

# ACTA CIENTÍFICA

Una revista transdisciplinaria de Puerto Rico y el Caribe

EDICIÓN ESPECIAL

**Más allá de la resiliencia: los efectos de los huracanes  
Irma y María en Puerto Rico y el Caribe**

SPECIAL EDITION

**Beyond resilience: the effects of hurricanes  
Irma and María in Puerto Rico and the Caribbean**



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## PORTADA



De izquierda a derecha y de arriba hacia abajo: primero, foto de las Dos Ceibas en la carretera PR-2 (antigua “carretera Militar”) en el Barrio Cocos de Quebradillas en 1988 (a inicios de las labores de construcción de la carretera PR-2). El título original de la foto: “Ceibas de Quebradillas, Puerto Rico, foto por Maribel Ruiz, Estudiante UPR-Arecibo 1988” tomado del relato “El manantial de mi infancia y la ceiba del manantial” por Amapola Pinocha Del Valle, colgado el 22 de abril de 2011 en el Blog Pinocha.net [<http://pinocha.net> ] mantenido por Margarita Agosto De Fernández bajo la licencia de Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported License). Las siguientes fotos de estas ceibas corresponden al 26 de septiembre de 2017 (seis días luego del Huracán María), 7 de octubre de 2017 (dos semanas y tres días luego del María) y 28 de noviembre de 2020 (tres años, dos meses y ocho días luego del María; inferior derecha) (fotografías por Neftalí Ríos). Así como el humano, con voluntad, adapta sus acciones para la transformación del paisaje en beneficio de la biodiversidad y su propia existencia, son estas ceibas símbolos del fenómeno adaptativo de la biota ante el paso milenar de los huracanes por Puerto Rico y el Caribe: en dos semanas, con hojas nuevas; a tres años, reorganizadas y listas para el próximo.

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# EDITORIAL

Este volumen de *Acta Científica: una revista transdisciplinaria de Puerto Rico y el Caribe (AC-PuR&C)* se hace realidad luego de un periodo de reformulación de la naturaleza de la revista que la precede y durante un tiempo atípico de tensión mundial producto de la pandemia por la COVID-19. Además, aquí comienzo mi labor como Editor en jefe para con una iniciativa extraordinaria, que por espacio de más de tres décadas, desarrollara y realizara el Dr. Ariel E. Lugo junto a un grupo de colegas comprometidos, tanto para la revisión, autoría y facilitadores de producción, involucrados en las muchas facetas del quehacer científico y social de Puerto Rico y más allá. Con un nuevo nombre, Junta de Editores y alcance, tanto en las ciencias naturales como en las sociales en Puerto Rico y el Caribe, expandimos el cúmulo de contribuciones referente al Huracán María y su influencia en las respuestas de la biota en Puerto Rico. Esta nueva fase de la revista es posible gracias a las gestiones realizadas por el Dr. Ernesto Medina para acceder a colegas de Caracas, que bajo la dirección de Pamela Navarro, proveen de la labor técnica y artística para la producción de la misma. La dirección, consejo, apoyo y contribución del Dr. Lugo a esta obra y su nueva faceta, así como del Servicio Forestal de los Estados Unidos de América, representa un

legado encomiable y ante esto, nuestro más profundo agradecimiento.

Este volumen 32 de *AC-PuR&C* cuenta con trabajos de estudiantes universitarios y profesores (tanto de Puerto Rico como de los Estados Unidos de América), personal del Servicio de Pesca y Vida Silvestre de los EE. UU. y Servicio Forestal de los EE. UU., un ensayo sobre la utilización de letras mayúsculas para nombres comunes en las ciencias biológicas y las Instrucciones para Autores revisadas y ampliadas, en español e inglés. Deseamos agradecer a los 21 autores que nos enviaron sus contribuciones y a los revisores, que sin su trabajo, sería imposible realizar el nuestro. Próximamente, *AC-PuR&C* deberá darle continuidad a la excelente iniciativa del trabajo que lo precede, relacionada con resúmenes de diversas actividades y síntesis de reuniones científicas y afines que normalmente se hacen en Puerto Rico. Esto, con el propósito de preservar el contenido de las mismas para el beneficio de aquellos que no tuvieron la oportunidad de participar y sobre todo, como reservorio histórico para beneficio de futuras generaciones. Luego de 31 años de apoyo a este foro de divulgación profesional esperamos igualmente el continuo apoyo a *Acta Científica: una revista transdisciplinaria de Puerto Rico y el Caribe*.

*Neftalí Ríos López*

Caguas, Puerto Rico



# FLORACIÓN, FRUCTIFICACIÓN Y GERMINACIÓN ABUNDANTE DE CÓBANA NEGRA, *Libidibia monosperma*, EN TERRENOS DEL RECINTO UNIVERSITARIO DE MAYAGÜEZ LUEGO DEL HURACÁN MARÍA: OBSERVACIONES Y RECOMENDACIONES

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## Resumen

Esta nota documenta las observaciones de un evento de floración, fructificación y germinación abundante de árboles de Cóbana Negra (*Libidibia monosperma*), una especie protegida, en terrenos de la Universidad de Puerto Rico, Recinto Universitario de Mayagüez (RUM), después del paso del Huracán María en septiembre 2017. A pesar de que los individuos de esta población de Cóbana Negra, la cual fue sembrada a mediados de siglo pasado, fueron completamente defoliados por el Huracán María, se observó floración y fructificación abundante entre cinco y siete meses luego del huracán en todos los individuos. Esto resultó en la germinación de cientos de plántulas bajo el dosel de los árboles parentales. La población de Cóbana Negra del RUM puede apoyar actividades de conservación, educación, e investigación para contribuir a la rehabilitación de la especie, tal como servir de fuente de semilla y plántulas para siembras de rehabilitación y facilitar estudios de métodos de propagación efectivos. En esta nota se elaboran éstas y otras recomendaciones para apoyar la conservación y rehabilitación de la Cóbana Negra y otras especies de árboles protegidos en terrenos del RUM y en Puerto Rico.

**Palabras clave** árboles, arboricultura, biología de conservación en el Caribe, biología reproductiva, dispersión de semillas, especies amenazadas, especies en peligro, especies vulnerables, manejo de árboles.

## Abstract

This note documents the observations of a copious flowering, fruiting, and germination event of trees of Cóbana Negra (*Libidibia monosperma*), a protected species, on lands of the University of Puerto Rico, Mayagüez Campus (RUM in Spanish), after the passage of Hurricane María in September 2017. Despite that the individuals of this population of Cóbana Negra, which was planted in the middle of the last century, were completely defoliated by the hurricane, abundant flowering and fruiting of mature individuals were observed between five and seven months after the hurricane in all individuals. This resulted in the germination of hundreds of seedlings of Cóbana Negra under the canopy of the parent trees. The population of Cóbana Negra in RUM can support conservation, education, and research activities to contribute to the rehabilitation of the species, such as acting as source of seed and seedlings for rehabilitation plantings and facilitating studies for effective propagation methods. These and other recommendations are elaborated to fur-

ther support current efforts for the conservation and rehabilitation of Cóbana Negra and other protected tree species on RUM lands and in Puerto Rico.

**Keywords** Caribbean conservation biology, endangered, threatened and vulnerable tree species, tree reproductive biology and seed dispersal, urban arboriculture and tree management.

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## INTRODUCCIÓN

Los terrenos del Recinto Universitario de Mayagüez (RUM) albergan una población madura de individuos de Cóbana Negra (*Libidibia monosperma* [Tul.] E. Gagnon & G. P. Lewis) (Mari-Mut 2014). La Cóbana Negra es endémica a manglares y pantanos costeros del archipiélago de Islas Vírgenes de Estados Unidos, Puerto Rico y el oeste de República Dominicana, y posee un reducido rango geográfico ocasionado por factores antropogénicos tales como la deforestación, cosecha excesiva por su valiosa madera, consumo de frutos por ganado y pérdida de hábitat (Little y Wadsworth 1964; U.S. Fish and Wildlife Service 1995). En consecuencia, la especie está clasificada como *en peligro* por la Unión Internacional para la Conservación de la Naturaleza (World Conservation Monitoring Centre 1998), *amenazada* por el Servicio de Pesca y Vida Silvestre de Estados Unidos (Department of the Interior, Fish and Wildlife Service 1990 y 2019) y *vulnerable* por el Departamento de Recursos Naturales y Ambientales de Puerto Rico (Departamento de Recursos Naturales y Ambientales 2004).

La población de Cóbana Negra en el RUM consiste de alrededor de una docena de individuos maduros localizados en terrenos adyacentes al edificio Jesús T. Piñero de la Facultad de Ciencias Agrícolas (FCA), dos individuos próximos al edificio de servicios médicos, un individuo próximo al área de estacionamiento en el edificio Doctoral en la Finca Alzamora, y otro cerca del laboratorio de artes gráficas (Mari-Mut 2014). Parte de la población próxima al edificio Piñero consiste de árboles sembrados alrededor de un terreno llano que es anegado estacionalmente,

mantenido como área verde y ocasionalmente utilizado como espacio de estacionamiento (Figura 1; Mari-Mut 2014). Este terreno ubica en la colindancia del RUM con la carretera PR-2R (ramal) y ha sido modificado de forma tal que contiene un desagüe para descargar el exceso de lluvias que se acumula en el terreno llano hacia el sistema de alcantarillados de la carretera. El resto de las cóbanas negras en las cercanías del edificio Piñero se encuentran en una pendiente y fueron sembradas al contorno en terrazas elevadas que rodean el terreno llano. Los individuos próximos a servicios médicos se ubican en una pendiente, el individuo en Finca Alzamora está sembrado en una isleta contenida por pavimento y el individuo cerca de artes gráficas en una zona riverense a la quebrada Del Oro que atraviesa el RUM.

Según el trabajo de documentación de historia natural del RUM del Dr. José Mari-Mut (2014), los árboles maduros más viejos de Cóbana Negra en el RUM incluyen aquellos cercanos al edificio Piñero y servicios médicos (i.e., cerca del Museo de Arte, MUSA), los cuales fueron sembrados entre 1936 y 1942 por iniciativa del Dr. Carlos Chardón. El árbol que se encuentra en las cercanías del edificio Doctoral (i.e., Laboratorio de Entomología) fue sembrado décadas después por José A. Ramos. La vegetación cercana a las cóbanas negras incluye árboles de matabuey (*Goetzea elegans*), palma real (*Roystonea borinquena*), zarzilla (*Leucaena leucocephala*) y cultivos hortícolas en las cercanías del edificio Piñero, árboles de algarrobo (*Hymenaea courbaril*), caoba hondureña (*Swietenia macrophylla*) y maría (*Callophyllum antillensis*) cerca de servicios médicos, y pino hondureño (*Pinus caribea*) cerca de artes gráficas. Los árboles de estas otras especies fueron en su mayoría sembrados y se

encuentran en terrenos designados y mantenidos como áreas verdes por el RUM. La colección de árboles del RUM es utilizada por como recurso educativo para cursos, laboratorios y talleres educativos.

Aunque no ocasionó la caída ni ruptura del tronco de ninguno de los árboles maduros de Cóbana Negra en el RUM, el Huracán María causó la pérdida del follaje en el dosel e incluso de ramas principales en algunos árboles. Durante los meses posteriores al Huracán María, se observó un evento mayor de floración y fructificación de los árboles maduros, y la germinación abundante de plántulas bajo éstos árboles. Esta nota documenta observaciones relacionadas a este evento y provee recomendaciones para apoyar los esfuerzos de conservación y rehabilitación de la Cóbana Negra y otras especies protegidas en el RUM y en Puerto Rico en general.

## OBSERVACIONES

Tras el paso del Huracán María en septiembre de 2017, los árboles maduros de Cóbana Negra del RUM florecieron y fructificaron abundantemente. Este huracán defolió cerca del 100% del follaje en las coronas y causó la caída de ramas en algunos individuos, pero no se observó mortandad de individuos maduros a corto plazo. El follaje del dosel de las cóbanas negras no se recuperó hasta aproximadamente diciembre de 2017 cuando llegó a niveles observados previo al Huracán María, descontando la pérdida de follaje de dosel a consecuencia de ramas caídas. Para febrero de 2018, los árboles mostraron floración y para abril de 2018 se observó fructificación abundante en todos los árboles de Cóbana Negra del RUM. Los frutos rojos, carnosos, de aproximadamente cinco centímetros de largo comenzaron a caer al terreno bajo los árboles parentales, persistiendo la caída durante los meses del verano, de mayo a julio. Durante el mismo verano de 2018 ocurrió la germinación de innumerables frutos resultando en una alta densidad de plántulas creciendo concentradas en

el terreno bajo las coronas de los árboles parentales. Para los meses de septiembre a noviembre del 2018, el cohorte de plántulas alcanzaba una veintena de individuos por metro cuadrado y una media en estatura de aproximadamente 20 centímetros basado en estimados oculares y datos recopilados para plántulas trasplantadas (Figura 1).

El retorno paulatino de las labores de mantenimiento en el RUM durante los meses posteriores al Huracán María resultó en que una proporción de las plántulas de Cóbana Negra que se encontraban creciendo en las áreas verdes fuera talada inadvertidamente por brigadas de mantenimiento. Consecuentemente, estudiantes y personal de la FCA coordinaron con el personal de mantenimiento del RUM para delimitar las áreas que contenían las plántulas de Cóbana Negra y evitar la tala. Paralelamente a este esfuerzo, estudiantes y personal de la FCA rescataron una proporción de las plántulas y las relocaron en el vivero de Finca Alzamora para su eventual trasplante y siembra en esfuerzos de rehabilitación de la especie (Figura 1).

## DISCUSIÓN

La temporada del evento de floración y fructificación abundante de la población de Cóbana Negra del RUM concuerda con observaciones reportadas en la literatura indicando floración regular anual entre los meses de febrero y junio dependiendo de los patrones de precipitación (Little y Wadsworth 1964; U.S. Fish and Wildlife Service 1995). Sin embargo, la fructificación tras el Huracán María parece haber ocurrido más temprano relativo a observaciones que indican su ocurrencia regular anual comenzando durante el mes de junio y con frutos madurando durante los meses de verano a otoño (U.S. Fish and Wildlife Service 1995). Es posible que la alta disponibilidad de agua tras el Huracán María haya facilitado una fructificación y maduración de frutos más temprana.



Figura 1. Individuos de Cóbana Negra (*Libidia monosperma*) en los terrenos cercanos al edificio Jesús T. Piñero y plántulas trasplantadas en el vivero de Finca Alzamora del Recinto Universitario de Mayagüez. (A) Tres árboles de Cóbana Negra creciendo en la terraza continua al terreno llano que se encuentra al fondo y un tocón de un árbol de padauk de Burma (*Pterocarpus macrocarpus*) en primer plano (la flecha señala un cuarto árbol de Cóbana Negra). (B) Dos de los árboles de Cóbana Negra (primer plano) de la primera foto pero vistos en dirección opuesta (al fondo, estudiantes de la Facultad de Ciencias Agrícolas durante un laboratorio y el edificio Piñero). El terreno en primer plano, de menor elevación y dominado por gramíneas, fue uno de los lugares donde se concentró la germinación de plántulas de Cóbana Negra. (C) Plántulas de Cóbana Negra listas para transplantarse.

Torres y Schwagerl (2006) reportaron la germinación abundante (aproximadamente 100 plántulas) de Cóbana Negra bajo árboles parentales que fueron sembrados a partir de 1980 en proyectos de rehabilitación de la especie en el Refugio Nacional de Vida Silvestre de Cabo Rojo (Weaver y Schwagerl 2008). En ese caso, las plántulas también se concentraron bajo árboles parentales. Observaciones contemporáneas en poblaciones silvestres indican que los frutos de la Cóbana Negra podrían ser dispersados por algunas especies de murciélagos y cangrejos terrestres (Department of the Interior, Fish and Wildlife Service 1990; U.S. Fish and Wildlife Service 1995). La aparente limitada dispersión de Cóbana Negra fuera de la sombra de lluvia de semillas de árboles parentales en el RUM pueda deberse a falta de dispersores adecuados y es posible que el Huracán María haya exacerbado una de por sí la limitada disponibilidad de posibles agentes dispersores, tal como murciélagos, que pudiesen ser agentes dispersores importantes en entornos urbanos (Abelleira 2017). A pesar de que mis observaciones fueron casuales y limitadas a los terrenos en las inmediaciones de las cóbanas negras del RUM, merece estudiar la ocurrencia y los agentes de dispersión de frutos de la Cóbana Negra puntualmente para poder entender el posible rol de procesos de dispersión y sucesión natural en apoyo a esfuerzos de rehabilitación de la especie. La ger-

minación abundante y crecimiento de plántulas bajo árboles parentales también pudo haber sido facilitada por la alta disponibilidad de agua en el terreno después del María permitiendo condiciones anegadas, similares a las encontradas en su distribución geográfica original, por un mayor periodo de tiempo relativo a otros años.

Durante el verano del 2019, temporada durante la cual ningún huracán afectó directamente a Puerto Rico, no se observó un evento de floración y fructificación de cóbanas negra tan abundante como el observado el año anterior en respuesta al María en el RUM. Aunque no realicé observaciones puntuales sobre el nivel de floración y fructificación en tiempos previos al Huracán María, mi recolección es que el nivel de fructificación en temporadas de verano previas a este huracán no fueron tan llamativas y comparables a lo que observé en el verano de 2018. Similarmente, aunque eventos de germinación abundante y crecimiento de plántulas de Cóbana Negra en los terrenos bajo árboles parentales en el RUM pueden haber ocurrido previo al Huracán María, no hay información disponible para constatarlo. Sin embargo, los niveles de germinación y crecimiento de plántulas en verano del 2019 no fueron comparables a los del 2018, posiblemente debido a una floración y fructificación de árboles parentales menos abundante.

Se conoce poco acerca de la biología reproductiva de la Cóbana Negra y merece documentar si eventos de floración y fructificación abundante en respuesta a huracanes son generalizados a través de las poblaciones de la especie en su estado silvestre, en aquellas sembradas para rehabilitación, y en entornos urbanos (U.S. Fish and Wildlife Service 1995). La presencia de plántulas de Cóbana Negra regenerándose en las áreas verdes del RUM a altas densidades puede ser recurrente por huracanes y merece ser documentado si tal evento ocurre en otros entornos urbanos y en poblaciones silvestres sujetas a menor influencia antropogénica. Densmore (1987), citado por U.S. Fish

and Wildlife Service (1995), indica que las plántulas y árboles juveniles de Cóbana Negra crecen más vigorosamente en pleno sol, lo cual puede facilitar su propagación en viveros, siembra en áreas deforestadas, y la expansión del rango geográfico de la especie. Sin embargo, no se deben ignorar los individuos y poblaciones en áreas urbanas o contextos manejados, (i.e., fincas agrícolas o patios), que bien pueden sobrepasar el centenar de individuos maduros conocidos de poblaciones silvestres en Puerto Rico. Los árboles de Cóbana Negra que han sido sembrados en áreas urbanas pueden estar aportando inadvertidamente a la rehabilitación de la especie y a conservar su diversidad genética, quizá hasta incrementándola por entrecruzamiento.

## RECOMENDACIONES

Este informe resalta observaciones que sirven de base para las siguientes recomendaciones relevantes a la conservación de la Cóbana Negra en el RUM y en Puerto Rico. Primero, el esfuerzo combinado en la delimitación de áreas que albergan la población de Cóbana Negra en el RUM y la capacitación del personal de mantenimiento puede evitar la tala de plántulas de Cóbana Negra a corto plazo. Aún así, es recomendable el establecer un plan institucional especial para un mantenimiento adecuado de la población enfocado en evitar afectar los individuos de esta especie a largo plazo. Esto puede incluir un manejo enfocado en el eventual remplazo de individuos maduros que puedan sufrir mortandad natural con el crecimiento de plántulas en el lugar, protegiéndolas hasta que puedan alcanzar madurez y capacidad reproductiva.

En segundo lugar, los árboles maduros de Cóbana Negra creciendo en estas áreas representan una fuente de semillas y plántulas que pueden aportar al desarrollo de técnicas de propagación, trasplante, siembra y establecimiento de poblaciones viables en otros lugares, ampliando así los esfuerzos de rehabilitación

de la especie (U.S. Fish and Wildlife Service 1995; Santiago y Rivera 2019). En este sentido, la población de Cóbana Negra del RUM provee una oportunidad de conservación e investigación irremplazable que permitirá el desarrollo y mejor entendimiento de métodos de propagación y siembra exitosa en beneficio de la especie. Por lo tanto, recomiendo que algunas de estas áreas en el RUM, en particular la población adyacente al edificio Piñero, sean consideradas para designación como un área especial protegida para la Cóbana Negra donde se permita un proceso de sucesión natural que puede ser manejado para favorecer el crecimiento y supervivencia de plántulas y árboles maduros de la especie, y su permanencia en el lugar.

Finalmente, cabe destacar la desinteresada y minuciosa labor del Dr. José Mari Mut en recopilar y documentar información acerca de los recursos históricos y naturales de Puerto Rico, en este caso particular los aspectos agrícolas, biológicos, históricos y silvícolas de las especies, y hasta de individuos particulares, de árboles creciendo en terrenos del RUM (Mari-Mut 2014). La institución puede asegurar la continuidad de este tipo de labor invirtiendo en actividades de educación, extensión e investigación que apoyen la conservación de sus recursos naturales y el desarrollo de capacidad institucional para poder cumplir con dicho objetivo. Por ejemplo, la falta de información acerca de la biología reproductiva de la Cóbana Negra y otras especies protegidas en Puerto Rico se puede atender aplicando métodos estandarizados de monitoreo de aspectos fenológicos, tanto de plantas como animales, que puedan realizarse periódicamente por estudiantes y voluntarios, y cuya información pueda ser recopilada y mantenida en bases de datos (Denny et al. 2014). Métodos innovadores tal como éste, implementados como actividades programáticas en cada una de las unidades de la UPR, pueden contribuir a salvaguardar la diversidad de especies, asegurar la disponibilidad de germoplasma, y perpetuar el patrimonio histórico y natural para satisfacer necesidades agrícolas, silvíco-

las y de conservación de la sociedad puertorriqueña. Estas recomendaciones son cónsonas con la Política Ambiental de la Universidad de Puerto Rico (Universidad de Puerto Rico 1996) y servirán para mejor contribuir a la conservación, estudio y rehabilitación de la Cóbana Negra y otras especies protegidas en Puerto Rico.

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#### Errata:

Abelleira Martínez, O. J. 2017. El huracán María en Añasco y sus efectos en sistemas sociales-ecológicos del norte y oeste de Puerto Rico. *Acta Científica* 31: 60–78.

En página 66, último párrafo, tercera oración, donde lee “urbanización Jardines” debe leer “urbanización Brisas”.

# SHORT-TERM EFFECT OF HURRICANE IRMA AND MARÍA IN THE POPULATION OF *Gesneria pauciflora* (GESNERIACEAE)

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## Abstract

The Caribbean was recently struck by two hurricanes (Irma and María) considered among the most powerful since 1928 in that region. These hurricanes brought intense and continuous rainfall, which likely impacted plants inhabiting riparian areas through flash floods and landslides. We conducted a post-hurricane assessment of *Gesneria pauciflora*, an endemic riparian species of conservation concern in Puerto Rico, to determine the number of individuals of this species, their distribution and their response to the influence of these natural phenomena across its distribution range; also, the assessment was an opportunity to survey additional sites within and outside of the Maricao Forest Reserve. A total of 79 colonies were surveyed during the study period (56 known colonies and 23 new records), yet seven of the known colonies were extirpated due to landslide or flood-driven habitat modifications. The survey yielded 7,853 plants distributed across three sub-watersheds with non-reproductive plants comprising 65.2% of the plants surveyed, followed by reproductive adults (25.3%) and seedlings (9.5%). Plants were found in a variety of habitats associated with riparian environments. Results from colonies that had pre-hurricane information suggest that plant mortality could have been as high as 89% with variation likely resulting from differences in their location within the riverine system (higher mortality for colonies in the main channel of the watershed). There was approximately an 11% reduction in estimated canopy cover at the site, and percent plant mortality showed a negative association with canopy cover after the hurricanes. While the number of individuals is higher than expected for a threatened species, the patchy distribution of its populations justifies the continuation of monitoring activities for the species at larger spatio-temporal scales to examine potential delayed responses to these hurricanes.

**Keywords** Caribbean, disturbance, endemics, plant conservation, riverine ecosystem.

## Resumen

El Caribe fue golpeado recientemente por dos huracanes (Irma y María) considerados entre los más poderosos desde 1928 en esa región. Estos huracanes trajeron lluvias intensas y continuas que probablemente impactaron en plantas que habitan áreas ribereñas a través de inundaciones repentinas y eventos de deslizamientos de terreno. En este estudio,

realizamos una evaluación post-huracán del estado poblacional de *Gesneria pauciflora*, una especie ribereña endémica de Puerto Rico y de interés de conservación, específicamente para determinar el número de individuos de esta especie, su distribución y la influencia de estos fenómenos naturales sobre los individuos en su área de distribución. Esta evaluación representó además una oportunidad para explorar lugares adicionales dentro y fuera de la Reserva Forestal de Maricao en búsqueda de poblaciones desconocidas al momento. Evaluamos 79 colonias durante el período de estudio (56 colonias conocidas y 23 nuevos registros), mas sin embargo, siete de las colonias conocidas fueron extirpadas debido a deslizamientos de tierra o modificaciones de hábitat generadas por inundaciones. La evaluación resultó en 7,853 plantas distribuidas en tres subcuencas hidrográficas donde las plantas no-reproductivas representaron el 65.2%, seguidas de adultos reproductivos (25.3%) y plántulas (9.5%). Las plantas se encontraron en distintos microhábitats asociados a ríos. Para las colonias con información previa al huracán, los resultados sugieren que la mortalidad de plantas alcanzó hasta un máximo de 89% con variaciones entre colonias dependiendo de la ubicación dentro del sistema fluvial (mayor mortalidad para las colonias localizadas en el río principal de la cuenca hidrográfica). Hubo una reducción del 11% en la cobertura estimada del dosel y el porcentaje de mortalidad de plantas mostró una asociación negativa con la cobertura luego de los huracanes. Si bien el número de individuos aparenta ser relativamente alto para una especie considerada amenazada, la distribución geográfica restringida de sus colonias justifica el continuar los monitoreo de las mismas a mayor escala espacio-temporal, para examinar posibles respuestas tardías de sus individuos ante estos huracanes.

**Palabras clave** Caribe, conservación de plantas, disturbio, ecosistema riverino, endémico.

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## INTRODUCTION

Caribbean forests frequently experience tropical storms, which often become major natural phenomena transforming their structure, composition, and ecosystem function, and large-scale catastrophic events to infrastructure (Boose et al. 1994; Lugo 2000; Van Bloem et al. 2003, 2005, 2006). Visible hurricane effects include massive defoliation, snapped and wind-thrown trees, large accumulation of debris, landslides, debris flows, and altered stream channels, among others (Lugo 2008) noticeable over the short-term and relatively well documented in the literature. Invisible effects are less understood as they require well-focused research both in the short- and long-term time scales. Even though these natural phenomena might favor the survival and growth of some species (i.e., Boucher and Mallona 1997), it may also

diminish the persistence of others either by direct mechanical damage or changes in species interactions. For example, hurricanes may promote immediate or delayed mortality in trees through complete defoliation and severe branch damage (Frangi and Lugo 1998), facilitate the establishment of pioneer and shade-intolerant species in disturbed sites within the forest (Brokaw 1985, 1987), increase herbivory rate (Hunter and Forkner 1999) and even help accelerate the spread of invasive plants (Bellingham et al. 2005; Lynch et al. 2011; Bhattarai and Cronin 2014). For species of conservation concern in the Caribbean, understanding the effects of these natural events on them is a priority in order to increase their chance of recovery, with assisted rehabilitation, in response to these events.

Puerto Rico receives hurricanes at a rate of one every 21 years historically, but between 1852 and

1998, that rate reduces to one every 11.2 years when thirteen hurricanes affected the island including Hurricane Georges, a category-3 hurricane in 1998 (Scatena and Larsen 1991; Feng et al. 2018). In September 2017, however, Puerto Rico received the impact of two higher-category hurricanes (Irma and María). On 6 September 2017, the trajectory of Hurricane Irma (category-5) crossed about 85 km East-Northeast from San Juan, with maximum-sustained-winds of 295 km/h. Even though the eye of Hurricane Irma was away from the U.S. Virgin Islands (it struck the British Virgin Islands and moved upwards into the Atlantic Ocean), tropical storm and hurricane conditions were reported for Puerto Rico (Cangialosi et al. 2018). On 20 September 2017, the eye of Hurricane María made landfall near Yabucoa, southeast coast of Puerto Rico, as a top category-4 storm with maximum-sustained-winds of 250 km/h (Pasch et al. 2018). Hurricane María crossed the island exiting it from the north coast between the municipalities of Camuy and Quebradillas at around 1800 h (Pasch et al. 2018). As Hurricane María made landfall on the island, damage to infrastructure and natural areas was evident (Hu and Smith 2018). It is estimated that Hurricane María may have killed or damaged more than 20 million trees (Feng et al. 2018) with massive wind-driven defoliation leading to the browning of forests throughout the landscape (Burnett 2017).

During hurricane events, rainfall may become extreme, increasing the number and intensity of flash floods and landslides (Scatena and Larsen 1991; Larsen and Torres Sanchez 1992). Species associated with riparian ecosystems might be especially vulnerable to the action of flashflood events and landslides, possibly experiencing extirpation following these events when extreme. If the number and intensity of hurricanes in the Caribbean increase as predicted by models (Emanuel 2005), species endemic to riparian areas and of conservation concern could face a much more complicated scenario in the near future. *Gesneria pauciflora* (Gesneriaceae) is

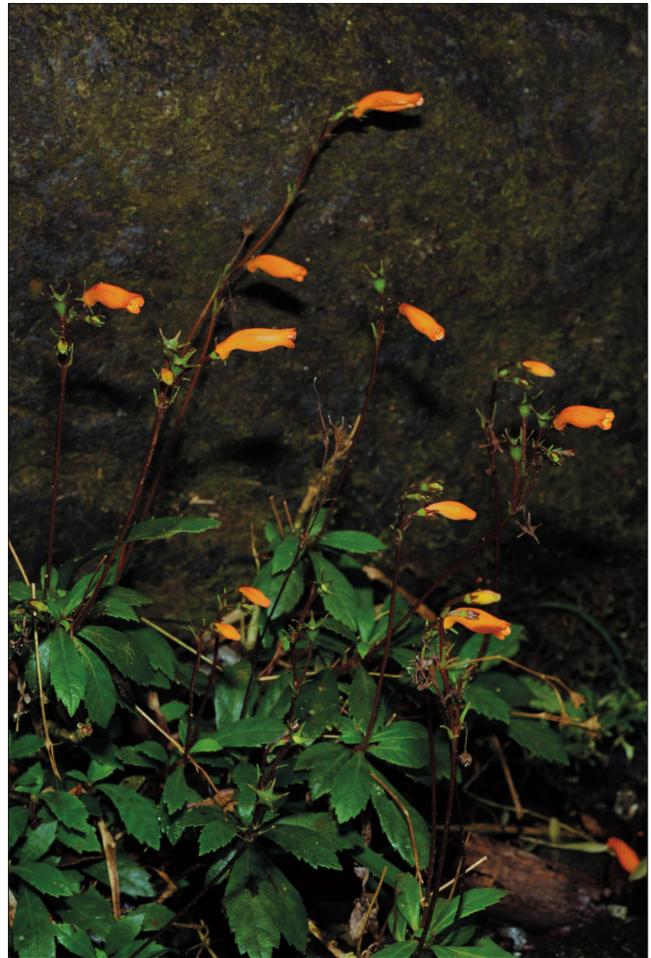


Figure 1. *Gesneria pauciflora*, an endemic species from Puerto Rico. Photo by O. Monsegur-Rivera.

the only one of five endemic Gesneriaceae species to Puerto Rico (Skog 1976) (Figure 1), classified as Threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1995). This riparian species was listed due to its narrow distribution restricted to serpentine soils in the western part of Puerto Rico (i.e., Maricao Forest Reserve boundaries), and the potential for population extirpation due to the threats from large-scale natural phenomena (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). Populations of *G. pauciflora* at the reserve inhabit riverine environments and are established on wet rocks near to the river flow. Some of

these populations have been monitored since 2013, and we expected that populations might have experienced consequences of intense and prolonged duration because of hurricanes Irma and María. One hypothesis is that colonies (i.e., patch level) with more individuals were more susceptible to plant mortality or extirpation. Likewise, flooding events may lead to differential mortality across plant stages if, for example, different plant stages were to be differentially impacted by the incoming water during flash flood events, and small individuals may be more likely to be washed than juveniles or adults.

In this study, we took advantage of ongoing studies to assess the post-hurricane condition of 11 colonies of *G. pauciflora* for which there were plant counts before the hurricane events of 2017. We took the opportunity to visit all known colonies distributed in the Maricao Forest Reserve to conduct a full count of plants for this species. Also, we surveyed other watersheds outside of the reserve to evaluate the potential of occurrence of additional populations and provide more updated information on the distribution, general habitat, and the number of plants for this species. This information expands previous knowledge from other studies and allows us to make recommendations on the best practices to conserve and restore the population of this endemic and threatened species.

## METHODS

### Study Site

The Maricao State Forest Reserve (4,150 ha; Figure 2) is located at the western end of Puerto Rico within the municipalities of Maricao, Sabana Grande, and San Germán (Anadon-Irizarry 2006). The protected area's topography is dominated by rugged mountains and 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 Pujals and Padrón Vélez 2010). The mean temperature and rainfall at Maricao are 21.7°C and 2,326 mm, respectively (Tossas 2006). A seasonal trend in rainfall in the Maricao reserve is suggested, with a wet season from August to November and a dry season from January to April (Fogarty and Vilella 2002). Data from a period of 32 years (1985-2016; <https://waterdata.usgs.gov>) indicate highly variable streamflow in the Maricao River with the lowest monthly mean discharge reported in February (0.54 m<sup>3</sup>/s) and the highest in October (3.1 m<sup>3</sup>/s). The maximum discharge values for this river were reported in 1998, in September (8.7 m<sup>3</sup>/s) and October (204.8 m<sup>3</sup>/s), which were associated with Hurricane Georges. In 2017, rainfall associated to Hurricane María, between 19 to 21 September, was estimated within a range between 254 mm and 381 mm (Pasch et al. 2018), and the maximum daily mean discharge recorded for Maricao River was about 14.2 m<sup>3</sup>/s, also in September; there is no data on the maximum discharge of the Maricao River associated to Hurricane María, however, because most of the sensors were damaged. Nonetheless, flooding and landslides associated with Hurricane María caused unprecedented damage to the infrastructure and the Maricao River watershed (current and former staff from the Maricao Fish Hatchery, Department of Natural and Environmental Resources [DNER], personal communication).

### Field monitoring

Fifty-six previously known colonies of *G. pauciflora* were visited from March to April of 2018 (between five and six months after María impacted the island). At each colony, we counted the number of plants and classified individual plants in one of three categories or life-history stages using the classification scheme of Pérez et al. (2019): seedlings, non-reproductive, and reproductive. Individuals were considered

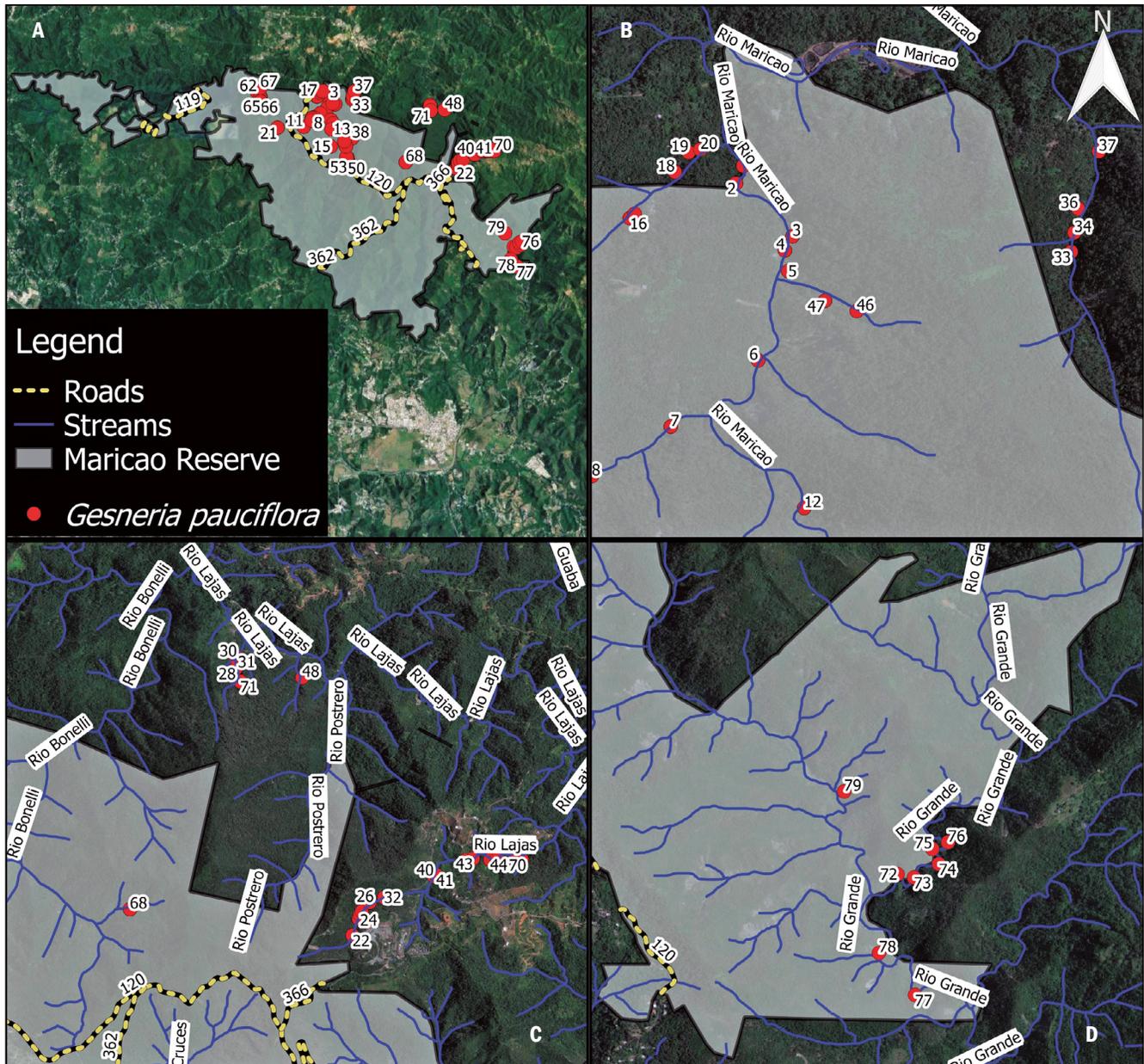


Figure 2. Distribution of the 79 colonies of *Gesneria pauciflora* distributed in the Maricao Reserve. (A) All of the colonies combined; (B–D) distribution of the 29 colonies located outside the limits of the Maricao Reserve. (B) Four colonies located at Quebrada Santa Rita and three in the Maricao River; (C) twenty colonies established along the Rio Lajas around the Salto Curet touristic place and Indiera Alta; (D) two colonies along the Rio Grande.

seedlings if they were small plantlets with a hyaline stem with two or four leaves (approximately less than 0.4 mm in high). Non-reproductive plants were those greater than 0.4 mm and smaller than 15 cm. Reproductive plants were those larger than 15 cm, but if plants smaller than 15 cm were flowering or had remnants of inflorescences, they were also categorized as reproductive individuals. For each plant, we

recorded the length of the largest branch, the number of inflorescences, flowers, and fruits (when present), and the frequency of floral herbivory. To characterize the habitat of each colony after the hurricane, we collected the following information: habitat type (i.e., cascade, rock wall, step, and pool), the surface area occupied by the species, percentage of area available for reintroduction (unoccupied space within

the colony, or available space with similar microhabitat conditions), canopy cover (estimated using a densitometer), and the presence of landslides. If new colonies were found, these were georeferenced, and we collected all parameters described above.

