Riparian zones are one of the most dynamic components of river ecosystems, with a range of processes and attributes that are inherently complex and nonlinear (Bigelow et al., 2007; Bendix and Stella, 2013). They are subjected to a plethora of natural disturbances and disturbance regimes that vary with catchment scale and stream size (Lee et al., 2017). Flood disturbance is generally considered as a primary driver of plant diversity and distribution within riparian ecosystems (Junk et al., 1989; Poff et al., 1997; Tockner et al., 2000), but flooding and other geomorphological processes are not equally distributed in space and time. Headwater areas tend to be more heavily influenced by debris movements, while downstream channels are more significantly influenced by floods (Johnson et al., 2000). Likewise, stream channels and riparian zones are a reflection of different disturbance histories and recovery trajectories (Bigelow et al., 2007; Naiman et al., 2010). Ecological data on riparian systems point to links between variation in geomorphological processes across riparian areas within watersheds and variation in demographic processes that in turn may lead to differences in species distribution (Dixon et al., 2002). Because of the variation associated with this broad complexity of riparian systems within a watershed, conservation scientists have stressed the importance of applying available scientific knowledge about disturbance regimes in riparian systems when designing management strategies to support biological conservation (Penaluna et al., 2018).

Variation across river channels in demographic dynamics of a riparian herb with threatened status: management and conservation implications

Mervín E. Pérez1,4,5, Elvia J. Meléndez-Ackerman1,2, and Omar A. Monsegur-Rivera3

PREMISE: Gesneria pauciflora is a rare, threatened plant in riparian forests. Periodic disturbances, expected in this habitat, could influence demographic dynamics on plant populations, yet their impact may not be the same across the watershed. We hypothesized that differences in disturbances between the main channel and tributaries may lead to spatial dissimilarities in population growth rate ($\lambda$), structure, and fecundity.

METHODS: In the Maricao River Watershed in Puerto Rico, 1277 plants were tagged and monitored for 1.5 years. Every 6 months, we measured plant size and recorded survival, fecundity, and appearance of seedlings. These variables were used in integral projection models to assess the population status of G. pauciflora.

RESULTS: Plants in the main channel were smaller but more likely to flower and fruit than those in the tributaries. Overall mortality was greater in the main channel and greater during the rainy season. At both sites, $\lambda$ ranged from 0.9114 to 0.9865, and survival/growth of larger plants had a greater effect on $\lambda$ (>0.90) regardless of site.

CONCLUSIONS: Values for population growth rates suggest that G. pauciflora is declining across the watershed. Higher mortality rates in the main channel (more-perturbed sites) might drive G. pauciflora to reproduce at smaller sizes, while tributaries (less-perturbed sites) might be better for growth and lead to larger plant sizes. Extreme climatic events are expected to increase in the Caribbean and might decrease the population if the population is left unmanaged. Management strategies that reduce the time plants require to reach larger sizes might be necessary to increase $\lambda$, and reintroduction using cuttings might be a possible solution.

KEY WORDS: Caribbean; Gesneria pauciflora; Gesneriaceae; integral projection models; natural disturbances; plant population dynamics; riverine ecosystems.
Endangered species with restricted distribution ranges are more susceptible to stochastic events (natural and anthropogenic) due to their low abundances (Schemske et al., 1994). While the extent of occurrence, area of occupancy (i.e., Miller et al., 2013), and size of the population (Morris et al., 2002) are important ecological variables for rating the vulnerability of species and establishing monitoring priorities, they are not completely informative nor adequate to develop well-designed management plans to effectively prevent population reduction and extinction (Schemske et al., 1994; Morris et al., 2002). Even when rare species may have higher local adaptation due to habitat specialization (Raabová et al., 2007), climate change could alter habitat condition by increasing the frequency and intensity of natural disturbances (Dale et al., 2001), and consequently reduce the population below a threshold that may prevent self-recovery, resulting in extinction (Kreyling et al., 2011).

