampled those flowers halfway through their period of anthesis, then the estimated removal rates are 0.19 for Boven and 0.24 for the Quill population.

Our observations of the three sites overlapped for a 3-yr period (2011–2013). We compared the frequency of plants that produced fruit with that of those that did not among sites and years

using a Cochran-Mantel-Haenszel χ^2 test for count data. There were no significant differences detected ($M^2 = 0.088$, $df = 2$, $P = 0.96$). The proportion of fruit set (asymptotic CI) at each site was very low (Boven, 0.04 [0.02 – 0.06]; Quill, 0.025 [0.01 – 0.04]; Saba, 0.07 [0.05 – 0.10]), with totals of only 10, 8, and 35 fruits, respectively.

How much recruitment is needed for population stability? In all cases, the recruitment rate is well below that needed for a λ of 1 (table 5). The recruitment rates observed throughout the survey were very low. For the population to be stable and compensate for mortality at all stages, recruitment rates of seedlings must increase dramatically, from a low of 0.03 recruits per adult to a high of 24 recruits per adult, depending on the year and site.

How much fruit production is needed for population stability? Fruiting did not result in seedling recruitment that we could detect for the Quill and Saba populations. In the 3-yr span in which the Boven population produced 10 fruits, 11 recruits were detected, but only three survived at the end of our study. If we assume that those three become effective recruits (survive to reproduce—a big assumption), then the population would need to produce 1.1 fruits for every effective recruit each year. And because the population is decreasing by 5–10 plants per year, it would take seed production of 5.5–11 fruits per year, at the very least, to attain a stable state.

Herbivore Activity

Leaf herbivory was detected at all three sites. At Boven, 18.6% of the plants had evidence of herbivory, whereas Quill had 30.4%, and Saba had 32.1%. These frequencies, though, were