**Table 1.** Population structure and habitat characterization of *Gesneria pauciflora* colonies. Life history stage: Seed = seedlings; NRP = non-reproductive plants; RP = reproductive plants. Habitat characteristics: R = rock-wall; C = cascade; S = step; P = pool; CC = canopy cover; AfR = area for restoration. \* = grand mean of all sites.

Locality	Life history stage						Habitat characteristics					
	Seed		NRP		RP		Patch surface				CC (mean %)	AfR (m <sup>2</sup> )
	Total	%	Total	%	Total	%	R	C	S	P		
Bonelli	—	—	—	—	—	—	0	1	0	0	—	—
Lajas	0	0	953	65.3	506	34.7	10	6	4	6	70.8	89.7
Maricao	447	8.7	3,419	66.3	1,288	25.0	8	16	10	10	79.7	158.3
Prieto	217	17.5	749	60.4	274	22.1	3	1	6	0	71.4	30.3
Total	664	8.5	5121	65.2	2,068	26.3	21	24	20	16	76.5*	278.3

## Hurricane Impacts

We have pre-hurricane count data (number of plants per life-history stage) for a subset of 11 colonies (out of the 56 previously known colonies), located in the Rio Maricao watershed. For these 11 colonies, we used post-hurricane counts of plants to estimate percent mortality (i.e.,  $\{[\text{number of plants in 2017} - \text{plants in 2018}]/[\text{number of plants in 2017}]\} * [100]$ ) for the whole colony and by stage. We analyzed changes in the number of plants per colony before (June 2017) and after (April 2018) these hurricanes and tested if the difference between the pre- and post-hurricane count of plants was significantly different among plant stages using a Negative Binomial General Linear Model (NBGLM) and a post hoc analysis using the “e means” package in R (R Core Team 2018). At each colony, we also estimated changes in canopy cover after Hurricanes Irma and María by taking hemispherical photographs (using a Nikon Coolpix 8400 camera and fish-eye lens FC-E9) before (October 2016) and after the hurricanes (April 2018). The percent of canopy cover at each colony was estimated from the images with the software ImageJ (Rasband 2014) using Hemispherical 2.0 macro (Beckschäfer 2015). We conducted a paired t-test to determine if the difference in the percentage of canopy cover before and after hurricanes was significant. The relationship of the percentage of plant mortality with canopy cover and initial population size was analyzed using regression analysis. All statistical analyses were conducted using R (R Core Team 2018).

## RESULTS

The overall survey resulted in 79 colonies (23 new ones), which expanded the inventory of *G. pauciflora* colonies; 29 colonies were located outside the Maricao Forest Reserve limits (Figure 2). Also, 46 colonies were in a third-order stream, 30 in a second-order, and 3 in a fourth-order stream. After the hurricanes, seven colonies were extirpated. These were mostly located in second- and third-order streams in the lower part of the basin; five of these colonies were extirpated because of landslides. For the 72 extant colonies among the three sub-watersheds, colony size varied from 4 to 476 individuals with larger colonies concentrated in the upstream within the watershed. Among all colonies, we found 7,853 individuals quantified and classified as follows: 8.5% seedlings, 65.2% non-reproductive, and 26.3% reproductive plants (Table 1). Most of the colonies had at least one individual classified as a reproductive adult (> 15 cm in length), and only 397 (5.1%) out of the 7853 individuals had reproductive structures. At the time of the survey, reproductive adults were developing 105 inflorescences (average = 1.61/plant,  $\pm 0.22$  [standard error of the mean]), and produced 375 flower buds (2.27/plant  $\pm 0.13$ ), 76 open flowers (1.18/plant  $\pm 0.06$ ), and 1914 fruits (3.59/plant  $\pm 0.19$ ). Overall, floral herbivory was minimal (2.9% of the plants presented damages), and the level of damage from herbivory varied between 0% and 25% per colony. Colonies of *Gesneria* were distributed across

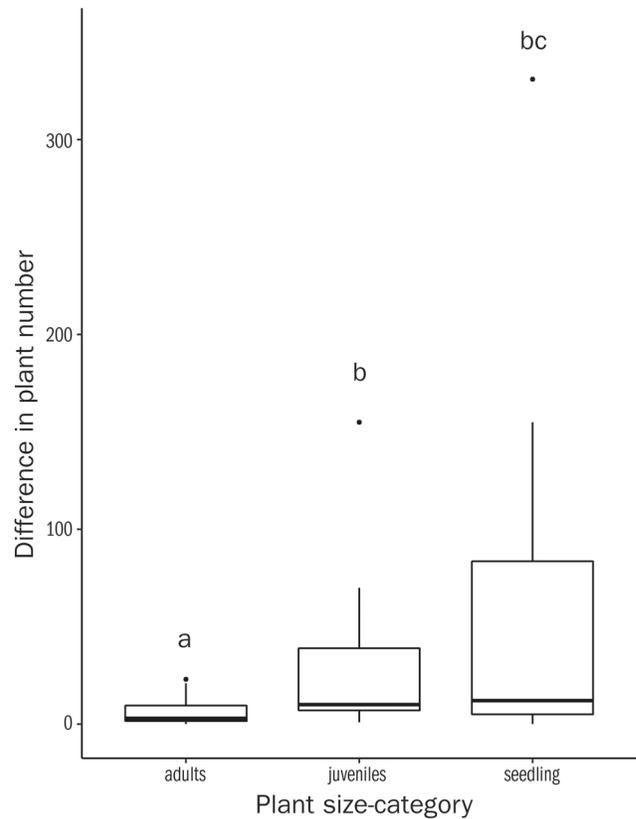
**Table 2. Number of plants (n) and reproductive individuals (Reprod.), before and after hurricanes Irma and María, and percent mortality per colony in each of two riverine localities. ext. = extirpated.**

Locality	Colony	Pre-hurricane		Post-hurricane		Mortality (%)
		n	Reprod.	n	Reprod.	
Main Channel	1	16	1	5	1	68.8
	2	251	14	44	2	82.5
	3	40	3	5	0	87.5
	4	14	1	ext.	—	—
	5	573	45	63	5	89.0
	6	225	29	42	3	81.3
Tributary	7	36	5	13	1	63.9
	8	1	0	ext.	—	—
	9	21	5	5	2	76.2
	10	219	17	129	6	41.1
	11	241	8	174	4	26.1

four types of microhabitats (in decreasing percentage): cascades (29.6%), rockwalls (25%), steps (24.6%), and pools (19.8%) (Table 1). On average, the area occupied by colonies was 20.2 m<sup>2</sup> (± 4.4), and the average canopy cover was 76.5% (± 1.73). The average available space for reintroduction within a colony was 4.5 m<sup>2</sup> (± 0.9); the total area available for reintroduction among the three watersheds was approximately 278.3 m<sup>2</sup>.

Out of eleven colonies monitored for reproduction and mortality before hurricanes Irma and María, two were extirpated: one was in the main channel and another in a tributary of the Maricao River. The two extirpated colonies had the lowest number of plants before the hurricanes (Table 2). Colonies located in the main channel exhibited an average rate of mortality of 81.2%, while colonies in the tributary had an average rate of 51.8% (Table 2). The average number of plants per colony was significantly lower six months after the hurricanes: it changed from 148.8 plants (± 52.9) to 44 plants (± 17.8) (NBGLM:  $X^2 = 3.86$ ,  $p = 0.049$ ) (Table 2). Changes in the number of plants were related to plant stage, but changes were larger for seedling than for juveniles when compared with adults (Figure 3).

Overall, survivorship was higher in the juvenile and adult size-categories with 48.5% and 56.7%, respectively (Table 2). The average number of reproductive individuals changed from 11.6 (± 4.25) per colony to about 2.7 (± 0.7) before and after the hurricanes, respectively



**Figure 3. Difference in the number of individuals before and after the hurricane events as a function of plant stage (adults, juvenile, and seedlings). The full model (see text) was expressed as the difference = 1.92 + (1.54) juveniles + (2.25) seedlings (all significant at  $p < 0.01$ ). Different letters in the figure indicate significant differences at  $\alpha = 0.05$  among groups.**

(NBGLM:  $X^2 = 10.52$ ,  $p = 0.03$ ). Colonies 5 and 6 (see Figure 2b) had the greatest number of reproductive plants before the hurricanes, but also scored the highest reduction (Table 2). The percent of canopy cover ranged between 79.4% and 98.7% (average = 93.8 % ± 1.6) before the hurricanes, and between 71.6% and 93.6% (average = 82.9% ± 2.3) after the hurricanes (NBGLM:  $X^2 = -5.94$ ,  $df = 10$ ,  $p = 0.0001$ ). Percent mortality of plants per colony was negatively related with canopy cover after hurricanes (Estimate ± standard error of the mean =  $-2.6 \pm 0.51$ ,  $F_{1,9} = 25.85$ ,  $p = 0.0006$ ) (Figure 4a) and a positive relationship with the percent canopy cover change (Estimate ± standard error of the mean =  $2.3 \pm 0.94$ ,  $F_{1,9} = 6.1$ ,  $p = 0.0350$ ) (Figure 4b) and these models explained 71.3% and 40.4% of the total variation in plant mortality, respectively. Initial population

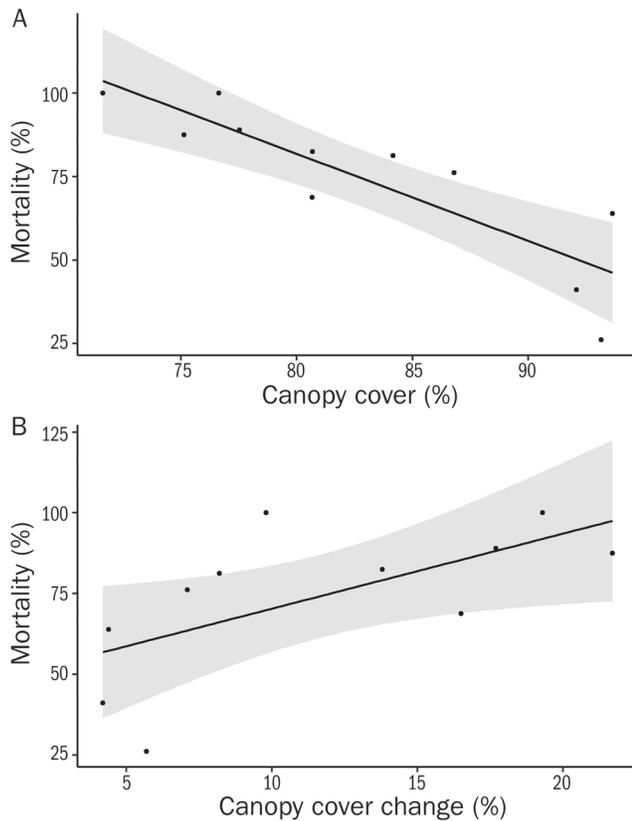


Figure 4. Relationship between percent plant mortality of *Gesneria pauciflora* among colonies as a function of (A) percent canopy cover and (B) percent canopy cover change after the 2017 hurricane events at the Maricao Forest Reserve in Maricao, Puerto Rico.

size did not explain the percent mortality of plants per colony ( $F_{1,9} = 0.21$ ,  $p = 0.6600$ ).

## DISCUSSION

As expected, hurricanes Irma and María induced higher plant mortality rates, which is partly consistent with theory. For example, theory predicts that small populations are usually more vulnerable to environmental stochasticity (Colling and Matthies 2006). In fact, our results showed that 1) changes in canopy cover (higher mortality occurred in areas with less cover); 2) the location within the riverine system (main channel vs. a tributary); 3) and stochastic events (landslide extirpating some of the colonies) were factors that explained most of the variation in plant mortality and population persistence. Theory

also predicts that populations with less than six plants are more likely to be extirpated (or extinct in the case of whole species) (Matthies et al. 2004; Öckinger and Nilsson 2010). Contrary to theory, however, our results showed that few colonies were extirpated and that the initial number of individuals in a colony was not a significant factor explaining plant mortality after these hurricanes. Most likely, environmental variation may play a greater role in plant mortality than frequently acknowledged (see next).

Colonies of *Gesneria pauciflora* appear to be associated with shaded environments (Pérez et al. 2018). Hurricane María defoliated most forests across Puerto Rico massively (Miller et al. 2019). Canopy cover and changes in it were significantly associated with percent mortality of plants among colonies, with higher mortality in colonies located in more-open forest areas or where the reduction in the percent canopy cover was highest. Also, plant mortality seemed to be highest in seedlings relative to juveniles and adults following these hurricanes. Several hypotheses may explain these results. First, evapotranspiration rates of plants increases in an opened canopy, and these increases are higher in seedlings relative to other plant stages by virtue of having a higher surface to volume ratios (Zotz et al. 2001) Also, and in the case of seedlings, they may have a less developed root system relative to juveniles and adults and thus, are less able to access groundwater, which makes them more susceptible to drought stress due to an open canopy. In addition, our observations frequently revealed plants slightly detached from the substrate and showed drying symptoms, which suggest that seedlings may be more susceptible than other stages of plant development to mechanical forces from water currents.

Overall, the rate of plant mortality ranged from 68% to 89% in the main channel, while in the tributary, it was between 26% and 76%. Colonies along the main channel were likely to be subjected to greater volumes of water and sediment that scraped the vegetation along river margins due to the flooding events

associated with hurricanes Irma and María. Prior demographic studies of *G. pauciflora* suggest that plants in different locations along the river system may exhibit life-history trade-offs that are consistent with different disturbance regimes along the river (Pérez et al. 2019). Although we did not have data to quantify and compare the discharge in the main channel and the tributary, structural damage of the forest was higher along the main channel where more landslides and greater accumulation of rocks and sediments were evident (M. Pérez, personal observation).

Plants documented in this study are distributed among 79 local patches in the forest, and only 63.2% of patches are currently protected, and at least 29 colonies are located outside areas managed for conservation. Also, even when the number of plants detected for the species could be considered high (> 7,000 individuals), and that 11 “new” colonies were added to previous surveys, only a quarter of plants sampled were flowering and capable of sexual reproduction. Even when this species is capable of some autogamy (i.e., autonomous pollination), fruit production is often pollination limited (Pérez et al. 2018). Pollen limitation on sexual reproduction may be even stronger if these natural phenomena also affected populations of pollinators like hummingbirds, which are the main visitor to individuals of *G. pauciflora* (Pérez et al. 2018).

In this study, we did not measure plant damage nor reductions in plant size, which likely occurred during the hurricane-driven flood events as plants can be broken easily. Plant damage following hurricanes, however, may lead to delayed mortality and decrease reproduction and recruitment in the long term. For example, the reproductive effort of two epiphyte orchid species did not return to pre-hurricane condition, and one of them, *Dendrophylax lindenii*, showed a decline in the population growth rate that continued eight years after Hurricane Ivan struck Cuba in 2004 (Mújica et al. 2013; Raventós et al. 2015). Similarly, over a period of nine years, values of the population growth rate of the cactus *Mammillaria*

*gaumeri* were lower than unity and were associated with the flooding period that occurred in the Yucatán Península due to the Hurricane Isidore in 2002 (Ferrer-Cervantes et al. 2012). Therefore, although it was beyond the scope of our study, we need to continuously monitor colonies of *G. pauciflora* to assess its long-term response to the influence of these hurricanes, particularly the survival, growth, and fecundity of its individuals at a larger spatio-temporal scale.

## Management Recommendations

We provide recommendations based on the quantitative and qualitative information herein discussed. After the hurricanes, there were plants slightly detached from the rock or hanging from their roots. Thus, we recommend that following a hurricane, plants under such conditions (detached from the rock) should be glued to the rock (based on preliminary experiments we recommend using Loctite® marine adhesive sealant) or relocated in microhabitats with environmental conditions similar to those of pre-hurricane conditions and mostly undisturbed. The species can generate roots from vegetative material within a period of two or three months (Pérez et al., unpublished data). Relocation of large plants (i.e., adult plants) after a hurricane seems to provide an acceptable management strategy for some epiphyte orchids after hurricane events (Tremblay 2003; Raventós et al. 2015). Therefore, relocating adult plants of *G. pauciflora* also might be a plausible strategy, at the population level, to increase their probability of survival.

The spatial location and microsite conditions where the establishment of plants is most successful should be known before relocating plants or establishing new colonies (Tremblay 2003; Tremblay and Castro 2009; Vale et al. 2013). Colonies distributed in the second- and third-order streams may be more vulnerable than the ones in the upper part of the basin (first-order streams) during extreme natural events because they showed higher mortality of plants after

these hurricanes. Fortunately, our surveys within the Maricao Forest Reserve revealed available space for reintroduction, either in sites in which colonies were extirpated, in sites where colonies were reduced in number, or in new microhabitats that share ecological features similar to pre-hurricane conditions. Therefore, these new microhabitats may represent adequate options for future relocations if deemed necessary. Also, we recommend monitoring all colonies documented here, at least once a year, to detect signs of delayed mortality before it reaches unsustainable levels. Likewise, we need to study the reproductive activity because recent population models of *G. pauciflora* suggest that populations are declining in numbers across the main watershed examined here (Pérez et al. 2019). Finally, we recommend executing efforts to educate and integrate surrounding communities and private stakeholders in conservation efforts for this species, given that recent surveys suggest that 36.7% of colonies lie outside the Maricao Forest Reserve boundaries.

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# 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 surge de este estudio es valiosa para esfuerzos efectivos de manejo y conservación de esta especie.

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

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## 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 (Pacifi 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

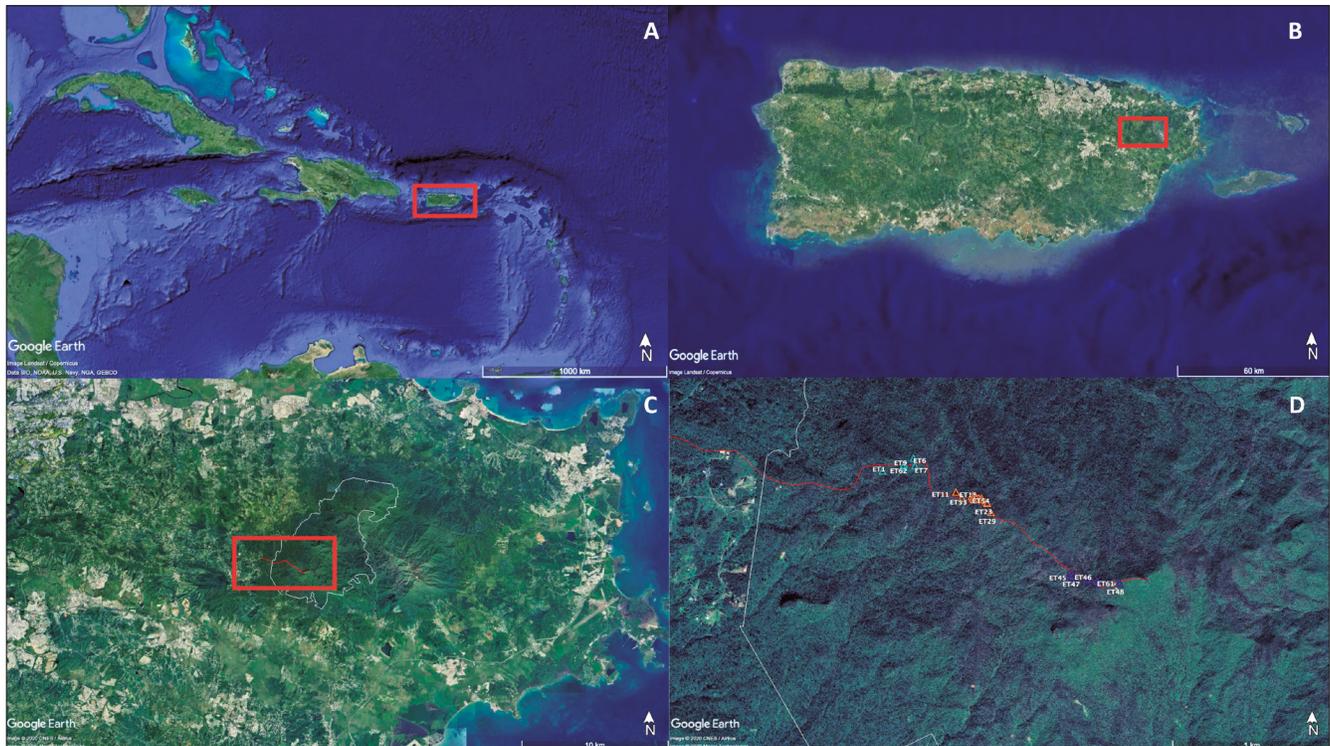


Figure 1. Location of study site: (A) Caribbean, (B) El Yunque National Forest (EYNF) in Puerto Rico, (C) Wilderness area within EYNF, and (D) El Toro Trail and populations sampled (different colored symbols with letters) (images based on ©Google Earth, 2020).

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  $\times$  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 sintensisii* 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.

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  $([1 - \text{number of orchids before}] / [\text{number of orchids after}])$  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.

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,

### 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  $2 \times 3$  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 pairwise-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  $\pm$  standard deviation: cluster 1 = 34.2 cm  $\pm$  8.8 cm,  $n = 5$ ; cluster 2 = 17.4 cm  $\pm$  7.9 cm,  $n = 17$ ; cluster 3 = 17.3 cm  $\pm$  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  $\pm$  35.5 m; cluster 2 = 942.3 m  $\pm$  62.5 m; cluster 3 = 1,035.2 m  $\pm$  49.2 m (Figure 3B). The mean elevation between adjacent clusters varied

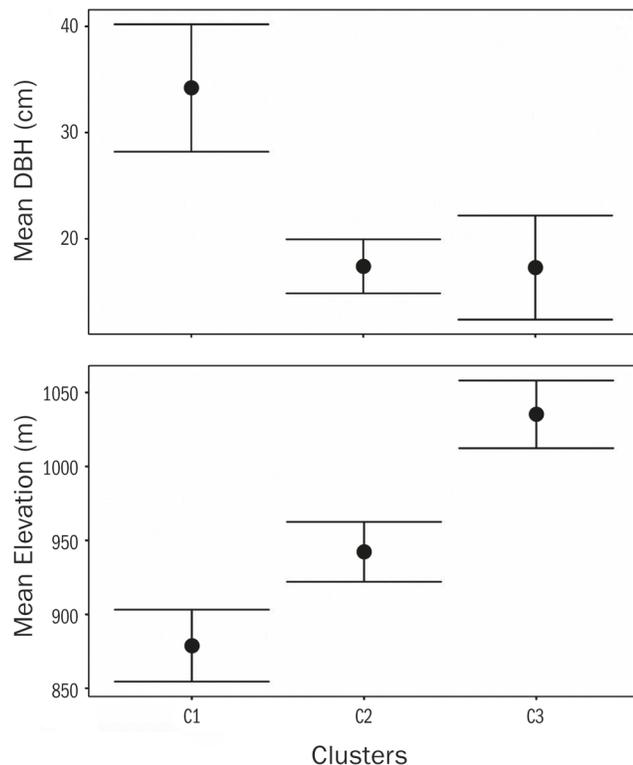


Figure 3. Differences in mean diameter at breast height (DBH) of host trees of *Lepanthes eltoroensis* and the mean elevation of orchid hosts by geographic cluster (C1, C2, C3) along the El Toro Trail. Data was analyzed with one-way ANOVA for (A) difference in DBH among clusters/ phorophytes ( $F_{2,28}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

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 ( $r_s = -0.41$ ,  $p = 0.05$ ,  $n = 31$ ).

### 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 clusoides*, *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

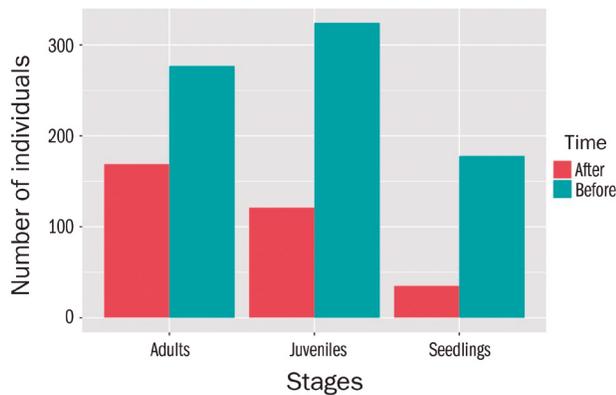


Figure 4. Number of individuals of *Lepanthes eltoroensis* by life stage documented at each study site along El Toro Trail. Seedling; Juvenile; Adult (plants with dry or live inflorescences). Bars represent the number of plants before and after Hurricane María in 2017. Only plants from host plants tagged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

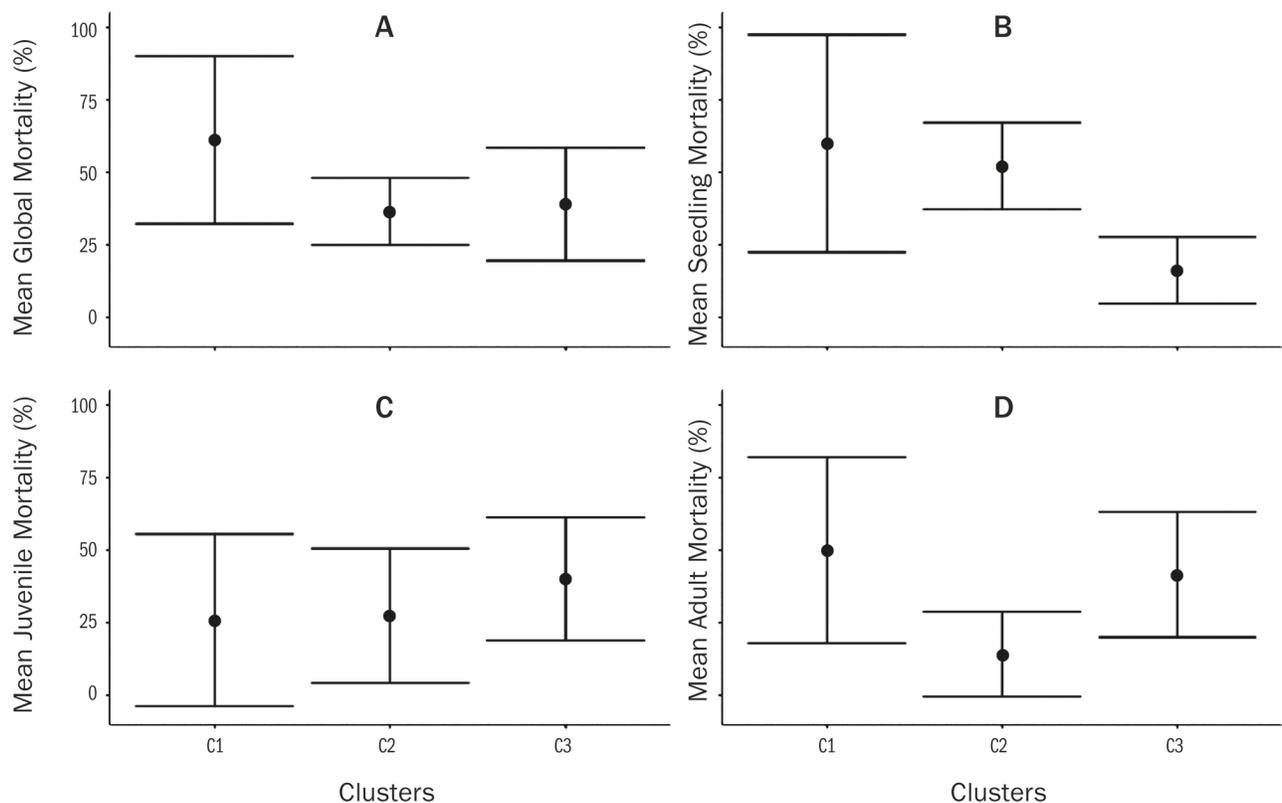


Figure 5. Mean orchid mortality (= 1 – survival) per host plant in the designated clusters along the El Toro trail, Luquillo Experimental Forest/El Yunque National Forest in Puerto Rico six months after Hurricane María: (A) Global population (all populations merged); (B) Seedlings; (C) Juveniles; and (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 ( $\Delta S$ ), juvenile plants ( $\Delta J$ ), seedlings and juvenile plants combined ( $\Delta SJ$ ), adult plants ( $\Delta A$ ), and subpopulation (all categories combined;  $\Delta POP$ ). Asterisks highlight levels of significant correlations: \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ .**

	dbh	elevation	$\Delta S$	$\Delta J$	$\Delta SJ$	$\Delta A$	$\Delta POP$
dbh	-						
elevation	-0.41*	-					
$\Delta S$	-0.02	0.10	-				
$\Delta J$	0.07	-0.08	0.80***	-			
$\Delta SJ$	0.02	-0.05	0.91***	0.96***	-		
$\Delta A$	-0.19	0.10	0.51**	0.74***	0.66***	-	
$\Delta POP$	-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 (Rodríguez-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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# DRIVERS OF HURRICANE STRUCTURAL EFFECTS AND MORTALITY FOR URBAN TREES IN A COMMUNITY OF SAN JUAN, PUERTO RICO

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## Abstract

As it is accepted in the scientific community, the frequency of hurricanes is expected to increase due to climate change, possibly affecting the tree's provision of ecosystem services and resilience to urban cities. This study assessed hurricane-related structural effects after hurricanes Irma and María for an urban community in San Juan, Puerto Rico. Tree's structural characteristics, such as height, dbh, and crown width were obtained from previous tree inventories. The type of structural change was recorded for each tree after each hurricane, and mortality was estimated. A total of 61 trees were assessed after Hurricane Irma and 44 after Hurricane María. We found that wind structural effects and mortality were higher after Hurricane María than after Hurricane Irma and that taller trees and trees with wider crowns were more vulnerable to hurricane structural effects and mortality. Structural variables showed significant relationships after Irma and not after María. We suggest that changes in structure during the first storm could have influenced how trees respond structurally to the second storm. Larger tree sizes may be more susceptible to hurricane events, which suggests the need for size management of urban trees as a potential strategy for maintaining functional trees' resources and services.

**Keywords** urban trees, urban forests, hurricane effects, Hurricane Irma, Hurricane María, hurricane frequency.

## Resumen

La comunidad científica proyecta que el cambio climático debe causar un aumento en la frecuencia de los huracanes. Es posible que de este aumento ocurrir se afecte las provisiones de servicios ecosistémicos de los árboles urbanos y también la resiliencia de las zonas urbanas. Para este estudio se evaluaron los efectos estructurales en los árboles asociados a los huracanes Irma y María para una comunidad urbana en la ciudad de San Juan, Puerto Rico. Las características estructurales de los árboles, tales como su altura, diámetro a la altura del pecho, y ancho de la copa, se obtuvieron de un inventario de árboles. Luego de cada huracán, cada árbol fue evaluado para el tipo de efecto estructural observado y se determinó la mortandad. Un total de 61 árboles fueron evaluados después del Huracán Irma y 44 después del Huracán María. Encontramos que los efectos estructurales y la mortandad fueron mayores después del Huracán María comparado con los efectos después del Huracán Irma. Los árboles altos y/o con anchos de copa extensos mostraron mayor vulnerabilidad y mortandad asociada a los huracanes. Las variables estructurales mostraron asociaciones significativas para el Huracán Irma, pero no para el Huracán María. Una posible explicación podrá ser que los cambios en estructura durante el primer

evento podrían influenciar la forma en la cual los árboles urbanos responden estructuralmente al segundo evento. Como los árboles más grandes son los árboles que podrían estar más susceptibles a los efectos asociados con algún evento atmosférico, sugerimos que se implementen medidas estratégicas de manejo de árboles urbanos. De esta forma se reduce el efecto hacia estos y se mantienen los recursos y servicios que estos árboles brindan en la comunidad urbana.

**Palabras clave** árboles urbanos, bosque urbano, efectos causados por un huracán, Huracán María, Huracán Irma, frecuencia de huracanes.

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## INTRODUCTION

The last two decades have seen an increase in awareness of the importance of urban trees to the provision of resilience and sustainability to cities (Duryea and Kampf 2007; Wagner et al. 2016). Trees provide important benefits to urban residents. Among them, carbon dioxide sequestration, improvement of air quality, thermal comfort are among the most important services that trees provide to urban areas (Nowak et al. 2010, 2013; Summers et al. 2018) and all these and more increase community-wellbeing (Nesbitt et al. 2017). However, rising temperatures and the predicted increase in the frequency of extreme weather events (e.g., hurricanes, droughts, frost), all of which can influence tree health and growth are of concern if the goal is to manage urban trees such that they produce services that promote better quality life to urban citizens (Nesbitt et al. 2017).

Hurricanes are a common disturbance of Caribbean ecosystems with the potential to change forested areas (Sanford et al. 1991; Staudhammer et al. 2011; Zimmerman et al. 2014). While we have a considerable amount of information as to how trees respond in a forested setting, we know less about trees in urban areas although some studies do exist. In urban and forested areas a general observation is that even when hurricane effects are directly proportional to wind speed, species and structural characteristics such as height, crown width, and diameter at breast height (dbh) may also influence the extent of hurricane effects and mortality rate of trees at least under some circumstances (Duryea et al.

2007a,b). For example, after hurricane Ivan struck cities in the Florida panhandle in 2004, researchers found that certain species in urban cities such as *Carya illinoensis* showed significantly more effects related to uprooting than breaking while other species showed no difference (Duryea et al. 2007). Another study found that large forest trees that exceeded 80 cm of dbh and 16 m of height were more likely to be uprooted after a major storm event (Rossi et al. 2017). Because urban ecosystems haven't been broadly studied until recently, from the perspective of urban management, it is important to understand how tree structural change will materialize not only as a function of their structure but also in response to multiple hurricane events as it is predicted for the Caribbean region.

The 2017 hurricane season was one of the most active and costly in recorded history (NOAA 2017). During the month of September of 2017, Puerto Rico received tropical storm and hurricane grade winds from hurricanes Irma and María, respectively. The National Weather Center reported that the center of Hurricane Irma did not pass directly over Puerto Rico, yet tropical storm sustained winds were registered at a maximum of 88 k/h for San Juan on September 7, 2017. From September 5 to September 7, rainfall associated with Hurricane Irma ranged from 254 mm to 381 mm (Cangialosi et al. 2018). On September 20, 2017, two weeks after Hurricane Irma, Hurricane María made landfall on the main island of Puerto Rico. Although the National Weather Center classified the latter hurricane as a category 4 storm, they acknowledged that stronger sustained winds equivalent of a category 5

hurricanes were registered in some areas (Pasch et al. 2019). The maximum registered rainfall for Hurricane María was just below 965.2 mm.

This study assessed hurricane-related effects in the community of Buenos Aires at Santurce, Puerto Rico, where previous tree inventories were made before the hurricane passage. The following questions were addressed by this work: (1) what types of hurricane structural effects are observed in urban trees? (2) Do these differ between hurricane events? (3) How are tree structural effects and mortality associated with tree size, crown condition, and previous tree injuries? We expected that the woody structure of trees would suffer some sort of effect, but we expected these to be more frequent after Hurricane María than after Hurricane Irma due to the difference in the intensity of wind forces between storms. We also expected that the probability of structural effect and tree mortality would be influenced by variables related to tree size and crown structure based on what we know from how hurricanes in the region may affect trees in non-urban areas. To address these hypotheses, the work had the following objectives: (1) perform a rapid assessment of the types of structural changes caused by each hurricane, (2) correlate structural characteristics of marked trees collected before the hurricane season of 2017 with the type of structural change observed after the season (3) contrast data for structural tree effects collected after hurricanes Irma and María. The results of this study contribute to the understanding of how structural characteristics may influence tree responses in urban sites vs. non-urban sites and to what extent these relationships need to be considered in the management of urban trees within the context of achieving resilient and functional cities.

## METHODS

This study conducted hurricane-related effects assessments on urban trees that were hit by hurricanes Irma and María in Puerto Rico on September 6 and

20 of 2017, respectively. Existent pre-hurricane tree inventory data were available on several communities of the Santurce Peninsula in the city of San Juan, Puerto Rico; two to four months before the hurricanes passed over the study area. The vegetation inventories used the i-Tree Eco standard methodology for urban tree inventories developed by the U.S. Forest Service, which provides a report on ecosystem services (U.S. Forest Service 2018). Information on species, height, dbh, crown width, and crown missing was recorded at 404.7-m<sup>2</sup> circular plots before and after the hurricanes. Around 200 plots were randomly chosen in Santurce to conduct the original inventory, yet only 61 trees (n = 61) from a single neighborhood (Buenos Aires) were assessed for this study due to safety and accessibility concerns after the hurricanes. The types of effects that were assessed are mostly associated with direct wind exposure such as broken bole, broken branches, uproot, and fall.

## Study Sites

Buenos Aires is located on the southeast side of the Santurce peninsula and is delimited by highway PR-1 to the north and west, and the Caño Martín Peña to the south and east of the community (Figure 1). Buenos Aires has an area of 0.497 km<sup>2</sup> with approximately 1,445 inhabitants where annual median household income is \$16,786 and 25.6 percent of residents have a bachelor's degree (U.S. Census Bureau 2012). Visually, fifty percent of Buenos Aires land use is public recreational/Institutional managed by the Department of Sports and Recreation of the Commonwealth of Puerto Rico. The remaining land use is divided into private multi-residential and private institutional land use. Demographic and ecological information is limited or non-existent to this community.

## Sampling Design

We revisited each plot up to two weeks after Irma and up to 4 weeks after María to visually evaluate

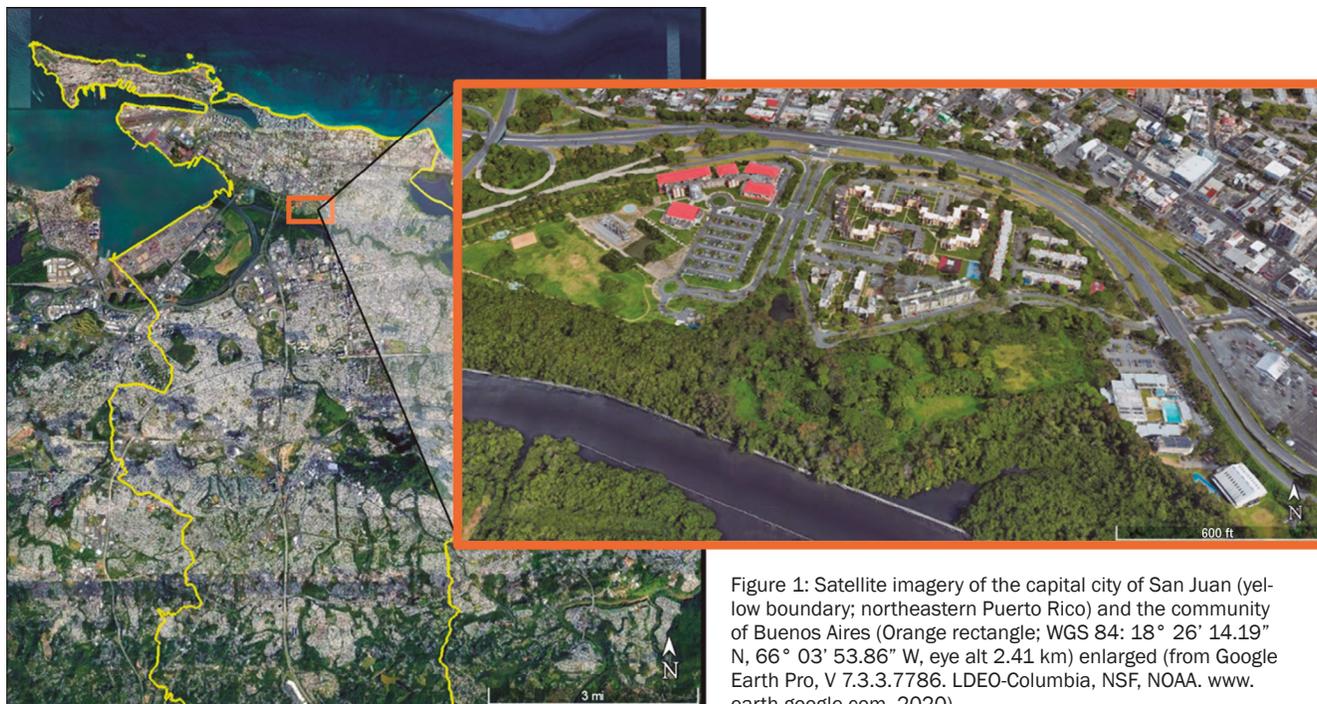


Figure 1: Satellite imagery of the capital city of San Juan (yellow boundary; northeastern Puerto Rico) and the community of Buenos Aires (Orange rectangle; WGS 84: 18° 26' 14.19" N, 66° 03' 53.86" W, eye alt 2.41 km) enlarged (from Google Earth Pro, V 7.3.3.7786. LDEO-Columbia, NSF, NOAA. [www.earth.google.com](http://www.earth.google.com). 2020).

structural effects on trees after each event. Hurricane effects were assessed using qualitative metrics adapted from Chapman (2008), Duryea et al. (2007b), Rojas-Sandoval et al. (2014), and Rossi et al. (2017). Due to safety concerns and time constraints, after locating each plot, each tree revisited was visually assigned an effect category depending on the type of structural change. The trees were classified as being uprooted (UpR) if it had fallen and mostly had exposed roots, fallen (F) if the tree was on the ground with minimal exposure of roots, broken bole (BB) if the bole was broken horizontally between crown and base, broken branches (BrBr) if branches were broken, and no effects (ND) if no visual alteration was identified. Trees that were BB and UpR were considered dead because researchers have argued that in urban settings, trees with these kinds of effects are usually removed (Francis 2000). Fallen was also considered for the mortality count due to similarities with the UpR classification. The researchers that conducted the initial survey reevaluated the same trees after both hurricanes to determine what

percentage of the tree was lost as a result of the hurricane. If a tree was assigned the effect category of UpR, BB, or F we considered that 100% of the tree was lost at the time of visit due to the hurricane.