Because demographic approaches are the best way to assess species and population status (Schemske et al., 1994; Morris et al., 2002; Tremblay and Hutchings, 2003), studies including these methods are necessary to provide quantitative trends that can determine a species’ threat category or potential for delisting and to improve management and conservation plans by detecting the demographic parameters that could prevent population decline (Schemske et al., 1994; Morris et al., 2002; Tremblay and Hutchings, 2003). Even though the use of demographic models are highly recommended for species protected by law, studies that incorporate these models to evaluate plant species populations are dominated by species not listed under the Endangered Species Act (ESA; Zeigler et al., 2013). The COMPADRE data base lists 468 studies that incorporate 598 plant (and algal), species with most of the demographic effort concentrated in North America, Europe, Australia, and Brazil, and fewer studies in areas considered as biodiversity hot spots (Salguero-Gómez et al., 2015). For example, in the Caribbean region, an important biodiversity hotspot (Myers et al., 2000; Olson et al., 2001), there are only 11 plant species that do include demographic models (eight in the Orchidaceae family; Calvo, 1993; Tremblay, 1997; Tremblay and Hutchings, 2003; Schödelbauerová et al., 2010; Olaya-Arenas et al., 2011; Wiegand et al., 2013; Crain, 2014; Tremblay and McCarthy, 2014; Raventós et al., 2015a, b; Tremblay et al., 2015; Falcón et al., 2017), one in the Cactaceae (Rojas-Sandoval and Meléndez-Ackerman, 2013), one in the Cycadaceae (Nigrón-Ortiz et al., 1996), and another in the Melastomataceae (Pascarella et al., 2007). Of those species, only three have been assigned risk categories. Lepanthes eltoroensis Stimson has been classified as “Endangered” under the ESA (U.S. Fish and Wildlife Service, 1991), the cycad Zamia eosa O.F.Cook & G.N.Colins is considered “Vulnerable” under the IUCN criteria (IUCN Red List of Threatened Species, 2018) and the cactus Harrisia portoricensis Britton is considered as “Threatened” under the ESA (U.S. Fish and Wildlife Service, 1990). Puerto Rico has 52 plant species that are considered at risk and need protection by law, but only 4% of the species have demographic models to evaluate their population dynamics, so clearly, demographic models are needed for more of these species.

The tribe Gesneriaceae (Gesneriaceae) is endemic to the Caribbean with five species endemic to Puerto Rico (Skog, 1976), but only G. pauciflora is labelled as threatened under the ESA (U.S. Fish and Wildlife Service, 1995). This riparian, herbaceous species was listed due to its narrow distribution (i.e., restricted to the western part of Puerto Rico), the potential for population extinction due to the threats from large-scale natural disturbances (i.e., hurricanes, landslides, flooding) and from human activities (i.e., modifications in the river hydrology due to water extraction; U.S. Fish and Wildlife Service, 1995). The monitoring of this species’ demography was identified as a recovery action outlined in the “Recovery Plan for Gesneria pauciflora” (U.S. Fish and Wildlife Service, 1998). Nevertheless, the plant lacks information to appropriately estimate current population dynamics and to determine the demographic vulnerabilities from environmental factors. The species inhabits riverine environments and establishes on wet rocks near the stream flow. Frequent disturbances from flash floods are expected in this type of habitat, but the impact is not necessarily the same across stream orders or segments because topography is an important driver of flash flood behavior within a watershed (Lee et al., 2017). Thus, one hypothesis is that differences in the intensity and frequency of flash floods across riverine locations within the watershed (i.e., more intense and more frequent in the lower watershed and less intense and less frequent in the headwaters) may lead to differences in the population structure of G. pauciflora patches across sites. From this premise, several hypotheses can be developed about the demographic behavior of G. pauciflora. First, to the extent that different topographic locations within the watershed translate into differences in exposure to flash floods, we hypothesized that population patches near more disturbed sites (i.e., near the main river channel) may be less stable (will have more variable lambda) than those of less disturbed sites (i.e., tributaries). Plant history evolution and disturbance ecological theory also predict that the frequency and intensity of perturbations may selectively influence plant traits (i.e., plant sizes, reproduction frequencies or reproductive mechanisms, Trémolières, 2004; Borne et al., 2008). For example, plants in more disturbed areas may be smaller and reproduce vegetatively more often. If such is the case for G. pauciflora, different management actions may be needed among stream locations throughout its distribution.

The goal of this study was to implement a demographic-based study in the Maricao Forest Reserve evaluating the influence of site characteristics on the demographic behavior of G. pauciflora. We sought to identify the current population status of G. pauciflora to make informed management recommendations that can lead to the eventual recovery of populations and future delisting. This work addressed the following questions: (1) What is the current population status of G. pauciflora and which processes in the life cycle of G. pauciflora have a greater influence on its finite population growth rate? (2) Is the population growth rate, population structure, and fecundity influenced by site? We used results to re-evaluate its vulnerability status and provide recommendations for its management and conservation.

