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Population Ecology of a Caribbean Epiphyte Trichocentrum undulatum (orchidaceae): Defining Habitat and the Effects of Herbivory and Hurricanes at Its Peripheral and Core Range

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

POPULATION ECOLOGY OF A CARIBBEAN EPIPHYTE *TRICHOCENTRUM UNDULATUM* (ORCHIDACEAE): DEFINING HABITAT AND THE EFFECTS OF HERBIVORY AND HURRICANES AT ITS PERIPHERAL AND CORE RANGE

A dissertation submitted in partial fulfillment of the
requirements for the degree of
DOCTOR OF PHILOSOPHY
in
EARTH SYSTEMS SCIENCE
by
Haydee Borrero

2022

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Haydee Borrero, and entitled Population Ecology of a Caribbean Epiphyte *Trichocentrum undulatum* (Orchidaceae): Defining Habitat and the Effects of Herbivory and Hurricanes at its Peripheral and Core Range, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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Date of Defense: January 19, 2022

The dissertation of Haydee Borrero is approved.

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Vice President for Research and Economic Development
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Florida International University, 2022

DEDICATION

I dedicate this dissertation to my family. My husband, Paul Michael Nuñez, who keeps me grounded and encouraged me over the years. To my parents, Carelia Carcaño and John Borrero, who have both provided me their unconditional love, support, and patience. To my sister, Karina Queupumil, who has that special way of making me laugh when I need it most.

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ABSTRACT OF DISSERTATION

POPULATION ECOLOGY OF A CARIBBEAN EPIPHYTE TRICHOCENTRUM UNDULATUM (ORCHIDACEAE): DEFINING HABITAT AND THE EFFECTS OF HERBIVORY AND HURRICANES AT ITS PERIPHERAL AND CORE RANGE

by

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Florida International University, 2022

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Professor Hong Liu, Major Professor

Population ecology studies are central to species conservation. My dissertation focused on the Florida state-listed endangered orchid, *Trichocentrum undulatum* at its northern-most range in the Everglades National Park (ENP), Florida and multiple populations throughout its core range in Cuba. Through surveying populations of *T. undulatum* across this range from 2013-2021, I made a new reporting on the occurrence of a specialized insect herbivore, *Melanagromyza miamensis* in Cuba (Chapter 1). This flower-crippling herbivore was previously known only in the ENP. With this discovery I assess the intensity and impacts of this herbivore, as well as others on *T. undulatum* across the populations (Chapter 3).

During the orchid population surveys in Cuba, I determined the orchid’s host tree diversity and preference throughout my study sites (Chapter 2). I ranked a list of host trees with two levels of host preference, including a compilation of host diameters and orchid heights. The information provides management recommendations for the species in Florida and can guide the site selection of future species restoration plans.

Finally, I conducted repeated demographic censuses documenting individually marked plant survival, growth, and seedling recruitment. These data allowed me to conduct deterministic and stochastic population modeling (Chapter 3). The finite and stochastic population growth rates (λ and λ_s) show that the ENP population is declining, although experiencing rare and high episodic recruitment. Populations in Cuba are more stable, with λ values closer or equal to one. Life table response experiments (LTRE) show that the higher λ value is linked to higher rates of adult survival. Alongside the documented herbivory from both *M. miamensis* and *Diaspis boisduvalii*, the category 3 storm Hurricane Irma caused increased mortality at the ENP in 2017. Following the hurricane, the ENP site exhibited a decline in herbivore attacks, and a surge in short-term survival and growth. The surge in growth is possibly linked to forest canopy gaps and increased sunlight. The projected long-term population growth rate increased when simulating the removal of leaf herbivory under historical hurricane frequency at the ENP, but is still less than one. My study showed that the population at ENP is under multitude of threats, including that from sea-level rise to host tree habitats that is not studied. The complexities of combating these threats leads to my recommendation of using existing host species information as well as the population viability analysis to guide restoration activities that are essential for the species survival in the northern-peripheral range.

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INTRODUCTION

RESPONSE TO A CHANGING WORLD: A FOCUS ON PERIPHERAL POPULATION CONSERVATION

All species have a range of tolerances that play a role in their distribution. The range for a species is rarely, if ever, constricted to a single plot of uniform land, rather a range is made up of multiple microclimates, geological formations, and species interactions that differ across the landscape. It is currently thought that the most climate sensitive and limiting areas for a species across their distribution are those that are found at low elevations or at the trailing and leading boundaries of populations – while at the core of a species' distribution conditions for persistence are ideal (Parmesan et al. 1999; Parmesan and Yohe 2003; Gibson et al. 2009). Due to global changes species must either adapt to different environmental factors or move and track their tolerable ecological limits to persist, oftentimes poleward or to higher elevations (Thomas and Lennon 1999; Parmesan and Yohe 2003; Hickling et al. 2006; Chen et al. 2011; Poloczanska et al. 2013; Mason et al. 2015). Evidence of shifting distributions and of changes to dispersal abilities of species, which have been well documented, shows that species can make the move and adapt, yet the interactions between species as well as the habitat quality in the limits of their expanding range remains unknown or understudied (Thomas 1991; Davis & Shaw 2001; Walther et al. 2002; Parmesan 2006).

As conditions change from the equator poleward, the central "core" of a species' range may no longer have ideal conditions and population declines may follow (Lawton 1993; Coristine & Kerr 2015; Hastings et al. 2020). This is termed "core-periphery pattern" in which the core will become less than ideal as climate changes (Lawton 1993;

Vucetich and Waite 2003), though not all species are distributed in this core-periphery pattern due to the varying complexities of abiotic and biotic factors that are species and habitat specific (Hampe and Petit 2005; Hughes et al. 2007; Sexton and Dickman 2016). Yet generally, the edges of species distributions are important for conservation due to the potential for genetic differentiation as a result of genetic drift, founder effects, differing selection pressures and adaptive responses to other abiotic or biotic factors (Hampe & Petit 2005). The differences in genetics, biotic and abiotic adaptations at the margins of a species distribution may allow for populations to buffer against the effects of climate change more readily. Peripheral populations have the highest likelihood of successful poleward migration in a warming climate, especially for those species that do not have long-distance dispersal as a part of their life history (Gibson et al. 2009; Kostyack et al. 2011).

As range expansion occurs boundary populations are sources of dispersal and genetics (Durka 1999; Sexton et al. 2016). Populations experiencing reductions in environmental quality have been observed improving their dispersal abilities with the success of more dispersive morphs. Species that naturally have high dispersal abilities have been linked to improved gene flow, larger populations in newly colonized patches, and a decrease in fitness as a trade-off. For example, the small seed sizes of orchids, long-winged seeds of pines, and large wings on insects facilitate extended dispersal distances (Thomas et al. 2001; Hughes et al. 2003; Simmons & Thomas 2004; Ilves et al. 2016). Species that disperse long distances may be able to colonize new areas, but these habitats may lack the conditions for establishment and persistence. Leading boundaries, where poleward and altitudinal expansion is born with the release of previous climate limitations, will have an increased likelihood of extinctions due to the less than ideal site conditions from non-climatic stressors as well as the potential change up of community composition and genetic traits of migrant populations (Gibson et al. 2009; Louthan et al. 2015: Forsman et al. 2016; Keret et al. 2020). Yet movement must occur prior to the observations of repercussions, if any, in the community composition in these novel Anthropocene ecosystems (Thomas 2020). Conservationists, through assisted migrations or adaptive management of species redistributions, can limit the deleterious effects of abrupt species range shifts (Liu et al. 2012; Melbourne-Thomas 2021). The biotic component influencing a species distribution has gone vastly overlooked (and is less obvious than the abiotic) when considering the movement and adaptation of the "natural" (excluding invasion ecology) redistribution of boundaries (Louthan et al. 2016). Of course not all species have thermal limitations on their boundaries, but they may have other limitations of consequence such as precipitation and prey abundance (Woodward 1987; Coristine & Kerr 2015; Hantson et al. 2021). Shifts in the species' interactions with the abiotic and biotic environment may or may not be of prime consequence, but change is a given with a newly expanded and novel range (Thomas et al. 2001; Hughes et al. 2003; Parmesan 2006). The differences in peripheral versus core range is often defined spatially, with the "core" representing dense populations in the most ideal conditions and the "peripheral" margins harboring less population density and fitness (Sagarin & Gaines 2002). A shift in defining the range of species based on their ecology, encompassing the abiotic and the complex biotic across different populations, is necessary to reflect the realities of complex species distributions. In this dissertation, I define the core range of a species as exhibiting the highest habitat quality and general community diversity of the existing populations rather than geographically.