### Statistical Analysis

The analyses for this research include descriptive analysis, observation frequency, and regressions. For this study, variables of effect type will be considered mutually exclusive. To calculate the extent of effects (% affected population) after each hurricane, we compared the total population that was assessed with the number of individuals that were affected (reported structural change or mortality) after Hurricane Irma. Due to mortality after Hurricane Irma, to estimate the extent of effects after Hurricane María, we used the remainder trees post-Irma and compared them with the number of affected individuals after Hurricane María. Therefore, the sampling size for analyses conducted for Hurricane María was lower.

**Table 1. Species of trees assessed after hurricanes Irma and María in the urban community of Buenos Aires in San Juan, Puerto Rico. A dash represents unknown species of trees. Numbers (including [n] in Grand Total) under Irma and María represent trees per species.**

Species	Family	Abbreviation	Irma	María
<i>Albizia procera</i>	Fabaceae	AP	22	14
<i>Azadirachta indica</i>	Meliaceae	AI	1	0
<i>Bucida buceras</i>	Combretaceae	BB	2	2
<i>Carica papaya</i>	Caricaceae	CP	1	0
<i>Leucaena leucocephala</i>	Fabaceae	LL	4	0
<i>Pithecellobium dulce</i>	Fabaceae	PD	1	0
<i>Roystonea borinquena</i>	Arecaceae	RB	2	2
<i>Swietenia mahogani</i>	Meliaceae	SM	13	13
<i>Tabebuia heterophylla</i>	Bignoniaceae	TH	7	6
<i>Terminalia catappa</i>	Combretaceae	TC	1	1
<i>Washingtonia robusta</i>	Arecaceae	WR	4	4
-	-	-	3	2
<b>Grand Total (n)</b>			<b>61</b>	<b>44</b>

Three Chi-square tests were conducted to determine if the distribution of hurricane structural effect, mortality, and extent changed after each hurricane. Binomial logistic regression tests were conducted to evaluate if initial structural characteristics and previous hurricane effects were predictors of hurricane extent of structural effects and mortality after each hurricane. Several regressions were run, and the lowest Akaike Information Criterion (AIC, an estimator for selecting the best model among a set of models from

a given dataset) for structural effects and mortality. Initial structural characteristics included height, maximum dbh, basal area, number of stems, crown width north to south, and percent crown missing. For the i-Tree methodology, crown missing is an interval categorical variable, therefore, for the regression, we converted it to a continuous numerical variable by assigning the middle value of the originally assigned range. For example, if a tree has a percent crown missing between one and five percent, the continuous numerical value is three percent. The percentage of the tree that was lost sampled after Hurricane Irma was used as a previous hurricane effect for the regression models of Hurricane María.

## RESULTS

### Tree Mortality and Structural Effects

We assessed 61 trees from 11 species and 9 families after Hurricane Irma, but after Hurricane María, that number was reduced to 44 (17 trees died after Irma). In the urban community of Buenos Aires, the most dominant tree species were *Albizia procera* (tall *Albizia*) and *Swietenia mahogani* (West Indian mahogany), with 22 and 13 stems evaluated after Irma, and 14 and 13 evaluated after María (Table 1). Out of these two species, *Albizia* had the highest mortality rate with 47% after Hurricane Irma and 64% after Hurricane María. Before the hurricane events, the tallest trees on average within the community were those of *Leucaena leucocephala*, the highest maximum dbh was recorded for *Washingtonia robusta* and the species with the widest crown from north to south was recorded for *Bucida buceras* (Table 2).

The mortality of trees after Hurricane Irma was significantly lower

**Table 2. Initial structural characteristics and measurements of assessed species of trees in an urban community of San Juan, Puerto Rico before the effects of hurricanes Irma and María. Standard deviation is in parenthesis where applicable and missing values are represented with a dash.**

Sp*	Height (m)	Crown width N-S (m)	Crown missing mid value (m)	Number of Stems	Basal Area (cm <sup>2</sup> )	Maximum dbh (cm)
AP	9.35 (5.56)	7.32 (3.8)	31.94 (34.73)	1.19 (0.51)	16.48 (12.25)	14.49 (10.63)
AI	7.50	6.20	-	1.00	9.00	9.00
BB	9.35 (7.57)	8.50 (0.57)	32.00 (21.21)	1.00 (0.0)	21.65 (7.42)	21.65 (7.42)
CP	3.40	3.00	27.00	2.00	14.90	9.10
LL	10.33 (3.81)	5.38 (2.84)	3.00	1.50 (1.0)	8.65 (11.20)	4.45 (2.88)
PD	11.16	8.00	37.00	2.00	135.00	70.00
RB	9.15 (1.48)	5.90 (0.28)	0.00 (0.00)	1.00 (0.0)	33.90 (2.26)	33.90 (2.26)
SM	7.82 (2.88)	6.52 (1.95)	10.17 (8.88)	1.25 (0.87)	20.33 (8.02)	18.45 (7.52)
TH	6.20 (1.59)	4.10 (0.97)	29.33 (20.45)	1.29 (0.49)	15.49 (6.15)	12.99 (4.84)
WR	5.84 (1.18)	4.53 (2.04)	18.50	(22.87)	1.00 (0.0)	52.50 (2.95)
-	7.19 (1.0)	7.50 (2.26)	3.50	(4.95)	3.50 (0.71)	38.15 (22.42)

\*Species acronyms are: AP = *Albizia procera*; AI = *Azadirachta indica*; BB = *Bucida buceras*; CP = *Carica papaya*; LL = *Leucaena leucocephala*; PD = *Pithecellobium dulce*; RB = *Roystonea borinquena*; SM = *Swietenia mahogani*; TH = *Tabebuia heterophylla*; WR = *Washingtonia robusta*.

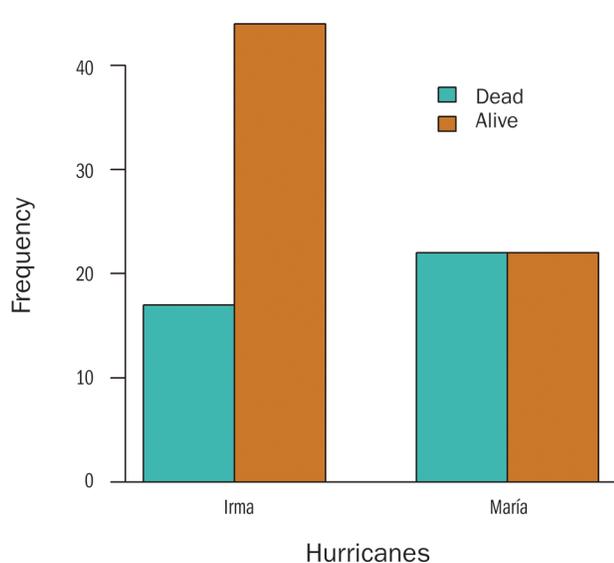


Figure 2: Distribution of mortality of trees after hurricanes Irma and María in Buenos Aires, San Juan, Puerto Rico.

than after María (Irma: 28%, María: 50%,  $X^2 = 5.36$ ,  $df = 1$ ,  $p = 0.02$ ) (Figure 2). The frequency distribution of trees with and without structural effects was also significantly different between hurricane events, with 48 % of trees showing effects after Hurricane Irma and 86% after María ( $X^2 = 16.68$ ,  $df = 1$ ,  $p < 0.0001$ ). Following both hurricane events, woody components of trees exhibited four types of structural effects: fell, were uprooted, had broken branches, or a broken bole. The frequency distributions of different effect categories, however, were

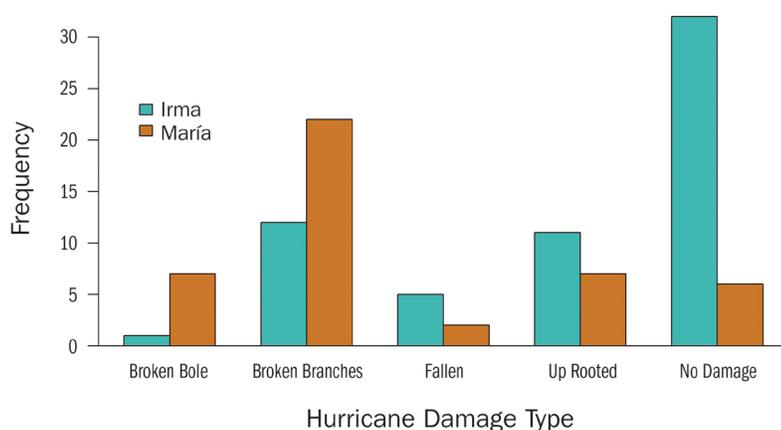


Figure 3: Distribution of the type of damage of trees after hurricanes Irma and María in Buenos Aires, San Juan, Puerto Rico.

significantly different between hurricane events ( $X^2 = 25.32$ ,  $df = 4$ ,  $p < 0.0001$ ). For Hurricane Irma, most trees (52%) fell within the “no effect category” but following Hurricane María, most trees had effects in their woody components and the frequency of trees with broken bole and broken branches were significantly higher (Figure 3).

### Correlates of Tree Effects and Mortality

Logistic regression analyses detected significant associations between the probability of finding an affected tree after Hurricane Irma and the height of trees before that hurricane event, but it did not detect significant associations with the prior state of other structural characteristics related to tree size (dbh, number of stems, crown width, basal area) and structure (i.e., crown missing) (Table 3A). According to this analysis, there was a positive association between the likelihood of becoming affected and tree height. The odds-ratio for height was equal to 1.29 indicating that for each unit increase in height, the probability of becoming affected was increased 1.29 times or by 29%. Logistic regression analyses also detected significant associations between the probability of finding affected trees after Hurricane María and their initial structural state, but this time, the probability of finding an affected tree was only associated with the width of the crown. For every unit increase in the crown, wider trees were 7.8 times more likely to become affected after Hurricane María (Table 3B).

When we analyzed the correlation between tree structure and tree mortality after Irma, the analyses showed significant associations between the probability of tree mortality and initial structural values but not all in the same direction (Table 4A). The probability of mortality was negatively associated with the tree’s initial dbh and crown width but positively associated with

**Table 3. Binomial logistic regression evaluating the relationship of structural effects after hurricanes Irma (A) and María (B) and initial structural characteristics of urban trees in a community of San Juan, Puerto Rico (n = 44). Significant values with p < 0.05 are denoted with an asterisk (\*).**

A - Hurricane Irma Predictor Variables	Coefficient	SE	z value	p-value	Odds ratio
Maximum dbh (cm)	-0.524	0.279	-1.876	0.061	-
Basal area (cm <sup>2</sup> )	0.391	0.262	1.489	0.136	-
Height (m)	0.255	0.12	2.131	0.033*	1.29
Crown width N-S (m)	0.098	0.155	0.631	0.528	-
Number of stems	-3.094	2.184	-1.417	0.157	-
Crown missing mid value (%)	-0.005	0.014	-0.366	0.714	-
AIC = 73.65 Number of Fisher Scoring iterations: 7, McFadden's Pseudo R <sup>2</sup> = 0.24, p-value = 0.0038*					
B - Hurricane María Predictor Variables	Coefficient	SE	z value	p-value	Odds ratio
Maximum dbh (cm)	-45.813	11030.290	-0.004	0.997	-
Basal area (cm <sup>2</sup> )	45.693	11030.290	0.004	0.997	-
Height (m)	-0.568	0.399	-1.423	0.155	-
Crown Width N-S (m)	2.059	1.044	1.972	0.049*	7.839
Number of Stems	-339.723	82224.15	-0.004	0.997	-
Irma Woody Damage (%)	-0.082	0.071	-1.158	0.247	-
AIC: 27.47, Number of Fisher Scoring iterations: 3, McFadden's Pseudo R <sup>2</sup> = 0.61, p-value = 0.0018*					

**Table 4. Binomial logistic regression evaluating the relationship of mortality after hurricanes Irma (A) and María (B) and initial structural characteristics of urban trees in a community of San Juan, Puerto Rico (n = 44). Significant values with p < 0.05 are denoted with an asterisk (\*).**

A - Hurricane Irma Predictor Variables	Coefficient	SE	z value	p-value	Odds ratio
Maximum dbh (cm)	-0.365	0.142	-2.572	0.01*	0.69
Basal area (cm <sup>2</sup> )	0.206	0.085	2.411	0.016*	1.23
Height (m)	0.587	0.184	3.187	0.001*	1.80
Crown width N-S (m)	-0.447	0.228	-1.961	0.05*	0.64
Number of stems	-1.709	1.028	-1.662	0.096	-
AIC: 54.405, Number of Fisher Scoring iterations: 6, McFadden's Pseudo R <sup>2</sup> = 0.38, p-value = 0.0002*					
B - Hurricane María Predictor Variables	Coefficient	SE	z value	p-value	Odds ratio
Maximum dbh (cm)	-44.409	7485.732	-0.006	0.995	-
Basal area (cm <sup>2</sup> )	42.933	7485.732	0.006	0.995	-
Height (m)	1.422	0.814	1.748	0.081	-
Crown Width N-S (m)	1.789	0.98	1.825	0.068	-
Number of Stems	-319.614	55477.28	-0.006	0.995	-
Crown missing mid value (%)	0.136	0.087	1.572	0.116	-
Irma Woody Damage (%)	0.169	0.09	1.88	0.06	-
AIC: 29.593, Number of Fisher Scoring iterations: 21, McFadden's Pseudo R <sup>2</sup> = 0.761, p-value << 0.0001*					

the tree basal area and height. For every unit change in dbh and crown width, the probability of mortality was lowered by 30.6% and 36.1% respectively. Meanwhile, for every unit change in basal area and tree height, the probability of a tree dying was increased by 23.8% and 79.9% respectively. When we analyzed the correlation of tree structure and tree mortality after María, the model was significant but individual coefficients for size and structural variables were not statistically significant (Table 4B). According to this

model, the presence of structural effects from Hurricane Irma neither was significantly associated with the probability of tree mortality (Table 4B).

Pearson correlation analyses showed that dbh was positively and highly correlated with the basal area (p < 0.001), while basal area was positively correlated with the number of stems (p = 0.018) before the hurricanes. Likewise, tree height also showed a positive correlation with dbh (p = 0.014) and crown width (p < 0.001 for both cardinal orientations, E-W and N-S) (Figure 4).

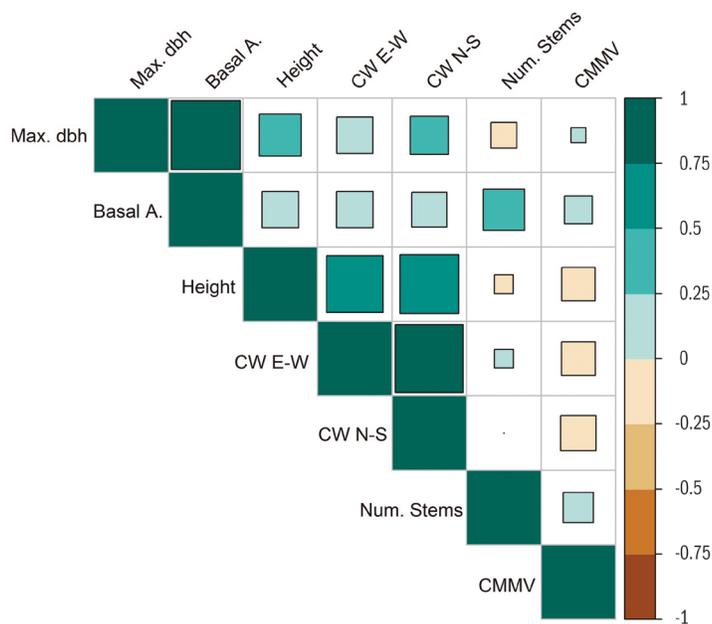


Figure 4: Correlation diagram of the relationship among the initial physical conditions of trees before hurricanes Irma and María, based on the binomial logistic regression for the community of trees in Buenos Aires, San Juan, Puerto Rico. Colored scale represents 0.25-range increments of Pearson's correlation coefficient; the relative size of squares is proportional to the strength of the correlation. Abbreviations and units as follow: Max. dbh = Maximum dbh (cm); Basal A. = Basal area (cm<sup>2</sup>); Height in m; CW E-W = Crown width (m) East-West cardinal direction; CW N-S = Crown width (m) North-South cardinal direction; Num. Stems = Number of stems; CMMV = Crown missing mid-value (%) (also see Table 3 for changes in physical conditions of trees after hurricanes Irma and María).

## DISCUSSION

Tree species on urban areas in Puerto Rico responded differently to hurricanes Irma and María. Hurricane Irma, although a category-5, did not pass directly over the island of Puerto Rico bringing only the equivalent of tropical storm winds (Cangialosi et al. 2018). On the other hand, Hurricane María struck Puerto Rico directly as a strong category-4 storm (Pasch et al. 2019). As expected, our study shows that trees were indeed more affected after Hurricane María than after Hurricane Irma, which is consistent with studies of catastrophic hurricanes on both urban and forest settings (Hook et al. 1991; Francis and Gillespie 1993). In both events, broken branches were the most frequent form of tree effects. Results of the distribution of different tree effect categories are consistent with studies of forested areas in the Caribbean,

where researchers have found that branch breakage or loss is the most common effect category associated with hurricanes (Ostertag et al. 2005; Eppinga and Pucko 2018). The uprooting and broken bole distributions found in urban areas after Hurricane María are similar to the distributions of affected trees found in forested areas after Hurricane María (Eppinga and Pucko 2018; Uriarte et al. 2019), yet different than Hurricane Georges (Uriarte et al. 2019). Some studies have found that uprooting and broken bole for urban trees are species-dependent (Duryea et al. 2007a,b) while other studies found that dbh is a better predictor for the hurricane response of forest and urban trees (Lugo 1983; Wiersma et al. 2012). The death rate following Hurricane María in our study site was higher than the recorded in forest settings for the same storm in the Caribbean (Eppinga and Pucko 2018; Uriarte et al. 2019) and higher than eight different hurricanes on urban forests between Florida and Puerto Rico (Duryea and Kampf 2007).

As predicted, our results suggest that multiple structural factors related to tree size can influence the occurrence of hurricane-related structural effects and mortality of urban trees, but that multiple hurricane effects can influence these relationships. We found strong evidence that taller trees and trees with wider crowns were more vulnerable to hurricane effects and mortality, which is consistent with other studies conducted tropical forested areas in past storms (Ostertag et al. 2005). These results were also consistent with a study of tree effects in San Juan, Puerto Rico following Hurricane Georges in 1998, where tree height also had a positive influence on the probability of tree structural change (Francis 2000). A meta-analysis of hurricane effects on urban forests in coastal cities evaluating the effects of different storms also found that in general species with larger trees tended to lose more branches than small and medium species (Duryea et al. 2007a). A hypothesis to explain these relationships

is that larger trees offer more wind resistance than smaller ones, thus more prone to breakage. At least one experimental study exposing trees from different pruning treatments (i.e., crown sizes) to different simulated storms showed that smaller crowns experienced reduced upper crown movements than larger crowns at all windspeeds including a simulated category 2 storm (Gilman et al. 2008).

There are nuances to the relationships between the probability of stem structural effects and mortality and different variables related to tree size and crown structure or condition. The combined results from our study and other studies point to the fact that is not always possible to predict which variable is the most important at influencing tree structural effects or mortality. For example, in our study, the positive effect of tree height on structural change and mortality was only apparent in Irma and not during María. Structural variables showed significant relationships in Irma and not in María. One possibility for these relationship changes is that changes in structure during the first storm could have influenced how trees respond structurally to the second storm. Based on studies conducted in Puerto Rican forest after Hurricane María, Uriarte et al. (2019) proposed that Hurricane Irma caused a change in the crown of trees that could have altered the structure and stability of the tree making it more rigid and more prone to breakage regardless of its structural variation. Another possibility (not mutually exclusive) for the lack of relationship between certain variables with structural effects and mortality may be a purely statistical one. Namely, a reduction in the statistical variation of structural variables by the first storm through woody structural effects and defoliation may have reduced the variation in the tree structure to the point that it was hard to detect in the second storm given our small sample sizes.

One unexpected result from our data was that the relationship between dbh and crown width with the likelihood of tree mortality was a negative one.

When relationships between tree structure and mortality are detected, most studies in urban (Wiersma et al. 2012; Ridge and Towns 2013) and non-urban areas have shown that trees with larger dbh have an increased probability of falling (Lugo 1983; Uriarte et al. 2019). We suggest that the wood density of *Albizia*, the dominant species in our study area, probably is more important than dbh to predict mortality due to its fast-growing properties where height is favored over dbh growth.

Hurricanes are expected to increase in frequency and intensity in the future (Gould et al. 2018). Data on how trees may respond to hurricanes can be extremely helpful in urban forest management to maintain resilient green infrastructures, which is something already being considered in other cities (Escobedo et al. 2017). Ideally one would like to make recommendations on which trees species to plant and the types of management to undertake. One limitation of this study was the small sample size for the limited number of species available. The Buenos Aires community was dominated by two species (both introduced) that behave differently in terms of structural effects and mortality. Trees of *Swietenia mahogany* experienced less structural changes and died less than *Albizia* trees. These differences are likely the result of lower wood densities as *Albizia* is considered a light to medium density wood (0.58–0.72 g/cm<sup>3</sup>) while *S. mahogany* is generally considered a high-density wood (0.56–0.85 g/cm<sup>3</sup>; Francis 2003; Carsan et al. 2012). Even with these limitations, our overall results are consistent with the fact that larger tree sizes may be more susceptible to hurricane events, which suggests the need for size management of urban trees as a potential strategy for maintaining functional trees resources in the wake of these events.

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# MISSING THE TREES FOR THE FOREST: POST-HURRICANE UNDERSTORY VEGETATION IN RELATION TO SPATIAL VARIATION

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## Abstract

Within a forest, differences in landform spatial variation (i.e., geomorphic settings: valley, slope, and ridge) could affect the species richness and distribution present at a particular site. Previous studies have confirmed that plant species richness and biomass changes after a hurricane and such values can vary among geomorphic settings. Understory vegetation, including ferns, herbs, climbers, graminoids, and shrubs, accounts for more than two thirds of flora in tropical ecosystems, but there is limited information of the effect of hurricanes on these communities. We evaluated the structure and composition of understory vegetation in a post-hurricane forest in relation to geomorphic settings. This study was conducted in El Verde Research Area in the Luquillo Experimental Forest, Puerto Rico. We established 1-m<sup>2</sup> plots within three geomorphic settings: riparian valley, slope, and ridge. Within each plot we identified species, estimated percent of cover and collected biomass samples. Additionally, we estimated species accumulation curves and analyzed species composition among geomorphic settings using multivariate ordination. The relative species abundance of vegetation life-forms was similar among geomorphic settings, but graminoids and climbers exhibited differences in species composition. Higher forest understory biomass and percent vegetation cover was observed at this immediate post-hurricane period than what was reported pre-hurricane. The understory of valley areas had a more distinct species composition than what was observed among ridge and slope areas. The understory vegetation patterns observed would need to be followed through time and among the landforms to confirm the hurricane disturbances effects at these understory scale.

**Keywords** tropical, hurricane, understory, ridge, slope, valley, species composition, biomass.

## Resumen

Dentro de un bosque, las diferencias en la variación espacial de los entornos geomórficos (valles, pendientes y crestas) podrían afectar la riqueza y distribución de especies presentes en un sitio en particular. Estudios previos han confirmado que la riqueza de especies y la biomasa de plantas cambian después de un huracán y tales valores pueden variar entre entornos geomórficos. La vegetación del sotobosque, que incluye helechos, herbáceas, trepadoras, gramíneas y arbustos, representa más de dos tercios de la flora en los ecosistemas tropicales, pero aun la información sobre el efecto de los huracanes en estas comunidades es limitada. Evaluamos la estructura y composición de la vegetación del sotobosque en un bosque post-huracán en relación con los entornos geomórficos. Este estudio se realizó en el Área de Investigación El Verde, en el Bosque Experimental de Luquillo, Puerto Rico. Establecimos parcelas de 1 m<sup>2</sup> dentro de tres entornos geomórficos: valle ribereño, pendiente y cresta. Dentro de cada parcela

identificamos especies, porcentaje estimado de cobertura y recolectamos muestras de biomasa. Adicionalmente, estimamos las curvas de acumulación de especies y analizamos la composición de especies con ordenación multivariada en relación con entornos geomórficos. La abundancia relativa de especies por cada tipo de vida vegetal fue similar entre los entornos geomórficos, pero las gramíneas y trepadoras exhibieron diferencias en la composición de especies. Se observó una mayor biomasa del sotobosque y porcentaje de cobertura vegetal en este período inmediatamente posterior al huracán que lo que se reportó para antes del huracán por otros estudios. El sotobosque en los valles tenía una composición de especies más distinta que la observada entre las áreas de crestas y pendientes. Los patrones de vegetación del sotobosque observados deberían seguirse a lo largo del tiempo y entre los entornos geomórficos para confirmar los efectos de las perturbaciones de los huracanes a esta escala del sotobosque.

**Palabras clave** biomasa, composición de especies, cresta, huracán, pendiente, sotobosque, tropical, valle.

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## INTRODUCTION

Within a forest type there can be differences in the landforms which influence the spatial distribution of ecosystem properties, these in turn, could affect the distribution and quantity of species present at a particular site. In the tabonuco forest at the Luquillo Experimental Forest (LEF) in Puerto Rico some of these differences have been observed in the geomorphic settings (e.g., ridge, slope, and valley) that characterize its landforms and topography (Scatena and Lugo 1995). The distribution of tree species, together with their biomass, structure and composition have been associated with these geomorphic settings in this forest (Scatena et al. 1993; Heartsill Scalley et al. 2010). In addition to geomorphic settings, hurricane disturbances also have a role in shaping the structure of plant communities in the tabonuco forest. Most research conducted to assess the effects of hurricane disturbance on forest dynamics in Puerto Rico has been devoted to understanding the effects on tree species (Heartsill Scalley 2017). Previous studies in the tabonuco forest have confirmed that plant total number of species increase after a hurricane and sometimes surpasses the pre-hurricane levels (e.g., Heartsill Scalley et al. 2010; Royo et al. 2011). As found by Heartsill Scalley et al. (2010), after 15 years from Hurricane Hugo tree species richness of a tabonuco forest was significantly higher in riparian valleys than

in the ridges, compared to their pre-hurricane values.

Despite the record of research on hurricane effects on forests, little is known about the effects of hurricanes on the understory, focusing on non-arborescent species. The few studies that have focused on changes in the understory plant community through time have not yet explored variation in relation to geomorphic settings. It has been shown that the understory plant community accounts for a more than two thirds of plants in tropical ecosystems and comprises the majority of tropical flora (Gentry and Dodson 1990; Chinaea 1999; Royo et al. 2011). We broadly classify the species inhabiting the understory as: ferns, herbs, climbers, graminoids and shrubs, some of which have been documented to respond to the effects of a hurricane by increasing, decreasing or remaining unchanged (Royo et al. 2011). Based on previous research in this forest, we asked whether the understory plant community exhibited differences in relation to geomorphic settings six to nine months post-hurricane disturbance.

This study evaluates the structure and composition of understory vegetation (ferns, herbs, climbers, graminoids, shrubs, and tree seedlings) in the understory of the tabonuco forest in a post-hurricane environment using three different approaches: (1) identifying non-arborescent understory species; (2) estimating the percent of coverage of each species; and (3) sampling the biomass of non-tree species. We present these

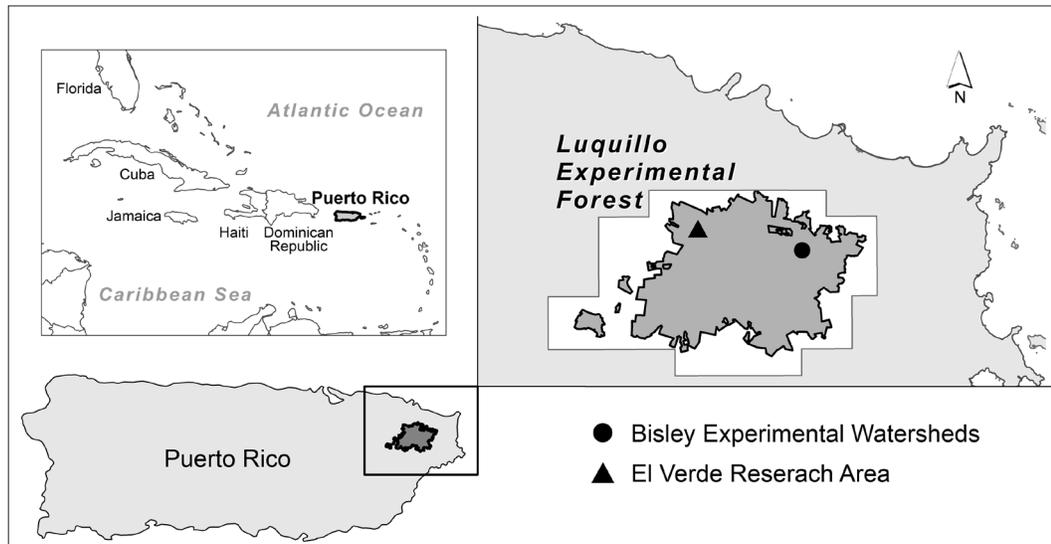


Figure 1. Study sites El Verde Research Area and Bisley Experimental Watersheds, within the tabonuco forest at Luquillo Experimental Forest, Puerto Rico.

components of the understory species community by describing them in terms of composition and number of species in relation to their location in riparian valley, slope, and ridge setting.

## METHODS

### Study Site

This study was conducted in the LEF located in northeast of Puerto Rico ( $18^{\circ}32'12''\text{N}$   $65^{\circ}81'99''\text{W}$ ; Figure 1). The forest vegetation in the LEF is influenced by periodic disturbances such as hurricanes, tropical storms, and droughts (Harris et al. 2012). In addition, forest vegetation communities are also associated with different scales of disturbances including treefalls and landslides (Brokaw et al. 2012; González et al. 2013). Over the past three decades there have been several hurricanes that affected the LEF at different intensities with Hurricane María being the most recent and most intense (category 5; September 20, 2017) since Hurricane Hugo in 1989.

The *Dacryodes-Sloanea* forest, also known as the tabonuco forest, dominates the low elevations of the LEF (< 600 m), receives an average of 3,482 mm/yr of rainfall and encompasses 70 percent of the LEF

(Harris et al. 2012). Common tree species in this forest type include the ausubo (*Manilkara bidentata*), guaraguao (*Guarea guidonia*), granadillo (*Buchenavia capitata*), laurel geo (*Ocotea leucoxylon*) and motillo (*Sloanea berteriana*) trees. Previous studies on understory non-arborescent vegetation in this forest type have found 43 species of ferns, 96 species of forbs and herbs, 28 species of vines and 20 species of shrubs (Chinae et al. 1993). Throughout the tabonuco forest, lianas (i.e., woody vines) and climbers contribute to the extent of the canopy while epiphytes tend to be most abundant in riparian areas. Ferns dominate the understory in this forest, and they can comprise up to 34 percent of total vegetation (Heartsill Scalley 2012). The geomorphic settings found in this forest type include valleys, which tend to have poorly drained soils, the least biomass, and lowest tree species richness; slopes, which receive runoff from upland areas and transmit runoff to valleys; and ridges which have well drained soils, more aboveground biomass, greater species richness and are mostly occupied with the dominant tabonuco tree species (Johnston 1992; Scatena and Lugo 1995; Heartsill Scalley et al. 2010).

For this study, we collected data at two sites in the tabonuco forest (Figure 1). The first site was the Bisley Experimental Watersheds (Bisley) on the east side of

the LEF, where data were collected six months after Hurricane María. The second site was the El Verde Research Area, part of the El Verde Field Station (El Verde) on the west side of the LEF, where data were collected nine months after Hurricane María.

### Non-arborescent Vegetation Sampling

At El Verde we quantified 31 1-m<sup>2</sup> plots in sites selected at random to include the riparian valley or valley, slope, and ridge settings. These locations were outside of permanently sampled research areas. Areas sampled were (1) the section east of Quebrada Prieta as it exits the LFDP, (2) along Quebrada Caoba, west of the main trail, and (3) south of Quebrada Sonadora west of the hanging bridge. The geomorphic settings sampled were: the ridge, which are the highest areas within the tabonuco forest; the slope, which is the steepest area located between the ridge and the valley; and the valley or riparian valley, which is the lowest part, close to stream flow or located between two slopes. For the riparian valley, the plot was established 5 m away from the stream water edge.

For each plot we identified all understory species and estimated the percent of coverage of each species. We identified species to the lowest taxonomical level possible, but for species that were difficult to identify precisely in the field, we took photos, and identified them in the laboratory, or categorized them. For species that we were unable to identify, we report them in the lowest taxonomical level possible. In addition to vegetation characterization, we estimated canopy openness above the sampled plot with a horizontal photograph at 1.5 m in height as a relative measure of light exposure condition among plots. These photographs were analyzed by placing a grid over the image and classifying grid areas as open sky or vegetation. In 9 of the 31 plots, we collected biomass (three plots per geomorphic setting). Aboveground biomass was determined by harvesting all vegetation in the plot and classifying the collected biomass per the lowest taxonomical level possible and

placed in paper bags. All understory vegetation located within the space defined by vertically projecting the perimeter of the 1-m<sup>2</sup> plot to 1.5 m in height were sampled, regardless of whether vegetation was rooted in the plot or not (following the procedure in Royo et al. 2011). We identified tree seedlings located in the plots but did not harvest them.

### Biomass Sample Processing

We took the biomass samples to the Analytical Chemistry Laboratory of the USDA Forest Service, International Institute of Tropical Forestry in Río Piedras and dried them at 65 °C to constant weight (estimated time of three days each sample). Then we weighed all the sampled vegetation to three decimal places.

### Statistical Analyses

For all plots in Bisley ( $n = 25$ ) and El Verde ( $n = 31$ ;  $n = 9$ ), species percent cover (%) and biomass (g/m<sup>2</sup>) were calculated, along with species counts (richness). Species accumulation curves were estimated using the program EstimateS Win9.1.0 software (Colwell 2013). We also calculated richness, percent cover and biomass by vegetation life forms groups: ferns, herbs (which include forbs category), climbers (herbaceous vines and woody lianas), grasses and shrubs (i.e., multi-stemmed woody plant with mature height < 5 m, as defined in the species list by Royo et al. [2011] and USDA Plants Database). To compare understory vegetation characteristics (richness, percent cover, biomass) among geomorphic settings (ridge, slope, and riparian valley) at El Verde and among life forms at both study sites, a Kruskal-Wallis test (KW, H) was conducted. Statistics were considered significant at a level of 0.05 (Heartsill Scalley et al. 2010). All mean values for El Verde, except mean biomass, were based on 31 plots ( $n = 31$ ). For biomass samples, the mean values were based on nine plots ( $n = 9$ ). Based on the nine plots we calculated biomass for the most common species found (the ones

**Table 1. Species per vegetation life form found in the understory of the tabonuco forest, six to nine months after Hurricane María, El Verde Research Area, Luquillo Experimental Forest, Puerto Rico.**

Life Form	Species	Native Status	Life Form	Species	Native Status	
Fern	<i>Adiantum</i> spp.	Probably Native	Palm	<i>Eugenia</i> spp.	—	
	<i>Blechnum occidentale</i> L.	Native		<i>Eugenia stahlii</i> (Kiaersk.) Krug & Urb.	Native	
	<i>Danaea nodosa</i> (L.) Sm.	Native		<i>Faramea occidentalis</i> (L.) A.Rich.	Native	
	<i>Tectaria</i> spp.	Probably Native		<i>Guarea guidonia</i> (L.) Sleumer	Native	
	<i>Thelypteris deltoidea</i> (Sw.) Proctor	Native		<i>Hirtella rugosa</i> Thuill. ex Pers.	Native	
	Other unidentified fern species			<i>Inga laurina</i> (Sw.) Willd.	Native	
Graminoid	<i>Ichnanthus pallens</i> (Sw.) Munro ex Benth.	Native		<i>Inga vera</i> Willd.	Native	
	<i>Olyra latifolia</i> L.	Native		<i>Ixora ferrea</i> (Jacq.) Benth.	Native	
	<i>Pharus latifolius</i> L.	Native		<i>Manilkara bidentata</i> (A.DC.) A.Chev.	Native	
	Poaceae	—		<i>Nectandra turbacensis</i> (Kunth) Nees	Native	
Herb	<i>Scleria canescens</i> Boeckeler	Native		<i>Ocotea leucoxydon</i> (Sw.) Laness.	Native	
	Boraginaceae	—		<i>Psychotria berteriana</i> DC.	Native	
	<i>Commelina diffusa</i> Burm.f.	Native		<i>Psychotria brachiata</i> Sw.	Native	
	<i>Euphorbia</i> spp.	—		<i>Sapium laurocerasus</i> Desf.	Native	
	<i>Heliconia caribaea</i> Lam.	Native		<i>Schefflera morototoni</i> (Aubl.) Maguire, Steyererm. & Frodin	Native	
	<i>Catopsis floribunda</i> L.B.Sm.	Native		<i>Simarouba amara</i> Aubl.	Introduced	
	<i>Peperomia rotundifolia</i> (L.) Kunth	Native		<i>Sloanea berteriana</i> Choisy ex DC.	Native	
	<i>Phytolacca rivinoides</i> Kunth & C.D.Bouché	Native		<i>Tabebuia heterophylla</i> (DC.) Britton	Native	
	<i>Pilea</i> spp.	—		<i>Tetragastris balsamifera</i> (Sw.) Oken	Native	
	<i>Pilea inequalis</i>	Native		Vine	<i>Prestoea acuminata</i> var. <i>montana</i> (Graham) A.J.Hend. & Galeano	Native
	<i>Rhynchospora radicans</i> (Schtdl. & Cham.) H.Pfeiff.	Native			<i>Roystonea borinquena</i> O.F.Cook	Native
	<i>Ruellia coccinea</i> (L.) Vahl	Native	<i>Cayaponia racemosa</i> (Mill.) Cogn.	Native		
	<i>Sauvagesia erecta</i> L.	Introduced	<i>Cissus verticillata</i> (L.) Nicolson & C.E.Jarvis	Native		
	<i>Spermacoce ocyimifolia</i> Willd. ex Roem. & Schult.	Native	<i>Dioscorea polygonoides</i> Humb. & Bonpl. ex Willd.	Native		
	<i>Tillandsia utriculata</i> L.	Native	<i>Dolichandra unguis-cati</i> (L.) L.G.Lohmann	Introduced		
	<i>Wulfschlaegelia calcarata</i> Benth.	Native	<i>Heteropterys laurifolia</i> (L.) A.Juss.	Native		
	Shrub	<i>Urera baccifera</i> (L.) Gaudich. ex Wedd.	Native	<i>Hippocratea volubilis</i> L.	Native	
		<i>Gonzalagunia hirsuta</i> (Jacq.) K.Schum.	Native	<i>Ipomoea alba</i> L.	Native	
<i>Miconia racemosa</i> (Aubl.) DC.		Native	<i>Ipomoea tillicea</i> (Willd.) Choisy	Native		
<i>Microgramma piloselloides</i> (L.) Copel.		Native	<i>Marcgravia sintensisii</i> Urb.	Native		
<i>Neurolaena lobata</i> (L.) R.Br. ex Cass.		Native	<i>Mikania</i> spp.	Probably Native		
<i>Piper glabrescens</i> (Miq.) C.DC.		Native	<i>Mikania cordifolia</i> (L.f.) Willd.	Native		
<i>Piper hispidum</i> Sw.		Native	<i>Mikania fragilis</i> Urb.	Native		
<i>Piper umbellatum</i> L.		Native	<i>Paullinia pinnata</i> L.	Native		
<i>Solanum torvum</i> Sw.		Introduced	<i>Philodendron hederaceum</i> (Jacq.) Schott	Native		
Tree		<i>Alchornea latifolia</i> Sw.	Native	<i>Pinzona coriacea</i> Mart. & Zucc.	Native	
	<i>Andira inermis</i> (Wright) DC.	Native	<i>Rourea surinamensis</i> Miq.	Native		
	<i>Buchenavia tetraphylla</i> (Aubl.) R.A.Howard	Native	<i>Schlegelia brachyantha</i> Griseb.	Native		
	<i>Byrsonima spicata</i> (Cav.) Rich. ex Kunth	Native	<i>Securidaca virgata</i> Sw.	Native		
	<i>Casearia sylvestris</i> Sw.	Native	<i>Smilax domingensis</i> Willd.	Native		
	<i>Cecropia schreberiana</i> Miq.	Native				
	<i>Cordia borinquensis</i> Urb.	Native				
	<i>Dacryodes excelsa</i> Vahl	Native				

found in most of the plots). All values are shown as mean  $\pm$  2 standard errors.