**MATERIALS AND METHODS**

**Study site**

The Maricao State Forest Reserve (4150 ha) is located at the western end of Puerto Rico within the municipalities of Maricao, Sabana Grande, and San Germán (Anadon-Irizarry, 2006). The topography is dominated by rugged mountains and hills with steep slopes (between 40–60%), and the majority (90%) is characterized by serpentine soils. This particular geological soil type distinguishes the Maricao Reserve as an important ecological area due to a high number of associated endemic species (Ricart
Rainfall in the Maricao Reserve is seasonal with a wet period from August to November and a dry season from January to April (Fogarty and Vilella, 2002). The mean temperature is 21.7°C, and mean precipitation is 2326 mm (Tossas, 2006). Long-term data from 1985 to 2016 (https://waterdata.usgs.gov) also suggest that monthly mean discharge in the Maricao River is also variable, with the lowest in February at 0.5 m³·s⁻¹ (±0.16) and highest in October (3.1 m³·s⁻¹ ± 1.4). The maximum discharge recorded for this period was reported in 1998 in September (8.7 m³·s⁻¹) and October (5.8 m³·s⁻¹), which overlapped with events related to Hurricane Georges. The reserve has an elevation from 150 to 875 m a.s.l. that includes subtropical wet, moist forest and lower montane, wet life zones (Tossas, 2006). For this study, we used a fragment of the Maricao River Watershed from 450 to 700 m a.s.l. Eleven colonies of *G. pauciflora* were located, and 1277 individuals were tagged (Fig. 1). Six colonies were located at the main channel (18.1661917, −66.9880556) of the river (stream order 1), and five were distributed in tributaries (18.1600278, −66.992964) of stream order 2 and 3 (Fig. 1). The number of individuals per colony varied from one to more than 500. The colonies were distributed across the entire altitudinal gradient of the species’ distribution within the Maricao Reserve and along streambeds on exposed rock in the lower part of the river and on rock walls in the headwaters.

**Study system**

*Gesneria pauciflora* (Gesneriaceae) is a stemmed plant with a woody basal stem; branches are erect or decumbent (Liogier, 1995), and large plants tend to form creeping mats with fragile branches. Plants produce orange, tubular flowers that are about 2 cm long and are pollinated by hummingbirds (Pérez et al., 2018). *Gesneria pauciflora* is a self-compatible species capable of producing fruits and seeds via autogamy (Pérez et al., 2018). In the wild, individual plants produce an average of 140.3 (±26.2) healthy seeds with a germination rate in vitro estimated at 67.5% (±8.1%; Pérez et al., 2018). Even though flowering and fruiting occur throughout the year, these processes peak during the wet and dry season, respectively (M. Pérez et al., unpublished manuscript). Floral herbivory of the species is low (12%; Pérez et al., 2018) and appears to track flower bud production (M. Pérez et al., unpublished manuscript). The species inhabits riparian environments and is always associated to wet rocky habitat near to the stream flow.

**Field monitoring**

We monitored *G. pauciflora* colonies along a fragment of the Maricao River watershed that included portions of three different

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**FIGURE 1.** Study site map. (A) The Maricao Reserve in western Puerto Rico. (B) Closer view of Maricao Reserve to show location of study area. (C) Closer view of study area to show location of the 11 populations along the main channel (triangles) and tributary (circles) of Maricao River monitored over 1.5 years.
stream orders (Fig. 1). Plants were patchily distributed along the river, so we defined each one as a colony independently of the number of plants. We marked colonies between the limits of the Maricao Reserve (no colonies were reported below this point) to the junction of the first tributary (six colonies in this part of the river, Fig. 1). We then tracked plants in this first tributary and marked seven more colonies; no additional colonies were observed after the last colony (Fig. 1). The two segments had a linear distance of about 600–700 m each (Fig. 1). In December 2015, 1277 plants were tagged for the 1.5-yr study; 782 were located in the main channel and 495 in a tributary of the Maricao River. At each colony, we coded individual plants with tags attached to the rocks using Loctite marine epoxy (Rocky Hill, CT, USA). In December 2015, the length of the largest branch on all tagged plants was measured, and the number of leaves, presence of open flowers, and number of fruits was recorded. In June 2016, we revisited the 11 colonies and recorded the same information, whether the tagged plants had survived, and the number of new seedlings (small plantlets with a hyaline stem with two or four leaves). New seedlings were coded, the length of the stem measured, and the leaves counted. For following survival of seedlings, reference objects (usually eye bolts) were attached to the rocks using epoxy, and the distance from two references to the seedlings was used to relocate each individuals in consecutive censuses. To better characterize the reproductive performance of each individual and estimate the flowering probability and maximum number of fruits per plant (a proxy of plant fecundity), we revisited each plant every 2 weeks during the December 2015–June 2016. Two additional censuses were done (June 2016–December 2016, December 2016–June 2017) to assess the same attributes. Even though we revisited colonies every 2 weeks during census dates, semi-annual data sets were used as a reference to build each of the demographic models described below. Data collected from the main channel and from the tributary were used to construct two sets of demographic models. We used regression models to evaluate the relationship between plant vital rates (survival, growth, flowering probability, and the number of fruits per plant) as a function of size and compared the model outputs generated for each location type (main channel vs. tributaries).