Akin to a long, narrow land bridge, Peninsular Florida is a rare opportunity to observe the conduit of northern movement of Caribbean species to the continental United States. As Florida is also a “cool” range margin for different taxa in the Caribbean due to its sub-tropical clime, the location can be used as further evidence of the possible latitudinal shifting of range at the limits (Mason et al. 2015). Conservation management planning of novel habitats in the Anthropocene allowing for high quality species richness may benefit from the facilitation of endangered species that have limited movement (Menendez et al. 2006; Thomas 2020).

Epiphytes, orchids in particular, are sensitive to climate changes due to their sensitive physical positions (above ground with exposed roots), specialized natures and are indicative of tropical ecosystem health (Benzing 1998; Zotz et al. 2009). The tropics have a heavy representation of vascular epiphytes though little is known on the impacts of climate changes on these indicator species, other than on their significant carbon biomass capacity (Benzing 1998). The goals of the following chapters are to closely examine the ecology of *Trichocentrum undulatum* (Sw.) Ackerman & M. W. Chase with a focus on the population dynamics as well as the contrasting biotic and abiotic interactions across populations in the species’ northern peripheral and core range.

Study species

Trichocentrum undulatum is a tropical epiphytic orchid found in the United States (Florida), Cuba, Bahamas, and Jamaica (Ackerman 2014; Cetzal-Ix et al. 2016). Southern Florida is the northern limit of the species’ distribution and the only location within the continental United States. Historically, having been documented to occur as far inland as the Royal Palm Hammock area in the northern Everglades National Park (ENP). There remains one surviving population following the 19th century extraction and development that occurred across southern Florida (Gann 2009). This population can only be found in the southernmost salt marsh tip of the mainland peninsula within the ENP and are generally considered to be one large population of approximately 2,000 individual plants, although in this dissertation we report overall declines in population size (Gann 2009).

Chapters overview

Chapter 1 focuses on a rare herbivorous fly detected and described in the southern Florida population, *Melanagromyza miamensis* (Agromyzidae), which halts the development of *T. undulatum*'s inflorescence partially or entirely. The first documented voucher specimen of the fly dates back to the 1920's labelled with "orchid – larva destroys bloom (Spencer 1973)." Prior to the work we have undertaken, there has been no observations, of *M. miamensis* outside of southern Florida. Some have speculated that this "pest" has been introduced or is in fact an invasive (personal communications with local Florida naturalists), but it is equally possible if not more probable that it is a native. With the earliest known documentation of *M. miamensis* being a specimen collected in the early 1900s on an unidentified orchid from a site in southern Florida, it is doubtful that the insect was accidentally introduced to such an isolated location in the southern tip of the ENP. I report on the range expansion for the fly to include Cuba. The fly has yet to be observed on any other species of plant. The rates of attack are also documented in recent years with increasingly more detail in my third chapter.

In my second chapter I go into depth on the habitat differences across populations in both the northern-periphery population at ENP as well as select sites in the core range of Cuba. My goals were to (a) identify host trees of *T. undulatum* in the core range; (b) compare and contrast host plant community types in Cuba and in southern Florida; and (c) identify potential suitable but unoccupied habitats for *T. undulatum* in southern Florida where the species is highly threatened with extinction. Detailed host tree and habitat information is priceless when planning management strategies for endangered and threatened species. Targeted conservation strategies can increase the probability of success.

My third chapter focuses on the population dynamics of *T. undulatum* to determine the population viability as well as the main drivers in the difference in population stabilities among the populations by calculating the finite population growth rates (λ) and stochastic growth rates (λ_s), using life table experiments, and transient dynamic modeling. Stochastic events such as herbivory, hurricanes, episodic recruitment and logging have been modeled. Here I document the impacts of the stochastic factors on the long-term growth of these populations. Management recommendations are given for the species to improve the likelihood of success in restoration and conservation projects.

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CHAPTER I

SPECIALIZED HERBIVORY ON INFLORESCENCE STALKS OF *TRICHOCENTRUM UNDULATUM* (ORCHIDACEAE) BY *MELANAGROMYZA* SP. (DIPTERA: AGROMYZIDAE) IN CUBA.

1.1 ABSTRACT

Inflorescence stalk herbivory on the Mule Ear orchid (*Trichocentrum undulatum*) has been observed in Cuba, which resembles the specialized herbivory interaction seen in southern Florida between a specialized dipteran, *Melanagromyza miamensis* (Agromyzidae) and the Mule Ear orchid. We are able to identify the inflorescence herbivore to be the genus *Melanagromyza*. It is possibly the same species that can be found in southern Florida. The mule-ear orchid is endemic to the Caribbean region, i.e. Cuba, Jamaica and southern Florida. To our knowledge, this is the first report of an apparently specialized inflorescence stalk herbivory by Agromyzid flies on the Mule Ear orchid in Cuba. The herbivory can partially or completely destroy the flowering potential of the impacted plants.

1.2 INTRODUCTION

Trichocentrum undulatum (Sw.) Ackerman & M. W. Chase is an epiphytic orchid whose distribution extends from Jamaica, Cuba, and Bahamas to Florida (Ackerman 2014). The population in southern Florida is the northernmost limit of the species and is the only mainland North American population. In southern Florida, *T. undulatum* is rare and only found in a restricted area of coastal salt marsh found growing only on buttonwood trees (*Conocarpus erectus* L.). This Florida population is subject to specialized inflorescence stalk herbivory by *Melanagromyza miamensis* Spencer. Such herbivory has not previously been reported beyond southern Florida (Seavey & Seavey 2018, Higgins & Gann 2007, Spencer & Stegmaier 1973).

The dipteran genus *Melanagromyza* (Agromyzidae), consisting of over 300 species and is distributed worldwide (Spencer & Steyskal 1986). Not much is known about host plants used by the majority of Agromyzids due to the difficulties in capturing or rearing adult flies or difficulties with locating puparia within plant tissues (Spencer 1990). Herein we report inflorescence stalk herbivory of *T. undulatum* observed in four provinces within Cuba (Artemisa, Cienfuegos, Matanzas, and Sancti Spiritus).

1.3 METHODOLOGY

Trichocentrum undulatum can be found within every province of Cuba, in different habitats, and growing on a diversity of phorophyte hosts. Four populations of *T. undulatum* were visited in Cuba in the provinces of Artemisa, Cienfuegos, Matanzas, and Sancti Spiritus during the summers of 2016 and 2017. Transects were laid out within forest stands where the orchid was known to grow. A total of four transects were made at four wild populations in the Artemisa (one transect) and Matanzas (three transects) provinces. Inflorescence stalks were evaluated/collected for herbivore presence and collected at Macradenia Orchid Garden in Cienfuegos province (n= 6) and Comunidad 23 Orchid Garden in Sancti Spiritus province (n= 17). For every *T. undulatum* plant encountered on the transect, a search for other plants was made within a five meter radius. The length of the transects varied between 20 to 100 meters, depending on the forest size and habitat topography. Inflorescence stalks were collected from every individual that had flowered in February/March (the flowering season for the species) and had failed to produce fruit. The inflorescence stalks were labelled and later dissected to determine the presence of an inflorescence stalk herbivore. Exit holes were examined and any pupal casings found were photographed.

1.4 RESULTS

Although no adult fly exiting *T. undulatum* had been captured, we used larval casing characteristics to determine that the herbivores affecting inflorescences of *T. undulatum* within Cuba are a *Melanagromyza* species. Pupal casings were extracted from inflorescence stalks from all of the transects sampled. The larvae found in our orchid samples fitted the description of the genus *Melanagromyza* by having two sclerotized plates with pronounced "bulbs" atop the plates with a protruding "horn" in the center (Fig. 1) (Spencer & Steyskal 1986). This identification had also been confirmed by an Agromyzidae specialist (Scheffer pers. comm. 2017). Exit holes found on the inflorescence stalks were similar to those found in the southern Florida population (Fig. 2). No other Diptera larvae were found within the flowering stalks, leaves, or fruits of *T. undulatum*.

A total of 391 plants were located in the transects between the 2016 and 2017 surveys. Of these 149 (38%) produced inflorescences. The percentage of sampled flowering plants with *Melanagromyza* sp. presence was 48% (72 plants). The number of inflorescences produced by a plant generally varied between 1 to 6 stalks between the two surveys. A total of 198 inflorescence stalks were collected and examined. Of these, 87 inflorescences (44%) exhibited dipteran casing presence.

Despite approximately half of all flowering plants having been attacked by *Melanagromyza* sp., we observed fruit in both 2016 (two fruit out of 85 flowering plants) and 2017 (one fruit out of 64 flowering plants) (Fig. 3). Vouchers of the puparia casings and the inflorescence stalk tips exhibiting exit holes and boring architecture were deposited at the Onaney Muñiz National Herbarium from the Institute of Ecology and Systematics, Havana, Cuba.