To explore understory vegetation community species composition among ridge, slope, and riparian valley, a non-metric multidimensional scaling (NMS) ordination analysis was conducted. An NMS ordination was used because it has been used to efficiently reduce high “dimensional” multi-variable species

space (high number of species) to two dimensions, which makes it easy to plot simple two axis graphs. The NMS ordination was made for the El Verde data set in two ways; using per species biomass values and percent cover. The matrices for both ordinations were generated using Bray–Curtis distance in PC Ord-6 (McCune and Mefford 2011) in R version 3.4.0 (R Core Team 2017).

## RESULTS

### Distribution of Understory Vegetation Among Geomorphic Settings

A total of 95 species were found at El Verde, 85 of which belong to 49 different families. The remaining ten species were not identified, primarily because the seedlings were too small/young. From the 85 species, 8 species were identified to the genus level and 4

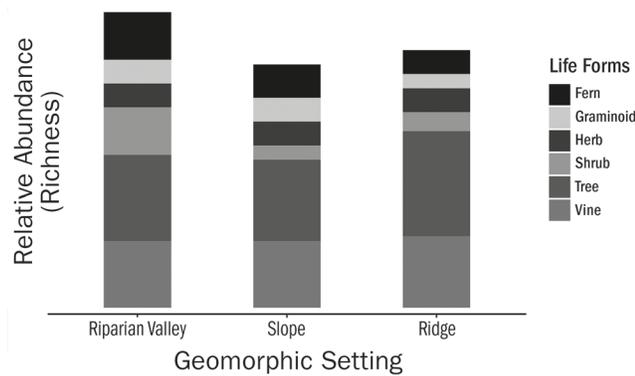


Figure 2. Differences in understory life forms patterns of relative abundance in terms of richness (number of different species) among geomorphic settings within the tabonuco forest six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico.

Table 2. Mean values for biomass and percent cover of the most common species in the understory of the tabonuco forest six to nine months after Hurricane María, El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. SE = standard error.

Life Form	Species	Mean $\pm$ 2 SE	
		Biomass g/m <sup>2</sup>	Cover (%)
Graminoid	<i>Ichnanthus pallens</i> (Sw.) Munro ex Benth.	89.57 $\pm$ 73.24	23.65 $\pm$ 10.34
Vine	<i>Dioscorea polygonoides</i> Humb. & Bonpl. ex Willd.	37.21 $\pm$ 40.86	6.65 $\pm$ 5.15
Tree/Shrub	<i>Psychotria berteriana</i> DC.	6.49 $\pm$ 11.42	2.39 $\pm$ 1.35
Vine	<i>Hippocratea volubilis</i> L.	3.55 $\pm$ 3.09	1.97 $\pm$ 1.12

species were identified to the family level, with only 4 being recognized as introduced species (Table 1). Tree (> 1.5 m in height) and vine species were the greatest contributors to species richness in the understory of the tabonuco forest at El Verde. The relative species abundance of understory vegetation was also similar among all three geomorphic settings (Figure 2). However, both, vines and trees were more abundant, in terms of richness and percent cover, in ridges than in riparian valleys. Fern species exhibited a trend of decrease from riparian valleys up to ridges. Shrub species were more abundant in riparian valleys than in slopes or ridges (Figure 3). The most abundant species

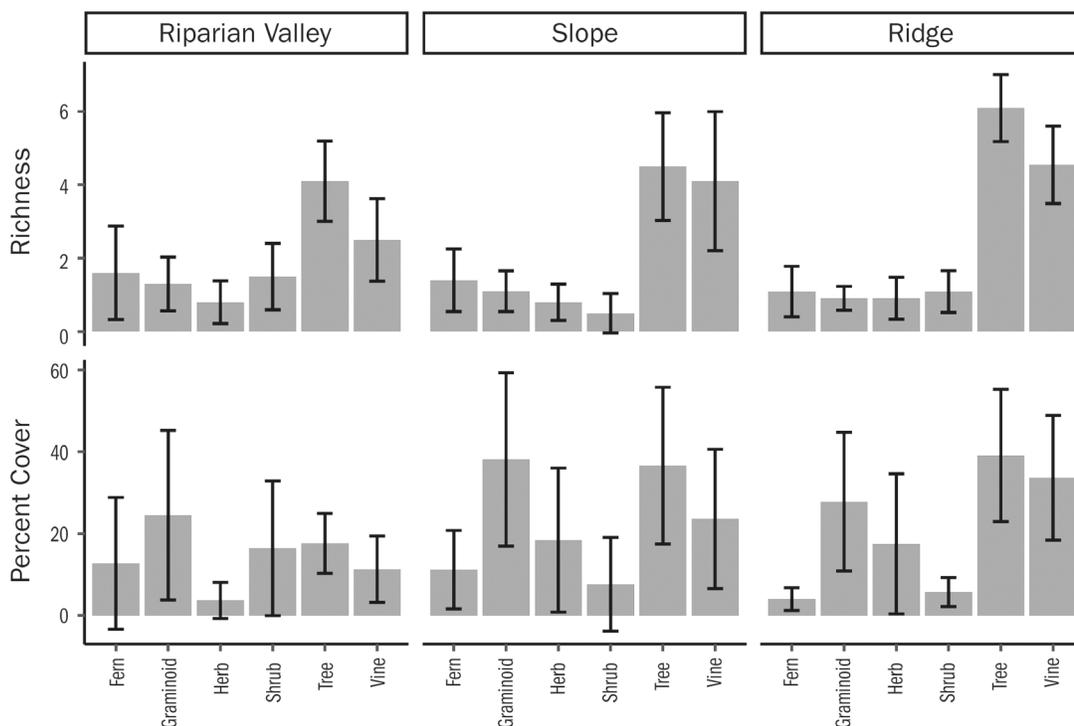


Figure 3. Mean richness (species per plot) and percent cover (%) values of understory species by life form among geomorphic settings within the tabonuco forest six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Mean values were based on 10 plots for Riparian Valley and Slope, and 11 plots for Ridge. Error bars represent two standard errors.

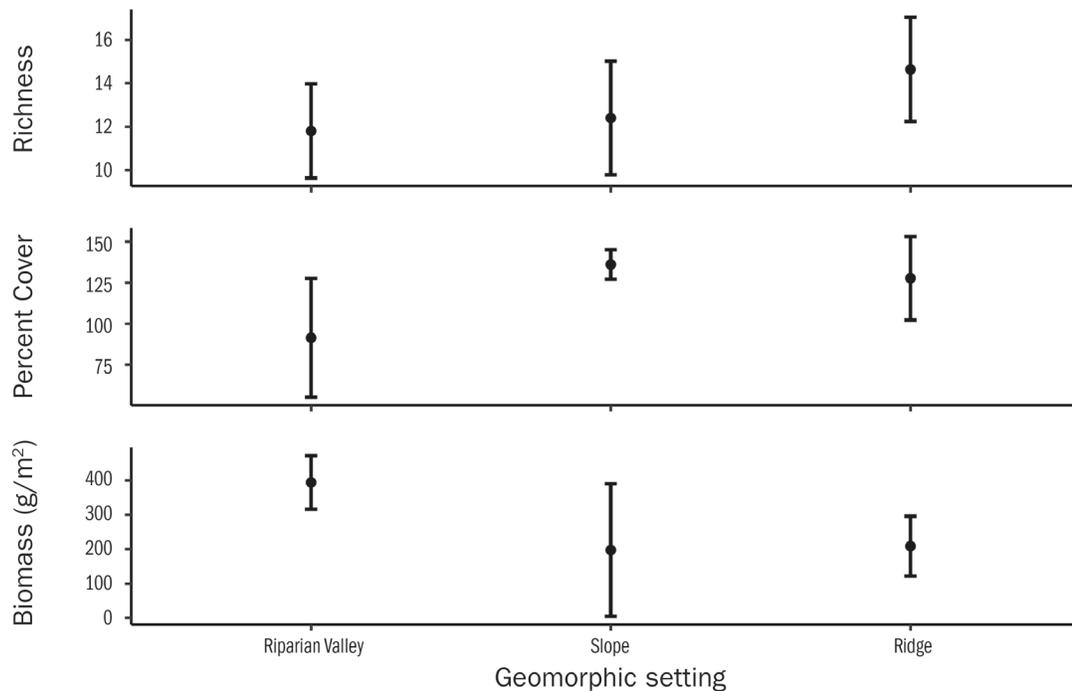


Figure 4. Mean richness (species per plot), percent cover (%) and biomass (g/m<sup>2</sup>) values of understory species for each geomorphic setting within the tabonuco forest six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Percent cover and richness values were Riparian Valley n = 10, Slope n = 10, and Ridge n = 11. Biomass values were Riparian Valley n = 3, Slope n = 3, and Ridge n = 3. Error bars represent two standard errors.

in terms of biomass and percent cover was a graminoid, the species *Ichnanthus pallens* (Table 2). Two vines (*Dioscorea polygonoides* and *Hippocratea volubilis*) and the tree/shrub *Psychotria berteronana* were the other top contributors to biomass and ground cover in the forest understory at El Verde.

Based on mean species richness per plot, trees seedlings and vines in the understory community at El Verde were the most abundant species among geomorphic settings (Figure 3). Tree seedling and vine mean cover exhibited a trend of increase from riparian valleys up to ridges, whereas shrub and fern cover decreased. In contrast, cover by graminoids tended to be more abundant on slopes. However, these tendencies were not statistically significant among vegetation life forms, both within the same geomorphic setting and among them (Figure 3).

### Forest Understory Vegetation Characteristics in Relation to Geomorphic Setting

Within the tabonuco forest at El Verde there were no statistically significant differences in terms of

richness (species per plot), percent cover, nor biomass for understory species among each geomorphic setting. A trend was observed for species richness to increase from riparian valleys up to ridges. Mean species cover was 45 percent less in riparian valley than in slopes, which had the most coverage. The aboveground biomass was comprised by every life form except tree seedlings. Riparian areas had the greatest amount of biomass and slopes the least (Figure 4). Each setting had a similar canopy cover with no significant differences among them.

### Variation in Understory Vegetation Life Forms Within Tabonuco Forest Sites

The understory at El Verde had more species per plot than what was observed in Bisley (Table 3) but had similar values for percent cover (El Verde,  $118.61 \pm 16.19$ ; Bisley,  $161.20 \pm 25.13$ ) and biomass (El Verde,  $266.75 \pm 91.14$ ; Bisley,  $174.99 \pm 48.03$ ). Tabonuco forest understory vegetation had greater species richness (species per plot) for tree seedlings at Bisley, compared to species richness for other understory vegetation

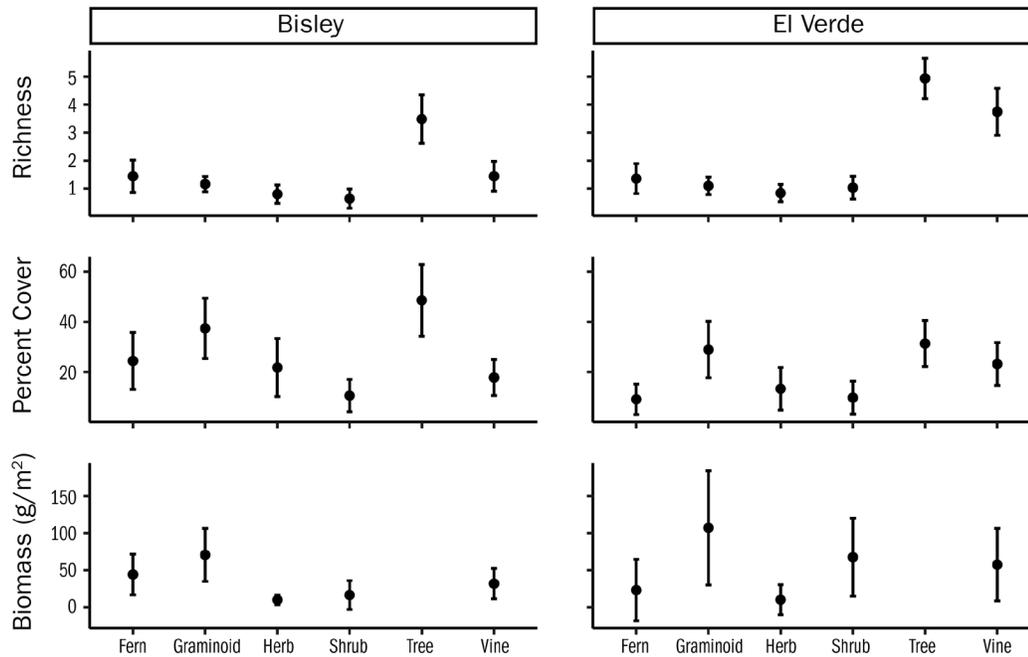


Figure 5. Mean richness (species per plot), percent cover (%) and biomass (g/m<sup>2</sup>) values of understory species by life form within the tabonuco forest six to nine months after Hurricane María at the Bisley Experimental Watershed and at El Verde Research Area. Bisley values n = 25 plots. El Verde values n = 31 plots for percent cover and richness; biomass n = 9 plots. Error bars represent two standard errors.

life forms (KW H = 38.348, p < 0.001; Figure 5). At the El Verde site, the tabonuco forest understory had greater species richness for both tree seedlings and vines, compared to other vegetation life forms (KW H = 85.347, p < 0.001; Figure 5). In terms of percent cover tree seedlings and graminoids were the most abundant at both sites (El Verde: KW H = 44.154, p < 0.001; Bisley: KW H = 26.983, p < 0.001).

One to two species of fern, graminoid, herb, and shrub were consistently found per plot at both Bisley and El Verde. At Bisley, trees were the most abundant life form of the understory, in terms of richness and percent cover. There were significant differences in terms of biomass per vegetation life forms (El Verde:

KW H = 11.331, p < 0.023; Bisley: KW H = 30.734, p < 0.001). Graminoids comprised the majority of biomass both at El Verde and Bisley, while herbs tended to have the least biomass in both sites.

### Understory Vegetation Composition in Relation to Geomorphic Setting

Species composition of the understory vegetation in the valley plots seems to have more species in common among plots, therefore high association in their species composition, as evidenced by their close location in the multivariate species space (Figure 6). This is observed in both, the ordination based on species biomass and the one based on percent cover. Some of the species associated to valley were in contrast, species composition in the ridge and slope plots seem to be more similar, as these plots converge and are occupying an overlapping area closer together multivariate species space (Figure 6).

In the tabonuco forest at El Verde, understory species composition is richer than what we were able to capture in our sampling during this study.

Table 3. Characteristics of understory vegetation of the two tabonuco forest sites sampled six to nine months after Hurricane María in the Luquillo Experimental Forest, Puerto Rico. El Verde Research Area n = 31 for species per plot and percent cover values, n = 9 for biomass values. Bisley Experimental Watersheds n = 25 for all values. SE = standard error.

Characteristic	Mean ± 2 SE	
	Bisley	El Verde
Species/plot	9.00 (± 1.31)	13.00 (± 1.42)
Percent Cover (%)	161.20 (± 25.13)	118.61 (± 16.19)
Biomass (g/m <sup>2</sup> )	174.99 (± 48.03)	266.75 (± 91.14)

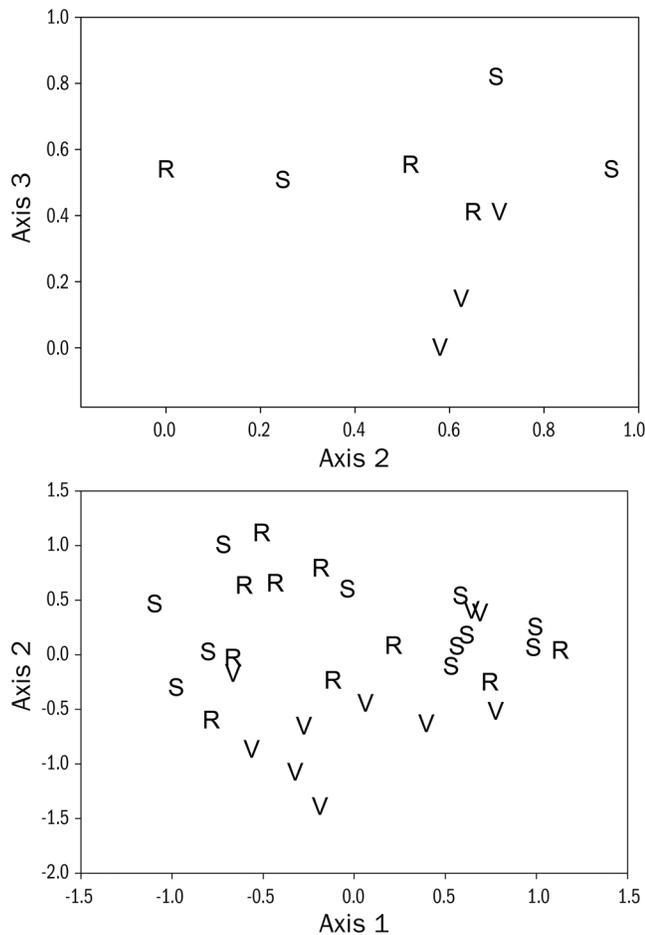


Figure 6. Ordination based on Non-metric Multidimensional Scaling (NMS) of understory vegetation community species composition among ridge, slope, and riparian valley plots six to nine months after Hurricane María in the tabonuco forest at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Top panel ordination on species composition based on biomass ( $\text{g}/\text{m}^2$ ) and bottom panel based on percent cover (%), symbols are V for riparian valley and valleys, S for slopes, and R for ridges.

Many species found during this study occurred only once or twice in the sampled plots (Table 1). In valley plots 40 percent of species found occurred only once. This is also evidenced by the species accumulation curves generated (Figure 7). Our samples were closer to approaching a maximum number of species in plots from ridge and slope sites in comparison to plots in valleys.

## DISCUSSION

Originally, we predicted that the understory community would show differences in terms of its

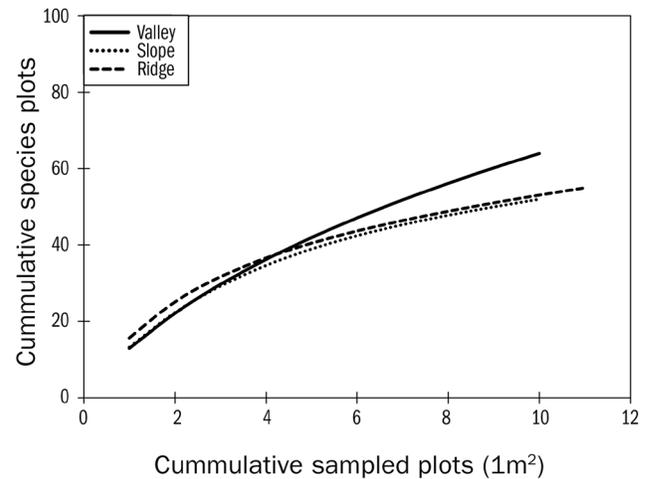


Figure 7. Species accumulation curves per geomorphic settings sampled six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Riparian Valley  $n = 10$ , and Slope  $n = 10$ , and Ridge  $n = 11$ .

structure and composition in relation to the geomorphic settings of the forest. Our results demonstrate that at the understory scale there could be differences in species composition among those settings. The tabonuco forest understory at both El Verde and Bisley has high biomass and percent vegetation cover at this post-hurricane period as was found by Chinaea (1999) and Royo et al. (2011). However, biomass values were not representative of percent cover and richness because most species found were tree seedlings that were not collected as biomass samples. Canopy cover was similar among geomorphic settings, so we rejected it as a possible factor affecting understory vegetation characteristics, such as low biomass values found in ridges, which tend to have the greatest values according to previous observations (Scatena et al. 1992; Scatena and Lugo 1995). Nonetheless and since ridges were observed to support the greatest tree seedling relative abundance and species richness, aboveground biomass values could have been underestimated, considering that tree seedlings were not collected for destructive sampling.

The lowest species richness and highest biomass in valley areas suggests a more distinct species composition than what was observed in ridge and slope

areas. The tendency of some vegetation characteristics to increase from one geomorphic setting to the other is another indicator of species composition variability in the understory. This variability in understory could be associated to differences in soil characteristics and species composition of the forest canopy dominants among geomorphic settings (Scatena and Lugo 1995). The low species richness at the Bisley site compared to the El Verde site could be associated to the different proportions of areas sampled, which in Bisley consisted mostly of slope regions. However, the overall species richness in the tabonuco forest understory is high at both sites as expected in this initial post-hurricane period (China 1999; Royo et al. 2011).

Even though the tabonuco forest was in the early stages of post-hurricane dynamics at the time of our field work, there were differences in vegetation characteristics among life forms at the spatial scale of geomorphic setting. The results reflect the structure and composition of the understory community in a post-hurricane environment, which contrasts to pre-hurricane conditions as reported in previous studies in this forest (China 1999; Royo et al. 2011; Kennard et al. 2020). Based on previous observations, the hurricane disturbance created opportunities for shade-intolerant graminoids and vines to thrive. Previous studies on post-hurricane disturbance effects on the understory have also found increases in certain vegetation life forms such as graminoids and lianas/vines, which have turned out to be only ephemeral increases in their biomass and ground cover that are gone after five years (Royo et al. 2011). The relative abundance of vine and graminoid in this study was significantly high, resembling the same response those previously studied post-hurricane environments.

During the post-hurricane period captured in this study, the understory of valley areas had a more distinct species composition than what was observed among ridge and slope areas which shared

more species. The species composition of the understory vegetation may indeed be different among geomorphic settings, but these differences might emerge more clearly once the canopy closes over the tabonuco forest.

## ACKNOWLEDGEMENTS

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# EFFECTS OF HURRICANES ON THE BRYOLOGICAL AND LICHENOLOGICAL FLORA OF PUERTO RICAN FORESTS

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## Abstract

Hurricanes drastically modify habitat structure and environmental conditions in forests of the island of Puerto Rico. In general, short- and long-term effects of hurricanes on most of the macrofauna and vascular flora in these ecosystems has been well characterized. Unfortunately, the effects of hurricanes on lichens and bryophytes, which are among the most diverse groups in these forests, are much less understood. The present review discusses potential short- and long-term effects of hurricanes on lichen and bryophyte communities on the island. General biological and ecological aspects of these organisms are provided first and are followed by a brief summary of important studies of Puerto Rican bryology and lichenology. We then combine firsthand field observations with current knowledge from the published literature to make inferences about how hurricanes, specifically how hurricanes Irma and María, might have affected lichens and bryophytes in our forests. Our work documents the scarcity of studies on hurricane effects on both groups, particularly in lichens. We present questions for future research and argue that properly studying typically overlooked groups, like lichens and bryophytes, will enhance our understanding of how this type of disturbances affect biodiversity on the island.

**Keywords** bryophytes, Caribbean, disturbances, lichens, Natural History, tropics.

## Resumen

Los huracanes afectan drásticamente la estructura de hábitats y las condiciones ambientales en los bosques de la isla de Puerto Rico. Los efectos a corto y largo plazo de los huracanes sobre la mayoría de la macrofauna y la flora vascular en estos ecosistemas han sido bien estudiados. Desafortunadamente, los efectos de los huracanes sobre los líquenes y briofitas, que están entre los grupos más diversos en estos bosques, son mucho menos comprendidos. La presente revisión discute potenciales efectos a corto y largo plazo de los huracanes sobre las comunidades de líquenes y briofitas de la isla. Aspectos generales sobre la biología y ecología de estos organismos es provista inicialmente y es seguida por un breve resumen sobre estudios importantes para la briología y liquenología de Puerto Rico. Luego combinamos nuestras observaciones de campo con conocimiento de la literatura científica para hacer inferencias sobre como los huracanes, en específico los huracanes Irma y María, pudieron haber afectado los líquenes y briofitas en nuestros bosques. Nuestro trabajo documenta la escasez de estudios sobre efectos de huracanes en ambos grupos, particularmente en los líquenes. Presentamos preguntas para investigaciones futuras y argumentamos que si estudiamos adecuadamente grupos típicamente ignorados, como los líquenes y las briofitas, mejorará nuestro entendimiento sobre como este tipo de disturbios afecta la biodiversidad de la isla.

**Palabras clave** briofitas, Caribe, disturbios, líquenes, Historia Natural, trópico.

## INTRODUCTION

Hurricanes are tropical cyclones that are formed over warm waters in the Atlantic Ocean, and that frequently make landfall in the Caribbean islands. The passage of hurricanes over the Caribbean islands, such as Puerto Rico, is linked to significant physical damage and disruption of biological processes in forests from this region. As a result of exposure over millennia, Caribbean ecosystems are generally adapted to hurricanes. Nevertheless, the effects from these events can pose serious challenges to species inhabiting these ecosystems, particularly over short temporal scales.

Known and potential effects of hurricanes to the biotas and physical elements of these forests were amply reviewed by Lugo (2000) and include, among others, sudden and massive tree mortality, increased opportunities for change in successional direction, high species turnover, and fast biomass and nutrient turnover. Many of these effects can certainly threaten vulnerable elements of these forests (e.g., pushing endangered species to the brink of extinction). However, the periodic passing of hurricanes over Caribbean forests seems to be important for maintaining a diverse mix of succession and climax species at particular sites (Zimmerman et al. 1994; Lugo 1998; Brokaw et al. 2012; Weaver et al. 2013). This suggests that despite their immediate catastrophic impacts, these events are critical for the maintenance of species diversity in these ecosystems (Lugo 1998). Similar observations have also been made for many other biotic elements including birds and amphibians (Waide 1991; Lugo 1998; Lugo 2008), reinforcing the view of hurricanes as important factors influencing biodiversity dynamics in Caribbean forests.

As briefly synthesized above, short- and long-term effects of hurricanes on major plant and animal groups inhabiting Caribbean forests are generally well understood. Little is known, however, about their effects on lichens and bryophytes, which are among the most speciose organisms to be found in these ecosystems (Pérez et al. 2012; Mercado-Díaz et al. 2015). While

poorly studied, lichens and bryophytes perform and/or mediate key ecological processes in tropical forests. They are important for soil formation and stabilization, water retention and nitrogen and carbon fixation (Nash 2008; Glime and Gradstein, 2018). These organisms also provide habitat to many invertebrates, serve as the staple diet for many insects and influence, either directly or indirectly, important biological interactions (e.g., potentially reduced predation through crypsis [see Lücking 2010]).

In this review, we will provide a brief description of what lichens and bryophytes are and the important roles they play in Puerto Rican forests. To offer a view on the current state of bryology and lichenology in the island, key studies that have been essential for understanding diversity patterns of these organisms will be summarized. We will combine our more than 20 years of field and research experience with current knowledge within these fields to hypothesize on the effects that hurricanes may have on lichen and bryophyte communities. While lichens and bryophytes grow on diverse substrates and are found in multiple forest ecosystems (see below), our observations focus mostly on epiphytic communities that occur in rainforests and/or other humid forests of the island. Anecdotal observations about potential short- and long-term effects of hurricanes Irma and María on these communities will also be discussed and used to propose questions for future investigation.

## THE LICHENOLOGICAL PERSPECTIVE

### Lichen Biology, Ecology, and Diversity Patterns

Lichens are traditionally defined as symbiotic associations between fungi and at least one photosynthetic partner (i.e., algae and/or cyanobacteria) (Figure 1). Most fungal partners, or mycobionts, are members of the phylum Ascomycota, but nearly one percent of the species form associations with Basidiomycetous



Figure 1. Growth forms of different lichens from Puerto Rico. (A) Crustose – *Thallopora rubromarginatum* from El Yunque National Forest (EYNF); (B) Foliose – *Sticta tainorum* from Bosque Estatal de Toro Negro, central Puerto Rico; (C) Fruticose – *Cladonia robusta* from Reserva Natural Laguna Tortuguero, northern Puerto Rico.

fungi (Nash 2008). Algae that are found in lichens usually belong to the genera *Trebouxia* and *Trentepohlia*, whereas lichenized cyanobacteria most commonly belong to the genus *Nostoc* (Friedl and Büdel 2008). Work by Spribille et al. (2016), Mark et al. (2020), and others, however, have begun to challenge the notion of lichens as static systems with fixed numbers of essential symbionts. This current view of lichens as more dynamic systems was elegantly summarized in the most recent definition of lichens provided by Hawksworth and Grube (2020): “A lichen is a self-sustaining ecosystem formed by the interaction of an exhibitant fungus and an extracellular arrangement of one or more photosynthetic partners and an indeterminate number of other microscopic organisms.”

Lichens are present in every major terrestrial biome and are capable of colonizing nearly every substrate (e.g., rocks, leaves, bark) available in those ecosystems (Nash 2008). In forests, lichens are known to contribute to soil formation and stabilization and therefore facilitate primary succession (Brodo et al. 2001). They potentially influence nutrient dynamics as many species are also capable of fixing atmospheric nitrogen (Forman 1975; Antoine 2004; Elbert et al. 2012). Lichens are also believed to play critical roles in the maintenance of water cycles (Green and Lange 1991; Beckett 1995; Zotz et al. 1998) and constitute an important staple in the diet of many animals in those ecosystems (Brodo et al. 2001; Storeheier et al. 2002). Close to 20,000 species of lichens have been formally recognized (Lücking et al.

2017). However, estimates indicate that global diversity might reach 28,000 species (Lücking et al. 2009), suggesting that nearly one-third of extant species in the planet are still to be discovered (Lücking et al. 2009).

While it was initially believed that lichens were more diverse in temperate ecosystems, recent work suggests that at smaller spatial scales, species diversity increases towards the tropics (Lücking et al. 2011). In fact, half of the estimated global number of species is predicted to be found in this biome (Lücking et al. 2009; Sipman and Aptroot 2001; Lücking et al. 2011).

Epiphytic lichens, which are lichens that depend on vegetation surfaces to grow, dominate the lichen flora in tropical humid and rainforests (Sipman and Harris 1989). Epiphytic lichen communities in these ecosystems are influenced by factors such as substrate characteristics (e.g., pH, degree of bark shedding, among others) and microclimate (Cáceres et al. 2007). Community composition of these organisms within these forests, on the other hand, vary along different spatial and temporal axes. Most variation, at least in short spatial scales, is possibly found between vertical forest layers (i.e., canopy versus understory) (Komposch and Hafellner 2000; Normann et al. 2010). Environmental conditions in the canopy have high diurnal variation, alternating between periods of high or low temperature and humidity, and increased solar radiation or shadiness. Due to these conditions, species in this layer likely have broader environmental tolerances if compared to those in the understory. Some families commonly found in this

layer are Asterothyriaceae, Parmeliaceae, Strigulaceae, Trypetheliaceae and the non-thelotremoid Graphidaceae (Sipman and Harris 1989; Komposch and Hafellner 2000; Lücking 2008). Understory communities, on the other hand, are exposed to less variable conditions. Most species are shade-tolerant and are adapted to high humidity conditions with the Pyrenulaceae, Coenogoniaceae, Porinaceae, Bacidiaceae and most thelotremoid Graphidaceae frequently found in this layer (Sipman and Harris 1989; Komposch and Hafellner 2000; Rivas-Plata et al. 2008). Canopy and understory communities also vary in the distribution of growth forms, the former containing a higher proportion of fruticose and foliose species, and the latter characterized by a high diversity of crustose and squamulose species (Forman 1975; Cornelissen and Ter Steege 1989; Komposch and Hafellner 2000). Together with bryophytes, lichens represent conspicuous elements of the non-vascular flora present in tropical forests. However, in comparison to their vascular counterparts, these organisms remain poorly characterized in tropical regions.

Although studies on the lichens of Puerto Rico are still scarce, the lichen flora of Puerto Rico is possibly the best known among the islands in the region (Mercado-Díaz and Santiago Valentín 2010). Ongoing inventory efforts based on published literature, information from online herbarium databases and collections from the first author indicate that nearly 1,500 species names have been recorded for Puerto Rico (Mercado-Díaz, unpublished). While this amount of species is similar to a previous estimate (~1,600 species, Lücking et al. 2009), the nomenclatural status of these names has not been revised, hinting that this number of species is likely inflated due to synonymy issues (see Dubois 2008 for an interesting discussion on this topic). This suggests that at least a small portion of the flora still awaits discovery.

### Lichen Studies in Puerto Rico

Mercado-Díaz and Santiago-Valentín (2010) provided the first historical account of lichen studies that have

shaped our understanding of lichen species richness in Puerto Rico. Two of the works cited in that review are notable in this respect. The first is Ismael Landrón-Concepción Ph.D. thesis on the genus *Ramalina* Ach. (Landrón-Concepción 1972). Landrón-Concepción is the first native Caribbean lichenologist, and his work represents the first formal taxonomic treatment for any lichen group in the region. Harris (1989) working keys to the lichen-forming fungi of Puerto Rico represents the second milestone. Besides providing keys to identify species within most micro- and macro-lichen genera present in the island, this work is of particular relevance to tropical lichenology as it constitutes the “first attempt to treat all the lichen-forming fungi in any tropical region” (Harris 1989). It also provided the first rough estimate of lichen species present in the island (i.e., 750 spp.).

While Puerto Rican lichenology remained inactive for nearly 20 years (1989–2009), the last decade witnessed an increase in the number of studies focusing on the ecology, taxonomy, systematics, and phylogenetics of these organisms. Four new species in the genus *Coenogonium*, all potentially endemic to Puerto Rico, were described by Mercado-Díaz and collaborators (Mercado-Díaz et al. 2013). Their findings have major conservation implications as these species were found in two threatened ecosystems (i.e., *Pterocarpus* wetlands and Non-calcareous dry forests), prompting the need to protect these habitats better. Mercado-Díaz et al. (2014) generated, on the other hand, one of the first studies to suggest that lichen endemism in islands is likely higher than previously assumed. This work resulted in two new genera and twelve new species in the family Graphidaceae, all apparently endemic to the Luquillo Mountains. The work by Mercado-Díaz et al. (2015) is particularly relevant as is the first to assess lichen diversity from an ecosystem-level perspective. Together with useful information for implementing forest health bioindication studies, Mercado-Díaz et al. (2015) provided general descriptions for lichen communities present in eight major ecosystem types in the island. Lastly, recent work by Mercado-Díaz et

al. (2020) is the first to combine traditional taxonomic approaches with molecular methods to elucidate diversity patterns of a lichen group in the Caribbean. Focusing on the genus *Sticta*, researchers found that species assemblages in the island resulted from multiple colonization events. They also suggest that nearly 70 percent of the species (eight newly described in that work) are endemic to the island, further supporting the idea suggested in Mercado-Díaz et al. (2014) that endemism in the Caribbean islands is probably underestimated.

### Effects of Hurricane Disturbances on Lichens

Lichens are often seen as “hardy” organisms mostly because many species are present in some of the most hostile environments in the planet (e.g., Antarctica). However, like any other species, lichens found in these environments adapt over evolutionary time to the specific conditions found in those areas. In this sense, lichens are also “fragile” because minimal alterations to the natural conditions of the preferred habitats in which they evolved can have detrimental effects on populations and communities. Since lichens are an association between two compatible (but usually unrelated) species, a specific set of environmental conditions are typically required for these species to develop and sustain a new individual. Disturbances, both non-anthropogenic and anthropogenic, could therefore pose major threats to the health, growth and survival of many species (Matthes and Feige 1983; Gries 1996; Tripp et al. 2019).

Only a handful of studies mention hurricanes and cyclones as a potential factor influencing organismal and species diversity patterns in lichens. Some of these hypothesize that these disturbances might serve as long-distance dispersal agents allowing species to expand their geographical ranges (Smith et al. 1997; DeLange and Galloway; 2015; Mercado-Díaz et al. 2020). Hurricanes along the US Gulf Coast might help maintain gaps in the shrub canopy, thereby benefiting the endangered species *Cladonia perforata*, which requires an

open habitat structure to thrive (Yahr 2000). In contrast, a study evaluating hurricane effects on survival and re-sprouting of Florida rosemary (*Ceratiola ericoides*) in that same region, linked dense coverage of reindeer lichens (*Cladonia* sp.) with longer hurricane return intervals (Bertz and Brewer 2013). These authors suggested that these lichens might be swept away or buried by widespread storm surge due to hurricane-induced overwash. Similar observations were made by Allen and Lendemer (2016) on their study on the effects of sea-level rise in coastal lichen biodiversity in the Mid-Atlantic Coastal Plain. According to these authors, hurricanes can drive the migration of barrier islands, which contain maritime forests that support distinct lichen communities. They anticipate that failure of maritime forests to migrate at the same rate as the barrier islands could result in negative consequences to lichens and other unique organisms that distinguish this habitat type.

At least in the short term, hurricanes most likely affect lichen communities in Puerto Rican forests indirectly by reducing canopy cover and increasing mortality of host trees. These structural changes can stimulate significant temperature increases and cause reductions in humidity and moisture. They should also reduce available substrates for colonization and result in higher solar radiation reaching the forest floor. Responses from lichen communities will be inextricably linked to these factors, and other more direct effects such as physical removal from substrates due to wind abrasion, as they can trigger increases in mortality and affect growth and survival rates in all groups. For instance, expected responses from these changes include reductions in species richness, abundance and diversity. In the short term, these changes will likely be more pronounced on canopy communities as these will lose more individuals due to defoliation, debranching, and tree-felling. Changes in understory communities will probably be most linked to environmental and microclimatic alterations resulting from structural effects on forests. Consequently, these will most likely be detected months or even years after an event.