**Demographic model and vital rate estimation**

For the integral projection models (IPMs), the essential element is the kernel function, which describes how the size distribution of individuals at time \( t \) changes over one-time step \( t + 1 \) (Easterling et al., 2000; Merow et al., 2014). The kernel \( (z', z) \) records the size distribution of individuals \( n(z) \) over a size interval \( \Omega \) from time \( t \) to time \( t + 1 \) by describing the individuals that survive, grow (or shrink), and reproduce and is expressed by the following equation:

\[
n_{i_{z'}}(z') = \int_{z}^{z'} K(z', z) \cdot n(z) \, dz,
\]

where \( z' \) is the plant size at \( t + 1 \) and \( \Omega \) represents the possible range of individual plant sizes (minimum and maximum sizes). So, the above integral performs a sum over all the possible ways of changing from size \( z \) at time \( t \) to size \( z' \) at time \( t + 1 \). The kernel is then the sum of two functions: one describing the survival probability and growth of survivors \((P \text{ kernel})\) and one describing the reproductive contributions of each individual and the size distribution of new recruitments in the next census \((F \text{ kernel}; \text{Metcalf et al., 2013; Merow et al., 2014.})\). For \( G. \ pauciflora \), the \( P \) kernel was constituted by the probability of an individual surviving from a time step, \( s(z) \), and the size distribution of the survivors, \( g(z'|z) \). The \( F \) kernel included the probability of flowering, \( P_{\text{flower}}(z) \), conditioned to surviving; the number of fruits produced per plant, \( F_{\text{fruits}}(z) \), conditioned to flowering; the establishment probability, \( P_{\text{estab}} \), a constant; and the size distribution of new seedlings, \( F_{\text{recruit size}}(z) \). Because all these rates are potentially a function of size in time \( t \), the complete kernel for \( G. \ pauciflora \) was formulated as:

\[
F_{\text{recruit size}}(z) = \int_{z}^{\infty} \int_{z}^{\infty} F(z', z) \cdot P_{\text{estab}} \cdot F_{\text{flower}}(z') \cdot F_{\text{fruits}}(z') \cdot P_{\text{flower}}(z)
\]

Semi-annual census data sets for \( G. \ pauciflora \) were divided into the main channel and the tributary, with two IPMs generated for each of the six census dates during the 1.5-year study. The length of the largest branch and the number of leaves were multiplied to obtain the size of each individual plant of \( G. \ pauciflora \) (details for choosing this size index are described in Appendix S1). The two variables combined in a size index best explained the size dependence of fecundity and survival (Merow et al., 2014) and the size dimensionality of the species. Therefore, this size index was used for the development of the IPMs. For subsequent analyses, the size index variable was log-transformed. We used logistic regression to evaluate the association of the size index with survival and flowering rates, generalized linear model using Poisson regression to evaluate the association of the size index with fruit production, and linear regression to evaluate the association of the size index with growth. To generate an establishment probability, we estimated the total number of seeds produced from time \( t \) to time \( t + 1 \) by multiplying the total number of fruits in census \( i \) by the estimated average number of seed produced per fruit in wild conditions (140.3 ± 26.2 seeds; Pérez et al., 2018), and divided the number of seedlings in census \( i \) by the number of seeds. We assumed that the size of new seedlings was independent of the maternal plant size (because it was not possible to link seedlings with individual plants) and fitted a linear regression model with the intercept only, and these parameters were included in the fecundity function assuming a normal distribution. Each regression was compared including different size combinations \((i.e., z−1; z−z; z−z+z^2)\) and the model with the lowest AIC (or the one that best explained the biology of the species) was chosen to build the IPM of \( G. \ pauciflora \). The selected regression models and their parameters are summarized in Appendices S2 and S3. Once the IPMs were created the population growth rates \((\lambda)\), stable size distributions, and reproductive values were estimated for the species using the IPMpack R package (Metcalf et al., 2013). An elasticity analysis in the same R package was used to identify the parameters that most affected the population growth rate. Uncertainty for all \( \lambda \) values were estimated following Bruna (2014) to test whether they differed from unity. All analyses were conducted in R version 3.5.1 (R Core Team, 2018).

**RESULTS**

**Summary statistics**

Overall, plant mortality for each census date was lower in the tributary than in the main channel (Table 1). The relative increase in plant mortality in the main channel over the tributary was also highest during the census period that included the rainy season (i.e., June–December) than during the ones that included the dry season (i.e., December–June). More new recruitments were found in June than in December, and the establishment probability was low (<2%) in both types of stream sites (Table 1). At both sites, the number of reproductive plants (those that produced open flowers)
was low compared to the total number of tagged plants. At the end of the study (June 2017), 1315 plants were reported for the main river channel and 605 for the tributary (Table 1).