1.5 DISCUSSION

Our study is the first to report the presence of inflorescence herbivory of *T. undulatum* by an Agromyzid fly in Cuba. Due to the host specialization nature of the Agromyzidae family (Spencer 1990), it is possible that the observed *Melanagromyza* in Cuba is the same species as that found in southern Florida, but this requires further taxonomical study by a specialist. *Melanagromyza* sp. has only been observed in the inflorescence stalks of *T. undulatum* and not on any other orchid species in the surrounding areas assessed in Cuba and southern Florida (Borrero unpubl. 2017).

In southern Florida, inflorescence herbivory intensity by *M. miamensis* was 90% and 100% between 2014 and 2015 in the largest known *T. undulatum* population within the Everglades National Park (n= 155 at a 1 km long transect and a total of 53 inflorescence stalks evaluated), resulting in a very low to no pollination opportunities (loss of flowers) and subsequently, limited fruit/seed production (Gann *et al*. 2009, Borrero unpubl. 2017). In contrast, only 48% of flowering plants assessed in Cuba experienced *Melanagromyza sp*. herbivory between 2016 and 2017. The lower attack rate in Cuba versus that observed in Florida could indicate that different biological and ecological factors exist between populations. Study is on-going in comparing the demography and ecology between the orchid populations in South Florida and Cuba.

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Fig 1.1 Pupal casings of a *Melanagromyza* sp. found within an inflorescence stalk in Cuba, summer 2016. The sclerotized plate with the doubled “horns” are apparent and particular for the genus.

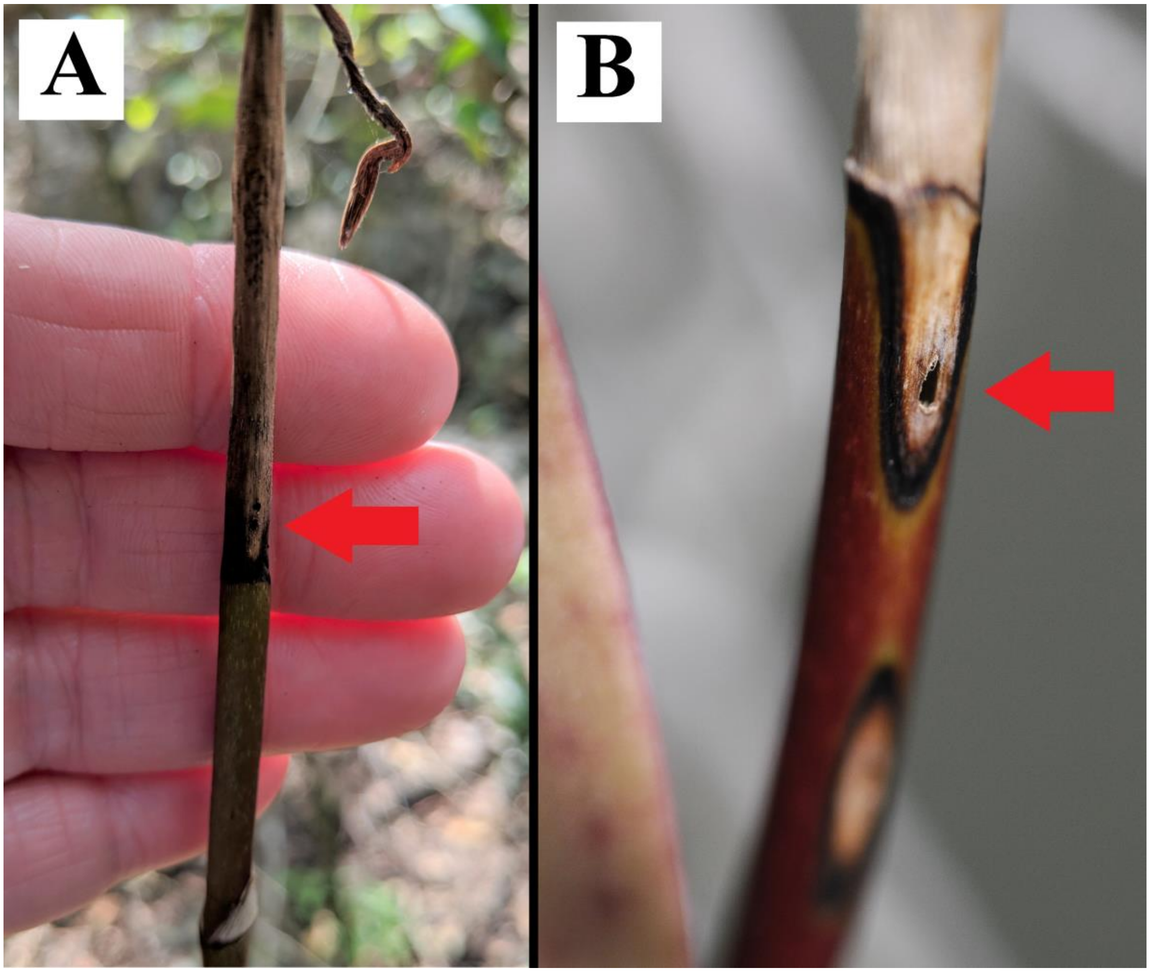

Fig 1.2 A) Exit holes made to accommodate the emergence of adult dipteran(s) from infested inflorescence stalks of *Trichocentrum undulatum* in Matanzas province, Cuba 2016. B) Exit holes made from emerging adult *Melanagromyza miamensis* from a *T. undulatum* inflorescence stalk in Florida, USA, 2014.

Fig 1.3 Uninfested fruiting inflorescence stalk where no *Melanagromyza sp*. herbivory was evident.

CHAPTER II

COMPARISONS OF HABITAT TYPES AND HOST TREE SPECIES ACROSS A THREATENED CARIBBEAN ORCHID’S CORE AND EDGE DISTRIBUTION.

2.1 ABSTRACT

Tropical forest ecosystems are rich in epiphytes that make up a significant portion of the overall plant diversity. However, epiphytic plants are often understudied due to inaccessibility and the lack of basic ecological information poses challenges to their conservation, particularly in a time of rapid global change. The mule-ear orchid, *Trichocentrum undulatum* (Orchidaceae), is a large flowering epiphyte found in southern Florida (USA), the Greater and Lesser Antilles including Cuba. The plant is Florida state-listed as endangered with only one remaining small and declining population in a coastal mangrove forest due to historical extraction and habitat destruction. Currently, there is no systematic understanding of the species' habitat requirements. To fill this void we compared the habitat and microhabitat of the species on its northern distribution edge (southern Florida) and the core range (in Cuba). The Florida population has only one host species, *Conocarpus erectus*, found in one habitat type. This is in sharp contrast to the 92 documented hosts and five habitats across seven provinces in Cuba. Based on our findings from Cuba we suggest conservation and restoration options in Florida by proposing potential suitable host plants and habitats. Proactive restoration of this species will help to ease the threat from sea-level rise to the species by securing and expanding range margins.

2.2 INTRODUCTION

Epiphytic plants constitute a significant proportion of the biodiversity in tropical forests (Gentry and Dodson 1987a, Kress 1985). However, they are often understudied due to accessibility issues and lack of resources. The absence of basic ecological information, e.g. habitat requirements, poses challenges in conserving epiphytes, particularly in a time of rapid global change. There is a need to plan population translocations to counter current and anticipated future threats, as is done with some endangered plants worldwide (Liu et al. 2015, Liu et al. 2020, Maschinski and Haskins 2012). The success of such actions depends on understanding the habitat limitations for the species of concern. For example, a good understanding of host species requirements can be used to inform conservation strategy of threatened epiphytic species (Benzing 1978, Callaway et al. 2002, Segovia-Rivas et al. 2018, Yang et al. 2017). Studies of this kind are rare in the tropics, especially on orchids, one of the most diverse plant families among tropical plants**.**

Throughout a species' range there exists a spectrum of habitats, defined by the species' degree of dependence on various biotic and abiotic factors, including the nature and quality of species interactions (Cassini 2013, HilleRisLambers et al. 2013, Louthan et al. 2015, Parmesan 2006). When species are threatened, conservation strategies depend on understanding those sustaining factors and also anticipating potentially rapid landscape changes (Katinas et al. 2009, Seddon et al. 2013). As one nears the edge of a species' distribution, habitat quality may decline until the distribution "limit" for the species is reached (Sexton et al. 2009). Distribution edges can include large swaths of habitat types, elevations, and climate zones extending across latitudes.