Effects at the ecosystem level are also expected. For instance, because there is a higher proportion of foliose and fruticose growth forms in the canopy (Forman 1975), higher losses in lichen biomass are likely to be more pronounced in that layer. Decreases in moisture and shade associated with hurricane passage over the forest are also detrimental to cyanobacterial species, which are known to potentially fix 1.5–8 kg of nitrogen per hectare per year in tropical forests (Forman 1975). Increased mortality associated with canopy changes could therefore diminish potential nutrient influx that might result from nitrogen fixation by cyanolichens.

## THE BRYOLOGICAL PERSPECTIVE

### Bryophyte Biology, Ecology, and Diversity Patterns

Bryophytes are distinct lineages of non-vascular plants that are closely related and include mosses, liverworts, and hornworts. As the group sister to the ancestor of the rest of land plants, bryophytes disperse by sexually produced spores and require water for reproduction. In bryophytes, as in all plants, two generations alternate to produce gametes (gametophyte) and to produce spores (sporophyte). The dominant photosynthetic and long-lived generation of a bryophyte is the gametophyte while the sporophyte is short-lived and dependent on the gametophyte (Figure 2A). Bryophytes are usually associated with humid environments but are found in a wide variety of substrates, in aquatic to terrestrial habitats, and from arctic to deserts. In these ecosystems, bryophytes play an important role in water storage, nutrient uptake from the rain, soil protection and succession, and provide habitats for animals and other plants (Frahm et al. 2003; Glime and Gradstein 2018).

Bryophyte species composition at a small geographical scale depends on the types of forests, microhabitats and substrates available, and the phylogenetic diversity of the region (Frahm et al. 2003). Elevation, annual

temperature, and humidity influence species richness in tropical forests (Frahm and Gradstein 1991; Vitt 1991). Other aspects of the landscape also influence the distribution and abundance of species such as forest interior to forest edge differences (Jiang et al. 2018) and distance from stream banks (Chinea et al. 1993). The principal drivers of epiphyte diversity in tropical forests with different land-uses are canopy cover, microclimate, and the characteristics of host trees such as bark structure and chemistry (Gradstein and Sporn 2010).

Global diversity of bryophytes is around 20,000 species making it the second-largest group of land plants. The most abundant are the mosses with an estimate of 12,700 species, followed by 6,000 to 8,000 liverwort species and 100 to 150 species of hornworts (Shaw 2009). Bryophyte species richness does not necessarily increase as latitude decreases, as observed for other organisms (Shaw 2009). Mosses are as diverse in tropical forests as in broadleaf, tundra, and boreal forest (Geffert et al. 2013). However, liverworts species richness is higher near the equator; it is hypothesized that tropical taxa have higher diversification rates than non-tropical taxa (Laenen et al. 2018). In fact, tropical America contains one-fourth of the total diversity of liverworts, with leafy liverworts being the most diverse, including the family Lejeuneaceae with hundreds of species (Gradstein et al. 2001). Hornworts are the least studied group of bryophytes and the one with fewer species. The highest diversity of species within this group are found in the tropics in India, Asia, and the Americas (Villarreal et al. 2010). In general, bryophyte species have a broader geographical range than flowering plants, probably due to their capacity for long distal dispersal (Patiño and Vanderpoorten 2018).

In Puerto Rico, bryophytes are represented with 526 species, in 217 genera and 69 families (Gradstein 1989; Sastre-D.J. and Buck 1993). Mosses and liverworts have the highest diversity with 284 and 237 species, respectively. Only five species of hornworts in 3 families are represented in the bryophyte flora of Puerto Rico. No endemic mosses are reported for Puerto Rico, and the



Figure 2. (A) *Philonotis* with sporophytes, five months after hurricane Maria near La Coca Falls, El Yunque National Forest (EYNF). (B) *Pogonatum* with sporophytes growing on exposed soil from a landslide, Trade Winds Trail at EYNF. (C) The liverwort *Plagiochila* growing among grasses in the understory at EYNF. (D) Patches of “burned” or decolored moss in a branch of a tree a year after the hurricane, Cienagás Las Cucharillas, Cataño, northern Puerto Rico. (E) Possible remains of *Thuidium* on a rock in a stream at El Verde Field Station, EYNF, two years after the hurricane. s = sporophyte; g = gametophyte.

number of endemic liverwort and hornworts is unknown (Sastre-D.J. and Santiago-Valentín 1996a). Considering that few phylogenetic studies include specimens from Puerto Rico and the Caribbean, the number of endemic and cryptic species might be higher.

### Bryological Studies in Puerto Rico

The bryophyte flora of Puerto Rico has been extensively studied. Early explorations by Europeans and US Americans described new species and records of bryophytes to the island (Pagán 1939; Crum and Steere 1957). Checklists and species descriptions were done

separately for mosses but combined for liverworts and hornworts. New York Botanical Garden scientists led surveys that included collections of bryophytes by Elizabeth Britton, a recognized bryologist and first female scientist to conduct research in the Luquillo Mountains and throughout Puerto Rico, and her husband, Nathaniel Britton (Sastre-D.J. and Santiago-Valentín 1996a,b). During this period Alexander W. Evans published the “Hepaticae of Puerto Rico” describing the Lejeuneaceae (Evans 1902–1912). In the 1930-40s the first Puerto Rican bryologist, Francisco M. Pagán, published a list of liverworts and hornworts of Puerto Rico that included the collections of A. W. Evans. Pagán

also described a new species of hornwort for Puerto Rico (Pagán 1942). The preliminary list reported 244 species of liverworts, including eight hornworts, and expanded the localities previously reported and added new records for the island (Pagán 1939). For mosses, the number of species increased with the publication of “The mosses of Porto Rico and the Virgin Islands” by Howard Crum and William C. Steere (Crum and Steere 1957). These authors reported 268 species of mosses, with 11 new species and provided the first comprehensive treatment of the mosses of Puerto Rico with keys and descriptions. Pagán was working on a similar treatment for the liverworts but was not completed because of his passing (Steere 1942).

Bryological work continued in the 1970s with studies of the liverworts (Fulford et al. 1970, 1971) and epiphytic mosses (Russell and Miller 1977) of the elfin forest in Luquillo Experimental Forest/El Yunque, and the development of a guide to the genera of the mosses of Puerto Rico (Miller and Russell 1975). Ecological studies and inventories in the Luquillo Experimental Forest included bryophytes, such as the irradiation experiments (Steere 1970), the flora of Bisley (Chinaea et al. 1993) and the nutrient content and biomass of bryophyte communities on wooden posts (Frangi and Lugo 1992). Studies of moss taxonomy and biogeography of the Caribbean by William Buck in the 1980s were important for creating the checklist of mosses of Puerto Rico (Sastre-D.J. and Buck 1993), the key for Pleurocarpous Mosses of the West Indies (Buck 1998), and motivated more bryological work in the island. A period of high bryological activity started in the late 1980s until recently; as Puerto Rican bryologist Inés Sastre-De Jesús began collecting, identifying and developing projects that included ecology, restoration, genetics, morphology and taxonomy of bryophytes, primarily of mosses. In addition, I. Sastre-De Jesús mentored students from Puerto Rico and Latin America, who were involved in projects that contributed to our understanding of the flora of Puerto Rico and the Caribbean. She invited bryologists from around the world to give

workshops and develop materials for identification of species on the island. A result of one of those collaborations is the key for the liverworts and hornworts of Puerto Rico published by Gradstein (1989) that included 237 species and is the most recent guide available for this group in Puerto Rico.

Floristic inventories of protected and non-protected forests around the island, have increased the number of species documented in these areas but did not significantly increase in the number of species for Puerto Rico (Reyes-Colón and Sastre-DJ 1998, 2000; Galva et al. 2008; Pérez and Sastre-De Jesús 2009; Pérez et al. 2012). Many species are only known from the original collections, and about 12 percent of the mosses listed to the island are now extinct. By the beginning of the 20th century, island-wide deforestation peaked, and most-likely caused the extinction of these species (Sastre-D.J. and Tan 1995).

### **Effects of Hurricane Disturbances on Bryophytes**

Disturbances such as hurricanes likely affect bryophyte communities by modifying or eliminating their microhabitats. Bryophytes are susceptible to changes in humidity, light intensity, and temperature (Glime and Gradstein 2018); all of these environmental factors can dramatically change after a hurricane. Bryophytes are tolerant to desiccation, but the degree, duration, and frequency of hydration/dehydration will have an effect on their recovery. When bryophytes dry and rehydrate, carbon and nitrogen are released to the surroundings. Plants adapted to dry environments are expected to experience less cellular injury and less nutrient loss than those of mesic or wet places (Slate et al. 2019). Higher resistance to desiccation occurs in tropical forests with low humidity and species in the canopy are more resistant to drying than those of the understory and can retain their photosynthetic capacity after longer periods of low humidity (Pardow and Lakatos 2013; Glime and Gradstein 2018). An increase in light intensity and

temperature also affect bryophytes, changes in coloration are noted with higher solar radiation, and with an increase of temperature above 25 °C, net productivity decreases (Glime and Gradstein 2018). This suggests that changes in canopy opening after a hurricane, can alter the microenvironmental conditions and potentially increase the frequency of hydration/dehydration cycles, thus affecting bryophytes' physiology.

Not many studies address the effects of hurricanes or storms to the bryophyte flora of the tropics. The strong winds of Hurricane Hugo's removed bryophytes from trees, but parts remaining from the surviving patches were left on the trees and probably facilitated recolonization and new growth (Glime 2019). A fertilization experiment to measure the effects on the vegetation of the influx of nutrients expected from leaf-litter and debris after Hurricane Hugo found that bryophyte biomass decreased three-fold after adding fertilizer every three months for three years (Walker et al. 1996). Bryophytes were measured only in one of the sites, Pico del Este, where *Sphagnum* is a major component of the terrestrial bryophytes, although *Marchantia*, *Philonotis*, and *Fossombronia* are also common. The decline in biomass is not surprising because bryophytes are sensitive to high levels of nutrients and can be outcompeted by vascular plants in those conditions (Glime 2017a).

A study describing the effect of hurricane Georges to the cryptogram flora of Toro Negro Commonwealth Forest found that effects to terrestrial plants (mostly ferns) were lower than to epiphytes (i.e., bryophytes and ferns; Rosado 2000). Visible hurricane effects to mosses and liverworts include yellowing (chlorosis), changes in color was evident in 9 (of 39) genera of liverworts and 6 (of 30) genera of mosses; while drying and reduction in plant size or abundance was found in one genus of liverwort and three genera of mosses. Death of individual plants was recorded for three genera of liverworts and one genus of moss, but the effects were not the same in all sites, and not all genera had the same responses. Before the hurricane, the most abundant and diverse groups were leafy liverworts from the Lejeuneaceae

and Plagiochilaceae, and mosses in the families Pilotrichaceae and Sematophyllaceae. After the hurricane, some genera remained abundant such as liverworts of the genus *Plagiochila* and the mosses *Leucoloma* and *Lepyrodontopsis*. In contrast, taxa with more visible effects were thallose liverworts Aneureaceae and Metzgeriaceae, and leafy liverworts in the Lejeuneaceae. Rosado (2000) speculated that mosses appear to be more tolerant to hurricanes than liverworts and that most of the effects occurred to the microhabitats. A study from Honduras found that bryophyte cover was significantly lower in trees located in areas more affected by hurricanes, years after the hurricanes (Batke and Kelly 2015). From these studies, we can hypothesize that hurricanes can reduce species richness and abundance at a small scale, such as in a specific microhabitat or phorophyte and not necessarily at a larger scale or forest area and that effects of hurricane disturbance on bryophyte communities can be long-lasting.

## LESSONS FROM OTHER EPIPHYTES

Many lichens and bryophytes are epiphytes; organisms that grow on other plants. Epiphytes in tropical forests also include bromeliads, orchids, species within the family Araceae, and ferns (Batke and Kelly 2015). Responses of other epiphytes to hurricanes can reasonably be extrapolated to lichens and bryophytes because life-history strategies among these groups are similar. One aspect to consider is the endurance of epiphytes to remain attached to their host tree. A study on the effects of Hurricane Hugo on the epiphytic orchid *Comparettia falcata* in Toro Negro found that about 70 percent of the plants had no meaningful damage (the rest of the individuals were detached from their host tree) and that less than 10 percent of the phorophytes were destroyed (Rodríguez-Robles et al. 1990). A recent inventory found that over 600 plants of the miniature orchid *Lepanthes eltoroensis* survived after Hurricane María, half of which were already recorded, and the rest were new records (Endangered and Threatened Wildlife and



Figure 3. Views of a rainforest understory in El Verde Field Station, El Yunque National Forest (EYNF), northeastern Puerto Rico, before (A) and after (B) hurricanes Irma and Maria.

Plants 2020). Most of the effects to populations were due to loss or host trees being knockdown; 30 percent of the individuals were still attached to fallen trees. These studies show that while hurricane winds can detach epiphytes from their hosts and destroy phorophytes, their effects are likely transient. The level of damage to the epiphytic community is contingent on the level of structural effects on the host tree and changes in the microenvironment. Many epiphytes can be observed growing with patches of lichens and bryophytes. After hurricanes, bryophyte cover and branch surface area influence epiphyte composition and diversity among tree branches (Batke and Kelly 2015). It is evident that bryophytes and lichens are important components of epiphytic communities and are key for the establishment and recolonization of other epiphytes. More studies will be needed to understand the scope of these interactions fully.

### POTENTIAL EFFECTS OF HURRICANES IRMA AND MARÍA TO BRYOPHYTE AND LICHEN COMMUNITIES

Very few studies document the effects of hurricanes on bryophytes and lichens. Furthermore, it is difficult to generalize or predict effects to lichens and

bryophytes based on those studies because hurricane effects on vegetation vary by location (exposure) in the landscape and by hurricane strength (López-Marrero et al. 2019). While lichens and bryophytes differ in many aspects of their organismal biology, both groups share similar habitats and growth forms and rely on similar ecological and physiological strategies to disperse, reproduce, and survive, hinting that responses to hurricanes might be similar. We have visited on a regular basis several natural protected areas of Puerto Rico after hurricanes María and Irma with the goal of determining how these events affected lichen and bryophyte floras and assessing similarities/differences in responses (Figure 3). The main attributes of these communities were well understood as these areas had been visited numerous times before these events. This allows us to hypothesize how large-scale effects of hurricanes might influence survival, growth, and reproduction of bryophytes and lichens in our forests.

### Ecological and Organismal Responses

High short-term mortality of individuals in both canopy and understory communities was likely the main response of lichens and bryophytes to hurricane disturbance. Populations of canopy species seem to

have been diminished as a result of major debranching, defoliation, and wind abrasion caused by hurricane winds. Understory populations, particularly those of ground-dwelling species, were consequently affected as many were buried under the large quantities of leaf litter and other organic debris that covered the forest floor. Spatial data from G-LiHT (Goddard's Lidar, Hyperspectral and Thermal Imager) estimated that about 40 to 60 percent of the trees in forests of the island were snapped or uprooted by these events, and the average canopy height of the Luquillo Experimental Forest/El Yunque National Forest (EYNF) was reduced by one third (NASA/Goddard Space Flight Center 2018). The visible effects caused by Hurricane María exceeded those of other hurricanes in recent years. At one experimental area in El Verde Field Station/Luquillo Experimental Forest, Uriarte et al. (2019) reported that twice as many trees died during Hurricane María compared to hurricane Hugo, while breaking of branches and

stems was on average tripled and uprooting of trees was widespread. Defoliation and canopy cover loss, which were exacerbated in higher elevations, were among the most visible and immediate effects that Hurricane María had on our forests (Munroe et al. 2018).

Three types of phenotypic responses, which are most likely linked to environmental changes induced by these hurricanes, were seen in several lichen groups after these events. The first is known as chorophyll bleaching (Gauslaa and Solhaug 1996). Bleaching manifests as a general whitening of the thallus and can have detrimental effects on individuals as it occurs after photosynthesis is severely inhibited by light stress (Gauslaa and Solhaug 1996). This response to light stress most likely occurred in green algal species such as *Chapsa thallorema* (Figure 4A) and *Coenogonium lepreurii* (Figure 4B). The second response could be termed "spotting". A thallus affected by spotting is easily distinguishable as it has discrete, white-to-beige



Figure 4. Presumed phenotypic responses of lichens to effects caused by environmental changes induced by hurricanes. (A) Signs of "bleaching" in the thallus of the otherwise dark-green species *Chapsa thallorema*, El Verde Field Station, El Yunque National Forest (EYNF). (B) An individual of *Coenogonium lepreurii* (a normally bright-green filamentous species) affected by "bleaching", El Verde Field Station, EYNF. (C) Individuals of *Sticta densiphyllidiata* from El Verde Field Station, EYNF and (D) Mt. Britton trail, EYNF, showing signs of "spotting" effects.

colored patches that appear to lack photobiont cells. This type of effect has so far been detected in *Sticta densiphyllidiata* (Figure 4C, D), but presence in green algal species and other cyanobacterial species is also likely. The third type of response is a general browning of the thallus, which is likely caused by the deposition of melanin in the outer layer of the upper cortex in light-stressed lichens (Gauslaa and Solhaug 2001). Browning has been recently seen in individuals from scattered populations of the newly described endemic species *Sticta tainorum* (Mercado-Díaz et al. 2020). Similar to our observations, these authors suggest that browning is likely a result of hurricane defoliation and concomitant increases in solar radiation. We suspect that damage from bleaching, spotting and browning may lead to long-term detrimental effects on populations of susceptible species. Additional studies are needed to understand causal links between hurricane-induced environmental conditions and these physiological responses.

Dead or dry mosses and liverworts was a recurrent observation from visitors to the forest after Hurricane María. In contrast to other plants, most bryophytes can withstand long periods of drying. When water is available, bryophytes will be physiologically active and photosynthesizing, and when the humidity of the atmosphere drops, they will dry and become dormant. However, drying combined with a rapid increase in temperatures and sunlight intensity resulting from canopy loss would increase the stress to the plants, thus reducing their survival (Glime and Gradstein 2018; Pardow and Lakatos 2013). In this novel environment, we can expect bryophytes to dry more frequently, for which they may not be adapted to, than in the previous humid forest. This could explain why parts of bryophyte patches were ‘burned’ after the hurricane and other parts survived (Figure 2D). Although sunlight exposure increased after Hurricane María, bryophytes of open areas such as *Philonotis* and *Plagiochila* seem to be unaffected and continued to grow and reproduce (Figure 2A,C).

## Responses to Changes in the Landscape and Effects on Riparian Communities

Landslides, which are largely caused by heavy rainfall during hurricane events, can dramatically change the landscape and result in significant modification of the habitat of many species. The highest density of landslides after Hurricane María was reported in the central mountain region (Bessette-Kirton et al. 2017), which has a high diversity of lichen and bryophyte species. Massive movement of rocks and soils associated with these events affected lichen- and bryophyte-covered areas and triggered reductions in populations from both groups. Paradoxically, landslides are likely important for the persistence of many species in these ecosystems. For bryophytes, bare areas resulting from landslides will eventually be colonized by groups like *Pogonatum* (Figure 2B) or members of the Pottiaceae, both of which have species that can be considered ruderal or early colonizers. Soil propagule banks can facilitate recolonization of disturbed or bare areas for a fraction of the mosses, particularly for acrocarpous mosses (Pasiche-Lisboa and Sastre-De Jesús 2014). Landslides are believed to be important for the persistence of many lichen species, including the genus *Stereocaulon*, which is found almost exclusively in roadcuts and areas where bare soil have been recently exposed (Walker and Shiels 2012; Mercado-Díaz et al. 2015). Heavy rainfall associated with hurricanes could also have affected lichen and bryophyte communities in riparian zones. Large amounts of water entering rivers at high speeds can detach individuals from rock surfaces and affect species inhabiting those areas (Figure 2D). Fortunately, some bryophytes can remain alive underwater for periods of time and resume growth if at least parts of individuals remain attached to rocks (Glime 2017b). For instance, medium to large patches of *Thuidium* persisted on rocks in the forest understory and in riparian zones of the El Verde Field Station in the Luquillo Experimental Forest/El Yunque National Forest two years after

Hurricane María. In this moss, changes in coloration from light green to brown orange were observed in plants under different light conditions. In contrast, many lichens in riparian zones (excluding those in surrounding vegetation) are endolithic and cannot be detached from rock surfaces by moving water. For these lichens, mortality will mostly be associated with individuals growing on rocks that could have been turned upside down during a flood event.

### **Responses by Forests Types and Modifications in Forest Structure and Composition**

The effects of hurricanes Irma and María on lichen and bryophyte communities were potentially variable within and among different forest types. High elevation forests, which host a high diversity of lichens and bryophytes (Sastre-D.J. and Buck 1993; Mercado-Díaz et al. 2015), were more affected as hurricane winds were generally stronger in these areas (Munroe et al. 2018). We have noted that in general, many species in both groups are able to recolonize and reestablish, suggesting they are likely adapted to these changes. Mercado-Díaz et al. (2020) suggested that *Sticta harrisii*, a relatively uncommon species in Luquillo Experimental Forest/El Yunque National Forest before 2017, might have increased in cover after these two hurricanes. Unfortunately, communities in other forests might face higher threats, particularly because hurricane effects are exacerbated by other types of disturbances. For example, conversion to agricultural, urban or industrial land uses has, and is still reducing the habitat available for lichen and bryophytes species in lowland forests, which host diverse species assemblages in both groups (Perez and Sastre De-Jesus 2009; Perez et al. 2012; Mercado-Díaz et al. 2015). The effects of land-use history on tree species composition remain evident after hurricanes and influence the recovery of the forests (Zimmerman et al. 1995; Lugo 2008). Effects from compounded

pressures from these disturbances will pose major challenges to already vulnerable elements in these communities, such as species with heightened risks of extinction that might exist in these forests.

The recovery and recolonization of bryophyte and lichen communities will also be linked to hurricane-induced changes in tree composition. Species like Palma de sierra (*Prestoea montana* syn. with *P. acuminata*), Yagrumo hembra (*Cecropia schreberiana*) and shrub species will be major woody components of the open-canopy vegetation during the first few years in high elevation forests (Heartsill-Scalley et al. 2010; Weaver 2013). These plants grow relatively fast but have straight stems and relatively homogeneous barks which would support less diversity of bryophytes (although possibly a higher diversity of lichens [Rosabal et al. 2013]). In addition, many bryophytes and lichens might be outcompeted due to the inevitable arrival of fast-growing herbs and vines. These species will temporarily displace the local flora but will eventually be replaced by bryophytes, lichens, and other native plants as the composition of the forest changes and the cover of the canopy increases.

### **Responses as a Function of Hurricane Frequency and Intensity**

The effects of hurricanes on lichen and bryophyte communities will ultimately depend on hurricane frequency and intensity. More frequent and severe storms will certainly alter forest species composition and the size assemblage of trees (Uriarte et al. 2018), and therefore the habitats in which lichens and bryophytes thrive. Yet, positive feedbacks on species richness and diversity at local scales could also be expected and will likely be maximized when these events are moderate in strength and frequency. For example, a high diversity of Cladoniaceae that has been noted in Laguna Tortuguero is likely explained by frequent canopy openings that are characteristic of this coastal scrub habitat and are possibly maintained by periodic hurricanes. Similar to

what has been observed for *Cladonia perforata* (Yahr 2000), maintenance of these openings might be critical for the survival of *Cladonia robusta*, a potentially endangered species that is endemic to this habitat. In the cloud forest, *Sphagnum portoricense* is abundant near trails and open disturbed areas, environmental modifications caused by hurricanes probably provide opportunities for this moss to expand its range and colonize new areas (Karlin 2006). Unfortunately, empirical data from lichen and bryophyte communities to test these ideas are lacking; therefore they should be taken as working hypotheses.

Work on the effects of hurricane disturbances on tropical tree species diversity has shown that beyond the frequency and magnitude of disturbances, the intensity in the spatial extent of damage is an important force driving patterns of species richness (Vandermeer et al. 2000). This observation hints that responses from lichen and bryophyte communities will vary depending on the spatial scale they are being analyzed. Thus, spatially explicit approaches to evaluate potential impacts will ultimately be needed to efficiently interpret and understand how responses relate to the frequency and intensity of these events.

## CONCLUSION

In this work, we synthesized general biological and ecological aspects of lichens and bryophytes in tropical forest ecosystems, briefly reviewed key bryological and lichenological literature from Puerto Rico and provided insights about potential effects of hurricanes, particularly hurricanes Irma and María, on lichens and bryophytes from the island. The dearth of literature about the effect of this type of disturbances in these organisms was evident but was more pronounced in lichens. Considering the high levels of endemism documented in lichens (Mercado-Díaz et al. 2014,2020), this scarcity of studies is troubling, and more studies are sorely needed to understand better short- and long-term effects of hurricanes in these organisms.

Because lichens and bryophytes are present in all forest types of the island, their abundance and diversity can serve as indicators of ecological continuity and forest health (Frego 2007; Rivas-Plata et al. 2008). We understand forest health as the production of current and future sustainable forest conditions, considering the interplay between human needs and the ability of ecosystems to persist, recur, and be resilient to disturbances. Useful guidelines on how to carry out studies of this type and evaluate forest health using lichen communities from the island are provided in Mercado-Díaz et al. 2015. Similar tools for bryophytes are currently being developed by the second author and are certainly an exciting avenue for future research.

Other areas of research also remain understudied with respect to the effects of hurricanes on lichen and bryophyte communities. Some important questions that should be investigated include: 1) What are the short-term physical and physiological changes, and phenotypic responses that occur to bryophytes and lichens after a hurricane? 2) How do species richness, abundance, and diversity change in the short- and long-term at the local and regional scales? 3) How does community succession operate in the new, modified microhabitats? 4) How hurricane effects on lichens and bryophytes affect ecosystem dynamics in terms of biomass, nutrient, and water cycles? 5) How do hurricanes alter between/within-species relationships of organisms that interact at the bryophyte/lichen community scale? 6) Are hurricanes important drivers of species diversity dynamics in lichens and bryophytes in these forests? The inclusion of lichens and bryophytes in after-hurricane surveys and long-term projects will give us a better understanding of the recovery process of the forest and of the organisms that depend on them.

The future of lichen and bryophyte communities will be further hindered by changes occurring at global scales, such as climate change. The intensity of hurricanes and tropical storms in the Atlantic has incremented since the 1970s (Mann and Emanuel 2006).

This increase is due to both longer and more intense storms and has been linked to rising sea surface temperatures in the Atlantic (Mann and Emanuel 2006; Lugo 2008). It remains to be seen how these changes will affect survival and subsistence of lichen and bryophyte communities on the island. Likewise, as in many tropical countries, biodiversity loss in Puerto Rico is strongly linked to changes in land-use and habitat fragmentation. We can hypothesize that in conjunction with frequent hurricane disturbances, anthropogenic-induced changes will also lead to further reductions in available habitats, and consequently, to potential losses in lichen and bryophyte species. Increased conservation efforts and accumulated knowledge on lichens and bryophytes will certainly play a critical role in buffering these effects. However, societal and political willingness will ultimately determine how effective we will be in addressing these pressing issues.

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# ENVIRONMENTAL CORRELATES OF LEAF STRESS SYMPTOMS IN THE MICRO-ORCHID *Lepanthes woodburyana* FOLLOWING HURRICANE MARÍA

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## Abstract

Cloud forest species face many threats including, but not limited to, climate change and increased extreme weather events. On September 20th, 2017, Hurricane María hit the island of Puerto Rico, changing the amount of coverage, structure, and microclimate of its forests. Cloud forest epiphytes can be particularly susceptible to such dramatic changes. Following Hurricane María, we studied the leaf characteristics potentially associated with reduced leaf health in the *Lepanthes woodburyana*, an epiphytic micro-orchid, endemic to Puerto Rico. We specifically assessed whether the environmental (e.g., microclimate, percent canopy cover, elevation) and biological factors intrinsic to the plant (e.g., plant size, life stage) were associated with variation in percent canopy cover, the number and the probability of occurrence of dark spots and discoloration on the leaves of *L. woodburyana*. We expected to find negative associations between variables related to plants that had dark spots and discoloration with forest cover and humidity, and positive associations between the occurrence of dark spots with plant size and temperature. Our results showed that dark spot formation was more frequent at lower elevations, open canopies and high temperatures, suggesting plant stress symptoms associated to canopy changes following hurricane events are not homogeneous throughout the forest.

**Keywords** *Lepanthes woodburyana*, dark spots, stress, leaf symptoms, climate change.

## Resumen

Las especies de bosques nublados se enfrentan a muchas amenazas, incluyendo, pero no limitándose a, el cambio climático y el aumento de los fenómenos meteorológicos extremos. El 20 de septiembre de 2017, el Huracán María azotó la isla de Puerto Rico, cambiando la cantidad de cobertura, estructura y el microclima de sus bosques. Las epífitas de los bosques nubosos pueden ser particularmente susceptibles a cambios tan dramáticos. Después del huracán María, estudiamos las características de las hojas potencialmente asociadas con la reducción de la salud foliar en el *Lepanthes woodburyana*, una microorquídea epífita, endémica de Puerto Rico. Evaluamos específicamente si los factores ambientales (microclima, cobertura porcentual del dosel, elevación) y biológicos intrínsecos a la planta (tamaño de la planta, etapa de vida) se asociaron con la variación en el número y la probabilidad de aparición de manchas oscuras y decoloración en las hojas de *L. woodburyana*. Esperábamos encontrar asociaciones negativas entre variables relacionadas con plantas que tenían manchas oscuras y decoloración con cobertura de dosel y humedad forestal, y asociaciones positivas entre la ocurrencia de manchas oscuras con el tamaño de la planta y la temperatura. Nuestros resultados mostraron que la formación

de manchas oscuras era más frecuente en elevaciones más bajas, doseles abiertos y altas temperaturas, lo que sugiere que las repuestas de estrés asociadas a cambios en el dosel luego de un huracán no son homogéneas a través del bosque.

**Palabras clave** *Lepanthes woodburyana*, manchas oscuras, estrés, cambio climático.

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## INTRODUCTION

Cloud forest ecosystems are typically covered by low clouds or mist where the influence of temperature and humidity is significant (Peh et al. 2011). They generally occur at altitudes of 1,200 meters on coastal and isolated ridges or on mountain summits at higher elevations where cloud formation is frequent (Brujinzeel et al. 1993). Global climate change models predict that these ecosystems (and species that inhabit these) will be negatively affected by climate change, given their unique environmental characteristics (Foster 2001; Nadkarni and Solano 2002). As a functional group, epiphytes exhibit high diversity and abundance in tropical cloud forests and play an important role in the light, hydrological and nutrient cycles of these ecosystems (Foster 2001; Giambelluca and Loope 1998; Still et al. 1999).

In the case of elfin cloud forests, epiphyte biomass constitutes less than 2% of its total dry weight, but the nutrients they contain are equivalent to up to 45% of the total nutrients contained in ecosystem foliage (Nadkarni 1984). They also act as capacitors in regulating the seasonal release of precipitation, thereby providing flood and erosion control in the rainy season and water storage in the dry season (Still et al. 1999). Evaluating the responses of epiphytes following changes in forest structure and condition may prove valuable in determining how epiphytic taxa can be managed within the context of environmental change. From a conservation perspective, it is also important to understand how species living in these systems may respond to environmental change.

The Caribbean region has been experiencing changes in weather patterns that may threaten the persistence of epiphyte species adapted to cloud forests

and endemic to the regions. Changes in the global hydrologic cycle and temperatures can influence hurricane formation (Dale et al. 2001). Current trends of increasing temperatures are expected to continue and to lead to increases in the frequency and intensity of hurricanes over time (Jennings et al. 2014). Hurricanes represent disturbances that can influence population dynamics in plants, altering their survival, growth, and reproduction, therefore defining their demography in the medium to long term (Tanner et al. 2014). These events can alter canopy structure significantly by defoliating many trees and can change the micro-environment, increasing light exposure and temperature and reducing relative humidity within Caribbean forests (Lugo 2008). These abiotic changes could, in turn, have direct and indirect effects on epiphytes.

Epiphyte loss following hurricane-driven changes in microclimate could occur due to dryness and low water availability, substrate damage, not enough bryophyte cover and changes in microclimate (Crain 2012; Jennings et al. 2014; Olaya-Arenas et al. 2011). Understory epiphytes that suffer drastic changes in light conditions after the opening of canopies may undergo photoinhibition (Le Gouallec et al. 1990). However, among the many abiotic factors involved in the survival of epiphytes, humidity is probably the main short-term limiting factor (Stancato et al. 2001).

Changes in leaf pigmentation can be an indication of changes in plant health, with chlorotic or discolored leaves indicating some level of plant stress. Low temperatures may lead to many symptoms of stress, such as leaf-yellowing, defoliation, or a reduced rate of growth (Zhang et al. 2018). With too much light, foliage may become yellowish-green or red, and sunburns can produce scorched blotches on leaves or overall yellowing of



Figure 1. A composite of pictures showing revealing the extent of changes in the vegetation at El Toro Trail on 6 March 2018, approximately six months after Hurricane María struck the island of Puerto Rico. Photographs kindly provided by Jonathan A. López.

the plant (Missouri Botanical Garden, n. d.). Reddish purplish pigmentation can be a sign of high light intensity or overheating, a sign of stress (Bottom 2017).

On September 20th, 2017 Hurricane María struck the island of Puerto Rico substantially reducing forest cover and changing forest structure across the island. A post-Hurricane María assessment using remote sensing techniques suggests that Puerto Rico suffered massive defoliation and estimates that 23–31 million trees may have died on the island (Feng et al. 2018). We expected epiphytic species in high elevation areas such as cloud forests to be particularly affected by these changes. This study evaluated indicators of plant stress in the micro-orchid *Lepanthes woodburyana*, an epiphytic understory species focusing on a population located at the Luquillo Experimental Forest, also known as El Yunque National Forest, within cloud forest habitat. This work addressed if environmental factors (e.g., light exposure, canopy cover, air temperature) were associated with variation in the probability of occurrence of dark spots, and discoloration on leaves of *L. woodburyana*. After Hurricane María, we observed plants

to have leaves with dark spots and some even appeared burned. If these were symptoms of plant stress, we expected a negative association between their presence and frequency with abiotic factors such as low light exposure and high canopy cover and air temperatures.

## METHODS

### Study Site

This study was conducted at the El Toro Trail (18.281159° N, -65.858139° W), within the Luquillo Experimental Forest (El Yunque National Forest). The El Toro trail extends from 370 to 1,074 m above sea level (asl) and is located in an area classified as wilderness area since 2005 (Weaver 2011). This trail contains four forest types: lower montane rain forest between 150 and 600 m asl, palm breaks above 450 m asl, montane rain forest between 600 and 900 m asl, and most importantly, cloud forest above 900 m asl (Tremblay and Castro 2009; Weaver 2011). This habitat is found near ridges, at the upper edges of the Sierra Palm and Palo Colorado forests.

A characteristic of the habitat within the trail is that trees tend to be small or stunted and have an epiphyte laden vegetation (Weaver 2011). The canopy surrounding the El Toro Trail opened considerably following hurricanes Irma and María in 2017 (Figure 1).

## Study Species

*Lepanthes woodburyana* Stimson is a small epiphytic orchid, and the most common and widespread *Lepanthes* species in Puerto Rico (Stimson 1969) (Figure 2). It is infrequently pollinated and has a low frequency of fruit set (Ackerman and Castillo 1992). The flower has a peculiar mushroom-shape of the middle lobe of the lip, a distinctive feature from any of the other Puerto Rican *Lepanthes* (Stimson 1969). It flowers all year long and flowers last approximately 6–8 days (Ackerman and Castillo 1992; Tremblay et al. 2006). This plant is generally found at mid to high elevations in the wet forests of Luquillo, Sierra de Cayey and Cordillera Central of Puerto Rico and can also be seen at the El Toro Negro Forest (Ackerman and Castillo 1992; Tremblay and Salguero-Farías 2001). In *Lepanthes*, adult plants can be recognized by the presence of an inflorescence which may be active or dry, while juvenile plants show no evidence of reproductive activity and can be distinguished from seedlings by the presence of a lepanthiform sheath (Tremblay and Hutchings 2002).

## Study Design

Our data were collected from November 2018 to March 2019. We took advantage of ongoing work with *Lepanthes eltoroensis* by the University of Puerto Rico, which had georeferenced hosts that also had *L. woodburyana* plants ( $n = 15$  hosts). For each host, *L. woodburyana* plants were counted and classified according to their demographic stage (adults, juveniles, and seedling). For each plant, we recorded its height above ground (m) within the host tree, its angular direction using a compass, its leaf size, the number of leaves, and,

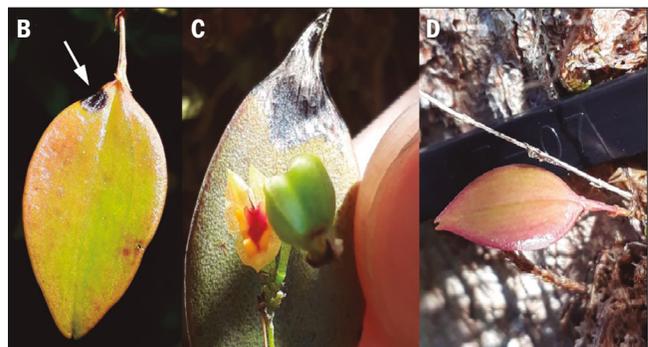
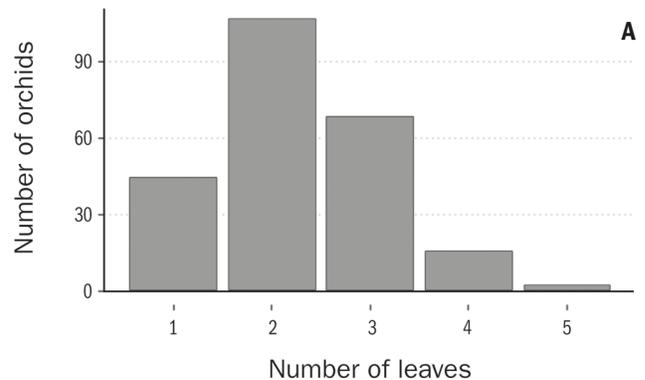


Figure 2. (A) Frequency distribution of the number of leaves per individual of *Lepanthes woodburyana*, and (B) a juvenile with chlorotic leaf and a dark spot (white arrow); (C) a reproductively-mature adult with a leaf tip burned; (D) a juvenile with discolored leaf compared to that in (B) (also see main text).

if they were reproductive, we recorded the number of flowers and fruits. Each plant was also checked for dark spots and discoloration, and the number of leaves showing those signs was recorded. Plants were classified as “healthy” if leaves were green and “damaged” if otherwise, leaves showed dark spots or else were discolored. For each plant, we also recorded the proportion of leaves with spots and the proportion of unhealthy colored leaves. Several environmental variables associated with each host plant were evaluated using complementary methodologies. Monthly temperature (minimum, maximum, and mean) and relative humidity (minimum, maximum, and mean) were extracted from 21 HOBO® sensors, located at three different elevations. At each tree, we took four measurements of percent canopy cover with a densitometer next to the tree trunk and positioned at 1.37 m from the ground, with each measurement taken at four cardinal points.

## Statistical Analyses

Descriptive statistics were developed for all biological and environmental variables measured. We tested for associations among variables using correlations analyses. We conducted binomial logistic regression analyses to evaluate variable association to three categorical variables that indicate symptoms. These variables were (1) the presence of dark spots, (2) the presence of unhealthy coloring, (3) and the variable “presence of stressed leaves”, which refers to any sign of leaf stress regardless of the symptom. All dependent variables were treated as categorical and coded as “1” when the condition was present and as “0” when the condition was absent.