### Vital rates as a function of plant size

Survival probability had a positive and significant association with plant size regardless of site and season (all $P$ values were < 0.001; see Appendix S3 and Fig. 2). Larger individuals were most likely to survive in both the main channel and the tributary, and seedlings were the most vulnerable (Fig. 2). However, the fitted line of the logistic models was somewhat variable in time and space and indicated that survival probability of smaller plants could vary by season and location (Fig. 2). For example, in the first census (June 2016), the approximate threshold size in which smaller individuals had more than 50% probability to survive was equal or greater than a log size index of −1.7 (about 0.1 cm and two leaves) in the main channel compared with a log size index of 0.57 (about 0.4 cm and five leaves) in the tributary. Yet, in the last census (June 2017), the trend was the opposite (−1.7 in the tributary, −0.2 [about 0.2 cm and four leaves] in the main channel). Plant size at time $t + 1$ was significantly related to the size at time $t$ in the main channel and in the tributary ($R^2 > 0.85$; $P < 0.001$; Fig. 3). Some plants had a dramatic reduction in size and represented outliers in our models; nonetheless, these values had low leverage and did not affect the slope if included (see Appendix S4 for details of models with and without outliers). The probability of plants having open flowers was significantly related to plant size in all the logistic models ($P < 0.001$; Fig. 4). However, for plants in the main channel, the size at which plants reached a 50% probability of flowering was smaller (range, log size index: 6.5–6.7 [about 11.6–13.1 cm and 57–62 leaves]) than for plants along the tributary, which were larger (range, log size index: 8.8–10.3 [about 44.8–108.0 cm and 148–275 leaves]) but less likely to have flowers (Fig. 4). The number of fruits was also significantly related to plant size ($P < 0.001$), but for any given plant size, the expected number of fruits produced per plant was higher in the main channel than in the tributary (Fig. 5).

### Outputs from the IPMs

All the regression models explained above were used to construct the IPMs for both sites. The IPM estimated that the population growth rates ($\lambda$) for the main channel and the tributary were both below unity in all semi-annual censuses (Fig. 6). In the main channel, $\lambda$ values ranged from 0.9416 to 0.9848, while in the tributary they ranged from 0.9114 to 0.9865. Uncertainty in $\lambda$ values were below unity as well (Fig. 6), suggesting that the populations are declining at both locations. Moreover, the confidence intervals estimated from the two sites overlapped in all censuses, suggesting that population growth rates were similar. Proportional changes in the survival and growth components of the model had the greatest impact on $\lambda (>0.95)$ with transitions from the most-abundant expected size class being the most important influence (Fig. 7). In the first two censuses in the main channel, the survival and growth of medium and larger sizes had a greater influence on $\lambda$, while in the third census only the larger plants had a greater effect (Fig. 7). In the tributaries, the greatest influence was for plants ranging from a log size of 7 to 8 in the first census, and larger individuals (greater than a log size index of 9) being more influential in the next two censuses (Fig. 7). The observed size distribution in *G. pauciflora* was different in the two sites and did not match the expected stable size distribution at either site (Fig. 8A–F). Medium and small plant sizes dominated the main channel (Fig. 8A, C, E), while the tributary showed a bimodal size distribution dominated by small (log size index ≤ 0) and large plants (log size index ≥ 5; Fig. 8B, D, F).

### DISCUSSION

Our results suggest that the overall population of *G. pauciflora* at Maricao is declining, which justifies its threatened status. Lower $\lambda$ values have been reported for other species of special concern such as the endangered herb *Iresine rhizomatosa* Standl. (Amaranthaceae, Schwartz et al., 2016), the orchid *Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe (Raventós et al., 2015a, b), and the threatened cactus species *Mammillaria gaumeri* (Britton & Rose) Orcutt (Ferrer-Cervantes et al., 2012). All these species and our target species were similar in terms of elasticity analyses, where the survival and growth of larger plants contributed most to the changes in the population growth rate. This trend was also observed for the endangered herb *Silene tatarica* (L.) Pers. (a temperate riparian species) where stasis had the highest elasticity value followed by growth (Jäkäläniemi et al., 2005). In the case of *G. pauciflora*, this result was probably related to the fact that larger plants contributed the most to reproduction in both sites. Even though $\lambda$ values were lower than unity, the estimated value in the last two censuses were higher, suggesting that population was not decreasing as fast as in the first census. With the observed trend in $\lambda$ variation, the population could probably decrease at a lower rate if the trend was temporally consistent. Nevertheless, Puerto Rico was recently exposed to two hurricanes events (directly hit by Category 4 Hurricane Maria, indirectly by Category 5 Irma),

### TABLE 1. Overall semiannual descriptive information of *Genseria pauciflora* in two localities (main channel and tributary) of the Maricao River, Puerto Rico.

