SHORT-TERM EFFECTS OF HURRICANE MARÍA ON POPULATIONS SIZE AND INDIVIDUAL SURVIVAL IN *Lepanthes eltoroensis* (ORCHIDACEAE) AT THE LUQUILLO EXPERIMENTAL FOREST, PUERTO RICO

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Abstract

Plants endemic to the Caribbean region have evolved in response to hurricanes. These natural phenomena appear to be more frequent and more intense in the Caribbean region, which requires the study and understanding of their influence on responses by these plants – particularly if rare and with limited geographic distribution within the region – as a priority for conservation. We took advantage of long-term monitoring studies at the Luquillo Experimental Forest/El Yunque National Forest in Puerto Rico to evaluate the short-term changes in population size and the distribution of life stages of *Lepanthes eltoroensis*, a species listed as endangered under the Endangered Species Act of 1973, in response to Hurricane María. We expected there to be reductions in overall population size, and also that plants at smaller developmental stages (seedlings and juveniles) would be more affected by hurricanes compared to larger plants (i.e., adults). To examine these predictions, we conducted a rapid assessment (six-month after the storm) of inventoried subpopulations of this species, and that also are georeferenced before the 2017-hurricane season. This information is valuable for effective management and conservation efforts for this species.

Keyword **orchid, Caribbean, epiphyte, endangered, cloud forest.**

Resumen

Las plantas endémicas de la región del Caribe han evolucionado en respuesta a los huracanes. Estos fenómenos naturales aparentan ser más frecuentes e intensos en la región del Caribe por lo que es necesario comprender cómo su influencia incide en la respuesta de estas especies y establecer su estudio como una prioridad de conservación particularmente para especies raras y con una distribución limitada en la región. En este estudio aprovechamos datos de monitoreos poblacionales a largo plazo de *Lepanthes eltoroensis* – una especie listada como en peligro bajo la Ley de Especies Amenazadas del 1973 – en El Bosque Nacional El Yunque en Puerto Rico y evaluar su respuesta a corto plazo al Huracán María, tanto en el tamaño poblacional como en la distribución de individuos a distintas etapas de vida. Esperábamos reducciones en el tamaño general de la población de *L. eltoroensis*, así como una mayor respuesta de individuos en pequeñas etapas de desarrollo (plántulas y juveniles) comparado con individuos adultos. Para examinar estas predicciones, realizamos una evaluación rápida, a seis meses después del Huracán María, de subpoblaciones inventariadas y georeferenciadas desde antes de la temporada de huracanes de 2017. La información que surje de este estudio es valiosa para esfuerzos efectivos de manejo y conservación de esta especie.

Palabras clave orchid, Caribbean, epiphyte, endangered, cloud forest.

INTRODUCTION

Increases in regional temperature in the Caribbean – related to increases at a global scale – are expected to increase the frequency and intensity of extreme tropical storms and other weather events (Gould et al. 2018). Although it is assumed that native species in hurricane-prone areas have evolved in response to the influence of hurricanes (Lugo 2008), these natural phenomena change the forest structure and microclimate considerably in the short term. These changes may include extirpation of populations of rare species, which requires studying how such species will respond to hurricanes as their frequency and intensity increase in the foreseeable future. Under a scenario of climate change, rare species and unique ecosystems may be vulnerable (Pacifici et al. 2015; Ponce-Reyes et al. 2012; Bruijnzeel et al. 2011; Jarvis et al. 2010; Singarayer et al. 2006). Species could either adapt or face the prospect of going extinct (Koh et al. 2004). This could be a challenge for the maintenance of biodiversity in the Caribbean, which is considered a biodiversity hotspot given its high proportion of rare, endemic species (Myers et al. 2000).