Southern Florida lies at the northern edge of the distribution for many tropical plant species, orchids included, that have their core range in the Caribbean or tropical America (Nieto-Blázquez et al. 2017, Santiago-Valentin & Olmstead 2004, Trejo-Torres & Ackerman 2001). The subtropical climate of southern Florida may not be as ideal for tropical species, but the varied transitional climate may be tolerable, due to tropical seasonality, despite occasional frost events (Downing et al. 2016, Obeysekera et al. 1999). The north-ward movement of species from the Caribbean and tropical America to southern Florida has already been documented for species with strong dispersal capability naturally (Paulson 2001) or aided by human activities (Pemberton & Liu 2007, Pemberton & Liu 2008a,b, Skov & Wiley 2005), and it is likely that more species will follow suit. For endangered species that have limited dispersal abilities, or small populations at the limit of a distribution, range shift or expansion into nearby unoccupied yet desirable habitat may be difficult (Liu et al. 2012, Martin 2001). Under such circumstances, a conservation strategy might be to identify suitable habitats for assisted dispersal, which should enhance the probability of establishment and reproductive success (Munzbergova et al. 2004).

The dust-like wind dispersed seeds of orchids may readily disperse to great distances, but can be site limited due to their dependencies on mycorrhizae for germination and other periods of their life histories (McCormick & Jacquemyn 2014, Yang et al. 2017). Determination of host tree diversity and substrate specificity for epiphytic orchids is a critical component to understanding their life histories and habitat suitability as a baseline for conservation planning (Adhikari et al. 2012, Ilves et al. 2016, Laube & Zotz 2006, Migenis & Ackerman 1993, Tremblay et al. 1997a, Xiqiang 2005). Comparison of host identities and associated plant communities between the core and edge distribution of an orchid species may offer insight on the limiting factors along its distribution range. The goals of this paper are to: (a) identify host trees of *Trichocentrum undulatum* (Sw.) Ackerman & M.W.Chase in the core range area, i.e. Cuba; (b) compare and contrast host plant community types in Cuba and in southern Florida, the species' northern distribution edge; and (c) identify potential suitable but unoccupied habitats for *T. undulatum* in southern Florida where the species is highly threatened with extinction.

Study species

Trichocentrum undulatum is an epiphytic orchid with a distribution in the Greater and Lesser Antilles and southern Florida of the United States (Cetzal-Ix et al. 2016). The orchid can be found throughout the entirety of the island country of Cuba and in historically large numbers in Jamaica, with these two islands being the core range in the Caribbean (Ackerman 2014, Ackerman & Chase 2001). Current conservation status of the species in Jamaica is unknown but populations were reported in decline following high levels of wild harvest and habitat destruction (NEPA 2007). Only one population is currently known to persist in the United States and it is limited to a thin coastal stretch on the southernmost border of peninsular Florida. Southern Florida is considered the northern latitudinal limit of the species. Throughout the entire distribution of this species it is subject to anthropogenic threats such as habitat alteration, destruction, collection, and natural forces like hurricanes and specialized herbivory (Borrero et al. 2018, Gann et al. 2007).

Study site

Populations of *T. undulatum* were studied across the species core range on the island of Cuba as well as the leading northern edge of the species distribution in southern Florida, USA. Cuba, the largest of the Caribbean islands, is home to over 312 orchid species and is thought to be the center of radiation for many wind-dispersed plant species like orchids and bromeliads (Ackerman 2014). Due to Cuba’s geological age, as well as its mountainous landscape, there are diverse habitats and microclimates from which these wind-dispersed species can spread (Borhidi & Muñiz 1985, Nieto-Blazquez 2017). In contrast, the Everglades National Park (ENP) is lower in elevation than much of Cuba, ranging from 0 to 2.4-m above sea-level. The ENP is the largest wetland preserve in the United States covering over 64,238-ha in Miami-Dade, Monroe, and Collier counties (https://www.nps.gov/ever/learn/news/parkstatistics.htm). Boasting a diverse sub-tropical region of its own, the ENP houses 39 native orchid species.

2.3 METHODOLOGY

Field methods

Study sites were selected based on prior knowledge of the species distribution and legal accessibility. Over the 4-year (2015-2019) study period, we visited a total of 29 sites with *T. undulatum* populations in Cuba across seven provinces including Artemisa, Cienfuegos, Matanzas, Mayabeque, Pinar del Rio, Sancti Spiritus, and Santiago. In this study we defined a population of *T. undulatum* as a collection of all individuals that occur at a site. We surveyed plant communities at eight sites using transects at four provinces in Cuba: Matanzas, Mayabeque, Pinar del Rio, and Sancti Spiritus. A single transect was also surveyed at the ENP site in the USA. The transects range from 499 km in distance from each other with a median of 216 km. The identity of each host tree species for every *T. undulatum* encountered was documented at all sites. Non-host species were also documented along the transects.

Population and plant community sampling via transects

At each site where plant community sampling was possible, a 1-km non-linear transect was set up where *T. undulatum* occurrence was deemed representative of the site. Most of these transects were along informal forest trails, including the one at the ENP. Once we encountered *T. undulatum*, we would search all trees within a 5-m radius for additional individuals. This approach was taken to maximize the probability of locating *T. undulatum* individuals for the orchid's population study (not presented here). A transect ended when it reached one km in length. Both host and non-host trees, shrubs, and lianas were identified to species for the entire transect length. Shrubs and lianas were included in the plant community study because they were occasional hosts of *T. undulatum* (pers. obs.). Diameter at breast height (DBH) of the host and the height at which the individual *T. undulatum* was found were recorded. In addition, abundance of host and non-host species were categorized into the following five categories within the transects: (1) very abundant, with 15 or more individuals, (2) moderately abundant, between 11-14 individuals, (3) somewhat abundant, between 6-10 individuals, (4) occasional presence, between 3-5 individuals, and (5) species with a rare presence, 1-2 individuals within the study area. While the transects were not a random sample as they maximized inclusion of host species, they nonetheless generated reasonable quantification of host and non-host species diversity and relative abundance where *T. undulatum* occurred. For the nine plant communities where a transect was sampled, South Florida included, habitat description was based on vegetation types as defined by Borhidi (d1991).

Data analyses

To assess the thoroughness of our sampling effort, we plotted in Cuba two species accumulation curves: one for all recorded tree species and another for just the orchid host species (Fig. 3 a & b). Only plants that were identified to species level were plotted. Differences in mean host tree DBH and height frequencies at which *T. undulatum* occurred were compared among sites using one-way ANOVA in SPSS 26 (SPSS, Chicago, Illinois, USA). Host preference was evaluated both qualitatively and quantitatively. Qualitatively, host preference was evaluated in three ways, to provide a range between liberal and conservative evaluation scenarios. The most inclusive interpretation for host preference includes as a host every species that has been observed with the presence of a *T. undulatum* across all study sites. An intermediate interpretation is provided by creating species-wide abundance categories for every plant recorded along the Cuban transects, as follows: (1) 10 or fewer individuals, (2) between 11 and 30 individuals, and (3) 31 or more individuals. We then classified the species with the least abundant score and being a host as preferred hosts. The 3rd approach, also the most conservative, was to calculate a host proportion using the abundance of host species at the transect sites divided by the overall abundance for every plant species. This preference interpretation criterion used a host proportion of equal to or greater than 0.5 occurrence for each species.

Quantitatively, for species that are identified as preferred host in the strictest sense, the total number of trees encountered for each species and the number that were observed as hosts was compared to the total number of trees of all species and the total that were hosts, using Chi-square tests (Vergara-Torres et al. 2010). The species must have been observed at a minimum of three times to be tested statistically. The significant p value was adjusted by Bonferroni method.

2.4 RESULTS

Habitat and host species in Everglades National Park, Florida, U.S.A

The ENP population site is known as a coastal transitional buttonwood woodland or hammock (TBH) with a calcitic marl substrate and thin detritus layer at approximately 0.3 m elevation above sea-level (25°10'18" N, 80°54'28" W) (Rutchey et al. 2006, Saha et al. 2009). Flooding at the site between the months of May and October occurs between the open salt marsh and tropical hardwood hammock. Post-storm disturbances can cause an influx of sea water at the site (Saha et al. 2009, Saha et al. 2015). The ENP site consists of a predominant canopy of buttonwood trees, *Conocarpus erectus*, with occasional occurrence of other woody plants such as *Sideroxylon celastrinum* and *Randia aculeata*, and an understory of herbaceous plants including *Alternanthera flavescens, Chromolaena frustrata*, and *Dicliptera sexangularis* (Saha et al. 2015, Wendelberger 2016). The TBH habitat is considered a threatened habitat type and is shrinking due to increasing salinity and sea-level rise at the ENP (Saha et al. 2009). This vegetation type can also be found in shallow coastal regions of Cuba (Borhidi 1991), but we have not yet located populations of *T. undulatum* in these habitats (personal observations).