We conducted binomial logistic regression analyses to evaluate factors associated with each categorical variable. For these analyses, we followed the guidelines in the “*Introduction to Statistical Learning with Applications*” (ISRL) in R by James et al. (2017). These analyses included the following independent variables: temperature, canopy cover, relative humidity, azimuth, area (i.e., clusters of plants that were grouped), height (plant distance above the ground), host tree elevation, life-history stage, and the number of leaves of each orchid. Seedlings did not show spots, therefore for the analysis evaluating drivers of the presence of dark spots, life-history stage, originally a trinomial variable, was included into the model as binomial by pooling “seedlings” and “juveniles” into one category (i.e., young plants). This was done as it was detected that including the seedling stage led to inflation of estimates which often occurs from having sample sizes and rare events (Mansournia et al. 2017). All other analyses were run with life stage as a categorical variable with three classes. For each dependent variable, we explored many regression models and the best model was selected based on the lowest “Akaike’s Information Criterion” (AIC) among models (i.e., the one which explained most of the variation with the minimum number of parameters; the best models for consideration are those with the lowest AIC). We

examined between 34 and 37 models per dependent variable (as an example, see Appendix 1 for a summary of the process of model selection for the dependent variable “presence of spots”). Kendall’s ( $\tau$ ) correlations were used to evaluate how well environmental and plant-host related factors related to the proportion of leaves with dark spots and the proportion of unhealthy colored leaves. The incidence of reproductive adults with and without spots was below our statistical ability to test for relationships between plant reproductive activity and plant stress. Therefore, these relationships were not evaluated. We used the “*circular*” package for R to do circular statistics to determine the mean angle for plant location (i.e., azimuth in degrees) around the tree trunk, and to conduct the Rayleigh test of uniformity (Notar and Thomas 2018) to examine if plants are randomly distributed around the host tree. All analyses were done in R (R Core Team 2013).

## RESULTS

We sampled 240 individuals across those 15 hosts. Of these, 11.7% were reproductive adults (A1), 6.3% were non-reproductive adults (A0), 58.8% were juvenile (J), and 23.3% were seedlings (S). In general, plants had between one and five leaves with most plants having two leaves (Figure 2A). Also, we found symptoms like dark spots, unhealthy and discolored leaves in *Lepanthes woodburyana* (Figure 2B-D). Out of 240 individuals, 14.6% of the individuals had dark spots (Figure 3A), 29.2% had discolored leaves (Figure 3B), and 5% had both symptoms (not shown), but in general, plants showing some form of damage on their leaves was 38.8% (Figure 3C). However, plants found without these symptoms were not assessed as “healthy” as other responses attributed to stress could exist and were not apparent to plain sight. Finally, plants did not show a significant angular direction in terms of their location around the tree trunk (Figure 4).

Binomial logistic regression analyses for the presence of spots showed significant negative associations

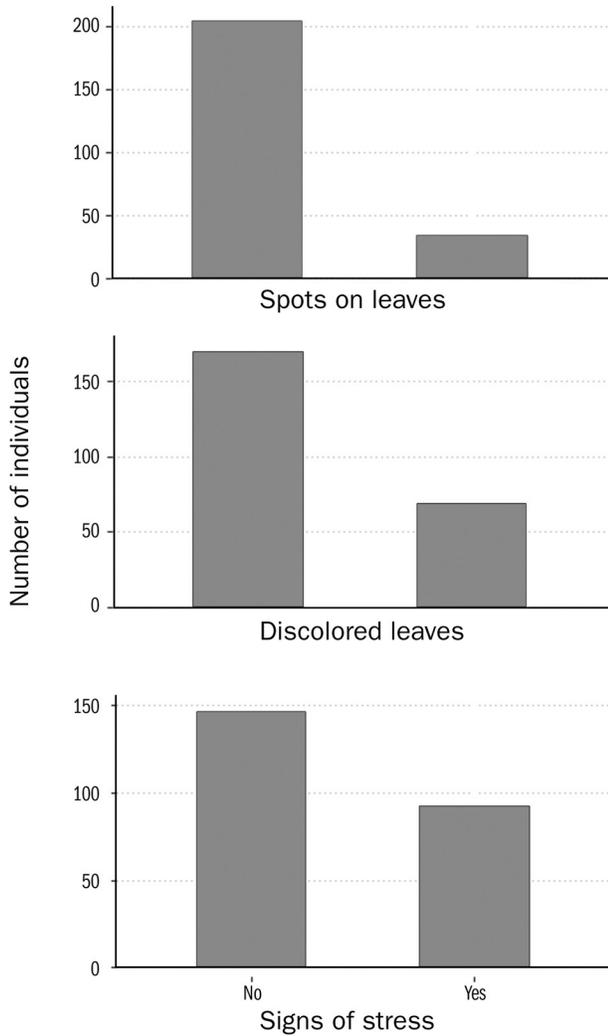


Figure 3. Frequency distribution of categorical variables examined in *Lepanthes woodburyana*: (A) plants with dark spots on leaves; (B) plants with discolored leaves; (C) plants deemed with signs apparent of stress.

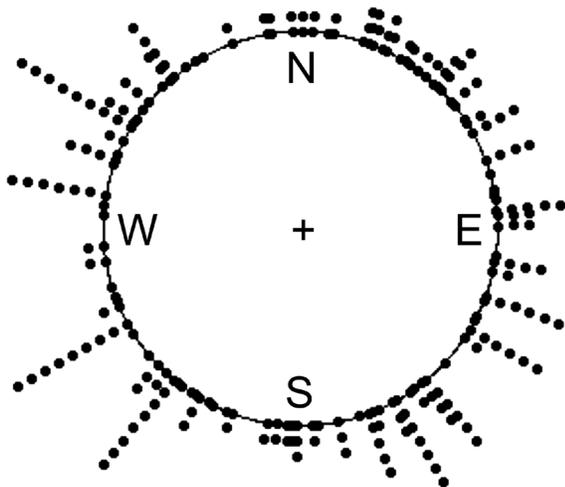


Figure 4. Circular histogram – azimuth projection on the compass – of the distribution of orchids of *Lepanthes woodburyana* on host trees. Rayleigh Test of Uniformity:  $p = 0.41$ .

between the presence of dark spots and, canopy cover, elevation, and maximum relative humidity (Table 1A; best model out of 37 evaluated) (Appendix 1). It also showed a significant positive association for the presence of spots with the number of leaves per orchid (i.e., larger plants had a higher probability of showing dark spots) (Table 1A). Plants that had more leaves and that were located in areas with low canopy cover, at low elevation and with low relative humidity were more likely to show dark spots. The model analyzing the presence of leaf discoloration color showed significant negative associations with the number of leaves, mean temperature, canopy cover, and mean relative humidity; and positive associations with maximum and minimum temperature (Table 1B; best model out of 34 evaluated). Overall, in areas with higher mean temperatures, low canopy cover, and low relative humidity, plants had a higher probability of showing discolored leaves. The binomial logistic regression model analyzing the presence of pooled leaf damage (dark spots and/or leaf discoloration) showed significant negative associations with life stage, elevation, mean temperature, and canopy cover. Meanwhile, a positive association was found with the maximum temperature (Table 1C; best model out of 37 evaluated). Overall, plants were more likely to show some form of leaf damage if (1) they were adults, (2) they were located at low elevations, (3) in areas with high mean and maximum temperatures, (4) and in areas with low canopy cover.

Kendall's correlations analyses evaluating associations between independent variables with the proportion of spots and the proportion of unhealthy colored leaves showed significant negative associations between the proportion of spots with elevation, canopy cover and significant positive associations with the number of leaves and the minimum and mean temperature (Table 2). Plants showed a higher proportion of spots at lower elevations, and in areas with low canopy cover. Likewise, for the proportion of unhealthy colored leaves, we found significant negative correlations with canopy cover and number of leaves, and positive correlations with maximum relative humidity and

**Table 1.** Binomial logistic regression analyses evaluating the probability of occurrence of leaf condition variables (presence of spots, presence of discoloration, and presence of any sign of leaf stress) as a function of environmental and plant size correlates in *Lepanthes woodburyana* following Hurricane María at the Luquillo Experimental Forest (El Yunque National Forest). **Model (A)** = Dependent variable: “presence of spots” (AIC = 187.11); **Model (B)** = Dependent variable: “leaf discoloration” (AIC = 231.09); **Model (C)** = Dependent variable: “presence of any leaf stress” (ie. combination of both symptoms) (AIC=257.75). Sample size = 240 individuals.

<b>Model (A): Independent Variables</b>	Estimate	Std. Error	Z-value	p-value
Elevation	-0.008	0.004	-2.24	0.02
Number of Leaves	0.61	0.21	2.87	0.004
Canopy Cover	-3.48	1.15	-3.02	0.002
Maximum Relative Humidity	-0.07	0.03	-2.50	0.01
Mean Relative Humidity	0.03	0.02	1.41	0.16
<b>Model (B): Independent Variables</b>				
Number of Leaves	-0.37	0.20	-1.81	0.07
Canopy Cover	-5.90	1.27	-4.65	< 0.0001
Maximum Temperature	0.29	0.14	2.10	0.03
Minimum Temperature	1.75	0.54	3.22	0.001
Mean Temperature	-2.01	0.42	-4.76	< 0.0001
Mean Relative Humidity	-0.04	0.02	-2.20	0.03
<b>Model (C): Independent Variables</b>				
Juvenile Life Stage	-0.12	0.41	-0.30	0.77
Seedling Life Stage	-1.85	0.55	-3.35	0.008
Canopy Cover	-7.04	1.15	-6.13	< 0.0001
Mean Temperature	-1.57	0.45	-3.45	0.0005
Maximum Temperature	0.27	0.12	2.17	0.03
Elevation	-0.007	0.003	-1.92	0.05

minimum relative humidity. In other words, plants showed a higher proportion of leaves with some form of damage in areas with low canopy cover and low relative humidity (maximum and minimum).

## DISCUSSION

Cloud forests are habitats with unique abiotic characteristics (low light in the understory, high relative humidity, low temperatures (Foster 2001), which are bound to change dramatically following hurricane events. Leaf photodamage (i.e., the photooxidation of chlorophyll and cell death) is a possible outcome when plants are exposed to extreme environmental stress. For example, when shade-adapted plants are suddenly exposed to prolonged sunlight when the canopy opens, which bring an excess of light and solar radiation. This excess exacerbates stress with increasing

**Table 2.** Kendall's  $\tau$  and significance between the proportion of leaves with signs of leaf stress – i.e., dark spots, unhealthy leaf coloration – and environmental and plant-related parameters.

Variables	Dark spots		Unhealthy	
	Kendall's $\tau$	p-value	Kendall's $\tau$	p-value
<b>Environmental parameter</b>				
Minimum temperature (°C)	0.11	0.04	0.12	0.03
Maximum temperature (°C)	0.03	0.53	-0.01	0.78
Mean temperature (°C)	0.10	0.05	0.05	0.34
Minimum relative humidity (%)	0.006	0.92	0.08	0.16
Maximum relative humidity (%)	-0.04	0.43	0.20	0.0005
Mean relative humidity (%)	-0.08	0.14	0.18	0.001
Canopy cover (%)	-0.17	0.002	-0.34	<< 0.0001
<b>Plant-related parameter</b>				
Elevation of host tree (m)	-0.17	0.001	-0.05	0.35
Height of orchid on host (m)	-0.07	0.15	-0.05	0.28
Number of leaves/orchid	0.11	0.05	-0.14	0.01
Area (m) covered by orchids/host	-0.13	0.02	0.08	0.17
Azimuth (°) of orchid on host	-0.01	0.78	-0.01	0.78
Proportion of unhealthy	0.03	0.57	-	-
Proportion of dark spots	-	-	0.03	0.57

temperature to extreme levels, which combined with dry spells, cause even more stress (Lovelock et al. 1994; Robinson 2000). It has been argued that most species of orchids living in forested areas cannot be exposed to direct sunlight for long periods since photoinhibition may occur (Osmond 1978; Winter et al. 1983) and that most orchids require low irradiance levels to carry out photosynthesis (Chang et al. 2011; Zhang et al. 2007). In some orchid species, increases in light exposure may even cause injury to their photosynthetic apparatus (Pires et al. 2012) and lead to irreversible changes in leaves (Pastenes et al. 2003). In our study, the responses of *L. woodburyana* to the changing environment following Hurricane María supported previous findings of the consequences of rapid changes in abiotic variables on leaf health in this species.

Even when a considerable fraction of the population showed leaves with symptoms of stress, most plants (62%) did not show these symptoms. Prior work had reported that in tropical rain forests, most orchids experience canopy openings at some point in their lifetime and that most seem to have the capacity to recover from them (Ackerman 2014). Our study began one year after the hurricane events of 2017. Therefore, one possibility is

that by the time we began studying *L. woodburyana* at the El Toro trail, plants were on their way to recovery, which would explain the moderate incidence of leaf symptoms. Another possibility is that this particular species of *Lepanthes* has enough intraspecific variability such that many individuals are capable of adjusting to sudden changes in forest structure and their associated changes in abiotic conditions. In addition, plants with more severe damage could have died by the time our census was conducted, and our surveyed individuals represented those *L. woodburyana* orchids that could withstand the most stress and survive. Of all the *Lepanthes* species endemic to Puerto Rico, *L. woodburyana* is the most common and widespread (Stimson 1969) known to occur throughout an elevation range that spans the 300 m to 1,200 m asl (Ackerman 1995).

Published work indicates that some *Lepanthes* species (including *L. woodburyana*) that experience higher than optimal temperatures and drier microclimates become stressed (Crain and Tremblay 2017). Research also suggests that stresses like water deficits and increases in temperature can interact with photoinhibition to cause greater leaf injury than either factor alone (Bjorkman and Powles 1984; Lovelock et al. 1994; Robinson 2000). The conditions to create environmental stress for the orchid seem plausible. Not only was the canopy more open, but also our HOBO<sup>®</sup> sensors recorded a maximum temperature during our study that reached as high as 33.3°C and a maximum relative humidity that only reached 72.8%. This contrast from historical average values of monthly temperatures that range between 17°C and 21°C, and relative humidity that is often close to 100% (Weaver 2012).

To the extent that leaf symptoms were indicative of plant stress related to photoinhibition, heat, drought and other factors (which would need testing), then many of the relationships found between the presence of spots, leaf discoloration and abiotic environments were consistent with expectations. For example, we did find that the incidence of plants with visible signs of stress was higher in areas with higher

temperatures, low canopy cover (i.e., an indicator of high light exposure) and low relative humidity. However, physiologically speaking, small plants are more susceptible to temperature and water stress changes (Hietz, 1997; Zotz 1998; Zotz and Thomas 1999). Thus, we expected them to show more signs of stress, and that was not our result. Indeed, small plants (juveniles and seedlings) in our study were less likely, relative to adult plants, to show stress symptoms in the way of dark spots and discoloration. One possibility is that there is variation in the way different life stages would handle the combined effects of multiple stressors. Another possibility is that these younger plants germinated sometime after the hurricane event and have been exposed to the “harsh” environmental conditions for a shorter period of time.

The difference between smaller (seedling and juveniles) and larger (adults) individuals may suggest variation in the way different life stages would handle the combined effects of multiple stressors. It should be emphasized that the occurrence of relationships between leaf symptoms and indicators of environmental stress in this study are not a test for the presence of photoinhibition or leaf stress but instead are hypotheses about the mechanisms leading to the occurrence of visible damaging leaf stress symptoms. Photoinhibition and leaf stress should be tested as both can have negative consequences on plant growth, reproduction, and survival as it has been shown in other plant systems.

We found the presence of spots and leaf damage was not related to the cardinal position in which the orchids were located around the host stems. In a prior study with *L. eltoroensis*, a related species with populations restricted to the elfin cloud forest of the El Toro Wilderness, plants of that species were preferentially distributed on the northwestern side of the tree stems of their hosts (Tremblay and Castro 2009). That study proposed that better abiotic conditions on those locations could be driving the uneven distribution of orchids. In our study, we found no such preference which suggests that perhaps *L. woodburyana* may be less

susceptible to environmental stresses relative to the less widespread *L. eltoroensis*. We did find that the presence of dark spots was negatively associated with elevation. A study at this site, found that canopy cover following the hurricane was negatively related to elevation (Hernández-Muñiz et al., this issue) so it is possible that differences in forest structure, between high and low elevation sites, were responsible for this observation.

## CONCLUSION

Epiphytes are an important component in tropical cloud forests and knowing how these species react to upcoming changes like climate change means coming up with better conservation and management practices. Studying plants like *L. woodburyana* could be used as a model system to help us understand how other *Lepanthes*, also epiphytes and some of which are protected may behave and how resilient this genus can be when faced with changes in microclimatic conditions. Our results showed that dark spot formation was more frequent at low elevations, open canopies and high temperatures. Further studies should focus on trying to capture the mechanisms that produce leaf deterioration and to what extent these symptoms translate into reduced growth and survival. Additional questions could center on how spatial differences in canopy structure following hurricane disturbances can influence plant stress following these events.

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## Appendix 1.

A summary of results for the selection of the best binomial logistic regression model for the dependent variable “presence of spots” in leaves of *Lepanthes woodburyana* (Model [A] in Table 1; other models not shown, but we follow a similar process for their selection). For this variable, the lowest “Akaike’s Information Criterion” (AIC) was 187.11 from a model that included five parameters: number of leaves, canopy cover, elevation, mean RH, and max. RH. We then selected this model as the one that explained most of the variation of presence of spots on leaves (also see the main text). For simplicity, min., max., and mean RH and T = minimum, maximum, and mean relative humidity and temperature, respectively.

AIC	Parameters	Variables in the model
187.11	5	Number of leaves, canopy cover, elevation, mean RH, and max. RH.
187.49	5	Number of leaves, canopy cover, elevation, min. RH, and max. RH.
187.85	4	Number of leaves, canopy cover, max. RH, and elevation.
188.26	6	Number of leaves, canopy cover, elevation, mean RH, height, and max. RH.
188.31	5	Number of leaves, canopy cover, elevation, max. T, and max. RH.
188.53	6	Number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. RH, and elevation.
188.53	7	Number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. T, max. RH, and elevation.
188.59	5	Number of leaves, canopy cover, elevation, mean RH, and max. RH.
188.91	5	Number of leaves, canopy cover, elevation, mean T, and max. RH.
189.01	5	Number of leaves, canopy cover, elevation, height, and max. RH.
189.09	6	Number of leaves, canopy cover, elevation, mean RH, angle, and max. RH.
189.11	6	Number of leaves, canopy cover, elevation, mean RH, leaf color, and max. RH.
189.43	5	Number of leaves, canopy cover, elevation, min. T, and max. RH.
189.48	3	Number of leaves, canopy cover, and elevation.
189.79	5	Number of leaves, leaf color, canopy cover, max. RH, and elevation.
190.31	8	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. T, max. RH, and elevation.
190.40	7	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. RH, and elevation.
190.53	9	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. T, max. RH, min. RH, and elevation.
191.87	7	Life stage, number of leaves, proportion of discolored leaves, canopy cover, max. T, max. RH, and elevation.
191.97	8	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, min. T, max. RH, and elevation.
192.21	2	Number of leaves and canopy cover.
192.22	7	Life stage, number of leaves, leaf color, canopy cover, max. T, max. RH, and elevation.
192.52	10	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. T, min. T, max. RH, min. RH, and elevation.
192.69	3	Number of leaves, canopy cover, and max. RH.
193.32	2	Number of leaves and elevation.
193.62	9	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. T, min. T, min. RH, and max. RH.
194.16	11	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. T, min. T, max. RH, min. RH, mean RH, and elevation.
194.17	5	Life stage, number of leaves, canopy cover, max. RH, and elevation.
195.84	12	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, max. T, min. T, mean T, max. RH, min. RH, mean RH, and elevation.
196.22	1	Canopy cover.
196.97	13	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, height, max. T, min. T, mean T, max. RH, min. RH, mean RH, and elevation.
197.55	1	Elevation.
197.89	1	Number of leaves.
198.95	14	Life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, angle, height, max. T, min. T, mean T, maximum RH, minimum RH, mean RH, and elevation.
200.93	15	Life stage, area, number of leaves, leaf color, proportion of discolored leaves, canopy cover, angle, height, max. T, min. T, mean T, max. RH, min. RH, mean RH, and elevation.
201.07	16	All Variables: host, area, life stage, number of leaves, leaf color, proportion of discolored leaves, canopy cover, angle, height, max. T, min. T, mean T, max. RH, min. RH, mean RH, and elevation.
201.83	1	Life stage.

# PRELIMINARY ESTIMATE OF THE IMMEDIATE EFFECTS OF HURRICANE MARÍA ON THE TREE STRUCTURE AND SPECIES COMPOSITION OF NOVEL FORESTS IN THE MOIST LOWLANDS OF PUERTO RICO

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## Abstract

Puerto Rico is regularly affected by the passing of hurricanes, resulting in assemblages of native tree species that are adapted to withstand hurricane effects. Tree species that were introduced for agricultural or ornamental purposes are now abundant in most secondary forests in Puerto Rico, increasing the ecological novelty of island forests and the uncertainty of their response to hurricane events. We report immediate and visible short-term effects of Hurricane María on the tree structure and species composition of four novel-secondary-forests found in the moist lowlands of Puerto Rico. We sampled the density (trees/ha), basal area (m<sup>2</sup>/ha), species richness and composition of large ( $\geq 10$  cm diameter at breast height; [DBH]) and small ( $\geq 2.5$  cm to  $< 10$  cm DBH) trees on each site before (between 2005 and 2017) and after (2018) Hurricane María, and used paired T-tests to evaluate the significance of differences observed between sampling dates. Contrary to expectation, we did not find a significant reduction in mean ( $n = 4$ ) values of tree density, basal area, and species richness on these four sites after the hurricane. In addition, we found no substantial changes in the relative dominance of species and no clear pattern of change in the percentage of introduced species across the four sites. The most extreme hurricane-induced changes in tree structure for pooled size-classes on any one site included 1) a reduction of 38% in density on one site, 2) an increase of 18% in density and a reduction of 26% in basal area on another site, and 3) an increase of 21% in basal area on a third site. Species richness of pooled tree size-classes increased by up to 50% or decreased by up to 30% on each site, and replacement of the dominant tree species was observed only in the small tree size-class and on one site only. Post-hoc Kruskal-Wallis tests revealed no significant differences in the magnitude or direction of changes in tree density, basal area, and species richness between large and small tree size-classes. Although the direction of changes in tree density, basal area, and species richness were highly variable among sites, the mean values of these variables were remarkably similar before and after the hurricane. These results suggest that the immediate effects of Hurricane María were offset by growth and recruitment within a relatively short time span. Our results also indicate that higher sample sizes may reveal patterns in hurricane effects arising from the distance of any given site to the trajectory of Hurricane María. Our findings show that, in the short-term, the tree structure and species composition of novel forests in the moist lowlands of Puerto Rico can be as resilient to immediate hurricane effects as that of the island's original, historic forests.

**Keywords** Anthropocene, Caribbean coastal and karst forests, introduced species, land-cover change, large infrequent-disturbances, short-term visible hurricane-effects.

## Resumen

Puerto Rico es afectado regularmente por el paso de huracanes, resultando en un arreglo de especies nativas adaptadas a resistir sus efectos. Árboles de especies introducidas, los cuales son abundantes en la mayoría de los bosques secundarios de Puerto Rico, han incrementado la novedad en los bosques insulares y la incertidumbre sobre sus respuestas a tales eventos atmosféricos. Reportamos los efectos visibles del huracán María a corto plazo sobre la estructura y composición de especies de árboles en bosques secundarios noveles encontrados en las tierras bajas húmedas de Puerto Rico. Muestreamos la densidad de árboles (árboles/ha), área basal ( $m^2/ha$ ), composición y riqueza de especies de árboles grandes ( $\geq 10$  cm diámetro a la altura de pecho; DAP) y pequeños ( $\geq 2.5$  a  $< 10$  cm DAP) en los cuatro sitios antes (entre 2005 y 2017) y después (2018) del huracán María y usamos la prueba T-pareada para evaluar diferencias observadas entre las fechas muestreadas. Contrariamente a lo esperado, no encontramos una reducción significativa en el valor promedio ( $n = 4$ ) de densidad de árboles, área basal, y riqueza de especies en los sitios después del huracán. Tampoco encontramos un patrón claro de cambio en porcentaje de especies introducidas, en la dominancia de especies, y las curvas de dominancia-diversidad de especies no indicaron cambios sustanciales en la dominancia relativa de especies. Los cambios más extremos en la estructura de los árboles para ambas clases de tamaños agrupadas por sitios incluyeron 1) una reducción de 38% en densidad en un sitio, 2) un aumento de 18% en densidad de árboles y una reducción del 26% en área basal en otro sitio, y 3) un aumento de 21% en área basal en un tercer sitio. A través de los sitios, la riqueza de especies de todos los árboles aumentó hasta por 50% o se redujo hasta por 30%, y el reemplazo de la especie de árbol dominante se observó solo en la clase de tamaño de árboles pequeños y solamente en un sitio. No encontramos diferencias en la magnitud o dirección de los cambios entre las clases de árboles grandes y pequeños. Aunque la dirección de cambios en la densidad, área basal, y riqueza de especies de árboles fueron altamente variables entre los sitios, los valores promedio fueron notablemente similares antes y después del huracán. Esto sugiere que los efectos del huracán fueron compensados por el crecimiento y el reclutamiento de árboles en un período de tiempo relativamente corto. Nuestros resultados indican que un mayor tamaño de muestra puede revelar diferencias en los efectos a corto plazo a raíz de la distancia del sitio a la trayectoria del Huracán María. Nuestros hallazgos muestran que la estructura y la composición de especies de árboles en bosques secundarios noveles puede ser tan resiliente como la de bosques históricos originales a eventos de huracanes, al menos a corto plazo.

**Palabras clave** Antropoceno, bosques costeros y cársicos del Caribe, especies introducidas, cambio en cobertura de terrenos, disturbios grandes e infrecuentes, efectos visibles de huracanes a corto plazo.

## INTRODUCTION

Due to its location in the Caribbean, Puerto Rico is regularly exposed to major hurricane events that cause cyclical and drastic changes to the island's ecosystems (López and Castro 2018). In Puerto Rico, hurricanes make landfall every decade, and their effects on forest

ecosystems include immediate and visible physical effects on tree structure and species composition that are observable in the short-term (i.e., up to three years after the event), and non-visible effects on ecosystem function and successional trajectory that are manifested in the long-term (Lugo 2008). The periodicity of hurricane landfalls in Puerto Rico appears to favor native tree

species with adaptations to fulfill ecological niches created by such large and infrequent disturbances (Basnet et al. 1993; Dale et al. 1998; Van Bloem et al. 2003). Relative to native tree species, those that were introduced to Puerto Rico prior to colonization by Europeans for agricultural and ornamental purposes may be in ecological disadvantage to adapt to short- and long-term changes in ecological space created in the aftermath of major hurricanes.

Just like hurricanes, humans play an important role in the successional trajectories of Puerto Rican secondary forests. Most of these forests constitute novel ecosystems that emerge as a natural response to high rates of anthropogenic changes and disturbances in the Anthropocene (Lugo 2009; Radeloff et al. 2015). The expansion of agriculture and population growth sped up deforestation rates in Puerto Rico in the 19<sup>th</sup> century up to the mid 20<sup>th</sup> century, when forest cover in the island reached a low of 5% that was mostly confined to mountain forest reserves, such as El Yunque in the northeast (March 1899; Álvarez et al. 2013). Today, it is estimated that forests cover 60% of the land area of Puerto Rico as a result of the abandonment of agricultural lands and an economy that is increasingly dependent on fossil fuels and external subsidies (Gould et al. 2017; González and Ma 2017). Centuries of intensive agricultural practices in the lowlands, which were chiefly used for sugar cane plantations, resulted in extensive modification of the land, loss of topsoil, and conditions that can hamper the establishment of native tree species (Silén 1993; Lugo 2004). However, some introduced tree species appear highly adapted to abandoned agricultural lands and in many cases eventually form nearly monodominant forest stands as a consequence of their arrival, colonization, and fast growth in deforested sites (Grau et al. 2003; Lugo 2004). Introduced species are now present throughout Puerto Rico and dominate the island's young secondary forest cover (Lugo and Helmer 2004; Martinuzzi et al. 2013; Marcano-Vega et al. 2015).

In September 2017, hurricanes Irma and María transformed the Puerto Rican landscape and affected the structure and functioning of its social and ecological systems (Cangialosi et al. 2018; Lugo 2018; Pasch et al. 2018). Although both were high-intensity major hurricanes (categories 4–5 in the Saffir-Simpson scale), Hurricane María was the one that made landfall and possibly caused the most significant effects on Puerto Rican forests and landscapes since Hurricane San Felipe's landfall in 1928 (López and Castro 2018). The immediate and visible effects of Hurricane María on forested areas included a reduction of 31% in canopy 'greenness,' estimated from remotely-sensed changes in leaf area, chlorophyll content, canopy cover, and structure at an island-wide scale (Van Beusekom et al. 2018). However, most long-term study plots, in which we base our current knowledge of hurricane effects on Puerto Rican forests, are located in the wet mountains of El Yunque and the dry forests in Guánica. Also, the information available for forests located in the lower elevation moist forest life-zone, which covers most lowlands and happens to be the most extensive on the island, is scant (Ewel and Whitmore 1973; Van Bloem et al. 2005; Brokaw et al. 2012). A notable exception is a study on the effects of Hurricane Georges on the tree structure and species composition in stands of novel forests in the moist lowlands, urban Río Piedras, northern Puerto Rico (e.g., Lugo et al. 2005b).

The moist lowlands of Puerto Rico have historically been subjected to the highest rates of land conversion for agriculture and urbanization, but these lowlands proportionally contain most of the island's novel-forests whose ecological properties, structure, and function are just beginning to be understood (Helmer et al. 2008; Lugo 2009; Martinuzzi et al. 2013). Lowland forests in Puerto Rico exhibit higher levels of ecological novelty due to their relatively young age, previous land use for intensive agriculture (e.g., sugar cane and grazing), high dominance by introduced tree species, and ephemerality due to high land conversion rates when compared to forests found in protected areas (Helmer

**Table 1.** Site descriptions for the four lowland novel-forest stands sampled in this study. Site elevation is from GPS measurements and topographic maps. Slope landforms are low side-slopes to moderately steep slopes for Guajataca and Río Hondo (Martinuzzi et al. 2007). Area sampled for the large tree size-class is followed by area sampled for the small tree size-class in parenthesis, and all area sampled values are rounded to the nearest 0.01 ha. Four trees per tree size-class were sampled on each point-quarter center method (PQCM) point (Cottam and Curtis 1956). On Pugnado, concentric 250 m<sup>2</sup> and 100 m<sup>2</sup> plots were used to sample large and small tree size-classes, respectively.

Site	Elevation (m)	Slope (°)	Aspect	Substrate and Landform	Year of Sampling		Area Sampled (ha)		PQCM points (plots in Pugnado)	
					Before	After	Before	After	Before	After
Cibuco II	10	0	None	Alluvial Floodplain	2005	2018	0.05 (0.03)	0.03 (0.01)	10	4
Guajataca Left	3–93	13–25	NW	Karst Slope	2017	2018	0.06 (0.02)	0.08 (0.01)	8	7
Pugnado	170	4	None	Karst Depression	2017	2018	0.03 (0.01)	0.03 (0.01)	1	1
Río Hondo	30–40	3–24	SW	Volcanic Slope	2015	2018	0.05 (0.01)	0.04 (0.01)	5	5

et al. 2008; Radeloff et al. 2015; Abelleira 2019). Nevertheless, detailed field-based assessments of short- to long-term hurricane effects on the tree structure and species composition of Puerto Rico's novel forests are scarce. The rarity of these assessments generates a significant gap in our knowledge and understanding of the effects of hurricanes on the island's current forest cover and impairs our capacity to anticipate and manage for extreme hurricane events in the future.

We sampled the tree structure and species composition of four lowland novel-forest sites before (2005, 2015, or 2017; Table 1) and after (2018) the passing of Hurricane María. Our objective was to quantify the short-term changes in tree density, basal area, and species richness that occurred as a result of the immediate and visible effects of Hurricane María on these four novel-forest sites. We expected that the hurricane would set back the process of ecological succession observed in Puerto Rico for secondary forests of this age range (35–60 yrs.), which is typified by an ongoing increase in tree density, basal area, and accumulation of species as forest growth proceeds toward ecological maturity (Aide et al. 2000; China 2002; Flynn et al. 2010). Specifically, we expected that tree density, basal area, and species richness would decrease as a result of the short-term, high-energy effects of Hurricane María, which were manifested by high-velocity winds and copious rainfall that caused extensive breakage of tree branches, tree uprooting, and treefalls. Our results constitute a preliminary estimate of the magnitude and direction of the immediate effects of Hurricane María on the tree structure and species

composition of novel forests in the moist lowlands of Puerto Rico. This study contributes to understanding Puerto Rico's current forest cover, which was largely shaped by large and infrequent hurricane disturbances in prehistoric times and is increasingly being shaped by anthropogenic land cover change and species introductions in the Anthropocene.

## METHODS

### Study Region, Site Selection and Description

The study sites lie in the lowlands located within the subtropical moist forest life-zone of Puerto Rico (Figure 1). In the moist life-zone, mean annual precipitation and air temperature range between 1,000 mm and 2,200 mm, and between 21°C and 25°C, respectively (Ewel and Whitmore 1973). We selected four study sites that are part of on-going studies focused on the ecological structure, function, and management interventions in novel forests dominated by introduced species in Puerto Rico (Abelleira et al. 2010; Túa and Abelleira 2019; Lugo et al. 2020). Two of the sites were dominated by *Spathodea campanulata* (Abelleira et al. 2010), a third site by *Albizia procera*, and a fourth site by *Terminalia catappa* (unpublished data). The location and landform of the study sites are, in order of their location from eastern to western Puerto Rico, the following (Figure 1): (1) Cibuco II, located on riparian alluvial floodplains; (2) Pugnado, located on a karst depression; (3) Guajataca Left, located

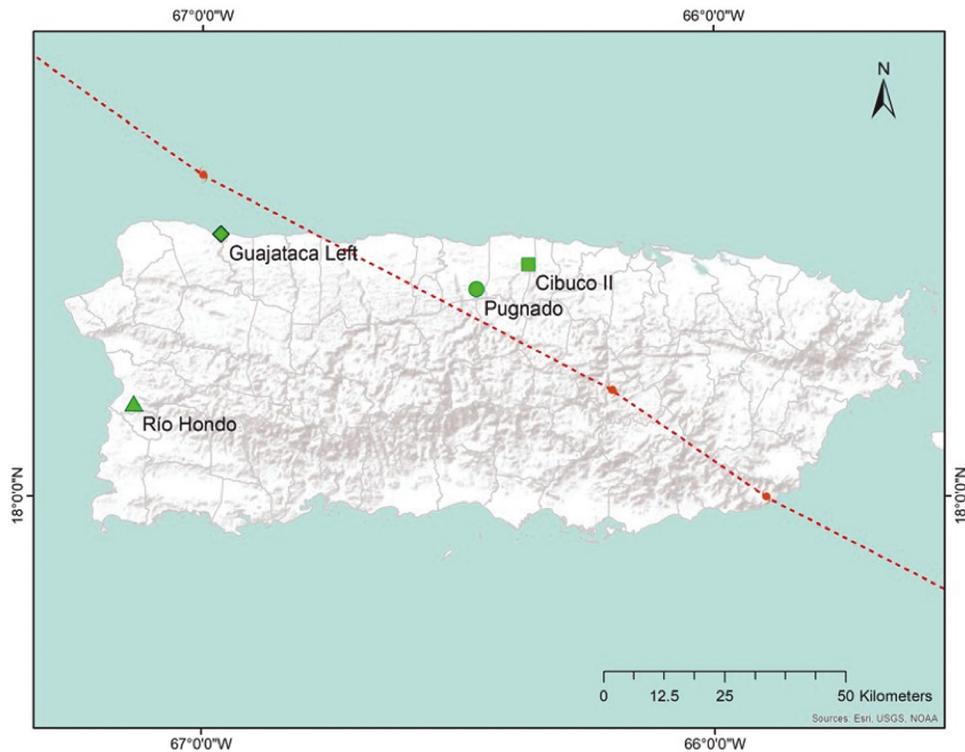


Figure 1. Location of study sites and the trajectory of Hurricane María in Puerto Rico.

in a low karst side slope about 100 m from the coastline; (4) and Río Hondo, located on a low volcanic side-slope (Martinuzzi et al. 2007; Gould et al. 2008). Cibuco II is on flat terrain, and Pugnado is enclosed within a depression that grades from a nearly flat slope at the bottom to a moderate slope on the side-slopes; therefore, these two sites have no aspect. The elevation of the four sites ranged from 10 m to 170 m above sea level (asl), and slope ranged from 0° to 25° (Table 1).

Age since abandonment, estimated from aerial photography coupled with informal interviews with neighbors, ranged from 35 to 60 years among the study sites. Previous land use included sugar cane plantations in Cibuco II and Río Hondo, subsistence farming in Pugnado, and grazing possibly occurring on all sites. The valleys where Cibuco II is located were used for sugar cane plantations since the 16<sup>th</sup> century, although it is not clear when the crop was first established on the site (Abelleira and Lugo 2008). Likewise, the first sugar cane plantations in the western alluvial valleys near Río Hondo date to the 16<sup>th</sup> century, yet the crop was

possibly established later on gentle, volcanic slopes in the western lowlands where Río Hondo is located (Silén 1993). Previous land use in Pugnado consisted of farming of fruit trees, tubers, and plantains intercalated with occasional grazing (Abelleira et al. 2010). Previous land use of Guajataca Left is less clear, but its close distance (< 50 m) to the coastal railroad tracks suggests the site was likely disturbed by the removal of carbonate rocks for constructing the mound atop which the tracks were placed. The coastal railroad was completed in 1890 and abandoned by the end of

the 19<sup>th</sup> century (Bergad 1978; Muñoz 2017). Given its proximity to alluvial flats currently used for hay cropping, it is possible that Guajataca Left was used for marginal grazing, but the site's topography and substrate would have made any agriculture and grazing difficult.

### Hurricanes Irma and María

On 6 September 2017, the eye of the category-5 Hurricane Irma was 92.6 km off the northern coastline of Puerto Rico; it developed a double-eyewall structure, had maximum winds of nearly 287 km/hr, and a large wind-field, but did not make landfall (Cangialosi et al. 2018). In contrast, on 20 September 2017, Hurricane María made landfall in the southeastern coast of Puerto Rico near the municipality of Yabucoa (Figure 1; Pasch et al. 2018). Also, Hurricane María crossed the island diagonally, from the southeast to the northwest, with maximum winds and rainfall accumulations of 150 km/hr and 96.3 mm, respectively, just below the threshold of a category-5 hurricane. On 21 September 2017, the eye

of Hurricane María exited between the municipalities of Camuy and Quebradillas, near the northwestern corner of Puerto Rico. Hurricane María is considered one of the most intense hurricanes documented as making landfall in Puerto Rico since Hurricane San Narciso (category-3) in 1867 (López and Castro 2018), along with Hurricanes San Ciriaco (1899), San Felipe II (1928), Hugo (1989), and Georges (1998). In our study, we mainly focus on the immediate effects of Hurricane María because we consider that the effects of Hurricane Irma on our study sites could be negligible for the reasons mentioned above. Nonetheless, we acknowledged that our estimates of changes in tree density, basal area, and species richness and composition could include the combined effects of hurricanes Irma and María, with the latter contributing to most of the changes in vegetation.

## Forest Sampling

We sampled the diameter (cm) at breast height (DBH; sampled at 1.4m above the ground) and identified the species of trees alive and standing on each site before and after Hurricane María to estimate changes in tree density, basal area, and species richness. On three of the study sites, we used the Point-Centered Quarter Method (PCQM) (Cottam and Curtis 1956; Ashby 1972) to sample large ( $\geq 10$  cm DBH) and small ( $\geq 2.5$  cm to  $< 10$  cm DBH) trees alive and standing before and after the hurricane (Table 1). On each of these three sites, we placed one PCQM line-transect (approximately 100-m long each), at random on the initial sampling period (i.e., before the hurricane), and set as many PCQM sampling-points as possible on each transect to record vegetation characteristics for large- and small-tree size-classes on each sampling date. On a fourth site, Pugnado, we established one circular concentric plot of 250 m<sup>2</sup> and 100 m<sup>2</sup> to sample trees alive and standing in the large and small tree size-classes, respectively, before and after the hurricane (Table 1). The concentric plot was placed randomly before the hurricane, and the DBH of all trees from each corresponding tree size-class was sampled on the concentric

plot before and after the hurricane. Comparisons of PCQM and plot-based methods for the sampling of tree density, basal area, and species richness have shown that estimates from both methods are in very close agreement when applied to novel-forest sites (Abelleira and Colón 2006). Each tree was identified to species following Little and Wadsworth (1964) and Little et al. (1988).