The orchid *Lepanthes eltoroensis* Stimson is a rare, epiphytic species endemic to Puerto Rico (PR) and restricted to the Luquillo Mountains, including the Luquillo Experimental Forest/El Yunque National Forest (LEF/EYNF; northeastern PR) (Stimson 1969; Woodbury et al. 1975). It was listed as endangered by the U.S. Fish and Wildlife Service on 29 November 1991 (Rivera, 1996). The species shows a distribution restricted to the upper elevation site of the cloud forest at LEF/EYNF (Stimson 1969). Globally, it has been suggested that cloud forests are one of the planet's most rare and endangered ecosystems (Bruijnzeel et al. 2011). In fact, downscale models on future climate change scenarios predict as a worst-case scenario in which temperature increases and precipitation declines – particularly in wetter regions like LEF/EYNF –, a shift in the distribution of life zones of PR, from humid to drier, with significant consequences to species whose distribution is restricted to higher elevations (Khalyani et al. 2016). For example, living under persistent cloud cover has adapted individuals of species at cloud forests to a unique microclimate, which includes reduced irradiance levels and temperatures (Bubb et al. 2004). These conditions, in turn, promote slow growth, short dispersal distances, and a patchy distribution of plant species in these forests (Foster 2001). Also, conditions at these forests, if changed rapidly relative to the rate of adaptability of their plants, may generate a disadvantage competitive scenario in a colonization-extirpation dynamic. For example, Tremblay (2008) and Benitez Joubert and Tremblay (2003) described the effects of hurricanes on populations of *L. eltoroensis*, when Hurricane Georges, a category-3 storm, struck the island in 1998. They concluded that hurricanes could lead to high mortality rates in this species as hurricane winds defoliate the canopy resulting in changes in microclimate conditions, and exposing individuals of *L. eltoroensis* (and other plants) in the understory to rapid changes that included increases in the intensity of light (e.g., increased radiative energy and temperature) and evapotranspiration. Tremblay (2008) proposed that these natural phenomena, although frequent in the Caribbean, have the potential to change the population size of these orchids negatively (Tremblay 2008).

On 6 September 2017, Hurricane Irma at Category 5 passed 92.6 km north of Puerto Rico with the island experiencing sustained winds of 88.9 k/hr and gusts of up to 118.5 km/hr (Cangialosi et al. 2018). Two weeks later, on 20 September 2017, the island of Puerto Rico was struck by Hurricane María, which was a high-end category-4 storm considered one of the strongest recorded for PR; winds reached 250 km/h, and pressure reached 908 millibars just before the landfall of its eye on southeastern PR (Yabucoa municipality; Pasch et al. 2018). In the Long-Term Forest Dynamics Plot of the LEF/EYNF, which has been monitored since 1989, Hurricane María led to immediate massive defoliation, tree mortality, increases in temperatures, and declines in relative humidity with forest effects that were more severe than what was experienced in Hurricanes Hugo and Georges both of which were Category 3 storms (Uriarte et al. 2019). Lugo (2008) reported increases in temperature of up to 4°C in some areas of LEF/EYNF. Therefore, given the restricted distribution of extant populations of *L. eltoroensis* to the cloud forest at LEF/EYNF, we expected – on the downside from a conservation perspective – large changes in its population size and distribution in response to Hurricane María.

In this study, we took advantage of ongoing monitoring of populations of *Lepanthes eltoroensis* at LEF/EYNF to evaluate the short-term changes in population size and the distribution of life stages of this species in response to Hurricane María six months after the event. We expected reductions in overall population size and that plants at earlier developmental stages (seedlings and juveniles) would be more affected by hurricanes than larger plants (i.e., adults). To examine these predictions, we conducted a rapid assessment (six-months after the storm) of inventoried subpopulations of this species that were also georeferenced before the 2017-hurricane season.

METHODS

Study site

We evaluated the fate of individuals of *Lepanthes eltoroensis* and their host plants (i.e., phorophytes) within a segment of the at El Toro Trail. This trail spans a distance of approximately 3.5 km from its entrance at road PR-186 in the municipality of Río Grande, northeastern PR to the end at the El Toro Peak (Figure 1). The trail, which runs from an east-west direction between roads PR-191 and PR-186, is situated in the protected wilderness area (i.e., El Toro Wilderness Area or ETWA) of the LEF/EYNF. The cloud forest area in our study site is classified as Elfin Forest due to its small stature and has an annual rainfall around 4,200 mm (data from Pico del Este weather station, eastern LEF/EYNF). Rainfall is seasonal: it peaks in October (low-end rainy season) and reaches low values around March (low-end dry season; Wang et al. 2003). Average monthly temperature ranges 17°C–21°C (Harris et al. 2012). The section of the trail included in our study lies between 875 meters above sea level (m asl) and 1,033 m asl.