<table>
<thead>
<tr>
<th>Census*</th>
<th>Site</th>
<th>n(t)b</th>
<th>Mortality (%)</th>
<th>Seedlings (%)</th>
<th>Reprod. plants (%)</th>
<th>Fruit prod. (%)</th>
<th>Estab. prob. (%)</th>
<th>n(t+1)c</th>
</tr>
</thead>
<tbody>
<tr>
<td>D15-J16</td>
<td>Main channel</td>
<td>782</td>
<td>13.4</td>
<td>388</td>
<td>15.6</td>
<td>289</td>
<td>0.009</td>
<td>1065</td>
</tr>
<tr>
<td></td>
<td>Tributary</td>
<td>495</td>
<td>10.7</td>
<td>152</td>
<td>16.5</td>
<td>151</td>
<td>0.005</td>
<td>594</td>
</tr>
<tr>
<td>J16-D16</td>
<td>Main channel</td>
<td>1065</td>
<td>30.9</td>
<td>112</td>
<td>11.9</td>
<td>237</td>
<td>0.003</td>
<td>848</td>
</tr>
<tr>
<td></td>
<td>Tributary</td>
<td>594</td>
<td>21.0</td>
<td>79</td>
<td>12.2</td>
<td>91</td>
<td>0.006</td>
<td>548</td>
</tr>
<tr>
<td>D16-J17</td>
<td>Main channel</td>
<td>848</td>
<td>17.8</td>
<td>467</td>
<td>13.3</td>
<td>247</td>
<td>0.014</td>
<td>1164</td>
</tr>
<tr>
<td></td>
<td>Tributary</td>
<td>548</td>
<td>12.6</td>
<td>57</td>
<td>6.9</td>
<td>70</td>
<td>0.006</td>
<td>536</td>
</tr>
</tbody>
</table>


n = total number of plants measured at time $t$ and time $t + 1$.

Reproductive plants = percentage of plants that flower in the given period.

Establishment probability = number of seedlings divided by the number seeds per census.
and the Maricao River and Reserve experienced heavy rainfall episodes, flash floods, and landslides (M. Pérez, personal observation). Hurricanes are common in the Caribbean and may have important negative effects in the population dynamics of many native and endemic plants. For example, in Cuba after Hurricane Ivan, the populations of two orchid species, the endemic Broughtonia cubensis
and Maria are likely to have impacted population dynamics of *G. pauciflora* especially in the main channel where higher and prolonged disturbances are expected. Plants inhabiting riverine ecosystems are prone to natural disturbances due to the frequency of...
flash flood and flooding events; thus, the challenges experienced by *G. pauciflora* have also been experienced by temperate riparian species. For example, in *Pedicularis furbishiae* S.Watson, the continued destabilization of the riverbank due to the increment of flood events makes the species more vulnerable in the face of the effects of climate change (Menges, 1990; Charney and Record, 2016). Similarly, and as a result of local processes, populations of *S. tatarica* might be extinct in the long term due to erosive forces.
of floods (Jäkäläniemi et al., 2005). Nevertheless, because the extinction of local population networks can be gradual in this type of habitat (Jäkäläniemi et al., 2005), there is an opportunity for actions to preserve vulnerable species.

The probability of flowering and the expected number of fruits were lower in plants in the tributaries than in the main channel. These results could be explained, in part, by the significant difference in canopy cover between the main channel (canopy cover ranged
from 79.4–96.6%) and the tributary (ranged from 93.4–98.7%; M. Pérez et al., unpublished manuscript). Some species tend to reproduce more with increased canopy openness due to light availability, and in orchids for example, this tendency seems to be related to a rise in flower and fruit production (Hurskainen et al., 2017). The same was observed for the herbaceous species *Vincetoxicum hirundinaria* Medik in which reproduction was positively associated with sun exposure (Ågren et al., 2008). Likewise, differences in shade conditions seem to influence the reproduction of the orchid *Lepanthes rupestris* in riparian habitats in Puerto Rico (Tremblay and McCarthy, 2014).