A total of 277 individuals of *T. undulatum* were documented on the 1-km transect at the ENP population site and all were found growing on the dominant canopy tree species, *C. erectus*. The heights above ground where *T. undulatum* were attached varied between 0.41 and 4 m (average = 1.36 ± 0.6 SD meter height for N=158). Host tree DBH ranged between 6 and 100 cm (average = 31 ± 18.5 SD cm, N=151).

Habitats in Cuba

The general plant communities identified for the Cuban transect sites were Semi-deciduous Mogote Complex (MC), Tropical Semi-deciduous Forest (TSF), Lowland Seasonal Rainforest (LSR), and Wet Montane Forest (WMF), all occupying an exposed limestone karst (Borhidi 1991).

A Semi-deciduous Mogote Complex (MC) is a type of Tropical Karstic Forest with four subdivisions that are based on species richness, location on the island, canopy height, and precipitation. Two MC subdivisions visited within this study include the *Spatheloio-Gaussian* Forest and the *Thrinacion-Punctulatae* Forest. The latter is a species-poor forest found between the Habana and Mayabeque provinces at 200-600 m elevation, while the former is a species-rich deciduous forest found in the western mountains exhibiting high endemism (Borhidi 1991). The *Spatheloio-Gaussian* Forest site (MC 1) visited was found near a popular hiker’s trail in Pinar del Rio (22°33'39" N, 83°49'58" W). The *Thrinacion-Punctulatae* Forest site (MC 2) transect was laid out near Ceiba Mocha, Mayabeque, on two small mogotes (limestone hills) surrounded by pasture (22°57'25"N, 81°46'05" W). The mogotes are steep and the rocky cliffs make it difficult for pastoral animals to climb and damage the vegetation.

The Tropical Semi-deciduous Forest (TSF) community is commonly found along coastal areas where seawater flooding is common. Sites on the coasts of Yaguajay, Sancti Spiritus (TSF 1) (22°16'03" N, 79°12'33" W), and Cienega de Zapata, Matanzas (TSF 2, TSF 3) are microphyllous communities also known as *Coccolobeto-Buresertum* (22°15'56" N, 81°07'05" W and 22°13'14" N, 81°08'08" W respectively). At the Guanahacabibes National Park, Pinar del Rio site (TSF 4) the coastal forest is known for the microphyllous *Bombacopsi-Catalpetum* plant community (21°55'24" N, 84°28'33" W) (Borhidi 1991).

Lowland Seasonal Rainforests (LSR) were historically widespread in Cuba, but most are now agricultural zones. The LSR that we visited, Comunidad 23, Sancti Spiritus, is a predominantly shade-coffee region with high epiphyte richness (21°52'06" N, 79°40'54" W) (pers. comm., Aliesky Gil Carballo). Our LSR transect was in a riparian area with limestone substrate that had not been converted to coffee plantations. Canopy trees in the LSR forest type can reach 40 m in height (Borhidi 1991).

Wet Montane Forests (WMF) are characterized by elevation (above 800 meters), annual precipitation of 1,700-3,000 mm, and a 20-25 m high canopy layer. They are found in the mountains of central to eastern Cuba (Borhidi 1991). One WMF was visited in the Sancti Spiritus Province along a river near the Banao Biology Research station in Jarico (21°51'36" N, 79°34'48" W).

Sampling efforts and observations of host and non-host species in Cuba

A total of 246 plant species were identified across the eight Cuban transects with 74 of them observed as hosts for a total of 1,021 *T. undulatum* (Table 1). The two MC sites had the highest recorded number of woody plant species and host trees with a total of 46 host and 160 non-host species between them (Figure 2 a&b). The most common host species at MC1 was *Adelia ricinella* and *Gymnanthes lucida* at MC2 comprising of

10% [N=245] and 6% [N=222] of the host species respectively. Thirteen percent of the orchids at MC1 were found growing epilithically (growing on the limestone substrate) with a majority of orchids (62%) at MC2 were found to be epilithic.

The TSF sites combined had a total 37 host species and 118 non-host species. The most dominant host species recorded at each site were *Oxandra lanceolata* (12 % at TSF 1) [N=71], *Bucida buceras* (55% at TSF 2 [N=281] and 30% at TSF 3 [N=23]), and *Adelia ricinella* (33% at TSF 4 [N=74]). The WMF and LSR sites had the least host richness with totals of nine host species [N=71] and six [N=34] respectively. *Syzygium jambos* made up the most common host species (55%) at the WMF site. The most common host recorded at the LSR site was *Guazuma ulmifolia* making up 33% of the host tree diversity. Few orchids were found growing epilithic at the WMF site (6%) and none at the LSR site.

We identified 92 host species at the 29 sites across seven provinces in Cuba, from a total of N=1,095 host tree observations (Table 2). Twenty-three of the 92 host species documented are native to both Cuba and southern Florida. Species accumulation curves show that sampling effort on the Cuban transects plateaus for both all species and host species encountered (Figure 3a&b).

Host tree DBH and orchid height on host tree

We recorded the heights of over 845 *T. undulatum* in the Cuban transects that ranged between 0.1 and 8 meters (Figure 1b). The lowest height that a *T. undulatum* was observed is for those orchids found on the ground (0 m). The MC 2 site had the lowest heights on a host which indicates where the *T. undulatum* germinated is 0.1 m for three host trees: *Bursera simaruba*, *Erythroxylum* sp., *Erythroxylum havanense*, and *Gymnanthes lucida*. The tallest that a *T. undulatum* was observed was on a *Bucida buceras* at 8 m at TSF 2 site. We measured 698 host tree DBH at the transects that ranged between 1 and 100 cm (Figure 1a). The largest DBH recorded was a *Ficus* sp. at 105 cm at TSF 3 site. The smallest host plants were recorded at MC 2 and measured 0.25 cm from a *Stigmaphyllon sagraeanum* and two *B. simaruba* plants at 0.6 and 0.65 cm. The mean DBH among and within the nine sites were statistically significant ($F_{8,803}$= 40.14, $P = 0.0014$) as well as the heights ($F_{8,937} = 18.31$, $P = 0.0014$). The most distinct sites with respect to DBH were the LSR, ENP, and WMF (Figure 2a) (Bonferonni post hoc; $P = 0.00139$) (Figure 1 a&b).

Host preferences

Our combined data from the eight transects show that *T. undulatum* was found growing on 74 species or 43% of the total species encountered (Table 1). Most species on the transects were found to not be hosts [N=171], although some were scored as very abundant (Table 2). The preferred host list generated using the intermediately conservative criteria includes a total of 36 species and the more exclusive preferred host list identifies 13 species (Table 1). Statistically, proportions of trees being hosts for all of the 13 species identified as preferred hosts using the strictest criterion were significantly higher than the overall proportion of trees being hosts with all species pooled. Specifically, for *Bucida buceras*, $\chi 2 = 116.7$, $P < 0.001$; for *Citharexylum caudatum*, $\chi 2 = 126.6$, $P < 0.000$; for *Clusia minor*, $\chi 2 = 52.4$, $P < 0.001$; for *Crescentia cujete*, $\chi 2 = 276.4$, $P < 0.001$; for *Hebestigma cubense*, $\chi 2 = 227.2$, $P < 0.001$; for *Petesiodes* *clusiifolium* ($\chi2 = 52.4$, $P < 0.001$; for *Syzygium jambos*, $\chi2 = 503.8$, $P < 0.001$; for *Thyana trifoliata*, $\chi2 = 135.2$, $P < 0.001$; and for *Volkameria aculeata*, $\chi2 = 99.5$, $P < 0.001$. The following were not subject to the chi-square tests because they violated the test assumptions, Clusia sp., Liana (unidentified 4), *Psidium guajava. Tabebuia calcicola*.

2.5 DISCUSSION

Our study illustrates that *T. undulatum* has a large number of host species in its core distribution, and it showed preference on a few of them. This information can be used to inform conservation strategy of this threatened species at its northern most range, as we will discuss in detail below. Studies of this kind are rare in the tropics, especially on orchids, one of the most diverse plant families among tropical plants (Tremblay 2008). There is often a lack in resources and time to study epiphytic species in their current ranges before stochastic events or other rapid environmental changes which demand emergency rescue and translocation actions. In some cases, it is difficult to know where a fallen epiphyte came from and prior knowledge on host species would be helpful to such actions (Tremblay 2008). Active restoration initiatives for anticipating threats to population growth of endangered plants is often needed (Liu et al. 2015, Liu et al. 2020, Maschinski & Haskins 2012). Success of such actions varies depending on the species habitat limitations. Restoration initiatives may have greater likelihood of success when out-planting occurs on trees of the right species and size, aided by a list of host trees with preference orders (Mujica et al. 2013, Segovia-Rivas et al. 2018, Tremblay 2008, Yang et al. 2017). Collecting baseline information for understudied species, like *T. undulatum*, can provide alternative solutions for conservation planners.