Study System

Lepanthes eltoroensis (Figure 2) is a small-sized epiphytic orchid endemic and restricted to the ETWA, along the trails named El Toro (to the west, starting at PR-186), passing just south of Mount Cacique (to the middle within the wilderness area), and Tradewinds (to the east, ending at road PR-191) at LEF/EYNF (Rivera 1996). Individual orchids have thin stems with a solitary leaf (3.8 cm long) and a one or few inflorescences that produce many small flowers (< 8 mm; Ackerman 1996) that produce fruits with many seeds. Like most orchids in the Genus, plants are pollinator limited (Tremblay et al. 2005). Also, they are protandrous and can be cross-pollinated (Tremblay et al. 2006). Although its main pollinator

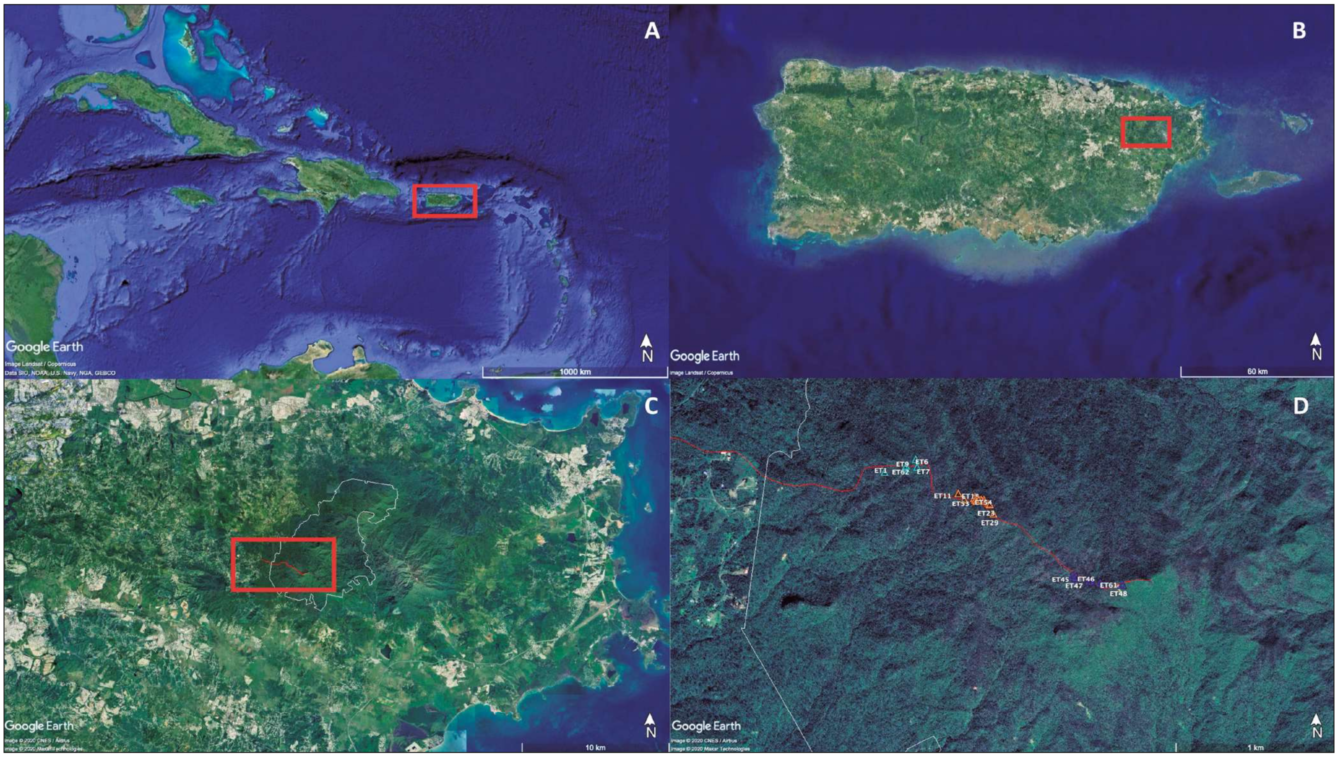

Figure 1. Location of study site: (A) Caribbean, (B) El Yunque National Forest (EYNF) in Puerto Rico, (C) Wilderness area within EYNF, and (D) El Toro Trail and populations sampled (different colored symbols with letters) (images based on ©Google Earth, 2020).