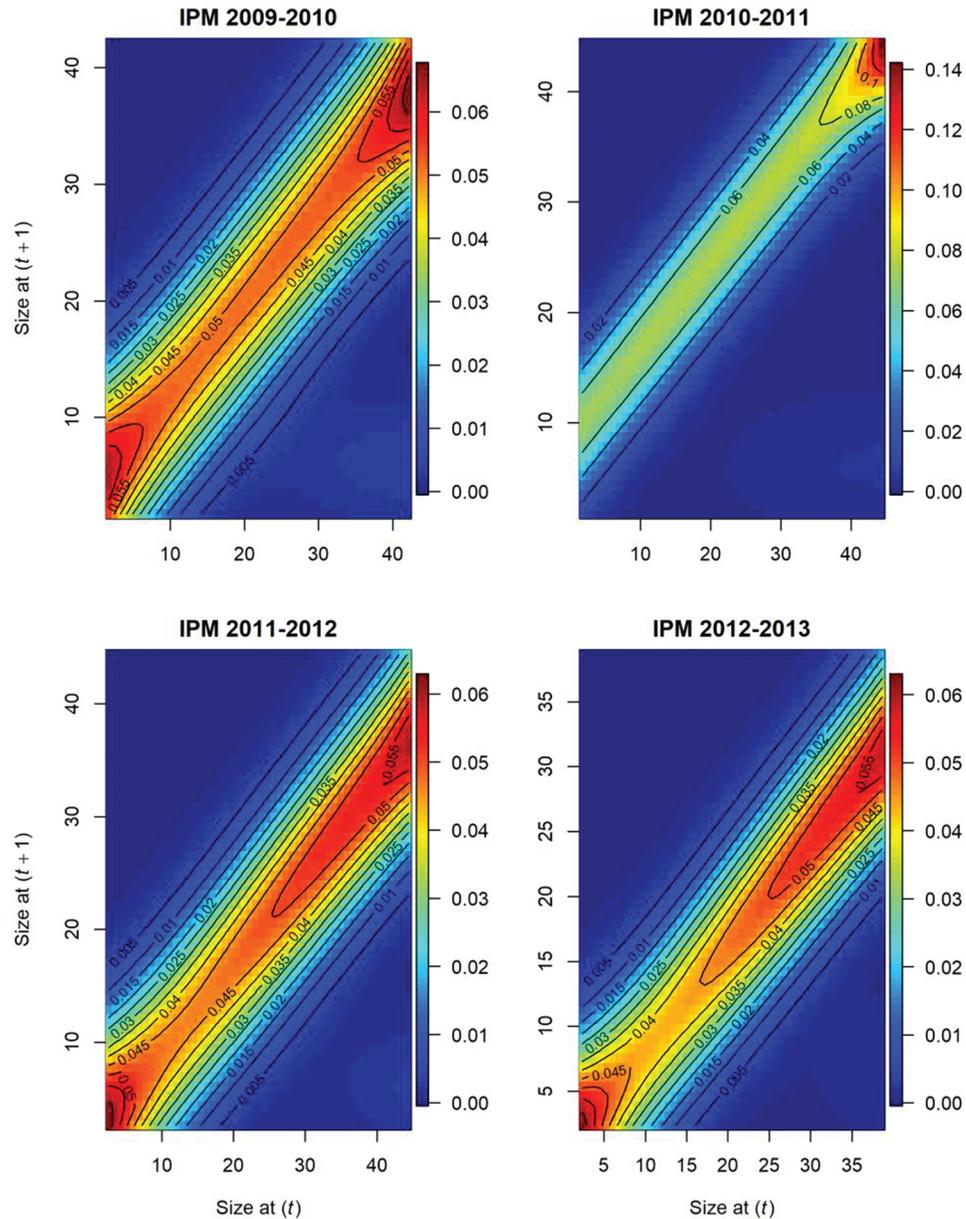


Fig. 6 Integral projection models (IPMs) describing survival/growth (diagonal lines) and fecundity of *Brassavola cucullata* at Quill over a 4-yr period. Red represents the greatest likelihood of transition in each plot. t = time.

not statistically different (contingency table analysis, $N = 145$, $\chi^2 = 2.51$, $P = 0.29$). We pooled the data for the three sites and found that plants with no evidence of herbivory were generally higher aboveground (mean = 187 cm) than those that had herbivory (mean = 135 cm; t -test assuming unequal variances, $t = -4.72$, $df = 94.5$, $P < 0.0001$). Logistic fit between the occurrence of herbivory and height aboveground shows that herbivory was rare above 200 cm and nonexistent above 250 cm (fig. 9). The Quill population reflected the strong relationship between height aboveground and herbivory. The other two sites showed similar trends, but CIs were very broad because few plants at Boven had herbivory, and at Saba few plants were above 200 cm.

Discussion

Populations on small islands are perhaps the least likely to show demographic stability. Environmental stochasticity may result in extinctions, underutilized niches may foster rapid population growth, and fewer links within interspecific interaction networks may reduce the capacity to buffer natural and human-made perturbations (MacArthur and Wilson 1967; Daehler 2003; Memmott et al. 2004). These and other factors conspire against stability. On the other hand, Cronk (1997) suggested that oceanic island floras are relatively stable, except for when parameters of anthropogenic disturbances exceed those of natural disturbance regimes. Castro-Urgal and Traveset (2014) also

Table 3

Transient Indexes Estimated for *Brassavola cucullata* Using Integral Projection Models

	Reactivity	Maximum amplification	Maximum attenuation	Inertia	Time maximum amplification/attenuation
Boven:					
2010–2011	.90588447	.8451	7
2011–2012	1.0872	1.2095	...	1.2095	17
2012–2013	1.0801	1.52391	...	1.5224	13
Quill:					
2009–2010	1.0040	1.01	...	1.01	16
2010–2011	.96439116	.9116	16
2011–2012	1.1510	1.6995	...	1.6996	30
2012–2013	1.2368	2.2963	...	2.2963	30

Note. Ellipses indicate that the index does not apply.

found stability on islands, with coastal pollination networks being stable because supergeneralist species with their asymmetric interactions are well represented and important for long-term survival of rare plants in small populations.