Habitats of *T. undulatum* as defined by hosts

The most diverse habitat in terms of host species was the Mogote Complex (MC) sites, which also have the highest percentages of epilithic plants. The *T. undulatum* plants at the MC sites are found at higher elevations and are possibly protected from both flooding and herbivory by large grazing herbivores (i.e. goats and cattle) (Aukema et al. 2007). We observed many plants growing on the Mogote rocky ground. Some orchid species are known to grow and recruit on rocky substrates (Kendon et al. 2020, Yokoya et al. 2015), but we did not observe any protocorms or seedlings of *T. undulatum* growing on rocky surfaces or crevices during the course of our study as we had on host trees. Judging from the size the plants on ground, it is likely that they fell from the host trees nearby. In habitats that experience periodic flooding, such as coastal TSF, BH or LSR sites, *T. undulatum* individuals are unlikely to survive while on the ground.

The three sites with the lowest host species richness were the ENP, WMF and LSR sites. The LSR and WMF habitats are particularly impacted by human presence. The LSR habitats are considered the most common habitat type in Cuba and are seen as ideal for agricultural usage, which makes these sites severely impacted by human presence (Borhidi 1991). Two of eight hosts documented at the WMF site are listed as invasive, including the most common host tree at the site, *Syzygium jambos*, which is found along rivers and waterways (CABI 2021). The ENP site is periodically flooded by saltwater, dominated by *Conocarpus erectus* trees throughout, and the population runs between an open saltwater marsh with no canopy tree species as well as manmade canals skirted by dense *Rhizophora mangle*. It comes as no surprise that *C. erectus* is the only host within this population due to a lack of alternative woody species in the area with a relatively open canopy. *Conocarpus erectus* were not reported in any of the Cuban vegetation assays and therefore not reported as a host in any of the *T. undulatum* populations in Cuba.

Trichocentrum undulatum is likely not microsite limited when germinating since such a wide-scale usage of tree species and growing locations were observed in Cuba. However, in southern Florida, coastal hammocks near the sole existing population were explored in search for more populations of *T. undulatum* but none have been found (pers. obs.). There may be pollination and seed limitations caused by *T. undulatum*'s deceptive pollination strategy and the lower pollinator availability in the southern Florida population (Ackerman et al. 1996, Turnbull et al. 2000). The presence of specialized herbivores as well as high herbivory rates found in the southern Florida population exacerbates fruit set and limits seed production, so although the habitat is there, the seeds may not be (Borrero et al. 2018, Higgins and Gann 2007). Varied mycorrhizal diversity between host trees and habitat types is also likely to be important, particularly because epiphytic orchids may depend on mycorrhizal fungi for water in harsh and dry conditions (Gowland et al. 2013, Kartzinel et al. 2013, Yoder et al. 2000). Bark rugosity, seasonal light penetration through canopy, as well as throughfall of nutrients adds yet more dimensions of complexity that may have an effect to some extent on host tree choices (Callaway et al. 2002, Hirata et al. 2008, Sayago et al. 2013, Zarate-Garcia et al. 2020).

Implications for management

This study is the first to evaluate the differences among habitats for populations of *T. undulatum* across its distribution. Our study is also a reflection of our best effort in understanding the orchid's hosts and vegetation communities in Cuba while access to natural areas is limited. Due to the diversity of host tree species, substrates, elevations, and plant species richness across the Cuban sites, we are certain that the Cuban *T. undulatum* populations are not host-specific (Ackerman et al. 2007, Nieto-Blazquez et al. 2017). The restricted southern Florida population occurred in mangroves with very limited tree diversity, and only one species, *Conocarpus erectus*, serves as a host tree for *T. undulatum*. It is not uncommon for specialist species to express stress characteristics on the leading edges of their distributions due to lower habitat quality (Franco et al. 2006). Yet there may be hope for *T. undulatum* since the wide range of hosts found in the core range overlaps with southern Florida (23 out of the 69 identified Cuban native host species are also native to Florida, USA). Our host list recommendations suggest that particular species be targeted in translocation and conservation projects in Florida, beginning with the species that are both native as well as noted as preferred, followed by intermediately preferred, and finally the more inclusive hosts. Unfortunately, there are no species in the most preferred host list that are native to mainland Florida, an indication that the habitats in South Florida are marginal.

The most similar habitat type in southern Florida to the sites observed in Cuba is the Tropical Hardwood Hammock or Rockland Hammock (G2/S2 Global/State Rank), in which 25 species have been recorded that are *T. undulatum* host trees in Cuba (Institute for Regional Conservation 2021). A listing of "exemplary" Rockland Hammocks that may be adequate planting sites for future projects focused on *T. undulatum* includes: Dagny Johnson Key Largo Hammock Botanical State Park, John Pennekamp Coral Reef State Park, and Lignumvitae Key Botanical State Park (all in Monroe County) as well as Matheson Hammock, Royal Palm Hammock, and Everglades National Park in Miami-Dade county (Florida Natural Areas Inventory 2010). Management of host tree species within orchid distribution is encouraged since available host trees can be a limiting factor for epiphytic orchid populations (Migenis & Ackerman 1993). Although sites in Cuba did have healthy individuals growing on the ground, recommendations for ground planting will not be made for future conservation work due to the flooding risk, ease of potential poaching, as well as increasing herbivory potential.

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Table 2.1: List of all observed host species for *T. undulatum*, host plant family, and vegetation types found at the Cuban and Florida transect sites. The “*” denotes a preferred host based on a species low abundance at sites, yet with the presence of a *T. undulatum* epiphyte (36 species). The “ψ” symbol is used to distinguish the strict interpretation of a preferred host species based on whether a plant species had an observed *T. undulatum* at a minimum of 50% of the time that species was encountered (13 species). Site vegetation where the host species were found are abbreviated with the following acronyms: Mogote Complex (MC), Wet Montane Forest (WMF), Semi-deciduous Mogote Complex (SMC), Tropical Semi-deciduous Forest (TSF), Buttonwood Hammock (BH) and Lowland Seasonal Rainforest (LSR). Following the host species name in brackets [C] means that the species is native to Cuba, [FL] native to Florida - USA and [E] for exotic.

Host Species	**Family**	**Vegetation Type**
Adelia ricinella L. [C]	Euphorbiaceae	TSF, LSR, MC
Albizia saman (Jacq) Merr. [E]	Fabaceae	WMF
Amphitecna latifolia A.H.Gentry [C,FL] *	Bignoniaceae	TSF
Annona glabra L. [C,FL] *	Annonaceae	TSF
Bucida buceras L. [C] $^{\psi}$	Combretaceae	TSF, MC
Bucida sp.	Combretaceae	
Bursera simaruba Sarg. [C,FL]	Burseraceae	MC
Canella winterana Gaertn. [C,FL] *	Canellaceae	MC
Casearia sylvestris Sw. [C] *	Salicaceae	MC
Cecropia peltata L. [C]	Urticaceae	TSF
Cecropia sp.	Urticaceae	
Cedrela odorata L. [C]	Meliaceae	TSF, LSR
Cedrela sp.	Meliaceae	
Celtis trinervia Lam. [C]	Cannabaceae	TSF, MC
Chrysophyllum cainito L. [C]	Sapotaceae	
Chrysophyllum oliviforme L. [C,FL]	Sapotaceae	TSF
Chrysophyllum sp.	Sapotaceae	TSF
Citharexylum caudatum L. [C] $^{*,\psi}$	Verbenaceae	TSF
Citharexylum spinosum L. [C,FL] *	Verbenaceae	TSF, MC
Citrus sp.	Rutaceae	
Clusia minor L. [C] $^{*,\psi}$	Clusiaceae	MC
Clusia rosea Jacq. [C,FL]	Clusiaceae	
Clusia sp. $^{*,\psi}$	Clusiaceae	TSF
Cojoba arborea (L.) Britton & Rose [C] *	Fabaceae	MC