is unknown, black-winged fungus gnats are likely to be the main pollinator of *Lepanthes eltoroensis* (Blanco and Barboza 2005). The mean population size of *L. eltoroensis* (i.e., the number of plants per host) can be low (11.6 individuals), and their spatial distribution is not uniform but exhibits a high mean-crowding index (47.6), with a mean distance of 38.6 m between populations (i.e., orchids on a host; Tremblay 1997). Also, individuals of *L. eltoroensis* have a relatively short life span (5.2 years; Tremblay 2000).

Pre-Hurricane Inventory

We searched and tagged host plants and orchids and collected count data for each cluster/population from July to August 2017 along the El Toro Trail. We inventoried all trees and lianas in a 30-m × 1,897.56-m long transect that was started parallel to the location of the lowermost *L. eltoroensis* subpopulation and was ended at the El Toro Peak. Before the hurricane, we marked 48 hosts of *L. eltoroensis*, which commonly included *Micropholis garciniifolia* Pierre, *Clusia clusioides* (Griseb.) D'Arcy, *Cyathea arborea* (L.) Sm., *Ocotea spathulata* Mez, and *Marcgravia sintenisii* Urban. Once a host plant was found, a 10-m radius circular plot was made around it, and we search for all trees and stems within to locate all *L. eltoroensis* present. For all hosts with *L. eltoroensis* plants, we recorded their geographic location, and counted all individuals of *L. eltoroensis* and classified the life stage of each as follows: (1) seedlings (small plants without a leaf petiole); (2) juveniles (individuals with at least one lepanthiform sheath on the petiole and without evidence of reproduction), (3) non-reproductive adults (non-flowering individuals that carry dry non-active inflorescences); (4) reproductive adults (individuals with photosynthesizing inflorescences) (Figure 2). For all hosts with *L. eltoroensis* on its surface, we recorded the diameter at breast height (dbh) and noted its elevation (m asl). Host plants tended to occur in

Figure 2. *Lepanthes eltoroensis* Stimson and its respective stages as: (A) Seedlings = only leaves, no "lepanthes sheet"; (B) Juvenile = leaves and at least one "lepanthes sheet"; (C) reproductively active adult plants with live inflorescences (photosynthetic with or without flowers and/or buds); (D) non-reproductive adult = plants with dry inflorescences. Photographs by Rayza M. Hernández-Muñiz.

clusters whose distribution was discontinuous along elevation (Figure 1), and we a priori assigned hosts to one of three categories of spatial clusters (groups of phorophytes): cluster 1 (C1, low elevation site), cluster 2 (C2, mid-elevation site), and cluster 3 (C3, high elevation site). Also, we determined the elevation of each host plant to document the mean elevation of their corresponding cluster, and conducted correlation analyses to determine the relationship between dbh and elevation of host plants (see Results).

Post-Hurricane Inventory

Previously tagged host plants found after the hurricane event (n = 31) were surveyed for damage and orchids along the El Toro Trail between 13 February and 1 March 2018. Also, we found seven new host plants with orchids and that were undetected in pre-hurricane surveys along the El Toro Trail but were not included in the pre-post hurricane analyses. For all hosts found, we recorded its state as live, dead, or missing, and its physical condition attributed either to the hurricane (e.g., broken branches, leaning trunks, defoliation, fallen, split, uprooted). For each host, we estimated the mortality of orchids as ([*1 - number of orchids before*]/[*number of orchids after*]) and mortality rate per for each life stage. Mortality attributed to the hurricane in *L. eltoroensis* (n = 779 evaluated individuals) was determined only using the pre-hurricane number of orchids from host trees that also were found after the hurricane.