We must clarify that although the PCQM can increase the efficiency of sampling efforts, it may need adaptations when applied to long-term studies (Lessard et al. 2002; Dahdou and Koedam 2006). Therefore, we note that although the location and extent of the transects used for placing PCQM points was the same on each of the three sites where PCQM was used on each sampling date (Table 1), the actual location of the points along each transect was randomized and resampled on each sampling date following the standard application of the PCQM (Cottam and Curtis 1956; Lessard et al. 2002). Since the exact point locations had to be randomized and placed within the initial extent of the lineal transect, the number of points per transect, and the area sampled per tree size-class per site, varied between sampling periods (before and after the hurricane; Table 1). In PCQM, the distances between points and trees are used to estimate tree density and basal area, and therefore a reduction in the number of trees (i.e., in tree density), as indeed happened in most of the sites, inevitably leads to potential overcrowding of PCQM points for any given extent of lineal transect. This is so because contiguous PCQM points on a lineal transect cannot share the same trees in the sample, which would create a condition (i.e., dependence of tree sub-samples between PCQM sample-points) that would invalidate the application of the method.

## Data Analysis

We estimated tree density (trees/ha), basal area (m<sup>2</sup>/ha), species richness, and species importance values (IV) for each tree size-class on each site before and after Hurricane María. For each variable, we also estimated the mean values, and corresponding

**Table 2.** Tree density (trees/ha), basal area (m<sup>2</sup>/ha), species richness, percentage of introduced species, and dominant species of large ( $\geq 10$  cm diameter at breast height; DBH), small ( $\geq 2.5$  cm to  $< 10$  cm DBH), and pooled size-classes of trees in four, lowland novel-forest sites, before and after Hurricane María. Codes for species: Sc = *Spathodea campanulata*; Tc = *Terminalia catappa*; Ap = *Albizia procera*; Gg = *Guarea guidonia*; Cc = *Calophyllum calaba*; Cs = *Casearia sylvestris*.

Site	Tree Density (trees/ha)		Basal Area (m <sup>2</sup> /ha)		Species Richness		Introduced Species (%)		Dominant Species: Importance Value (%)	
	Before	After	Before	After	Before	After	Before	After	Before	After
<b>Large Trees</b>										
Cibuco II	868	607	72.5	87.6	3	2	66.7	50.0	Sc: 84.3	Sc: 83.2
Guajataca Left	517	358	43.4	31.9	9	7	11.1	14.3	Tc: 48.9	Tc: 51.0
Pugnado	840	600	74.6	70.1	4	3	25.0	33.3	Sc: 75.1	Sc: 82.2
Río Hondo	366	552	12.7	14.5	5	7	40.0	42.9	Ap: 36.1	Ap: 38.2
Mean (S.D.)	648 (246.3)	529 (116.8)	50.8 (29.1)	51.0 (33.7)	5 (2.6)	5 (2.6)	35.7 (23.8)	35.1 (15.5)	61.1 (22.4)	63.7 (22.6)
<b>Small Trees</b>										
Cibuco II	1502	1820	2.8	3.5	3	6	66.7	16.7	Sc: 81.1	Gg: 57.3
Guajataca Left	1642	2179	5.5	4.1	12	12	8.3	8.3	Cc: 21.2	Cc: 31.8
Pugnado	1900	1100	3.8	2.1	9	6	25.0	33.3	Sc: 29.3	Sc: 30.3
Río Hondo	1529	1140	4.1	3.7	8	9	14.3	33.3	Cs: 28.4	Cs: 29.9
Mean (S.D.)	1643 (181.6)	1560 (528.8)	4.1 (1.1)	3.4 (0.9)	8 (3.7)	8 (2.9)	28.6 (26.4)	22.9 (12.5)	40.0 (27.6)	37.3 (13.3)
<b>All Trees</b>										
Cibuco II	2370	2427	75.3	91.1	4	6	-	-	-	-
Guajataca Left	2159	2537	48.9	36.0	16	15	-	-	-	-
Pugnado	2740	1700	78.4	72.2	10	7	-	-	-	-
Río Hondo	1895	1692	16.8	18.2	10	10	-	-	-	-
Mean (S.D.)	2291 (356.9)	2089 (456.0)	54.7 (28.6)	54.4 (33.2)	10 (4.9)	10 (4.0)	-	-	-	-

Notes: Species richness totals do not add up due to same species occurring in pooled tree size-classes.

standard deviation, for the four study sites. For each tree size-class, species IV's per site were estimated based on the relative density, basal area, and point frequency for each species in the three sites sampled with PCQM, and on relative density and basal area for each species in Pugnado. Changes (%) in the density, basal area, and species richness of trees on each site were estimated relative to values sampled before the hurricane. We used IV's to develop ranked-species dominance-diversity curves to assess changes in community structure due to the immediate effects of the hurricane.

We used paired-sample T-tests (two-tails) to compare the mean of differences (i.e., changes) in values of tree density, basal area, and species richness sampled before and after Hurricane María on each site for each tree size-class and for pooled (i.e., large and small) tree size-classes (n = 4). Although we initially did not expect any patterns of change in the IV of dominant species and the percentage of introduced species, we also used paired T-tests to compare the means of differences in these values before

and after the hurricane to further illustrate short-term patterns of species turnover in the large and small tree size-classes. Normality of data was tested with Shapiro-Wilk tests and homoscedasticity with F-Max tests. We conducted post hoc Kruskal-Wallis tests (non-parametric ANOVA) to compare the mean values of changes (%) in tree density, basal area, and species richness sampled in the large tree size-class (n = 4) to those sampled in the small tree size class (n = 4) to evaluate if immediate hurricane effects were homogeneous among large and small tree size-classes. We used Infostat (Di Rienzo et al. 2014) for all statistical analyses and adopted an alpha value of  $p \leq 0.05$  for statistical significance.

## RESULTS

### Density and Basal Area

The density of large trees ranged from 366 to 868 trees/ha on the four study sites before Hurricane María, and basal area ranged from 12.7 to 74.6 m<sup>2</sup>/

ha (Table 2). After the hurricane, the density of large trees ranged from 358 to 607 trees/ha, and basal area ranged from 14.5 to 87.6 m<sup>2</sup>/ha. The density of small trees ranged from 1,502 to 1,900 trees/ha before Hurricane María, and basal area ranged from 2.8 to 5.5 m<sup>2</sup>/ha (Table 2). After the hurricane, the density of small trees ranged from 1,100 to 2,179 trees/ha, and basal area from 2.1 to 4.1 m<sup>2</sup>/ha. We observed a smaller variation around the mean value of the density of large trees after the hurricane relative to the pre-hurricane value (Table 2). On the other hand, we observed the opposite pattern in the small tree size-class, where the variation around mean values of density of small trees was larger after the hurricane relative to pre-hurricane values. In contrast, we observed a somewhat larger variation around the mean value of the basal area of large trees after the hurricane relative to pre-hurricane values when compared with the corresponding pattern of variation observed for small trees before and after the hurricane (Table 2). Despite the wide range of variation in the mean values of density and basal area of large and small trees before and after Hurricane María, we found no significant changes in the mean values of these variables for both tree size-classes, and pooled tree size-classes, attributable to the hurricane (Table 3).

### Species Richness and Importance Values

Species richness of large trees ranged from 3 to 9 species per site before Hurricane María, and from 2 to 7 species per site after the hurricane (range of area sampled: 0.03–0.08 ha; Tables 1 and 2). Likewise, species richness of small trees ranged from 3 to 12 species per site before the hurricane, and from 6 to 12 species per site after the hurricane (range of area sampled: 0.01 to 0.03 ha; Tables 1 and 2). However, the mean values and the variation of species richness for the four sites were very similar in the large and small tree size-classes, and for pooled tree size-classes, before and after the hurricane; we found no significant changes in the mean values of

**Table 3. Changes in tree density (trees/ha), basal area (m<sup>2</sup>/ha), and species richness of four lowland novel-forest sites sampled before and after Hurricane María. Changes are expressed in percentual change from initial pre-hurricane values. Also shown are means and standard deviation in parenthesis, and the T-statistic and corresponding significance (p-value) of paired T-tests conducted on values recorded before and after the hurricane for large, small, and pooled size-classes of trees.**

Size-Class and Site	Density (% change)	Basal Area (% change)	Species Richness (% change)
<b>Large Trees</b>			
Cibuco II	-30.1	20.9	-33.3
Guajataca Left	-30.7	-26.5	-22.2
Pugnado	-28.6	-6.0	-25.0
Río Hondo	50.8	14.2	40.0
Mean (S.D.)	-9.7 (40.3)	0.7 (21.4)	-10.1 (33.8)
T-Statistic (p-value)	1.14 (p = 0.3)	-0.04 (p = 1.0)	0.58 (p = 0.6)
<b>Small Trees</b>			
Cibuco II	21.2	24.0	100.0
Guajataca Left	32.7	-25.4	0.0
Pugnado	-42.1	-44.7	-33.3
Río Hondo	-25.4	-10.4	12.5
Mean (S.D.)	-3.4 (36.0)	-14.1 (29.0)	19.8 (56.9)
T-Statistic (p-value)	0.27 (p = 0.8)	1.29 (p = 0.3)	-0.20 (p = 0.9)
<b>All Trees</b>			
Cibuco II	2.4	21.0	50.0
Guajataca Left	17.5	-26.4	-6.3
Pugnado	-38.0	-7.9	-30.0
Río Hondo	-10.7	8.2	0.0
Mean (S.D.)	-7.2 (23.6)	-1.3 (20.5)	3.4 (33.6)
T-Statistic (p-value)	0.67 (p = 0.6)	0.08 (p = 0.9)	0.48 (p = 0.7)

species richness of trees sampled before and after Hurricane María on these four study sites (Table 3).

The mean value of the percentage of introduced species in the large tree size-class remained similar before and after Hurricane María, and decreased slightly, by 6%, in the small tree size-class after the hurricane (Table 2). The percentage of introduced species was highly variable, ranging from 8.3% to 66.7% across sites in the large and small tree size-classes before and after the hurricane, but the variation around mean values was lower after the hurricane. The IV of the dominant species remained similar, and the identity of the dominant species remained the same on each site except for the small tree size-class on Cibuco II (Table 2). On Cibuco II, the IV of the dominant species in the small tree size-class decreased by 23.8% and the dominant species changed from *Spathodea campanulata* to *Guarea guidonia*. Overall, ranked-species curves of IV for

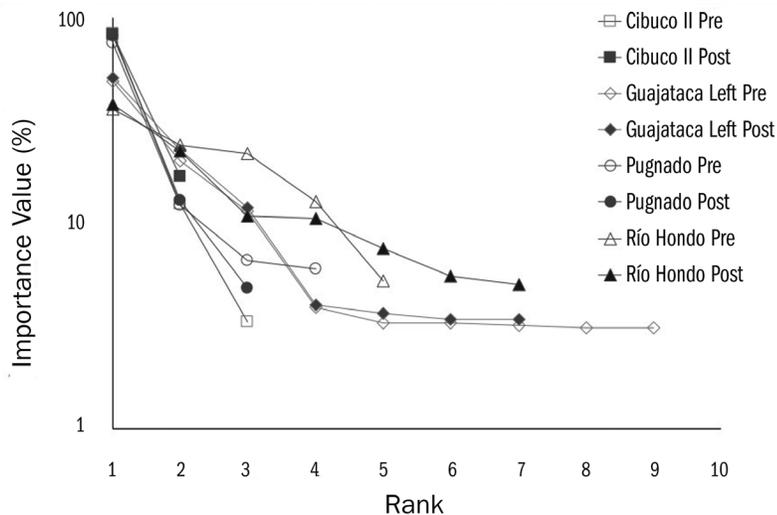


Figure 2. Ranked-species importance-values for large trees before (pre) and after (post) Hurricane María on four novel forests in the moist lowlands of Puerto Rico.

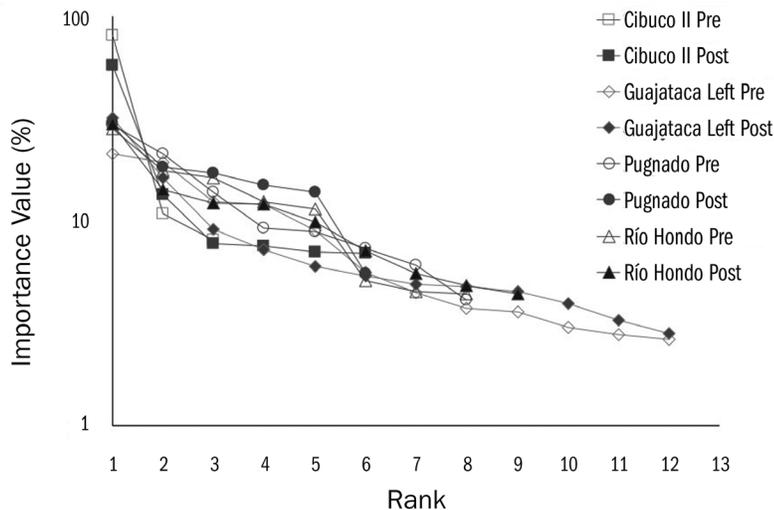


Figure 3. Ranked-species importance-values for small trees before (pre) and after (post) Hurricane María on four novel forests in the moist lowlands of Puerto Rico.

large and small tree size-classes on each site remained unmodified by the immediate effects of Hurricane María, with only the curves for the large tree size-class in Río Hondo exhibiting any perceptible modification (Figures 2 and 3).

### Patterns per Site

The density of large trees, basal area, and species richness of large trees tended to increase in all but one site, Río Hondo (Table 2). On the other hand, changes

in the density, basal area, and species richness of small trees exhibited a more variable pattern. For example, the density, basal area, and species richness of small trees increased in Cibuco II after the hurricane, but these variables decreased in Pugnado, and increased or decreased on the other two sites (Tables 2 and 3). The largest changes in the density, basal area, and species richness of large trees included a reduction of 33% in species richness in Cibuco II and an increase of 50% in density in Río Hondo. On the other hand, the largest changes in the density, basal area, and species richness of small trees included a reduction of 44% in density in Pugnado and a twofold (100%) increase in species richness in Cibuco II.

Changes in the density, basal area, and species richness of pooled size-classes of trees were also highly variable in direction (i.e., increased and decreased) when compared to changes in the large- and small-tree size-classes separately. However, the range of values was lower, and the means were overall closer to zero percent (i.e., ~no change) for the pooled size-classes of trees (Table 3). Post hoc Kruskal-Wallis tests showed there were no differences in the percentage of change in tree density, basal area, and species richness observed in the large-tree

size-class when compared to corresponding changes in the small-tree size-class among the four study sites ( $n = 4$ ,  $df = 1$ ,  $H \leq 0.52$ , and  $p \geq 0.5$  for all tests). Thus, we observed no clear tendency in the direction of changes in the density, basal area, and species richness among large- and small-tree size-classes. We also found no clear patterns or significant changes in the percentage of introduced species and the IV of the dominant species before and after the hurricane in the large- and small-tree size-classes (Table 2;  $n = 4$ ,  $T \leq 0.37$ , and  $p \geq 0.2$  for all paired T-tests).

**Table 4.** Summary of changes in tree density (trees/ha), basal area (m<sup>2</sup>/ha), species richness, and importance values of dominant species on two novel-forests in the short-term (1 yr.) and long-term (5–7 yrs.) aftermath of Hurricane Georges (from Lugo et al. 2005a,b). Trees were sampled on a 0.1 ha plot and classified as large (≥ 4 cm diameter at breast height [DBH]) and small (≥ 2 cm to < 4 cm DBH) in Caguana, a site on volcanic slopes in the moist to wet life-zone in the central mountains in the rural municipality of Utuado, Puerto Rico. Large (≥ 4 cm DBH) trees were sampled on circular 250 m<sup>2</sup> plots (n = 40) distributed across different landforms on moist lowland volcanic slopes and valleys in the New Millennium State Forest in urban Río Piedras, Puerto Rico. IV = Importance Value.

Size-class and site	Short-term changes (%)				Long-term changes (%)			
	Tree Density	Basal Area	Species Richness	Dominant Species IV	Tree Density	Basal Area	Species Richness	Dominant Species IV
<b>Large Trees</b>								
Caguana	27.2	-8.5	6.7	-22.2	56.4	10.4	33.3	-55.6
Río Piedras								
Valley	-	-	-	-	-5.3	0.0	4.4	-13.7
Sloping Valley	-	-	-	-	-2.2	-8.4	-5.1	4.6
Slope	-	-	-	-	-17.6	-19.8	2.8	-50.3
Ridge	-	-	-	-	-12.1	3.9	9.4	-15.8
All Landforms	-	-	-	-	-13.6	-7.1	-5.4	-18.8
<b>Small Trees</b>								
Caguana	-20.9	-22.3	0.0	11.1	23.0	15.1	4.5	22.2

## DISCUSSION

Our results stand in contrast to our expectations and to preliminary assessments of the effects of Hurricane María on Puerto Rico's forest cover, which suggested drastic reductions in tree density and basal area due to extensive tree mortality (Feng et al. 2018; Van Beusekom et al. 2018). Our results are comparable to the immediate effects of major (i.e., category-3 and higher) Hurricanes Betsy (1956), Hugo (1989), and Georges (1998) on the tree structure of wet forest stands in El Yunque observed in the short-term (< 3 years after the event), which include high and variable reductions in tree density (e.g., range of 27% to 63%, Brokaw and Walker 1991; Lugo 2008; Brokaw et al. 2012). We found similar reductions in tree density on two sites, but increments of equal magnitude on the other two sites, when data from large- and small-tree size-classes were pooled (Tables 2 and 3). Similar to patterns recorded in El Yunque, changes in basal area were not as large as for tree density and included more positive values (i.e., increments) among large trees, which suggest growth and recruitment into larger-tree size-classes in the short-term aftermath of Hurricane María. Nevertheless, changes in the mean values of density, basal area, and species richness of large and small trees for the four

study sites were close to zero (Table 3). This is surprising when considering the wide-spread extent of changes in vegetation-cover and mortality of trees reported throughout Puerto Rico in the immediate aftermath of Hurricane María (Feng et al. 2018; Van Beusekom et al. 2018).

### Changes in Forest Structure and Species Richness

Our results are comparable to the immediate effects of Hurricane Georges on a novel forest stand in Caguana, located in the municipality of Utuado in the central mountain range (Lugo et al. 2005a). In Caguana, the density of large trees increased, but the density of small trees and the basal area of both large and small trees decreased in the short-term aftermath of the hurricane (Table 4). In a study that included nine stands of novel forests dominated by *S. campanulata* in the wet mountains of Carite, near the municipality of Cayey in central south-eastern Puerto Rico, Pascarella et al. (2004) found short-term reductions in the density and basal area of large and small tree size-classes following Hurricane Georges. However, reductions in the density of small trees due to hurricane-induced mortality in Carite, although

comparably higher than for large trees, were offset by recruitment of juveniles found in the understory into the small tree size-class (Pascarella et al. 2004). In the short-term, the patterns observed in Caguana by Lugo et al. (2005a) are perhaps more similar to those that we observed in Río Hondo, and patterns observed in Carite by Pascarella et al. (2004) are more similar to those that we observed in Guajataca Left.

Similar to the immediate effects of major hurricanes on the tree structure of forest stands in Caguana, Carite, and El Yunque, species richness and the identity of the dominant species remained the same on our study sites in the short-term with the exception of small trees in Cibuco II, where species richness was doubled, and the dominant species was replaced after Hurricane María (Tables 2–4; Lugo 2008; Brokaw et al. 2012). Cibuco II, which is located on an exposed alluvial floodplain valley located near the trajectory of the eye of Hurricane María, stood out as the only site where the changes in the density, basal area, and species richness of small trees were all positive in direction, albeit considerable reductions in density and species richness of large trees (Figure 1; Tables 1–3). Before and after samples, however, were furthest spread apart in Cibuco II, which added uncertainty as to whether species turnover was directly related to the hurricane (Table 1). We elaborate further below on the implications of this and other caveats of sampling. Nevertheless, the high variation around the mean values of changes in the density, basal area, and species richness of large and small trees indicates that the immediate effects of Hurricane María that we were able to sample were highly uneven on the four sites (Tables 2 and 3). This high variation in changes observed due to the immediate effects of Hurricane María may amount to divergent trajectories of ecological succession, including contrasting rates of recruitment, biomass accumulation, species turnover, and dominant species identities, on these lowland novel forest stands in the long-term. Our results also indicate that the distance of forest stands to the trajectory of Hurricane María may have a significant effect

on the direction and magnitude of short-term changes in the density and basal area of trees, and possibly on long-term changes in tree species composition as well.

Río Hondo was the site located the furthest from the trajectory of Hurricane María, nearly as far from the hurricane's landfall as Guajataca Left, and its location on a gentle slope facing away from the hurricane eye's trajectory as it crossed the island possibly protected the site from direct winds of the highest velocity and, therefore, energy (Figure 1; Table 1; Lugo 2008; Pasch et al. 2018). Hurricane Irma's trajectory was located further north than Hurricane María's, and therefore Río Hondo, the site located furthest south, was also possibly less affected by the first hurricane relative to the other sites. Perhaps, in consequence, Río Hondo also stood out as the only site where the changes in the density, basal area, and species richness of large trees were all positive in direction (i.e., increased; Table 3). Río Hondo was also the only site where an increase in the density of large trees was observed and, along with Cibuco II, was one of the sites where most of the changes in the density, basal area, and species richness of large and small tree size-classes were positive in direction.

Overall, the positive changes (i.e., increments) observed in the density, basal area, and species richness of large and small trees on Cibuco II and Río Hondo after Hurricane María were offset by changes of similar magnitude, but of opposite direction (i.e., reductions), on Guajataca Left and Pugnado (Tables 2 and 3). Consequently, our statistical tests (i.e., paired-sample T-tests) found no significant changes in the density, basal area, and species richness of large and small trees on these four novel forest sites. Pugnado was the site closest to the trajectory of Hurricane María, nearly as close as Cibuco II to the hurricane's landfall, and therefore possibly the site subject to the strongest direct winds of highest velocity and energy (Figure 1; Pasch et al. 2018). This was manifested in notable reductions in the density, basal area, and species richness of both large and small trees in Pugnado (Table 3). Although Pugnado is located within a karst depression protected

by surrounding haystack hills (i.e., mogotes), the immediate effects of the hurricane on the tree structure were extensive and included a significant amount of felled, snapped, and uprooted large trees, which in turn caused direct structural changes to small trees.

In the long-term aftermath of Hurricane Georges, which was of lower intensity (category-3), Lugo et al. (2005b) found lower reductions in tree density, basal area, and species richness on novel forest stands located on low protected valleys relative to those located on the exposed hill and mountain slopes in urban Río Piedras (Table 3). This stands in contrast with our findings, in which the site located in a protected valley (i.e., karst depression), Pugnado, was subject to the highest reductions in tree density and basal area (Tables 1 and 3), and suggests that the intensity of Hurricane María was such that it offset any protection provided by landform and topography. In Guajataca Left, the site second closest to Hurricane María's trajectory and located on a coastal karst hill slope facing toward the trajectory of the hurricane's eye, all changes were also negative in direction except for an increase in the density of trees, and no change in species richness, in the small tree size-class (Figure 1; Table 3). It is possible that the traits of the dominant species in the large tree size-class in Guajataca Left, *T. catappa*, conferred some wind resistance to the forest canopy and made it less subject to crown branch breakage and fall to the forest floor. This may have buffered the forest understory from direct winds in Guajataca Left, and resulted in smaller structural changes to the small tree size-class on this site.

### Species Composition and Dominance

In spite of a possible tradeoff with flexibility, the higher wood density of *T. catappa* compared to the other two dominant species of large trees on our study sites, *A. procera* and *S. campanulata* (Francis and Lowe 2000), may have contributed to lower crown reductions by branch breakage and snapping in Guajataca Left. In fact, *T. catappa* is a pan-tropical coastal species native

to Indo-Pacific islands, which are subjected to intense, large, and infrequent disturbances that include typhoons and tsunamis (Francis and Lowe 2000; Lugo 2008). A lower amount of fallen branches could have protected the cohorts of small and juvenile ( $\leq 2.5$  cm DBH) trees already established in the forest understory in Guajataca Left. Previous observations indicated that the juvenile tree species composition in Guajataca Left was dominated by *Calophyllum calaba* before Hurricane María (unpublished data), and the increase in the IV of this species as dominant in the small tree size-class suggests that an advanced cohort of suppressed juvenile trees was released by the immediate effects of the hurricane (Table 2). Canopy opening from loss of foliage followed by high sunlight and nutrient availability from litter inputs to the forest floor may have favored the growth of *C. calaba* in Guajataca Left after the hurricane.

Although the dominant small-tree species in Guajataca Left remained the same (*C. calaba*), the increase in its dominance after the hurricane is consistent with empirical models (i.e., Vandermeer et al. 1996; Shimizu 2005): the replacement of small trees, which may be disproportionately subject to mortality induced by tree trunk and branch falls, occurred with smaller, juvenile trees that were established in the understory. The increase in the density of small trees observed in Guajataca Left is consistent with predictions of these models if it resulted from recruitment of juveniles into the small-tree size-class (Table 3). Likewise, the replacement of the dominant tree species was observed only in the small tree size-class on any site, but only in Cibuco II. Overall, this is also consistent with predictions of these models given the high abundance of the new dominant small-tree species (*G. guidonia*) in Cibuco II as a juvenile tree in the forest understory before the hurricane (Table 2; Abelleira et al. 2010). In contrast, we did not observe any substantial changes in the identity and IV of the dominant species of small trees on Pugnado and Río Hondo, and of dominant species of large trees on the four sites (Table 2). Also,

we did not find any differences in the changes in the tree density and basal area between large- and small-tree size-classes observed because of the hurricane (post-hoc Kruskal-Wallis tests), which suggests that any concomitant, long-term changes in the relative dominance of species due to changes in tree structure will proceed similarly on both tree size-classes.

The short-term effects of hurricanes on the composition and relative dominance of species of trees can be less predictable than changes in forest structure because species vary in ecological strategy, life-history, rates of resource-use and uptake (e.g., light-demanding pioneer species versus shade-tolerant late-successional species), and in adaptations to hurricanes (Lugo and Zimmerman 2002; Lugo 2008). For example, the roots of the late-successional and shade-tolerant canopy tree species *Dacryodes excelsa* graft between individuals in near monodominant stands in ridges in El Yunque, conferring superior stability when subjected to hurricane winds (Basnet et al. 1993). This adaptation can allow the standing and surviving trees of *D. excelsa* to maintain dominance at any given site in the aftermath of a major hurricane event. A shift towards a higher dominance of pioneer, light-demanding species, such as *Cecropia scheberiana*, is not necessarily observed in the short-term aftermath of hurricanes in El Yunque, which is characterized by a massive loss of foliage, downed trees and branches, and extensive canopy gaps that can significantly increase light and nutrient resources (Brokaw and Walker 1991; Scatena et al. 1993; Lugo 2008; Brokaw et al. 2012). Instead, the surviving trees resprout following crown-loss and uprooting, and the relative dominance of species at any one site is usually maintained, with factors such as aspect and topography influencing the magnitude of changes on the existing structure of the forest (i.e., resprouting and persistence-niche; Bond and Midgley 2001). We, therefore, lack previous well-founded reasons to expect any changes in the relative dominance (i.e., IV) and the identity of the dominant species in the large-tree size-class, which is mostly composed of

upper-canopy trees that are subjected to the most direct and strongest hurricane winds (Lugo 2008; Brokaw et al. 2012). If anything, our general expectation was a decrease in the dominance of introduced, light-demanding and fast-growing pioneer species, such as *A. procera* and *S. campanulata*, due to their frail and low-density wood (Francis 2000; Francis and Lowe 2000). Contrary to this general expectation, the IV of the dominant species in the large-tree size-class remained the same, and ranked-species IV curves for large- and small-tree size-classes were very similar in length, shape, and steepness before and after the hurricane on each site (Figures 2 and 3). This similarity in the shapes of ranked-species IV curves indicates only subtle short-term changes in tree species-dominance and diversity (Hubbell 2001).

In the short-term, our findings are comparable to those reported by Lugo et al. (2005a) on the immediate effects of Hurricane Georges on the relative dominance of tree species in a novel forest stand in Caguana (Table 4). In Caguana, the native and shade-tolerant treelet species *Miconia prasina* (Little and Wadsworth 1964) was and remained the dominant species in the large- and small-tree size-classes before and after the hurricane; its relative dominance (i.e., IV) also remained largely unchanged in the short-term (Table 4). However, the replacement of *M. prasina* by a native fast-growing and light-demanding pioneer species of tree, *Didimopanax morototoni*, was observed in the large-tree size-class seven years after Hurricane Georges in Caguana, along with considerable changes in the relative dominance of species. On the other hand, the shade-tolerant species *Hymenaea courbaril* and the light-demanding species *Tabebuia heterophylla* (Little and Wadsworth 1964; Francis and Lowe 2000), which are both native species, were the dominant species (along with *S. campanulata*) in the large-tree size-class of stands of novel forests in most landforms sampled by Lugo et al. (2005b) in Río Piedras. The relative dominance of these three species on any given stand remained largely the same when

sampled one year and seven years after Hurricane Georges (Table 4). These observations and our findings indicate that there can be a lag-time of at least a decade for the replacement of large tree species that dominate the canopies of lowland novel-forests in Puerto Rico. These examples also show that the replacement of the dominant large-tree species can be accelerated by ecological strategy or life-history traits, such as short stature in the case of *M. prasina*, which may not be favored in the long-term. We observed no consistent pattern of change in the percentage of introduced species in the large- and small-tree size-classes after the hurricane, which suggests that specific life-history traits, rather than biogeographical origin, mediate the influence of hurricanes on the relative dominance of tree species.

### Caveats of Sampling and Recommendations

Our study emerged as a necessity to assess the immediate and visible effects of Hurricane María on novel-forest sites where on-going studies were occurring and we, therefore, expand upon some considerations of the sampling design to provide context and ease comparisons with other studies. Since we only sampled trees that were alive, standing, and  $\geq 2.5$  cm in DBH, our preliminary assessment does not include changes in other attributes of trees and forest stands, for example, crown reduction and loss of main branches. Our assessment also does not quantify tree mortality and cannot be used to determine if the trees that were subject to the most remarkable structural-changes will survive in the long-term. Nonetheless, Lugo et al. (2005b) studied novel-forest stands on various landforms in Río Piedras seven years after Hurricane Georges (Table 4) and found that tree mortality amounted to an overall average of 3.8% per year for standing trees, including those standing trees with significant, visible effects.

Growth and recruitment of trees between sampling dates offset the changes caused by the

hurricane, particularly in Cibuco II. In fact, the basal area of trees sampled on Cibuco II after Hurricane María represented an increase to exceptionally-high levels, although within the range found for novel forests dominated by *S. campanulata* on alluvial floodplains in northern Puerto Rico (Abelleira et al. 2010). It is likely that the dozen years that elapsed between 2005, when the site was initially sampled, and the hurricane event in 2017, resulted in an even higher basal area immediately before the hurricane (i.e., right before September 2017) than after the event (i.e., in 2018) in Cibuco II. On the other hand, our implementation of the PCQM, which included randomization of points on both sampling dates, may have added some level of uncertainty to our estimates of immediate effects from the hurricane on three of our study sites, including Cibuco II, because the actual trees sampled before and after the hurricane were not necessarily the same on the three sites where the PCQM was used. Future studies can reduce the magnitude of this uncertainty by re-sampling the same PCQM points that were initially placed on sampling dates before the hurricane (i.e., no randomization). This would require the development of algorithms to deal with the possibility and problem of sampling the same tree on contiguous PCQM points, which can happen when the points are not randomized and are to be placed on lineal transects that are initially restricted in length. Comparing estimates obtained from both approaches to the method (i.e., with and without randomization of points in post-hurricane sampling) may help clarify the best approach to the method when applied to the long-term sampling of sites that may be subjected to the effects of major hurricanes.

Finally, future studies combining a larger sample-size with continued long-term sampling, can help evaluate if changes in the tree structure and species composition of Puerto Rican forests, at a regional level, are indeed related to the distance from the trajectory of Hurricane María. Establishing whether

this relationship holds across numerous sites can be useful to improve upon assessments of the effects of major hurricanes on the structure (e.g., biomass and carbon stocks) and species composition, including flora and fauna, of forests and other ecosystems in Puerto Rico and elsewhere in the Caribbean. Long-term sampling on novel-forest sites can improve our understanding of how novel-forest ecosystems respond to the effects of major hurricane disturbances, and how effects and responses compare with those of other secondary forests, primary forests, and other ecosystem types, such as herbaceous wetlands and prairies, in the Caribbean.

## CONCLUSION

We interpret our results to be consistent with high, net growth-rates and recruitment into size-classes of larger trees, which are characteristic of young secondary-forests that have been subject to major hurricane disturbances (Lugo et al. 2005a,b; Pascarella et al. 2004; Flynn et al. 2010). Contrary to our expectations, we found no consistent and general reductions in the density, basal area, and species richness of large and small trees on these four novel-forest sites. Similar to the well-documented case of El Yunque, our findings suggest that little changes in the species richness, composition, and the relative dominance of species in novel-secondary-forests can be expected in the short-term due to the visible and immediate effects of major hurricanes in Puerto Rico. In fact, our results are consistent with studies that report an increase in the variability in tree density, basal area, and species composition, as well as in growth rates and other ecological processes, in short- to long-term aftermaths of hurricanes in novel forests in Puerto Rico (Table 4; Lugo et al. 2005, b). Finally, our results suggest that the distance of any given site from the trajectory of a major hurricane could be a factor to consider in future studies to understand better the effects of hurricanes on the direction and magnitude of changes in

the structure and species composition of novel forests and other ecosystems in the Caribbean.

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# SOBRE EL USO DE MAYÚSCULA EN NOMBRES COMUNES: RECOMENDACIONES Y PROPUESTA PARA LA ESCRITURA CIENTÍFICA

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## Resumen

Examinamos aquí el uso de mayúsculas en los nombres propios y comunes en la escritura científica y técnica. Discutimos ejemplos y definiciones de términos relevantes, tanto en español como en inglés, destacando casos en los que carecemos de pautas categóricas sobre el uso uniforme de las mayúsculas en los sustantivos comunes. Además, destacamos casos en los que su uso entre las disciplinas de las ciencias biológicas y las normas ortográficas es bastante variable. Por tanto, proponemos la utilización de mayúsculas en los nombres comunes considerados nombres propios cuando se pretende mantener vínculos y contextos culturales, históricos e idiosincrásicos. Estos vínculos y contextos son fundamentales para mantener una comunicación eficaz en las ciencias biológicas, puesto que reconocemos que la escritura científica también es de origen humanístico.

**Palabras clave** escritura científica y técnica, mayúsculas, nombres científicos, nombres comunes, nombres propios.

## Abstract

In this essay, we examine the capitalization of common and proper nouns in scientific and technical writing. We discuss examples and definitions of relevant terms, both in Spanish and English, highlighting instances where we lack guidelines on the uniform use of capitalization of common nouns. Also, we highlight instances where its use between the disciplines of the biological sciences and the grammatical rules in linguistics is equivocal. Herein, we propose the capitalization of common names considered proper names when intended for maintaining cultural, historical, and idiosyncratic bonds and contexts. These bonds and contexts are fundamental to maintain effective communication in biological sciences as scientific writing is also of humanistic origin.

**Keywords** capitalization, common nouns, proper names, scientific and technical writing, scientific names.

## SOBRE EL USO DE MAYÚSCULA EN NOMBRES COMUNES: RECOMENDACIONES Y PROPUESTA

El uso de mayúsculas para nombres comunes de plantas y animales o incluso para otros sustantivos en idiomas como el inglés y español representa un

tema inconcluso, presumiblemente influenciado por la dicotomía entre claridad y convencionalidad en la norma lingüística, o como diría Amelia de Irazzábal, entre los especialistas y terminólogos con los lingüistas (de Irazzábal Nerpell 2004). De acuerdo con Puerto Sarmiento (2004: página 60), "...parece imprescindible hacer comprensible la ciencia a los

ciudadanos en su propia lengua, para lo cual es tan necesario normalizar el vocabulario científico, como hacer habituales los propios conocimientos científicos entre los ciudadanos”. [por tanto] “La tarea de hacer un vocabulario científico en castellano corresponde a las instituciones y a los propios científicos”. Culmina Puerto Sarmiento (2004): “Para ello, sería imprescindible el establecimiento de algún medio de comunicación científica en castellano, de gran prestigio, en donde pudieran exponer sus trabajos los pertenecientes a la segunda lengua del mundo en número de practicantes”. Aunque al presente el inglés sea el idioma indiscutible para la divulgación del conocimiento científico a nivel global (tal como en su tiempo el francés, el alemán, el holandés, el danés y el latín), el lector puede referirse, para consultas en español, al diccionario en línea del *Vocabulario Científico y técnico* de la Real Academia de Ciencias Exactas, Físicas y Naturales de España (disponible en [https://vctrac.es/index.php?title=Categor%C3%ADa:Biolog%C3%ADa\\_Da\\_Fundamental](https://vctrac.es/index.php?title=Categor%C3%ADa:Biolog%C3%ADa_Da_Fundamental)) y visitar el portal de la Real Academia de Ciencias Exactas, Físicas y Naturales (<https://rac.es/>) para asuntos relacionados y consultas.

El presente ensayo del tema en cuestión – el uso de mayúsculas para nombres “comunes” de especies – obliga al uso de referencias tanto en inglés como en español, muchas veces con el uso intercalado de ambos. Por ejemplo, el *Chicago Manual of Style* (2017; *Scientific Style and Format*), capítulo 22, *Taxonomy and Nomenclature*, plantea: “There is no authoritative source of guidance on writing vernacular names for plants, and there is inconsistency in how vernacular names are presented.” Igualmente, para nombres comunes de animales, este manual indica “*Lists of approved vernacular names for species in a number of phyla have been published: amphibians and reptiles [Collins and Taggart 2009], cnidaria and ctenophora [Cairns et al. 2002], mollusks [Turgeon et al. 1998], decapod crustaceans [McLaughlin et al. 2005; Williams et al. 1989], fishes*<sup>1</sup>

<sup>1</sup> FINS: the Fish Information Service. Fish index. Cambridge (MA): Active Window Productions, Inc.; c1993–2009 [accessed 2012 Sep 7]. <http://fins.actwin.com/species/>.

[Nelson et al. 2004], insects<sup>2,3</sup>, and birds<sup>4</sup> [Sibley and Monroe 1990].” (énfasis suplido). Estas listas son inconsistentes en cuanto al uso de mayúsculas en nombres denominados “comunes” y las mayúsculas son utilizadas libremente a *prima facie*. Entonces, no es de sorprender que el *New Oxford Style Manual* (2016: página 94; traducido libremente del inglés) también indique: “Es imposible establecer reglas absolutas para todos los aspectos de la aplicación de mayúsculas; como ocurre con el uso del guion y la separación silábica, el uso de mayúsculas en una palabra en particular dependerá de su función en la oración y también, hasta cierto punto, del gusto personal del escritor o del estilo de la guía/manual que se siga”.