Comocladia dentata Jacq. [C]	Anacardiaceae	MC
Conocarpus erectus L. [C,FL]	Combretaceae	BH
Cordia gerascanthus L. [C]	Boraginaceae	MC
Crescentia cujete L. [C] ψ	Bignoniaceae	TSF, MC, WMF
Cupania glabra Sw. [C,FL]	Sapindaceae	TSF
Damburneya coriacea Sw. [C,FL]	Lauraceae	
Drypetes lateriflora (Sw.) Krug & Urb [C,FL] *	Putranjivaceae	TSF
Erythroxylum areolatum L. [C]	Erythroxylaceae	MC
Erythroxylum confusum Britton [C]	Erythroxylaceae	TSF, MC
Erythroxylum havanense Jacq. [C]	Erythroxylaceae	TSF, MC
Eugenia farameoides A. Rich [C] *	Myrtaceae	TSF
Eugenia monticola (Sw.) DC [C]	Myrtaceae	MC
Exothea paniculata (Juss.) Radlk. [C,FL] *	Sapindaceae	TSF
Ficus americana Aubl. [C,FL]	Moraceae	
Ficus aurea Nutt. [C,FL]	Moraceae	MC
Ficus citrifolia Mill. [C,FL]	Moraceae	MC, WMF
Ficus maxima Mill. [C,FL]	Moraceae	MC
Ficus sp.*	Moraceae	TSF
Gaussia princeps H. Wendl [C]	Arecaceae	MC
Guaiacum officinale L. [C,FL]	Zygophyllaceae	TSF
Guapira obtusata (Jacq.) Little [C,FL] *	Nyctaginaceae	MC
Guazuma ulmifolia Lam. [C]	Malvaceae	TSF, LSR
Gymnanthes lucida Sw. [C,FL]	Euphorbiaceae	TSF, MC
Hebestigma cubense (Kunth) Urb. [C] ψ	Fabaceae	MC
Hibiscus elatus Sw. [C]	Malvaceae	
Jacaranda caerulea (L.) J. St.-Hil. [C]	Bignoniaceae	TSF, MC
Licaria jamaicensis Kosterm Ex Leon & Alain [C]*	Lauraceae	WMF
Lonchocarpus domingensis (Pers.) DC. [C]	Fabaceae	TSF
Maclura tinctoria (L.) D.Don ex Steud. [C]*	Moraceae	TSF
Mangifera indica L. [E]	Anacardiaceae	
Microcycas calocoma (Miq.) A. DC. [C]*	Zamiaceae	MC
Nectandra coriacea (Sw.) Griseb. [C,FL]*	Lauraceae	TSF
Ouratea elliptica (A. Rich.) M. Gomez [C]*	Ochnaceae	MC
Oxandra lanceolata (Sw.) Baill. [C]	Annonaceae	MC, TSF
Pachira cubensis (A. Robyns) Fern.Alon [C]*	Malvaceae	MC
Paullinia fuscescens Kunth. [C] *	Sapindaceae	TSF
Persea americana Mill. [E]	Lauraceae	
Petesiodes clusiifolium (Sw.) Kuntze [C] *,ψ	Primulaceae	WMF

Pisonia aculeata L. [C,FL]	Nyctaginaceae	MC
Plumeria obtusa L. [C]	Apocynaceae	MC
Psidium guajava L. [C] *,ψ	Myrtaceae	TSF
Roystonea regia (Kunth) O.F. Cook [C,FL]	Arecaceae	WMF
Savia sessiliflora (Sw.) Willd. [C]	Phyllanthaceae	LSR, MC
Senna tenuifolia H.S. Irwin & Barneby [C]	Fabaceae	MC
Sideroxylon foetidissimum Jacq. [C,FL]	Sapotaceae	MC, WMF, TSF
Spondias mombin L. [C]	Anacardiaceae	
Spondias purpurea L. [C] *	Anacardiaceae	TSF
Stigmaphyllon sagraeanum A. Juss. [C]	Malpighiaceae	MC
Syzygium jambos (L.) Alston [E] ψ	Myrtaceae	WMF
Tabebuia calcicola Britton [C] *,ψ	Bignoniaceae	MC
Tabebuia leptoneura Urb. [C]	Bignoniaceae	TSF
Tabebuia sp.	Bignoniaceae	WMF
Thyana trifoliata (Poit.) Ham. [C] *,ψ	Sapindaceae	LSR,MC
Trichilia hirta L. [C]	Meliaceae	TSF, MC
Urena lobata L. [C] *	Malvaceae	MC
Vitex divaricata Sw. [C]	Lamiaceae	TSF
Volkameria aculeata L. [C] *,ψ	Lamiaceae	TSF
Tree (Unidentified) 1		
Liana (Unidentified) 1 *		MC
Liana (Unidentified) 2 *		MC
Liana (Unidentified) 3 *		MC
Liana (Unidentified) 4 *,ψ		TSF
Liana (Unidentified) 5 *		TSF
Liana (Unidentified) 6 *		MC
Liana (Unidentified) 7 *		MC
Vine (Unidentified) 1 *		MC

Table 2.2: List of all plant species (236 taxonomically confirmed species, 72 families) recorded at eight 1-km long survey sites across 4 provinces in Cuba. Included is whether or not the plant species was observed as a host, vegetation types that the species was observed in, and the average abundance of the species at the sites. Vegetation types are as abbreviated in Table 2.1.

Species	**Family**	**Vegetation Type**	**No. Transects Present**	**Avg. Transect Abundance**	**Host (Y/N)**
Abrus precatorius L.	Fabaceae	MC	2	7.5	N
Acacia farnesiana (L.) Willd.	Fabaceae	LSR	1	10.0	N
Acacia tenuifolia (L.) Willd.	Fabaceae	LSR	2	12.0	N
Adelia ricinella L.	Euphorbiaceae	LSR, TSF, MC	6	8.5	Y
Ageratina havanensis (Kunth) R.M.King & H.Rob.	Asteraceae	TSF	1	5.0	N
Albizia saman (Jacq.) Merr.	Fabaceae	WMF, LSR, MC	3	5.0	Y
Alibertia edulis (Rich.) A.Rich. Ex DC.	Rubiaceae	TSF	1	2.0	N
Allophylus cominia (L.) Sw.	Sapindaceae	TSF, MC	4	5.0	N
Alvaradoa amorphoides subsp. *psilophylla* (Urb.) Cronquist	Picramniaceae	TSF	1	10.0	N
Ampelocera cubensis Griseb.	Ulmaceae	TSF	1	2.0	N
Amphilophium crucigerum (L.) L.G.Lohmann	Bignoniaceae	LSR, MC	2	3.5	N
Amphitecna latifolia (Mill.) A.H.Gentry	Bignoniaceae	TSF	1	5.0	Y
Amyris balsamifera L.	Rutaceae	MC	2	3.5	N
Amyris elemifera L.	Rutaceae	MC	1	10.0	N
Ancistranthus harpochiloides (M.Gómez) Lindau	Acanthaceae	MC	1	14.0	N
Andira inermis (Wright) DC.	Fabaceae	TSF	4	4.3	N
Annona glabra L.	Annonaceae	TSF	1	2.0	Y
Aristolochia bilabiata L.	Aristolochiaceae	MC	1	2.0	N
Aristolochia ringens Vahl	Aristolochiaceae	LSR	1	5.0	N
Ateleia gummifera (DC.) D.Dietr.	Fabaceae	TSF	1	5.0	N

Badiera propinqua Britton	Polygalaceae	TSF	1	2.0	N
Banisteriopsis pauciflora (Kunth) C.B.Rob.	Malpighiaceae	MC	1	5.0	N
Bignonia diversifolia Kunth	Bignoniaceae	TSF	1	2.0	N
Bomarea edulis (Tussac) Herb.	Alstromeriaceae	MC	1	2.0	N
Bourreria baccata Raf.	Boraginaceae	MC	1	10.0	N
Bucida buceras L.	Combretaceae	TSF, MC	3	17.7	Y
Bunchosia articulata Dobson	Malpighiaceae	TSF, MC	2	2.0	N
Bursera simaruba (L.) Sarg.	Burseraceae	WMF, LSR, TSF, MC	7	5.6	Y
Calophyllum brasiliense var. *antillanum* (Britton) Standl.	Clusiaceae	WMF, LSR, TSF	3	8.0	N
Calycophyllum candidissimum (Vahl) DC.	Rubiaceae	LSR	1	2.0	N
Calyptranthes pallens Griseb.	Myrtaceae	MC	1	2.0	N
Calyptronoma occidentalis (Sw.) H.E.Moore	Arecaceae	WMF, LSR	2	2.0	N
Canavalia nitida (Cav.) Piper	Fabaceae	MC	2	2.0	N
Canella winterana (L.) Gaertn.	Canellaceae	LSR, MC	2	3.5	Y
Capsicum annuum L.	Solanaceae	MC	1	5.0	N
Casearia aculeata Jacq.	Salicaceae	WMF, LSR, TSF, MC	6	4.5	N
Casearia guianensis (Aubl.) Urb.	Salicaceae	TSF, MC	3	5.0	N
Casearia praecox Griseb.	Salicaceae	TSF	1	2.0	N
Casearia sylvestris Sw.	Salicaceae	MC	1	5.0	Y
Catalpa macrocarpa (A.Rich.) Ekman ex Urb.	Bignoniaceae	TSF	1	5.0	N
Cecropia peltata L.	Urticaceae	WMF, LSR, TSF, MC	5	3.2	N
Cedrela odorata L.	Meliaceae	LSR, TSF, MC	5	2.6	Y
Ceiba pentandra (L.) Gaertn.	Malvaceae	TSF, MC	3	2.0	N
Celtis iguanaea (Jacq.) Sarg.	Cannabaceae	TSF	1	2.0	N