Statistical Analyses

We evaluated if there were significant differences between host clusters in the dbh of hosts and the actual elevation of hosts using One-way ANOVA. We use a 2 × 3 Chi-Square test to assess the difference in the frequency distribution of life stages before and after the hurricane. We also evaluated if orchid mortality (the proportion of missing orchids pre- and post-hurricane) per host was associated with the host's dbh and elevation using linear regression (based on the 'lm function' and proportions transformed using 'arcsine' function). Finally, we examined the relationship between the magnitude of the numerical change for the total subpopulation of a host (pre-hurricane – post-hurricane value) and that of the different life states with elevation and dbh using multiple pair-wise-correlation. For analyses including dbh, only standing hosts were included. All analyses were conducted using R (R Core Team 2013), and we adopted a significance level of *alpha* = 0.05.

RESULTS

Host-Habitat Characteristics

The dbh of host plants ranged 3.5–46.0 cm, and these plants were distributed across an elevation gradient that ranged 836.0–1,035.2 m asl. We found significant differences among the three clusters in their mean dbh (mean ± standard deviation: cluster 1 = 34.2 cm ± 8.8 cm, n = 5; cluster 2 = 17.4 cm ± 7.9 cm, n = 17; cluster 3 = 17.3 cm ± 10.5 cm, n = 9), but plants at cluster 1 had a larger value of mean dbh than those from clusters 2 and 3, which shared similar lower values of mean dbh (Figure 3A). In contrast, the mean elevation of host plants differed among all clusters: cluster 1 = 878.8 m ± 35.5 m; cluster 2 = 942.3 m ± 62.5 m; cluster 3 = 1,035.2 m ± 49.2 m (Figure 3B). The mean elevation between adjacent clusters varied between 63.5 m and 92.9 m asl. Although the mean dbh between clusters 2 and 3 was similar (Figure 3A), we found a significant negative correlation between the dbh and elevation among all host plants, with smaller plants at higher elevations (r_s = -0.41, p = 0.05, n = 31).

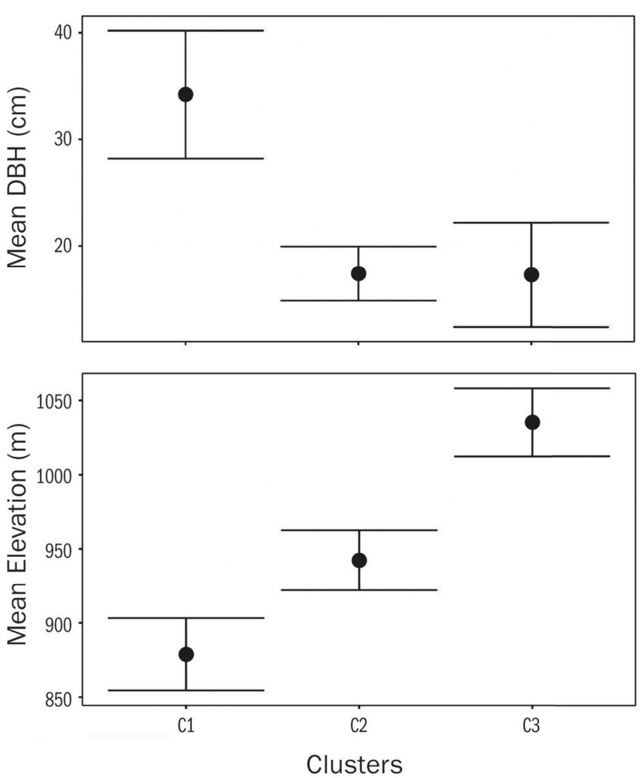

Figure 3. Differences in mean diameter at breast height (DBH) of host trees of *Lepanthes eltoroensis* and the mean elevation of orchid hosts by geographic cluster (C1, C2, C3) along the El Toro Trail. Data was Analyzed with one-way ANOVA for (A) difference in DBH among clusters/ phorophytes ($F_{2,28}$ = 58.5, p = 3.53e-12) and (B) difference in elevation among clusters ($F_{2, 28}$ = 3,072, p < 2e-16).