The small populations that we studied on two small islands of the Netherlands Antilles are dynamic, as expected. The populations behaved somewhat independently in that the behavior of one does not always predict the population behavior of another. Small plants were the most consistent. They suffered the highest mortality, and stasis in size class was more important than transitions, which is congruent with most demographic studies of epiphytic orchids and bromeliads (Mondragón et al. 2015).

Furthermore, fluctuations in mortality occurred in concert so that when one stage suffers a spike in mortality, all other stages suffer as well.

Predicted climate changes for the region are increasing temperatures and alteration of precipitation patterns (Neelin et al. 2006; Chou et al. 2009; Hsu et al. 2012; Stephenson et al. 2014; Taylor et al. 2018). During the period of our study, 2010–2014, monthly rainfall was quite irregular, with more than half of the months showing either high or low extremes. If such changes persist, they can cause regional shifts in the availability of suitable habitats (Zotz and Schmidt 2006), and populations of *Brassavola cucullata* may be sensitive to this variation. During the 2012–2013

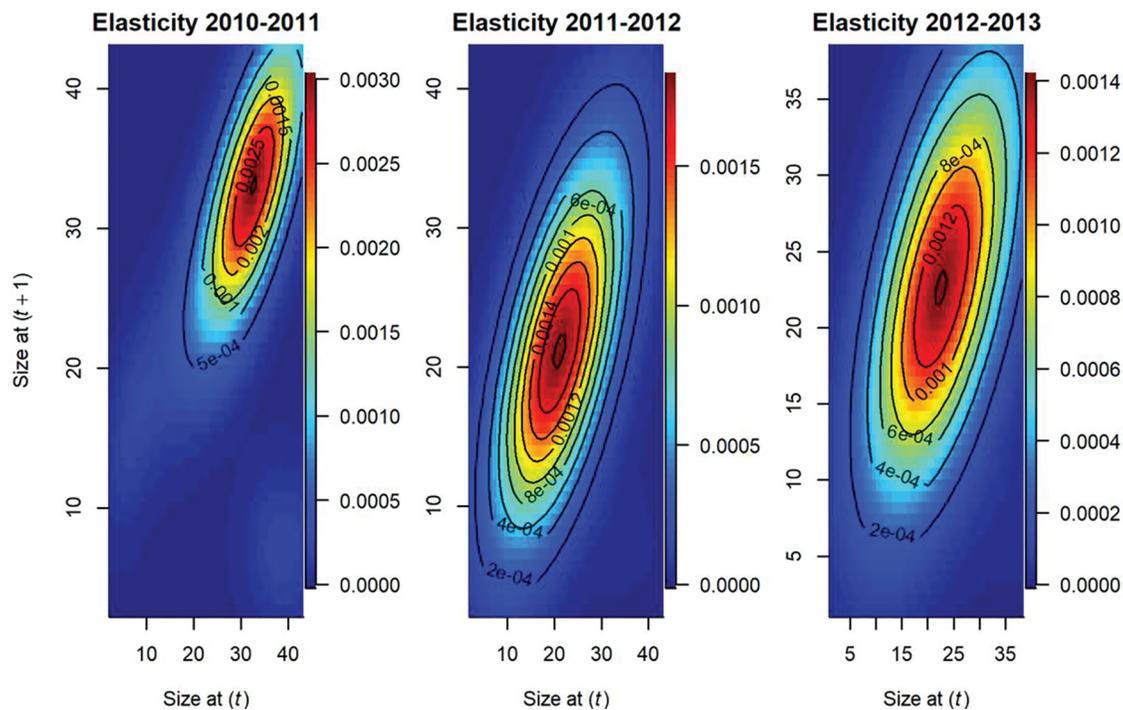


Fig. 7 Elasticity analyses for Boven over a 3-yr period. Overall, proportional changes in the survival and growth components (lines and colored shades over the diagonal) of the integral projection models had the greatest impact on λ (>0.96). The survival and growth of larger plants (>30 cm) had a greater significance for λ in the first year, while the survival and growth of medium plant sizes (15–30 cm) contributed more to λ for the two following years. t = time.