On the other hand, we also found a difference in the population structure of *G. pauciflora* between the main channel and the tributary, which was expected based on the premise that these sites probably differ in their exposure to disturbance regimes (i.e., flash floods). The main channel had smaller plants that were more likely to flower and thus produce more fruit, while in the tributary the trend was the opposite. Environmental factors that limit growth (i.e., limited resources availability) or increase mortality rate (i.e., disturbances) are known to support the start of reproduction at relatively small sizes (Bonser and Aarssen, 2009). Indeed, experimental studies with the herb *Cynoglossum officinale* L. suggest that in habitats in which the probability of survival and growth were lower, smaller plants were more likely to flowering (Wesselingh et al., 1997). Therefore, one hypothesis is that observed trade-offs between plant size and reproduction of *G. pauciflora* between the main channel and the tributary are related to differences in disturbance regimes between sites (i.e., more intense and more frequent flash floods in the lower watershed than in the headwaters). Such trade-offs between survival and reproduction are indeed consistent with what would be predicted by life-history evolutionary theory (Stearns, 1989). This theory describes the schedule of reproduction and survival by considering the benefit and cost that maximizes fitness (Brommer, 2000; Stearns, 2000), and this variation has important implication for species adaptation across environments (Bonser and Aarssen, 2009). Therefore, if species are subjected to greater stress, mortality might be higher, then selection could favor maturation and reproduction at smaller sizes (Reznick et al., 1990). Consequently, more intense and prolonged disturbance in the main channel (which also scored higher mortality) might influence the reproduction of *G. pauciflora* at smaller sizes, while at the less-perturbed site (i.e., tributary), undisturbed growth may lead to a larger individuals.

Even though the population structure varied between sites, there were large differences between the observed and expected stable size distribution in both sites. This trend suggests that the population is not at equilibrium, which might be associated with the temporal environmental variation that influences the vital rates in the species. This behavior has also been suggested for the cactus *Pterocereus gaumeri* (Britton & Rose) Th. MacDoug. & Miranda (Mendez et al., 2004) and *M. gaumeri* (Ferrer-Cervantes et al., 2012), and for the orchid *L. rupestris* (Tremblay and McCarthy, 2014). Therefore, the observed and expected size distribution might differ because habitat stability is unlikely (Bierzychudek, 1999). Having stable conditions in Puerto Rico or in riverine environments may be unattainable due to the frequent natural disturbances such as hurricanes and flash floods; thus, a mismatch in size distribution (observed vs. expected) could be expected in both localities. Nevertheless, the observed size distribution in the tributary included small and large plants, a pattern that fits expected distributions for less-disturbed river channels (Trémolières, 2004). Moreover, the main channel had small to intermediate plant sizes, which aligns with the size distribution expected in frequently disturbed river channels (Trémolières, 2004; Bornette et al., 2008). Overall, *G. pauciflora* might also present other traits associated with frequent disturbances in riverine ecosystems (i.e., reproduction at smaller sizes, body flexibility, plants firmly attached to the rocks, ease of vegetative growth, re-sprouting ability, self-compatible breeding systems, dispersion and establishment by vegetative propagules; Townsend and Hilder, 1994; Trémolières, 2004; Bornette et al., 2008; Merritt et al., 2010), and these attributes may give the species resistance and resilience in the face of frequent natural perturbations throughout its distribution range within the basin of the Maricao River.

**Management recommendations**

Elasticity analyses suggest that survival and transition toward larger reproductive plants could have a positive effect in the population growth rates of *G. pauciflora*. Thus, management actions to reduce the time required to reach a desirable size should be prioritized. The use of larger plants (i.e., adult plants) seems to provide a better management strategy for some epiphyte orchids (Tremblay, 2003; Raventós et al., 2015a); thus, one strategy to accomplish this goal is the reintroduction of vegetative material. The results of pilot studies suggest that 15-cm plant cuttings artificially attached in the field could reach a reproductive stage in 2 years (M. Pérez et al., unpublished manuscript). In the main channel, this plant size is highly recommended for reintroduction because it is in the range of sizes with greater probability to produce flowers (and fruits). Reintroduction strategies using seeds are also possible based on the higher frequency of seedlings observed in the main channel and the tributary. Even though the time to reach a reproductive size could be longer using this propagation technique, the use of seed could help to maintain higher genetic diversity in the population.

Emphasizing the need to forecast potential changes in the population dynamics of species to generate congruent management plans (Dietze et al., 2018), we projected the population using the IPMs from the last census in both sites. For this, we used the function

**FIGURE 6.** Semiannual population growth rate estimated for *G. pauciflora* in the main channel and tributary of the Maricao River. Filled and empty circles represent \( \lambda \) values; the lower and upper whiskers correspond to the 2.5% and 97.5% intervals, respectively, estimated by bootstrapping (\( n = 500 \) simulations). Dashed horizontal line represents \( \lambda = 1 \).
The output suggests that the population of *G. pauciflora* will be reduced in size in the next 5 years at both sites, so this might reduce the population growth rate of the species even more. Certainly, this trend was observed after the impact of Hurricanes Irma and Maria (Pérez et al., unpublished manuscript). Nevertheless, we caution the interpretation of this prediction due to the short duration of this study, and the extreme natural event on the island that could have affected the demographic vital rates of the populations at both sites. However, a continuous monitoring program is highly recommended so that management actions can be adapted for this species.