Short-term responses to hurricane

The hurricane led to considerable changes in forest structure. Before Hurricane María, 48 georeferenced host trees along the El Toro Trail harbored 1,258 orchids of *Lepanthes eltoroensis*, but immediately after the hurricane, 17 of those host trees could not be located (nor found), which also may represent 479 orchids missing. Of the 31 host trees found after the hurricane, seven fell to the ground but harbored live orchids. Also, 93% of host trees found (n = 28) had some physical damage, with the most frequent damage category being category 'broken branches' (Table 1). The 31 host plants found after the hurricane represented five species – *Chrysophyllum bicolor* Poir, *Clusia clusioides*, *Micropholis garciniifolia*, *Ocotea spathulata*, and *Cyathea arborea* – with *M. garciniifolia* being the most frequent host (70.9% or n = 22); most other host plants were represented by one individual. Also, after Hurricane María, the 31 host trees only carried 322 orchids, which may yield a 58.7% (= 457/779) estimated mortality compared to orchids alive immediately after the hurricane (i.e., n = [1,258

Table 1. Frequency distribution of damage categories for host trees (n = 28) of *Lepanthes eltoroensis* along El Toro trail at El Yunque National Forest. A host tree may be included in more than one category of damage.

Damage type	Number of stems	Proportion
Alive	15	0.22
Broken Branches	15	0.17
Defoliation	4	0.05
Leaning trunk	3	0.03
With Canopy	7	0.10
Fallen	6	0.10
Split	4	0.05
Uprooted	1	0.03

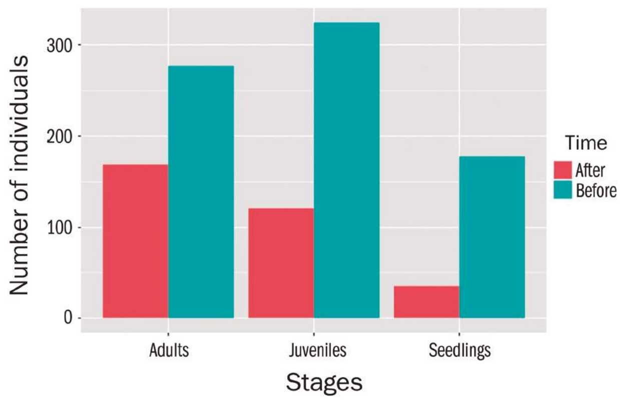

Figure 4. Number of individuals of *Lepanthes eltoroensis* by life stage documented at each study site along El Toro Trail. Seedling; Juvenile; Adult (plants with dry or live inflorescences). Bars represent the number of plants before and after Hurricane María in 2017. Only plants from host plants tagged in 2017 and that were recovered in 2018 were used in this analysis.

orchids alive before María – 479 orchids missing] = 779 orchids in the shorter term).

The frequency distribution of life stages following Hurricane María was significantly different from the pre-hurricane values ($X^2 = 112.9$, df = 4, $p < 0.001$), with seedlings being significantly overrepresented before the hurricane and significantly underrepresented afterward (Figure 4). Mortality rates were similar among different host clusters when mortality rates were pooled regardless of the category of life stages (Figure 5A). In contrast, when estimated by life stage, mortality was highest for seedlings (80.3%) (Figure 5B), followed by juveniles (62.6%) (Figure 5C), and adults (38.9%) (Figure 5D). The dbh of host plants nor mean elevation of clusters were correlated with the magnitude of the change in the total number of orchids nor the magnitude of change within life stages of orchids (Table 2). On the other hand, the magnitude of the numerical change of the different life stages and the total number of orchids on a host were positively correlated with each other (Table 2).