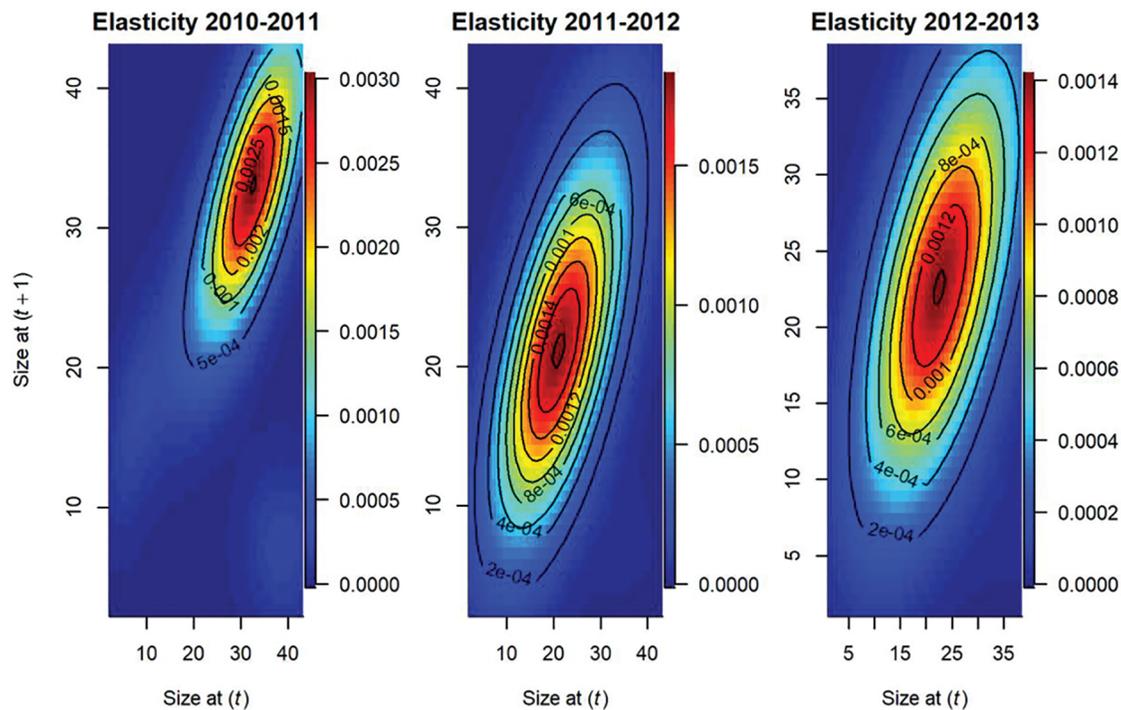


Fig. 8 Elasticity analyses for Quill over a 4-yr period. Overall, proportional changes in the survival and growth components (lines and colored shades over the diagonal) of the integral projection models had the greatest impact on λ (>0.97). The survival and growth of medium and larger plants (>15 cm) had a greater significance for λ in the first 2 yr, while the survival and growth of smaller plant sizes (<15 cm) contributed more to λ in the last 2 yr. $t =$ time.

period, which was relatively hot and dry, both St. Eustatius populations suffered the greatest reduction in the number of leaves per plant, which was also associated with a spike in death rates. Seed production and dispersal must keep up with such demographic pressures both locally and regionally for population persistence or rejuvenation via metapopulation dynamics (Tremblay et al. 2006; Winkler et al. 2009).