Recent studies have shown increasing trends in precipitation (using short- and long-term data) in both urban and natural environments (Méndez-Lázaro et al., 2014; Van Beusekom et al., 2015). In

**FIGURE 7.** Elasticity analysis of the two *Gesneria pauciflora* populations distributed in the main channel and tributary of the Maricao River. Censuses: December 2015–June 2016 (top), June 2016–December 2016 (middle), December 2016–June 2017 (bottom). The x- and y-axes are the plant size index (log-transformed) from time t to time t + 1, respectively. The differences in color (right-hand legend) represent the survival–growth transition (fecundity transitions are of small magnitude and thus do not appear in the graph).
addition, Puerto Rico is experiencing an increase in the occurrence of extreme heat events (Méndez‐Lázaro et al., 2015; Méndez‐Tejeda, 2017) and extreme floods associated to tropical cyclones (Hernández Ayala et al., 2017) that may impact ecological processes. The survival of *G. pauciflora* was negatively affected by flash floods and the accumulation of sand/rock after a heavy rain event. Assuming a scenario where extreme atmospheric events become more common for the Caribbean (McLean et al., 2015), we recommend continued monitoring efforts to assess the resilience of the species and to estimate the effect of hurricane disturbances in the main channel and in the tributaries of the Maricao River watershed.

**CONCLUSIONS**

*Gesneria pauciflora* had a $\lambda$ value lower than unity, suggesting the population is declining. Yet plants in the main channel were smaller and were more likely to flower, while the opposite was found in the tributary. This pattern is likely related to variation in the frequency and intensity of disturbances across topographic locations within the watershed. Survival and transition toward larger plants had the largest effect on $\lambda$; thus, management strategies to reduce the time to reach larger sizes might be necessary. The use of vegetative propagules could be a possible solution.

*Gesneria pauciflora* will face a difficult situation in the future based on climatic scenarios for the Caribbean and specifically for Puerto Rico. An increase in extreme events might decrease the population growth rate even more, based on the observed impacts from the recent hurricanes. We highly recommend monitoring the species’ resilience to advocate the best management and reintroduction action to conserve the endemic flora of Puerto Rico. Continuous monitoring can also help us to identify how much $\lambda$ departs from unity. For example, over 9 years, *M. gaumeri* had a $\lambda$ greater than one in the second and last year of monitoring (Ferrer‐Cervantes et al., 2012); thus, the study period used here for *G. pauciflora* might not be sufficient to sample the range of environmental variability experienced by the population (Bierzychudek, 1999).

Evolutionary–ecological studies of Gesneriaceae suggests that the evolution of breeding systems may respond to variation in uncertain habitat conditions (Martén‐Rodríguez et al., 2015). Our study suggests that the optimal size for reproduction in *G. pauciflora* may also respond to ecological variability.

**ACKNOWLEDGEMENTS**

Funds for this study were provided by U.S. Fish and Wildlife Service (Cooperative Agreement F12AC01556) and the Department of Natural and Environmental Resources (Cooperative Agreement 2014‐000057‐B). Thanks to the Center for Applied Tropical Ecology and Conservation, the Department of Environmental Sciences of the University of Puerto Rico at Rio Piedras, and LTER administrative staff for their logistical support. Thanks to Liza García for her collaboration in data collection during the study. We thank the two reviewers for their comments and suggestions, which helped to improve this manuscript substantially. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Use of trade names in this article does not imply endorsement by the United States government.

**DATA ACCESSIBILITY**


**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the supporting information tab for this article.
APPENDIX S1. A combination of different state variables (i.e., length of the largest branch and number of leaves) to estimate a size index for *Gesneria pauciflora*. All statistical parameters from the regression models are described in Appendix S1a.

APPENDIX S2. Graphs of model selection (Survival: Appendix S2a, b; growth: Appendix S2c, d; flowering: Appendix S2e, f; fruits: Appendix S2g, h) for the size regression analyses at each stream locality (main channel, tributary) and census date.

APPENDIX S3. Statistical parameters for all regression models selected to fit the vital rates and to build IPMs for *Gesneria pauciflora*.

APPENDIX S4. Growth linear regression models with (Appendix S4a1, S4b1) and without (Appendix S4a2, S4b2) outliers for *Gesneria pauciflora* in the two river sites (main channel, tributary). ANOVA parameters from these models are described in Appendix S4c.

LITERATURE CITED