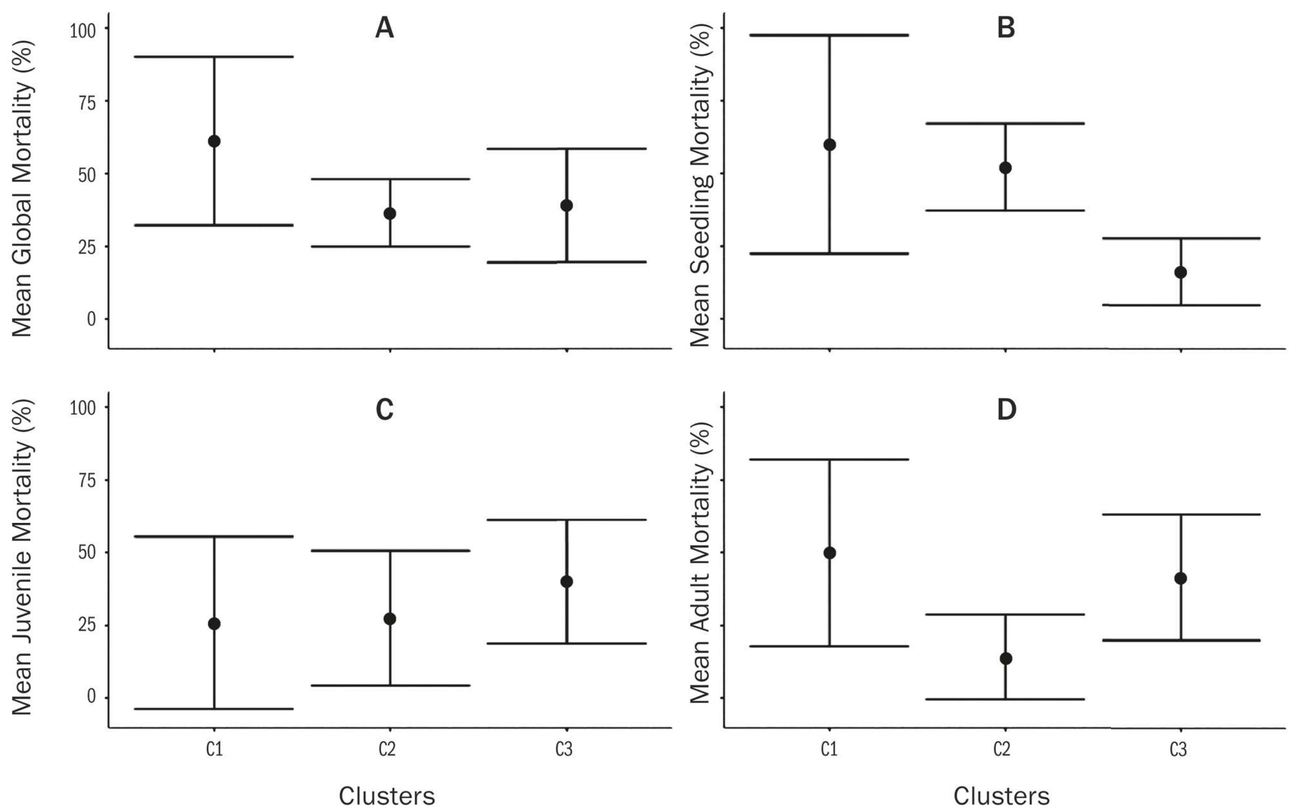

Figure 5. Mean orchid mortality (= 1 – survival) per host plant in the designated clusters along the El Toro trail, Luquillo Experimental Forest/El Yunque National Forest in Puerto Rico six months after Hurricane María: (A) Global population (all populations merged); (B) Seedlings; (C) Juveniles; and (D) Adults.

Table 2. Spearman Rank correlation coefficients for the relationship between the change in the number of orchids (at different categories) per host after Hurricane María and different variables. Variables are diameter at breast height (dbh) and elevation. Categories are: seedling (*△S*), juvenile plants (*△J*), seedlings and juvenile plants combined (*△SJ*), adult plants (*△A*), and subpopulation (all categories combined; *△POP*). Asterisks highlight levels of significant correlations: * = p < 0.05; ** = p < 0.01; *** = p << 0.001.

	dbh	elevation	*△S*	*△J*	*△SJ*	*△A*	*△POP*
dbh	-						
elevation	**-0.41***	-					
△S	-0.02	0.10	-				
△J	0.07	-0.08	**0.80*****	-			
△SJ	0.02	-0.05	**0.91*****	**0.96*****	-		
△A	-0.19	0.10	0.51**	**0.74*****	0.66***	-	
△POP	-0.02	-0.04	**0.87*****	**0.95*****	**0.98*****	**0.76*****	-