Hotter and drier conditions are not the only expected changes to regional climates; hurricane intensities are predicted to increase as well (Holland and Bruyère 2014). While damage to epiphyte populations by hurricanes can be mild, intense hurricanes can completely strip epiphytes from their hosts as well as destroy the hosts themselves (Rodríguez-Robles et al. 1990; Raventos et al. 2015). In 2017, Hurricane Irma struck both St. Eustatius and Saba, leaving 73% of trees with broken primary and secondary branches (Eppinga and Pucko 2018). Two weeks later, Maria skirted the two islands but struck Puerto Rico with category 4 strength, which tripled stem breaks and doubled tree mortality relative to previous category 3 Hurricanes Hugo in 1989 and Georges in 1998 (Uriarte et al. 2019). Thus, any increase in hurricane intensities will surely affect forest structure and epiphyte loads (Lugo et al. 1983; Walker et al. 1992; Migenis and Ackerman 1993).

Population Growth Rates

Changes in the vital rates of *B. cucullata* might be leading to a reduction of the population growth rates estimated over the study period. This has been observed in the Cuban orchid *Encyclia*

bocourtii, in which a decrease in survival and a retrogression in plant size lead to a decline in the population growth rate (Ortiz-Rodríguez et al. 2019). Plant survival of *B. cucullata* decreases from the first to the last census, which could be related to the overall continuous reduction in the asymptotic population growth estimated for the Boven and Quill populations. This decline might be the consequence of herbivory or environmental factors. Even though an increase in population growth rates was observed for some years, and they were even stable once for Boven and Quill, the overall trend is that populations in all localities are still far from stable growth rates (estimated stochastic $\lambda < 0.9715$).

In expanding populations, recruitment is robust, whereas in senescing populations, recruitment is usually minimal (Chung et al. 2011). We found virtually no recruitment at any of our

Table 4

Proportion of Plants with Flowers (Number of Plants with Flowers) at Each Site

Year	Boven	Quill	Saba
2009036 (2)	...
2010	.128 (6)	.243 (17)	.05 (1)
2011	.023 (2)	.063 (5)	.117 (31)
2012	.147 (10)	.186 (11)	.054 (7)
2013	.161 (9)	.091 (6)	.125 (4)
2014222 (16)

Note. Ellipses indicate that the locality was not surveyed in that year.

Table 5
Recruits Required to Attain Stable Population Growth

Site, transition year	No. recruits ($t + 1$)/ reproductive adults (t)	λ	No. recruits required per adult plant to attain stability ($\lambda = 1$)
Boven:			
2010–2011	.0002	.981	.07
2011–2012	.00008	.985	.03
2012–2013	.00011	.964	.7
Saba:			
2011–2012	.0001	.922	24.0
2012–2013	.0001	.938	8.0
2013–2014	.0002	.971	.4
Quill			
2009–2010	.0455	.926	3.5
2010–2011	.0002	.991	.07
2011–2012	.0456	.927	1.3
2012–2013	.0002	.904	15

Note. λ for the matrix with the estimated recruitment rates is in the original population projection model matrices. t = time.

three populations, which resulted in a predicted reduction in population size of approximately 4%–6% per year for the three sites (PPM analyses). We suspect that moisture conditions for germination and establishment are erratic at *B. cucullata* sites where cryptogam cover is mostly composed of patches of crustose lichens on boulders and sparse coverage on tree trunks. If recruitment occurs in boom years, we did not capture it at any of our three sites. However, this is not unusual. A survey by Mondragón et al. (2015) revealed that nearly two-thirds of epiphytic orchid populations had λ values <1.0 . Furthermore, they found, as we did, that populations tend to function independently and asynchronously, a phenomenon that characterizes metapopulation dynamics (Tremblay et al. 2006; Laube and Zotz 2007; Valverde and Bernal 2010). Thus, finding populations with negative growth rates may be normal and not necessarily cause for alarm.

However, variation in the number of recruits required for the population to be stable is enormous (table 5). This reflects the variation in survivorship and growth of the species across years and sites. It is unlikely that recruitment levels at any of these rates can be attained naturally except for in rare outstanding years where conditions for seed germination and survivorship (including reduced herbivory) are really high. For this species to persist, it will likely require human intervention, including hand pollinations and ex situ cultivation of plants followed by reintroduction to wild populations.