Consideremos el siguiente ejemplo en inglés, pero igualmente aplicable al español, que ilustra parte de la brecha en comunicación en el trato de nombres denominados comunes y propios de especies (taxonómicas, en el contexto biológico; Nichol 2011)<sup>5</sup>:

“Words that comprise the names of plant species are generally lowercase: ‘Lumber from the live oak is rarely used for furniture.’ Exceptions occur when one or more of the words is named after a person or a geographical location, as in the name of the California poppy. (The flowering plant bougainvillea is named after French explorer Louis Antoine de Bougainville, but plant names so inspired are still lowercase). An exception is also made for references to types of fruits and vegetables, such as Red Delicious apples or Early

<sup>2</sup> Entomological Society of America, Committee on the Common Names of Insects. Common names of insects and related organisms. Lanham (MD): ESA; c1995–2005 [accessed 2011 Nov 11]. <http://www.entsoc.org/common-names>.

<sup>3</sup> Iowa State entomology index of Internet resources. Ames (IA): Iowa State University, Entomology Department; c2005 [accessed 2011 Nov 11]. <http://www.ent.iastate.edu/list/directory/130/vid/4>.

<sup>4</sup> American Ornithologists’ Union (A.O.U.) Check-list of North American birds. 7th ed. McLean (VA): American Ornithologists’ Union; [accessed 2011 Nov 11]. <http://www.aou.org/checklist/north/print.php>.

<sup>5</sup> Nichol, M. 2011. When to Capitalize Animal and Plant Names. *Daily Writing Tips*, actualizado noviembre 2020. Disponible en <https://www.dailywritingtips.com/when-to-capitalize-animal-and-plant-names/>.

Girl tomatoes. Then there are names of cultivars, or cultivated varieties, of plants, such as that of a kind of broccoli, *Brassica oleracea* ‘Calabrese’. [...] as in the case of plant names, animal names are not capitalized (‘I spotted a red-tailed hawk,’ not ‘I spotted a Red-Tailed Hawk’), except when an element of the name is a proper noun, as in ‘Steller’s jay’ and ‘Siberian tiger.’ [...] The rules are complicated, but it’s a simple enough matter to get a ruling: Check the dictionary.”

Por el contrario, Gill et al. (2020)<sup>6</sup> se refiere al uso de mayúsculas para aves y sus nombres comunes como sigue:

“An important rule adopted at the outset was that the words of an official birds name begin with capital letters. While this is contrary to the general rules of spelling for mammals, birds, insects, fish, and other life forms (i.e., use lowercase letters), the committee believed the initial capital to be preferable for the name of a bird species in an ornithological context, for two reasons.

- 1) It has been the customary spelling in bird books for some years;
- 2) Because it distinguishes a taxonomic species from a general description of a bird. Several species of sparrows could be described as ‘white-throated sparrows,’ but a ‘White-throated Sparrow’ is a particular taxonomic species.

Jon S Greenlaw recently expanded this concept (in litt.) as follows: The value of capitalizing the English names of animals seems obvious to me. Somewhere deep in the history of our language, we came to regard vernacular and ‘common’

names as second-class citizens. Thou shalt not capitalize them. I believe that it has something to do with the (mis-) perception of species by folks in the humanities as ‘categories’ or ‘classes’ rather than as real entities (to the extent that we can know them). Well, biology has come a long way from that typological view. The standardized English names now have graduated from the realm of ‘common/vernacular’ names. From my perspective, the strongest argument for capitalizing the English names of birds is that we now have a single, unique name (see below) for each of the biological entities that we call bird species. These names must be regarded as proper nouns (thus receive capitals in all English publications), rather than as common nouns (vernacular names). My unabridged dictionary defines a ‘proper noun’ as (1) a word that is not necessarily preceded by an article (e.g., ‘the,’ ‘a’) and (2) denotes a particular person, place, or thing. A species is a particular thing or biological entity. We have other proper nouns in the English language that are composites as well. We talk about the ‘Great Lakes,’ the ‘Rocky Mountains,’ and the ‘Alps.’ In the same way, ‘American Robin’ says it all. No “the” is necessary except as grammatical stricture in a sentence may require one for proper nouns.”

De este ejemplo, parece revelarse un contexto cultural, histórico e idiosincrásico que permea significativamente los nombres otorgados a las especies de aves (y otros elementos naturales como veremos más adelante). Coincidentemente, es frecuente leer nombres comunes de especies escritos en mayúsculas en unas fuentes y en minúsculas en otras, sin importar – al menos en el caso del español y el inglés – el origen geográfico-político de la publicación. Este fenómeno sugiere varios asuntos: en primer lugar, pudiere existir la necesidad inherente del científico (con cierta formación humanística) de reconocer estas particularidades locales y referirse a un nombre considerado por unos “común” (si fuese en

<sup>6</sup> Gill, F., D. Donsker, and P. Rasmussen (eds). 2020. IOC World Bird List (v10.2). doi:10.14344/IOC.ML.10.2. *International Ornithological Committee’s (IOC) World Bird List* (Available at <http://www.worldbirdnames.org/new/english-names/spelling-rules/capitalization/>); Updated 25 Jul 2020 with version 10.2. Licensed under a Creative Commons Attribution 3.0 Unported License. Accessed November 2020.

estricto uso ortográfico) como uno propio. Segundo, pudiere existir una brecha en la comunicación entre las distintas disciplinas o, al menos, entre el remitente y el destinatario a base de sus trasfondos de interés y la aplicabilidad de la lingüística (ver de Irazazábal Nerpell 2004). Ya sea una o la otra, esta brecha manifiesta la necesidad de un contexto pragmático de la comunicación humana que no ha podido satisfacerse a plenitud en la literatura científica, técnica (y otras, inclusive).

El tema sobre la aplicabilidad de mayúsculas a nombres comunes y propios en el contexto taxonómico (biológico) parece complicarse ante el hecho que no contamos con una regla generalizada para el uso de mayúsculas en la literatura científica técnica, incluso en escritos no científicos pero que se refieren a especies en un contexto similar. Entonces, podríamos examinar los siguientes aspectos:

- 1) ¿Qué es un nombre “común” o “vernáculo” para las ciencias naturales (en relación con la taxonomía) comparado con otras ciencias como la lingüística (y en específico, su normativa ortográfica)?;
- 2) ¿Cómo aplicar la normativa ortográfica española a la literatura de las ciencias naturales teniendo presente la naturaleza del lenguaje como proceso dinámico de comunicación entre humanos?;
- 3) ¿Qué relación, si alguna, tiene un nombre “común” en la escritura en las ciencias naturales y el contexto cultural, histórico e idiosincrásico que carga dicho nombre?;
- 4) Ante la naturaleza dinámica de la lengua ¿existe prelación entre claridad y convencionalidad dentro del contexto extralingüístico (pragmática versus normativa)?

Trataremos el tema del uso de mayúsculas para nombres considerados “comunes” de especies más allá del contexto de la normativa ortográfica tradicional, pero utilizando definiciones y textos puntuales

de manuales y guías reconocidas de escritura en general. Específicamente, con una perspectiva que vincule la intención del uso del nombre para distinguir al sujeto por sobre otros clasificados en su mismo grupo (la definición misma de “nombre propio”). Al finalizar este ensayo, se hace obvia la reconceptualización de nombres no científicos como propios, en vez de comunes (autóctono o vernáculo), y se justifica el uso de mayúsculas para los mismos desde el contexto extralingüístico en la comunicación científica. Igualmente, se hace obvio el uso de mayúsculas cuando por antonomasia<sup>7</sup> se justifica su uso para otros nombres, por ejemplo, de fenómenos naturales. Así, proponemos la consideración extralingüística en el uso ortográfico normativo para nombres no científicos con la justificación de una comunicación efectiva y más precisa en la escritura científica técnica, y posiblemente no técnica, al preservar la carga cultural, histórica e idiosincrásica del nombre común convertido en propio.

### **Español—El significado de “nombre propio” y “nombre común” (autóctono o vernáculo)**

El *Diccionario de la lengua española*, Edición del Tricentenario, cuya versión del 2019 está disponible en <https://dle.rae.es/> es producto de la colaboración de las veintidós academias que constituyen la Asociación de Academias de la Lengua Española (ASALE), en la que, por supuesto, Puerto Rico está representado. El mismo indica:

- 1) nombre propio
  - a. “m. *Gram.* por oposición al común, nombre sin rasgos semánticos inherentes que designa un único ser; p. ej., *Javier, Toledo*”. (disponible en <https://dle.rae.es/nombre?m=form#7jtE0eh>).

<sup>7</sup> Término que “denota que a una persona o cosa le conviene el nombre apelativo con que se la designa, por ser, entre todas las de su clase, la más importante, conocida o característica” – tomado del *Diccionario de la Real Academia Española* (consultado en noviembre 2020). Disponible en <https://dle.rae.es/antonomasia>.

## 2) nombre común

- a. “1. m. *Gram.* nombre que se aplica a personas, animales o cosas que pertenecen a una misma clase, especie o familia, y cuyo significado expresa su naturaleza o sus cualidades. El sustantivo naranja es un nombre común. 2. m. *Gram.* nombre común en cuanto al género”. (disponible en <https://dle.rae.es/nombre?m=form#7JlxxL0>).

Por otro lado, cabe destacar en dicho diccionario el siguiente pasaje relacionado al “PLURAL. 2. OTRAS CUESTIONES RELATIVAS AL PLURAL” (<https://www.rae.es/dpd/plural>):

“2.8. **Nombres propios.** Puesto que los nombres propios, a diferencia de los comunes, no designan clases de seres, sino que **sirven para identificar un solo ser de entre los de su clase (énfasis suplido)**, no suelen emplearse en plural. Sin embargo, al existir seres que comparten el mismo nombre propio, sí cabe usar este en plural para designar varios referentes: *Los Javieres que conozco son todos muy simpáticos; En América hay dos Córdoba, una en la Argentina y otra en México*”.

La *Ortografía de la lengua española* (RAE-ASALE 2010) establece en el apartado relacionado con el uso de mayúsculas y minúsculas (página 455) que:

“La función principal de la mayúscula en español es la de distinguir el nombre propio del nombre común. Aunque su aplicación no presenta ningún problema en los miembros prototípicos de una y otra clase (nadie duda que Irene se escriba con mayúscula o tobillo con minúscula), **existe una casuística amplia y compleja de expresiones denominativas (énfasis suplido)** en las que el uso de la mayúscula puede plantear dudas a quien escribe”.

Continúa ASALE (2010; página 474), sobre **4.2.4.5.3. Nombres vernáculos de animales y plantas**, se plantea que:

“Los nombres con los que se designan en español las distintas especies de animales y plantas se escriben con minúscula inicial **por su condición de nombres comunes (énfasis suplido)**: el águila real, el alcaudón chico, la ballena jorobada, el buitre leonado, la comadreja, el oso pardo, el encina, el espliego, la palma de coco. No hay razón lingüística alguna para escribirlos con mayúscula, aunque así se vean escritos a menudo en textos especializados”.

No obstante, los ejemplos de nombres comunes de animales y plantas mencionados por RAE-ASALE (2010) en el pasaje anterior refleja la complejidad del asunto en cuestión: una brecha comunicativa entre los lingüistas con los especialistas y terminólogos (parafraseando a de Irazzábal Nerpell [2004]), desde el contexto socio-cultural-histórico de la ciencia. Por ejemplo, algo que tienen en común los nombres antes mencionados es que: (1) los ejemplos son de organismos con distribución espacial (geográfica) amplia, tanto a nivel continental como transcontinental y transoceánica; (2) cada ejemplo posee decenas de nombres comunes dependiendo de la región o país donde se encuentra el organismo en cuestión; (3) varios ejemplos de nombre común se utilizan para incluir muchísimas especies, por ejemplo, “comadreja” para agrupar al menos a las diecisiete (17) especies de mamíferos reconocidas en la taxonomía científica dentro del género *Mustela* o el ejemplo de “el espliego” o lavanda o alguno otro de los sobre 18 nombres comunes con los que se conoce a esta planta regionalmente. El siguiente ejemplo refleja una peculiaridad mayor y muy pertinente al presente ensayo: la carga cultural, histórica e idiosincrásica que justifica el uso de mayúsculas para un nombre común.

RAE-ASALE (2010) incluye el ejemplo del nombre común “encina”, conocido también como roble o charparro (del Vasco, txaparro; ver <https://dle.rae.es/>), para referirse presumiblemente a una de las especies de árbol del género *Quercus* sp. (género que alberga >350 especies distribuidas a nivel mundial). No obstante, es interesante notar el carácter cultural, histórico y

de identidad que carga el uso del nombre común “encina” en el titular del *Diario de Navarra*, “El original Encino de las Tres Patas de Mendaza” (véase *Diario de Navarra*, del 19 de febrero de 2020; <https://www.diariodenavarra.es/noticias/navarra/2017/07/17/el-original-encino-las-tres-patas-541934-300.html>). Este nombre común aparece destacado como nombre propio – “Encino de las Tres Patas de Mendaza” – para referirse al árbol que ubica en el paraje del monte La Laguna, en el consejo (o municipio) de Mendaza en Navarra, al norte de la Península Ibérica colindante con Francia. Este árbol (así como muchos otros) fue declarado Monumento Natural en 1991 (DECRETO FORAL 165/1991, de 25 de abril, del Gobierno de Navarra, por el que se declaran Monumento Natural determinados árboles singulares de Navarra; <https://docplayer.es/45221864-Gestion-de-monumentos-naturales-en-navarra-los-arboles-monumentales.html>). Note entonces cómo la nota periodística – uno de los medios de comunicación que para un pueblo representa una avenida asequible de educación continua una vez dejamos la escuela, en general, y la academia, en particular – destaca que: “*Los vecinos colocaron un cinturón de metal alrededor para parar la grieta originada por torsión en el tronco*”, una acción que, para muchos, significa el proteger lo que a todas luces representa una carga cultural, histórica y de identidad para esta comunidad: nuestra “encina”. En este contexto, el uso de mayúscula para distinguir a uno de entre su clase y por tanto, referirse a esta con un nombre propio cuando la identificación de la referencia es inequívoca. Este contexto en el uso de la mayúscula no se desprende de los ejemplos seleccionados por RAE-ASALE (2010) en estricta ortografía para justificar el uso de minúsculas para nombres comunes de animales y plantas. Por tanto, es posible que la comunicación efectiva del español en la ciencia pudiere conllevar algo más que la aplicación estricta de reglas gramaticales.

No debe sorprender entonces el hecho de que en RAE-ASALE (2010) también se establece, en varios

pasajes y con meridiana claridad, que (páginas 445–446):

“Las normas de uso de las mayúsculas en cada lengua son convencionales, por lo que no son inamovibles y están sujetas a cambio y evolución”.

“...en el uso de las mayúsculas influye, como en tantos otros aspectos de la ortografía, el peso de la tradición e intervienen otros factores, como la intención de quien escribe, el tipo de texto o el contexto de aparición”.

“Las normas de aplicación de la mayúscula que se exponen en el presente capítulo intentan de modo claro y sencillo del mayor número de casos, pero es a todas luces imposible prever y explicar todos los contextos en los que quien escribe puede optar por utilizar la mayúscula o la minúscula en función de variables muy diversas, sin que, en rigor, **ninguno de los dos usos pueda considerarse incorrecto**”. (énfasis suplido).

La RAE-ASALE, en su *Diccionario panhispánico de dudas* (2005), disponible en <https://www.rae.es/dpd/mayúsculas>, y visitado 31 de octubre de 2020, añaden sobre el uso de mayúsculas en nombres propios y comunes (capítulo 4):

“4. *Uso de mayúscula inicial independientemente de la puntuación*. Se escriben con letra inicial mayúscula todos los nombres propios y también los comunes que, en un contexto dado o en virtud de determinados fenómenos (como, por ejemplo, la antonomasia), funcionan con valor de tales, es decir, cuando designan seres o realidades únicas y su función principal es la identificativa”.

“4.22: Los nombres de marcas comerciales. Las marcas comerciales son nombres propios, de forma que, utilizados específicamente para referirse a un producto de la marca, han de escribirse con mayúscula: *Me gusta tanto el Cinzano como el Martini; Me he comprado un Seat*; pero cuando estos nombres pasan a referirse no exclusivamente a un objeto de la marca en

cuestión, sino a cualquier otro con características similares, se escriben con minúscula: *Me aficioné al martini seco en mis años de estudiante* (al vermú seco, de cualquier marca)”.

“4.27: Determinados nombres comunes cuando, por antonomasia, designan una sola de las realidades de su misma clase: *el Diluvio* (referido al diluvio bíblico), *la Reconquista* (referida a la de los territorios ocupados por los musulmanes, llevada a cabo por los reinos cristianos peninsulares durante la Edad Media), *el Muro* (referido al que separaba en Berlín los sectores oriental y occidental)”.

“4.7. [...] Los nombres comunes genéricos que acompañan a los nombres propios geográficos (*ciudad, río, mar, océano, sierra, cordillera, cabo, golfo, estrecho*, etc.) deben escribirse con minúscula: *la ciudad de Panamá, el río Ebro, la sierra de Gredos, la cordillera de los Andes, el cabo de Hornos*. Solo si el nombre genérico forma parte del nombre propio, se escribe con mayúscula inicial: *Ciudad Real, Río de la Plata, Sierra Nevada, los Picos de Europa*. **También se escriben con inicial mayúscula algunos de estos nombres genéricos cuando, por antonomasia, designan un lugar único y, por lo tanto, funcionan a modo de nombre propio. Estas antonomasias están lógicamente limitadas en su uso a la comunidad de hablantes que comparten una misma geografía, para los que la identificación de la referencia es inequívoca, como ocurre, por ejemplo, entre los chilenos, con *la Cordillera* (por la cordillera de los Andes) o, entre los españoles, con *la Península* (por el territorio peninsular español) o *el Estrecho* (por el estrecho de Gibraltar) (énfasis suplido)**. El hecho de escribir *Península Ibérica* con mayúsculas se debe a que con esta expresión nos referimos a una entidad de carácter histórico-político, y no a un mero accidente geográfico”.

Finalmente, se define “antonomasia” como (disponible en <https://dle.rae.es/antonomasia>) “1. loc. adv. Denota que a una persona o cosa le conviene el nombre apelativo con que se la designa, por ser, entre todas las de su clase, la más importante, conocida o característica”.

Por todo lo expuesto hasta aquí, las academias aparentan dar cierto espacio a la claridad por sobre lo convencional en cuanto al uso de mayúscula para un nombre genérico cuando el caso representa una antonomasia reconocible en una comunidad de hablantes que comparten una misma geografía o para quienes la identificación de la referencia es inequívoca en comparación con otros sustantivos similares. Igualmente, el trato en el uso de mayúsculas sobre el nombre de marcas provee de una analogía al trato similar de un “producto” (una sola de las realidades de su misma clase; aplicación de “nombre propio” con la aplicación de mayúscula que corresponde) o de una “marca” (como analogía, una especie).

### Inglés—El uso de mayúsculas para nombres propios y comunes

El *New Oxford Style Manual* (2016), capítulo 5, páginas 95–106 se refiere en términos similares a las academias de lengua española en cuanto al uso de mayúsculas y los nombres comunes:

“Capital letters in English are used to punctuate sentences, to distinguish proper nouns from other words, for emphasis, and in headings and work titles. It is impossible to lay down absolute rules for all aspects of capitalization; as with hyphenation, the capitalization of a particular word will depend upon its role in the sentence, and also to some extent on a writer’s personal taste or on the house style being followed. Also, certain disciplines, especially history, have their own particular styles of capitalization. However, some broad principles are outlined below. Editors should respect the views of authors, except in cases of internal discrepancies. Both authors and editors should strive for consistency: before writing or editing too much of a work, consider the principles that should govern capitalization, and while working through the material create a style sheet showing capitalization choices, and stick to it.” (página 95).

“Historians commonly impose minimal capitalization on institutional references; this may sometimes appear unconventional and should not be permitted if it will obscure genuine differences in meaning (as, for example, between the catholic church and the Catholic Church), although readers will seldom misunderstand lower-case forms in context. The style is common in, and appropriate to, much historical work, but editors should not introduce it without consulting with the author and/or publisher.” (página 96).

“It is as well, generally, to minimize the use of initial capitals where there is no detectable difference in meaning between capitalized and lower-case forms.” [...] “Overuse of initial capitals is obstructive, and can even confuse by suggesting false distinctions.” (página 96).

Finalmente, el *New Oxford Style Manual* (2016), páginas 105–106, en “*Trade Names*” (sección 5.15) sobre “*Ships, aircraft, and vehicles*” (sección 5.16) indica: “*In general proprietary terms should be capitalized...*” [...] y “*Capitalize names of ships and vehicles, using italics for individual names but not for types, models, or marques...*”. (énfasis suplido).

Un tema estrechamente relacionado es la estandarización de nombres científicos a base de guías y reglas que rigen la nomenclatura biológica (taxonómica). El tema de nomenclatura taxonómica es menos controversial y mucho más regulado internacionalmente: su objetivo es precisamente generar un lenguaje “universal” que incluye, al momento: (1) virus, (2) procariontes, (3) plantas, algas y hongos, y (4) animales. Estas guías son:

- 1) *The International Code of Virus Classification and Nomenclature* (disponible en línea en <https://talk.ictvonline.org/information/w/ictv-information/383/ictv-code>);
- 2) *International Code of Nomenclature of Prokaryotes, Prokaryotic Code*<sup>8</sup> (disponible en <https://ccug.se/>

<sup>8</sup> Parker, C. T., B. J. Tindall, and G. M. Garrity (eds.). 2019. International Code of Nomenclature of Prokaryotes, Prokaryotic Code (2008 Revision). *International Journal of Systematic and Evolutionary Microbiology* 69: S1–S111.

[documents/taxonomy/prokaryotic\\_code/2019\\_Parker-Tindall-Garrity\\_Prokaryotic%20Code%20-%202008%20Revision.pdf](https://www.ictvonline.org/documents/taxonomy/prokaryotic_code/2019_Parker-Tindall-Garrity_Prokaryotic%20Code%20-%202008%20Revision.pdf));

- 3) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)*<sup>9</sup> (disponible en español en <https://www.iapt-taxon.org/nomen/Shenzhen/Spanish/Spanish.pdf>);
- 4) *International Code of Zoological Nomenclature*<sup>10</sup> (disponible en español en <http://www.sam.mncn.csic.es/codigo.pdf>).

Ese *Código Internacional de Nomenclatura Zoológica* (en español) plantea con respecto al tema de nombres comunes en su “**Artículo 11. Requisitos**”:

“**Recomendación 11A. Uso de nombres vernáculos.** Una palabra vernácula sin modificar no debiera usarse como nombre científico. La latinización apropiada es el medio preferido en la formación de nombres a partir de palabras vernáculos”. (página 11).

Igualmente, el glosario de este Código define:

“**nombre, m.** (1) Palabra, o secuencia ordenada de las mismas, que se usan convencionalmente para indicar e identificar una entidad concreta (p. ej., una persona, un lugar, un objeto o un concepto). (2) Equivalente de nombre científico (véase). (3) Elemento del nombre de un taxón de nivel especie: véase nombre genérico, nombre subgenérico, nombre específico, nombre sub-específico” (página 113).

<sup>9</sup> Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smith (eds.). 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. Glashütten: Koeltz Botanical Books. DOI <https://doi.org/10.12705/Code.2018>

<sup>10</sup> International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth edition. Published by the International Trust for Zoological Nomenclature [ITZN], The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

“**nombre vernáculo.** Nombre de un animal o unos animales en una lengua de uso corriente en contraposición a un nombre propuesto sólo para la nomenclatura zoológica” (página 116).

Las referencias consideradas muestran diferencias en el modo en que los nombres “comunes” son escritos en la literatura científica, tanto en inglés como español. Igualmente, se refleja la intención de quien escribe de destacar la particularidad del nombre utilizado en un contexto pragmático, humanista, cuyos elementos culturales, históricos e idiosincrásicos se conserven en dicho nombre – algo que se pierde con el uso del término científico. Entonces, en este ensayo se hace hincapié en:

- 1) la intención de utilizar mayúsculas para nombres “comunes” (transformándolos en nombres propios con las reglas gramaticales aplicables) puede justificarse con el fin de destacar una “cosa” como la más importante, conocida o característica de entre todas las de su clase (definición de antonomasia);
- 2) que ciertas antonomasias pueden limitarse en su uso a la comunidad de hablantes que comparten una misma geografía, para quienes la identificación de la referencia es inequívoca;
- 3) que los nombres propios, a diferencia de los comunes, no designan clases de seres, sino que identifican un solo ser de entre los de su clase (ej. “Lagartijo Esmeralda” [nombre científico: *Anolis evermanni*] contrario a lagartijo esmeralda o lagartijos verdes);
- 4) que el nombre científico no presupone la eliminación del nombre autóctono de un organismo en el contexto pragmático del lenguaje;
- 5) la deseabilidad de mantener el contexto cultural, histórico e idiosincrásico de un nombre autóctono; y así, asignarle su nombre propio que, como destacamos antes, tampoco presupone la sustitución de un nombre científico, por ejemplo:

- a. “Guajón” como nombre de origen taíno con que se conoce únicamente a un anuro endémico de Puerto Rico (Hernández-Aquino 1977); no obstante, es uno de los varios nombres comunes con los que se conoce a *Beilschmiedia pendula* (Sw.) Hemsl. (o “Aguacate Cimarrón”, “Aguacatillo”, “Cedro Macho”, “Palo Colorado”; véase en [http://floraelverde.catec.upr.edu/especie\\_info.php?id=43](http://floraelverde.catec.upr.edu/especie_info.php?id=43));
- b. “Coquí Común” (nombre científico: *Eleutherodactylus coqui* Thomas 1966) como nombre propio de una especie de anuro endémico de Puerto Rico, contrario a solamente “coquí”, que en español se referiría al nombre común de todas las especies de *Eleutherodactylus* en Puerto Rico y a diferencia de “Coquí” como uno de los nombres comunes en inglés y con mayúscula de *Peliperdix coqui*, Smith 1836, un ave del continente africano (ver <https://avibase.bsc-eoc.org/species.jsp?avibaseid=ECD7C1D8CD5ECD48>).
- c. el nombre propio “Huracán” como referente a “el espíritu maligno” (Coll y Toste 1979; Academia Puertorriqueña de la Lengua Española 2016) en la cultura taína y así, “Huracán María” podría proponerse como referencia inequívoca de uno entre su “clase” en la región geográfica que cubrió (vea también el punto 4b a continuación).

### **Propuesta: uso de mayúsculas para nombres comunes en la escritura científica (Ciencias Biológicas y Afines)**

RAE-ASALE (2010: página 446) reconoce que: “... aunque la mayor parte de las normas que aquí se ofrecen son de carácter prescriptivo, existen casos en los que no pueden pasar de ser meras recomendaciones”. Y recordamos de Puerto Sarmiento (2004) que: “La tarea de hacer un vocabulario científico en castellano corresponde a las instituciones y a los propios científicos”. Por

tanto, proponemos, como esfuerzo para estrechar lazos de comunicación entre la escritura científica y técnica con la normativa, que:

- 1) En cada manuscrito científico y técnico en español, así como de divulgación en ciencia general, si decide incluir el nombre autóctono (“común”) de un organismo (o entidad; vea el punto 4b), escriba primero el nombre científico (taxonómico; según el código de nomenclatura aceptado) seguido del nombre propio en mayúsculas y entre paréntesis, ej. “*Eleutherodactylus coqui* (Coquí Común)”. Note que este formato puede aplicar igualmente en inglés.
- 2) Limite a uno o dos sinónimos, como máximo, la referencia al sustantivo en cuestión para mantener la coherencia del manuscrito. Note que aplica igualmente en inglés.
- 3) Escriba el artículo en minúscula si no forma parte del nombre común, a menos que inicie una oración, en cuyo caso el artículo irá en mayúscula (esto último aplica por igual en inglés).
  - a. Por ejemplo: “...la evidencia obtenida de estudios con el Coquí Común revela...” (correcto) en vez de “...la evidencia obtenida de estudios con El Coquí Común revela...” (incorrecto). Igualmente, “El Coquí Común es...” o “The Common Coqui is...”.
- 4) En inglés es común suprimir el artículo del nombre propio (a menos que inicie una oración) mas no así en español.
  - a. Entonces, si el tópico del escrito fuese el “Coquí Común” y así lo escribimos desde el inicio, podremos referirnos luego a “...en el Común...” y el lector sabrá que se refiere al “Coquí Común”;
  - b. Igualmente, si al inicio de nuestro manuscrito incluimos el tópico, digamos el “Huracán María”, entonces podemos escribir más adelante “...en el María...” (correcto) en vez de “...en María...”.

- 5) Finalmente, los avances en la búsqueda electrónica de literatura científica permiten hoy consultar, por ejemplo, la referencia original de la descripción de una especie y así, verificar la intención del autor al momento de describirla y asignarle un nombre común; si no se ha incluido dicho nombre, consulte la fuente local más antigua y revise trabajos subsiguientes hasta que localice la primera referencia del nombre común al organismo en cuestión; contrastelo con los incluidos en la literatura científica al presente: con mucha probabilidad, también será el más representado entre las citas disponibles. De lo contrario, habrá recuperado un pedazo olvidado de la historia cultural local, que en sí mismo ya es ganancia para la literatura científica y general.

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Para asegurar la consideración de su manuscrito, se aconseja prepararlo de acuerdo a las siguientes INSTRUCCIONES PARA AUTORES:

- 1) Incluya primero el nombre completo del autor (y coautores) seguido de sus apellidos. El orden de las secciones del manuscrito (mayormente para artículos mientras que para otro tipo de contribución es variable y debe ser discutido con el Editor previamente) es como sigue; Título de la página, Título del artículo, Resumen (no mayor de 400 palabras), palabras claves (hasta ocho palabras), el cuerpo del manuscrito con sus secciones principales (Introducción, Métodos, Resultados, Discusión, Reconocimientos, Literatura Citada [o Referencias]), Tablas (cada una en un archivo separado y rotulado según citado en el texto principal), Leyenda de las Figuras (en un documento separado y rotulado), figuras (cada una en un documento separado y rotulado según citado en el texto principal), y apéndices (cada uno en un documento separado y rotulado según citados en el texto principal). Utilice la voz activa (por ejemplo: “Estudiamos...” o “Analizamos...” en vez de “... fue estudiado...” o “... fueron analizados...”, etc.).
- 2) Texto del manuscrito:
  - Los trabajos pueden ser escritos en inglés o español y deben estar a doble espacio y en “Times New Roman” 12p.
  - Los trabajos deben ir acompañados de un resumen en español y en inglés (abstract), escrito a doble espacio y en hojas separadas, encabezadas por el título completo del trabajo. El título debe ser informativo y corto, generalmente no más de 12 palabras. El autor debe indicar un título más breve (no más de 40 letras), en el mismo idioma del trabajo, para ser utilizado como encabezamiento de cada página (*running head*).
  - Cada nueva oración debe ser antecedida por dos espacios.
  - Cada párrafo debe estar sangrado a 0.5 cm (del margen izquierdo).
  - Todas las páginas deben numerarse (al pié derecho de la página y numeradas de corrido), incluyendo la primera página (título).
  - Enumere todas las líneas de manera consecutiva, de inicio a fin del manuscrito; enumere también las líneas del texto de las figuras y apéndices pero no el de las tablas.
  - Citas textuales de un pasaje: las citas de más de 60 palabras deben colocarse separado del cuerpo del texto principal con una línea superior y otra inferior del mismo; en un párrafo con sangría de 1 cm desde los márgenes derecho e izquierdo y no es necesario que se incluya su texto entre comillas ni en cursivo. Las citas más breves deben ir en el texto, entre comillas dobles, excepto para una cita dentro de una cita, en cuyo caso las comillas dobles se usan con comillas simples internas (por ejemplo, si la cita original incluye texto citado de otra fuente).
  - Números y unidades: si tiene números con unidades tiene que incluir un espacio antes de la unidad; siempre utilice números para unidades antes de una abreviatura; tiene que deletrear los números hasta el diez inclusive (excepto cuando haya una combinación de números mayores a diez y otros igual o menores a diez – en este caso todos se expresan numéricamente); siempre añada una coma para los millares y números mayores en potencias de diez; siempre incluya un cero antes de cualquier decimal. Utilice el guion “n” (en Inglés, “en-dash”) para indicar rangos de números (pero no de años ni fechas, donde utilizará en cambio un guion sencillo corto) y para inserciones en una oración dentro de un texto particular; no utilice el guion “m” o largo; separe cada operador matemático utilizando un espacio sencillo a ambos lados del operador. Si utiliza el símbolo “~” no añada espacio a ambos lados del mismo. Preferiblemente, utilice Grados Decimales para identificar Latitud y Longitud (por favor, no olvide añadir el signo de negativo para las coordenadas Sur y Oeste si no escribe las direcciones o puntos cardinales); incluya el sistema de Dato Geodésico (p. ej., World Geodetic System [WGS] 84, en Inglés, u otro que aplique).
  - Escriba en mayúsculas toda referencia a secciones, figuras y tablas.
  - Letras en cursiva: aplique a nombres científicos (pero no a nombres comunes), palabras de otros idiomas utilizados en su escrito y título de libros. No utilice letras en cursivo para “p. ej.,” y otras abreviaturas de uso muy frecuente (o en Latín, cuando aplique), unidades de medidas, ni para símbolos de probabilidades y estadísticos.
  - Guía de nomenclatura aceptada para nombres científicos y autoría de los mismos:
    - Si es para virus utilice a:
      - The International Code of Virus Classification and Nomenclature (Disponible en <https://talk.ictvonline.org/information/w/ictv-information/383/ictv-code>; según actualizado a octubre del 2018).
    - Si es para procariotas utilice a:
      - Parker, C. T., B. J. Tindall, and G. M. Garrity (eds.). 2019. International Code of Nomenclature of Prokaryotes, Prokaryotic Code (2008 Revision). International Journal of Systematic and Evolutionary Microbiology 69: S1–S111. Disponible en [https://ccug.se/documents/taxonomy/prokaryotic\\_code/2019\\_Parker-Tindall-Garrity\\_Prokaryotic%20Code%20-%20202008%20Revision.pdf](https://ccug.se/documents/taxonomy/prokaryotic_code/2019_Parker-Tindall-Garrity_Prokaryotic%20Code%20-%20202008%20Revision.pdf). DOI 10.1099/ijsem.0.000778.
    - Si es para algas, hongos y plantas utilice a:
      - Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smith (eds.). 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. DOI <https://doi.org/10.12705/Code.2018> (versión en Español disponible en <https://www.iapt-taxon.org/nomen/Shenzhen/Spanish/Spanish.pdf>).
    - Si es para animales utilice a:
      - International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature. Fourth edition. Published by

the International Trust for Zoological Nomenclature [ITZN], The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (available online at <https://www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/>) (versión en español disponible en <http://www.sam.mncn.csic.es/codigo.pdf>, con la aprobación del ITZN [2009]).

- Si lo incluye, utilice mayúscula para el nombre común del sustantivo de una especie (de tenerlo); véase también el uso de mayúsculas por antonomasia en contextos geográficos y culturales.
  - Encabezamientos: **ACTA** usa encabezamientos primarios, secundarios y de ser necesario, terciarios.
    - Encabezamientos primarios deben estar en mayúscula, 12p ennegrecido, (centralizado, p. ej., **MÉTODOS**)
    - Encabezamientos secundarios deben estar en *title case*, 12p ennegrecido, centralizado, p. ej., **Descripción del Caso**
    - Encabezamientos terciarios deben estar en *title case*, 12p ennegrecido, justificado a la izquierda, p. ej., **Reserva Biológica Mata de Plátano**
  - **AGRADECIMIENTOS** y **REFERENCIAS**: en negrilla, en letras mayúsculas pequeñas y justificado a la izquierda.
  - Compagine las partes de sus manuscritos en este orden: página de título, resumen, texto, agradecimiento, literatura citada, anejos, tablas, leyendas de figuras, y figuras. Las figuras, fotografías y tablas no deberán estar insertadas dentro del texto sino sometidas por separado.
- 3) Las figuras deben tener una resolución no menor de 300 dpi (preferiblemente con un poco más de resolución si contiene texto, arte o dibujo lineal, y otros elemento lineales, y asegurándose que pueda ser enviada por medio de correo electrónico regular), debe ser enviado como un \*.PDF con toda letra o elemento ya incluido en la imagen (por ejemplo, flechas, símbolos o formas geométricas), \*.JPG o en \*.TIF (tendrá que guardar una copia en mayor resolución en tus archivos para fines de edición si fuese necesario solicitarlo y generar la versión final del mismo). De no ser posible, puede someter gráficas en Excel – un documento separado para cada gráfica – sin líneas de fondo y con su fondo blanco. Las fotografías deben estar en alta resolución (300 dpi o mayor y asegurándose que pueda ser enviada por medio de correo electrónico regular) como \*.TIF o \*.JPG de alta resolución. Cada figura debe enviarse en un archivo separado y nombrando cada archivo según el número de la figura citada en el texto principal. La manipulación de imágenes debe seguir las guías éticas aceptables (ver <http://microscopy.arizona.edu/learn/digital-image-ethics>). Finalmente, debe presentarse una lista de figuras junto con las leyendas de cada una, mecanografiadas a doble espacio en un archivo separado del texto principal del artículo con el título “Leyenda de Figuras”.
- 4) Las tablas deben: mecanografiarse a doble espacio, numerarse consecutivamente, tener un título breve, ser precisas y cada tabla debe presentarse en un archivo separado, nombrando cada uno según el número de la tabla citada en el texto principal. Las tablas deben ocupar como máximo el ancho de una página impresa (ya sea en un formato de página horizontal o vertical); puede ser necesario el uso de símbolos o abreviaciones para reducir el espacio de la información entre columnas (o filas). Cada tabla debe llevar un mínimo de líneas horizontales, preferiblemente en el margen superior, bajo el espacio de los títulos de las columnas y una al pie de la tabla; evite en lo posible el uso de líneas verticales. Verifique que las sumas en columnas correspondan al total de los valores de referencia y alinee todos los numerales al borde izquierdo. No deben repetir material en tablas y en figuras.
- 5) Los autores deben usar el sistema métrico para sus medidas. Consúltese el Sistema Internacional de Unidades (SI) como guía en la conversión de sus medidas. Al redactar texto y preparar figuras, nótese que el sistema internacional de unidades requiere:
- el uso de términos masa o fuerza en vez de peso.
  - cuando una unidad es expresada en denominador, se debe utilizar el sólido (p. ej., g/m<sup>2</sup>); para dos o más unidades en un denominador, use el sólido y un decimal (p. ej., g/m<sup>2</sup>·d).
  - use la “L” como el símbolo de litro.
  - use “Mg” como el símbolo para Megagramo (1 Mg = 1,000 kg ~ 1.102312 toneladas US o ~0.984207 toneladas imperial).
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    - **de una revista:**
      - Clark, C. M., and D. Tilman. 2010. Recovery of plant diversity following N cessation: effects of recruitment, litter, and elevated N cycling. *Ecology*.
    - **de un libro:**
      - Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principle and practice of statistics in biological research*. Third edition. W. H. Freeman and Co., New York, New York, USA.
    - **del capítulo de un libro:**
      - Hartshorn, G. S., and B. E. Hammel. 1994. Vegetation types and floristic patterns. Pages 73–89 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
    - **de un reporte gubernamental:**
      - Pardo, L. H., M. J. Robin-Abbott, and C. T. Driscoll. 2011. Assessment of Nitrogen deposition effects and empirical critical loads of Nitrogen for ecoregions of the United States. General Technical Report NRS-80. USDA Forest Service, Northern Research Station, South Burlington, Vermont, USA.
    - **de una disertación:**
      - Foster, S. E. 2007. The co-occurrence and interactions of large invertebrate predators in relation to the *Bythotrephes* invasion. Dissertation. University of Toronto at Mississauga, Mississauga, Ontario, Canada.
    - **de una página web:**
      - Keeland, B. D., and P. J. Young. 2004. Construction and installation of dendrometer bands for periodic tree-growth measurements. U.S. Geological Survey, National Wetlands Research Center, Lafayette, Louisiana, USA. <http://www.nwrc.usgs.gov/Dendrometer/index.htm>
    - **de un Software:**
      - SAS Institute. 2009. JMP version 8.0. SAS Institute, Cary, North Carolina, USA
  - 8) Le recomendamos a los autores que provean nombres e información de contacto de revisores potenciales de sus manuscritos para la consideración de la junta de editores.
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