DISCUSSION

The high mortality of orchids of *Lepanthes eltoroensis* herein documented may result from different factors and (direct and indirect) processes acting in synergism after Hurricane María and compared to Hurricane Georges that struck PR almost 20 years ago. First, Hurricane María was a more severe storm (category-4) than Hurricane Georges (category-3) and spent more time inland (~30 hours on 19-21 September 2017, compared to ~24 hours on 21-22 September 1998). In general, strong hurricane winds are known to strip epiphytes from the surface of host plants at LEF/ENFY (Migenis and Ackerman 1993) and, in particular, orchids in other forests in PR (Rodriguez-Robles et al. 1990). Moreover, host trees could also be stripped of their bryophyte cover, which is an element found to be important for the establishment of plants in other species of *Lepanthes* (García et al. 2009). Therefore, the differences in the percentage of mortality of *Lepanthes eltoroensis* between hurricanes María and Georges (i.e., 58.7% six months after María versus 47.6% 1.5 years after Georges) could be explained, in large part, by the direct influence of strong hurricane winds that removed orchids from the exposed surfaces of host plants at El Toro study site. Second, individuals could be lost via the mortality of their host trees (i.e., through severe uprooting or trunk damage) and extensive crown damage leading to orchids falling on the forest floor devoid of light and suitable microclimate conditions. For example, Tremblay (2008) and Benitez Joubert and Tremblay (2003) showed that after Hurricane Georges, individuals of *L. eltoroensis* could have died rapidly in just a few weeks if not relocated to suitable areas. It should be noted that our mortality rates may be underestimated as orchids occurring in hosts that were not found in the post-hurricane assessment were excluded from the estimate (i.e., 479 orchids missing from 17 host plants also missing). If we assumed that those missing host plants resulted in dead orchids (e.g., because orchids get buried within vegetation and soil, crushed by fell hosts and overshadowed by densely overgrown herbaceous vegetation; see next) our estimate of mortality most likely be higher at 74.4% (i.e., 936 total orchids deemed dead/1,258 alive before Hurricane María).

Mortality, however, could have also occurred through indirect effects such as changes in microclimate conditions besides direct physical removal from host plants. Although not assessed in this study, large differences in canopy cover could result in delayed physiological responses of orchids leading to increased mortality. For example, for shade-adapted species living in low irradiance environments and high humidity environments like those encountered in the cloud forest at El Toro, the opening of the canopy could bring orchids near their physiological limit because of an excess of light may interfere photosynthesis (e.g., as in *L. rupestris* in Zhang et al. 2017 and Zhang et al. 2018), and the associated increase in temperature and lowering of humidity may result in irreversible leaf damage (Lovelock et al. 1994; Robinson 2001). In contrast, Ackerman (2014) argued that epiphytic environments of orchids are highly variable and that as a group, epiphytic species may be able to recover from large changes in forest cover, which justifies the continued monitoring of populations of *L. eltoroensis* at a larger temporal scale.

Not all circumstances are dire for *Lepanthes eltoroensis*, however. Ongoing monitoring revealed that the number of individuals of *L. eltoroensis* is considerably higher compared to the known number of individuals at the time of the listing of the species in 1991. For example, the estimated number of orchids of *L. eltoroensis* before 1991 was 200 (Rivera 1996), but before Hurricane María, we identified 1,000 individuals in just one segment of the El Toro Trail; just in that segment of the trail, the numbers are still higher than what they used to be immediately before María. We also know much more about the natural history and ecology of *L. eltoroensis* since its listing in 1991, and we found 16 new host trees after Hurricane María, which suggests that *L. eltoroensis* may be more widespread and common at El Toro and similar microhabitats than frequently acknowledged. Whether this is a generality or a product of a false impression is yet still to be determined. Consequently, we need to continue monitoring efforts of this species currently in place by the USDA Forest Service, the U.S. Fish and Wildlife Service, and the University of Puerto Rico and develop a habitat suitability model for *L. eltoroensis* that allows identifying prospect locations of extant populations at LEF/EYNF. Although the Caribbean National Forest Act of 2005 designated 4,047 ha (10,000 acres) of the LEF/EYNF as El Toro Wilderness Area (USDA Forest Service 2016), our recommendations have profound consequences for the effective management and conservation of *Lepanthes eltoroensis* at a larger spatial scale.

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