Nonetheless, if a series of consecutive bad years with no recruitment and high death rates (8%–10%) occurred, population density could be reduced to very small numbers within a short period of time. The positive outcome of these analyses is that, for most years, very few effective recruits would be needed for the population to be stable. Effective recruitment rates (individuals that attain adulthood) of 5–10 individuals per year would be sufficient for a stable population according to PPMs, yet IPM analyses using a recruitment rate of five seedlings per year would still produce estimated population growth rates lower than 1. The stability and persistence of medium and large plants suggest that they are the least likely to perish and are more likely

to flower and fruit than smaller-size classes. Furthermore, these individuals are the ones contributing most to an increase in the population growth rate. Nevertheless, if a retrogression in plant size and a reduction in survival rates are observed, then our elasticity analyses suggest that conservation efforts must include strategies for the survival and growth of medium and small individuals as well. Our populations consistently produced few fruits, which is not unusual for orchids with food-deception pollination systems (Tremblay et al. 2005). While hawk moth (Sphingidae) pollinator populations can be sporadic, cyclic, and generally unpredictable (Haber and Frankie 1989; Bellotti et al. 1992), the pollinator service that they provide to deception-pollinated orchids on larger islands of the West Indies fluctuates little (Ackerman and Montalvo 1990; Ackerman and Moya 1996). Variation in fruit production in other epiphytic orchids is dependent on pollinator abundance, and recruitment is positively related to variation in fruit and seed production (Ackerman et al. 1996, 1997). Thus, *B. cucullata* populations may decline, persisting until appropriate conditions for both pollinator activity and seedling establishment coincide, rejuvenating populations or establishing new ones. Over our 5 yr of observations, we did not see this hypothetical boom year. Either infrequent boom years of recruitment occur, or our three populations are headed for extinction.

Transient Dynamics

Even though the trend for populations of *B. cucullata* is to decrease in the long term, transient dynamics might be regulating this tendency. For example, a projected maximum amplification was estimated for a population of *E. bocourti* just after a hurricane disturbance (lowest population growth rate estimated), and this matched the increment in the population growth rate 10 yr

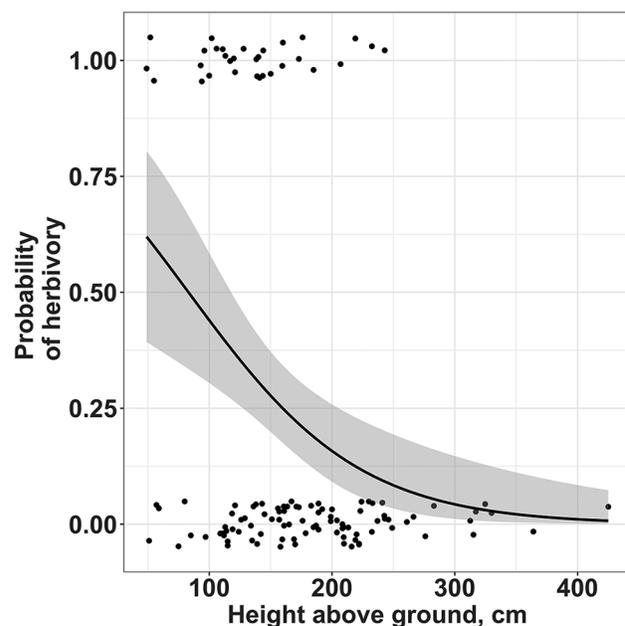


Fig. 9 Logistic fit between the occurrence of herbivory and the height aboveground for *Brassavola cucullata*. Because the herbivore community (goats, iguanas, and rats) was the same, and the occurrence of herbivory was not significantly different among sites, we pooled the data.

later (Ortiz-Rodríguez et al. 2019). Although our transient indexes might be suggesting a pattern similar to that of *B. cucullata*, long-term monitoring will be required to test this transient projection.

Since the smallest plants have the highest probability of death, it is not surprising that the first time-step attenuation suggests that a large reduction in density is possible, which is the worst-case scenario, and that the density is likely to be reduced even further, to a very small percentage of the original population size, in the long run (maximum attenuation). Most recruitment is destined to fail. Consequently, large plants are critical since they are the least likely to perish and are more likely to flower and fruit than smaller-size classes. Densities of populations dominated by large individuals are not likely to increase substantially in a short period (reactivity), but the long-term effects, as suggested by maximum amplification, could be substantial, perhaps 1.5–3 times the expected density of a population that began at SSD. The time to maximum amplification varies among sites, and the time to maximum amplification is very long for Saba; however, this may be misleading, as the rate of change is very small after 20 or so years (fig. 4).

The ability of traditional approaches to population projection analyses to predict future patterns is debatable (Schödelbauerová et al. 2009; Crone et al. 2013; Jäkäläniemi et al. 2013; Wootton and Bell 2014). Most assume that SSD is achieved; however, plant populations may not be at or close to SSD (Williams et al. 2011; Ellis 2013). In other species of epiphytic orchids, SSD was not commonly found (*Lepanthes rubripetala*, Schödelbauerová et al. 2009; *Lepanthes rupestris*, Tremblay and McCarthy 2014). If this is the case for *B. cucullata*, then it may limit our ability to use deterministic models for predicting future population densities.

Linear Elasticities and Transfer Functions

Linear elasticities suggest that the stage with the most influence on population growth rates in *B. cucullata* can vary among years and sites. The pattern that we observed is similar for orchids and epiphytes in general, where sensitivities and elasticities for survival tend to be larger than for growth or fecundity (Mondragón et al. 2015). Furthermore, the larger-size classes had the greatest influence. Results of transfer function analyses, which are the predicted change in λ as a function of the change in the parameter estimates, were not linear for many of the parameters (fig. A3). If only very small changes in the parameters occur, then traditional approaches would be sufficient; however, if larger changes occur, then the transfer function approach may be more informative. Interestingly, in almost all years, the stasis stage for the largest-size class showed the rate of change in growth rate to be steep. Thus, increasing and maintaining survival of this stage would have the largest positive impact on population growth rate.

Conservation Strategies

Models tell us that population persistence and growth will depend on seedling establishment, survival of small plants, and recruitment to the larger-size classes, yet knowledge of the environmental parameters and biological interactions that maximize orchid seed establishment and persistence in the wild is still in its infancy (Rasmussen and Whigham 1993; Bayman et al. 2002;

Wang et al. 2011; Zettler et al. 2011; Mújica et al. 2013, 2018). Successful recruitment would depend on the availability of the appropriate germination niche, which includes both biotic (mycobionts) and abiotic (light, moisture, phorophyte texture, and biochemistry) components. While Ackerman et al. (1996) showed that increased fruit and seed production results in an increase in the number of seedlings, the appropriate conditions for germination and establishment in our populations are apparently in existence irregularly so that broadcasting seed or augmenting fruit set may not be the best or most efficient strategies to rapidly stabilize or increase these populations. Alternatively, fruits may be collected in the wild; seeds asymbiotically germinated; seedlings and juveniles grown in controlled environments to a size of seven or more leaves, which would maximize survival upon introduction in the wild; and then plants transplanted to trees and boulders in appropriate sites at least 2–2.5 m above the forest floor to prevent goat herbivory. The results from the transient analysis suggest that plants that have 7–20 leaves are the best option for a reintroduction campaign, as this stage has higher inertia as compared with the stage with three to six leaves, and smaller plants (one or two leaves) have a high probability of mortality and thus need to be in a head start program before relocalizing in the wild. Furthermore, given the expected continuation of the regional warming and drying trend (Harter et al. 2015), plants should be transplanted to elevations at the higher end of local occurrence.

Conditions yet to be determined include the best position on the phorophyte or boulder for maximizing survival and reproduction. Moreover, removal of large plants from the population would result in a large decrease in the probability of population persistence, as clearly shown by the transfer function analyses and elasticities. Thus, effort should be continued to educate the local population in conservation aspects and the values of maintenance of these plants in the wild.

Presently, we observe no collection pressure on the natural populations of St. Eustatius and Saba, yet plants from asymbiotically grown seeds could be distributed to the local populations. This could result in two positive outcomes: reduction in the desire for collection from natural populations and instilling in the public a respect for nature by promoting a “save the panda”-type educational program. St. Eustatius and Saba are two of the Lesser Antilles where the local economy is mainly supported by tourism; promoting such a spectacular orchid could foster an additional positive view for conservation and tourism. Presently, tourism on both islands focuses on marine life, but if the wonders of local terrestrial treasures are highlighted, the tourist experience may be enhanced.

Conclusions

Small populations are expected to be more vulnerable to vagaries of their abiotic and biotic environments than large populations, and occupying small isolated islands can exacerbate this. Indeed, we have revealed negative population growth in three small island populations of *B. cucullata* where seedling recruitment was quite rare. This is consistent with most demographic studies of orchids. Decline of some orchids certainly may be attributed to collection pressures, while others may suffer from habitat changes, either anthropogenic or natural. On the other hand, metapopulation dynamics where populations come and

go may be at play, and those that decline are more common than those that are increasing in numbers, as growth phases may be more rapid than population declines. This may be the situation for *Brassavola* populations since they have persisted in the Lesser Antilles despite radical habitat changes caused by European colonization and exploitation. Furthermore, our populations show some degree of demographic independence and asynchrony, both diagnostic traits of metapopulations. Populations may persist for long periods of time without recruitment as long as large plants exist, these being the least vulnerable. Orchid populations are often localized, even when substrates and habitat appear to be abundantly available (Ackerman et al. 1996; Trapnell and Hamrick 2006; Kartzinel et al. 2013). When substrates are available, yet recruitment is sparse, either seed rain or conditions for germination and seedling establishment are wanting. From the year-to-year transitions across our three sites, we noted recruitment in only one population and in only one transition year. If these populations are not in long-term decline and are only passing through cycles, then we expect recruitment to be spasmodic and dependent on either ephemeral conditions for seedling establishment or a burst of fruit and seed production generated by either sudden increased availability of pollinators or increased flower production. While we have no data on phenotypic or genetic variation among populations of *B. cucullata*, the widespread distribution of the species and the virtual lack of described variants suggest that gene flow occurs sufficiently enough to establish and replenish populations, perhaps overriding local population differentiation via drift or selection (Tremblay et al. 2005).

Demographic models using PPMs and IPMs show similar trends in asymptotic population growth rates, higher λ values in the first censuses, and a decline in the population growth rates in the last two periods. Overall, those λ values estimated with IPMs were lower than those estimated with PPMs. Matrix dimensionality and sample size are the two factors playing an important role

in the estimation of population growth rate. Usually, less dimensional matrices (as the one used here, 4×4) will overestimate λ values compared with matrices with greater dimensionality (Ramula et al. 2009). On the other hand, when a smaller sample size is used, bias and variance of the estimated population growth are 1.6 times greater in PPMs than in IPMs; thus, IPMs are usually more accurate and more precise (Ramula et al. 2009). Nevertheless, we caution that, for IPMs, we assumed certain behavior in the vital rates of *B. cucullata* (survival and fecundity, specifically), so one must be cautious in interpreting the results. Regardless, the trend in the population dynamics of our species was similar using both methods, but a faster declining rate was estimated using IPMs, a trend that could be buffered in a short period of time on the basis of transient indexes estimated for the species. Thus, the demographic analyses are bleak in their predictions, but at the same time, they provide hope that perhaps spasmodic recruitment is the modus operandi of small populations of tropical epiphytic orchids.

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