Celtis trinervia Lam.	Cannabaceae	TSF, MC	4	5.5	Y
Centrosema virginianum (L.) Benth.	Fabaceae	MC	1	5.0	N
Chiococca alba (L.) Hitchc.	Rubiaceae	LSR, TSF, MC	5	5.0	N
Chrysobalanus icaco L.	Chrysobalanaceae	TSF	1	5.0	N
Chrysophyllum oliviforme L.	Sapotaceae	WMF, TSF, MC	4	4.3	Y
Cissus obovata Vahl	Vitaceae	MC	1	5.0	N
Cissus verticillata (L.) Nicolson & C.E.Jarvis	Vitaceae	WMF, TSF, LSR,MC	6	5.0	N
Citharexylum caudatum L.	Verbenaceae	TSF	1	10.0	Y
Citharexylum spinosum L.	Verbenaceae	MC	2	5.0	Y
Citrus reticulata Blanco	Rutaceae	MC	1	5.0	N
Clusia minor L.	Clusiaceae	MC	1	5.0	Y
Clusia rosea Jacq.	Clusiaceae	WMF, LSR, MC	4	3.5	Y
Clusia sp.	Clusiaceae	TSF	1	2.0	Y
Cojoba arborea (L.) Britton & Rose	Fabaceae	MC	1	5.0	Y
Comocladia dentata Jacq.	Anacardiaceae	LSR, TSF, MC	4	8.5	Y
Cordia bullata var. *globosa* (Jacq.) Govaerts	Boraginaceae	TSF	1	2.0	N
Cordia collococca L.	Boraginaceae	LSR, TSF	2	3.5	N
Cordia gerascanthus L.	Boraginaceae	WMF, LSR, TSF, MC	6	8.5	Y
Crescentia cujete L.	Bignoniaceae	WMF, LSR, TSF, MC	5	7.8	Y
Crossopetalum uragoga (Jacq.) Kuntze	Celastraceae	MC	1	2.0	N
Croton lucidus L.	Euphorbiaceae	MC	1	19.0	N
Cubanola daphnoides (Graham) Aiello	Rubiaceae	MC	1	5.0	N
Cupania americana L.	Sapindaceae	LSR, TSF, MC	3	5.0	N

Cupania glabra Sw.	Sapindaceae	WMF, LSR, MC, TSF	4	6.3	Y
Cupania juglandifolia A.Rich.	Sapindaceae	TSF, MC	2	5.0	N
Cynophalla flexuosa (L.) J.Presl	Capparaceae	MC, TSF	4	5.0	N
Dalbergia ecastaphyllum (L.) Taub.	Fabaceae	TSF	2	7.5	N
Dendropanax arboreus (L.) Decne. & Planch.	Araliaceae	LSR, TSF, MC	3	5.0	N
Dioscorea sp.	Dioscoreaceae	TSF	1	2.0	N
Dioscorea sp.	Dioscoreaceae	MC	1	2.0	N
Diospyros caribaea (A.DC.) Standl.	Ebenaceae	MC	1	2.0	N
Diospyros crassinervis (Krug & Urb.) Standl.	Ebenaceae	TSF, MC	2	3.5	N
Drypetes alba Poit.	Putranjivaceae	TSF	2	5.0	Y
Drypetes ilicifolia (DC.) Krug & Urb.	Putranjivaceae	MC	1	2.0	N
Ehretia tinifolia L.	Boraginaceae	MC	1	5.0	N
Erythrina sp.	Fabaceae	LSR	1	5.0	N
Erythroxylum areolatum L.	Erythroxylaceae	TSF, MC	5	6.8	Y
Erythroxylum confusum Britton	Erythroxylaceae	TSF, MC	3	5.0	Y
Erythroxylum havanense Jacq.	Erythroxylaceae	LSR, TSF, MC	7	11.9	Y
Eugenia axillaris (Sw.) Willd.	Myrtaceae	MC, TSF	2	7.5	N
Eugenia farameoides A. Rich.	Myrtaceae	TSF	1	5.0	Y
Eugenia ligustrina (Sw.) Willd.	Myrtaceae	TSF	1	5.0	N
Eugenia monticola (Sw.) DC.	Myrtaceae	TSF, MC	5	8.8	Y
Eugenia rocana Britton & P.Wilson	Myrtaceae	MC	1	2.0	N
Exothea paniculata (Juss.) Radlk.	Sapindaceae	MC, TSF	2	3.5	Y
Ficus americana Aubl.	Moraceae	MC	1	2.0	N
Ficus aurea Nutt.	Moraceae	LSR, TSF, MC	5	5.0	Y
Ficus citrifolia Mill.	Moraceae	WMF, TSF, MC	4	3.5	Y
Ficus crassinervia Desf. ex Willd.	Moraceae	TSF, MC	3	3.0	N
Ficus maxima Mill.	Moraceae	LSR, TSF	2	5.0	N

Ficus membranacea C.Wright	Moraceae	WMF, LSR, MC	5	4.4	Y
Ficus sp.	Moraceae	TSF	1	5.0	Y
Forestiera rhamnifolia Griseb.	Oleaceae	MC	2	2.0	N
Fridericia podopogon (DC.) L.G.Lohmann	Bignoniaceae	TSF, MC	2	3.5	N
Gaussia princeps H.Wendl.	Arecaceae	MC	1	14.0	Y
Genipa americana L.	Rubiaceae	LSR	1	5.0	N
Ginoria americana Jacq.	Lythraceae	LSR	1	10.0	N
Gouania lupuloides (L.) Urb.	Rhamnaceae	LSR, MC	2	10.0	N
Gouania polygama (Jacq.) Urb.	Rhamnaceae	LSR, MC	2	10.0	N
Guapira obtusata (Jacq.) Little	Nyctaginaceae	MC	1	2.0	Y
Guarea guidonia (L.) Sleumer	Meliaceae	WMF, MC	2	5.0	N
Guazuma ulmifolia Lam.	Malvaceae	WMF, LSR, TSF, MC	4	5.5	Y
Guettarda calyptrata A.Rich.	Rubiaceae	MC	2	5.0	N
Guettarda combsii Urb.	Rubiaceae	TSF	1	2.0	N
Gymnanthes lucida Sw.	Euphorbiaceae	TSF, MC	5	11.6	Y
Hamelia patens Jacq.	Rubiaceae	TSF	1	2.0	N
Hebestigma cubense (Kunth) Urb.	Fabaceae	MC	1	14.0	Y
Heteropteris laurifolia (L.) A.Juss.	Malpighiaceae	LSR	1	5.0	N
Hibiscus elatus Sw.	Malvaceae	LSR, TSF	2	7.5	Y
Hirtella triandra Sw.	Chrysobalanaceae	WMF	1	2.0	N
Hura crepitans L.	Euphorbiaceae	MC	1	5.0	N
Hypelate trifoliata Sw.	Sapindaceae	MC	1	2.0	N
Hyperbaena cubensis (Griseb.) Urb.	Menispermaceae	MC	1	2.0	N
Ilex cassine L.	Aquifoliaceae	TSF	1	5.0	N
Ipomea tiliacea (Willd.) Choisy	Convolvulaceae	MC	2	5.0	N
Ipomoea nil (L.) Roth	Convolvulaceae	MC	2	5.0	N

Ipomoea sp.	Convolvulaceae	LSR	1	5.0	N
Ipomoea tiliacea (Willd.) Choisy	Convolvulaceae	LSR	1	10.0	N
Ixora ferrea (Jacq.) Benth.	Rubiaceae	LSR	1	5.0	N
Jacaranda caerulea (L.) J.St.-Hil	Bignoniaceae	TSF, MC	2	6.0	Y
Jacquinia aculeata Druce	Theophrastaceae	LSR	1	5.0	N
Jacquinia curtisii (Britton) Lepper & J.E.Gut.	Theophrastaceae	TSF	1	2.0	N
Jatropha integerrima Jacq.	Euphorbiaceae	MC	1	5.0	N
Juglans jamaicensis subsp. *insularis* (Griseb.) H. Schaarschm.	Juglandaceae	MC	1	2.0	N
Koanophyllon villosum (Sw.) R.M.King & H.Rob	Asteraceae	MC, LSR	2	10.0	N
Lantana aculeata L.	Verbenaceae	MC	1	10.0	N
Lantana involucrata L.	Verbenaceae	TSF	1	5.0	N
Lasiacis divaricata (L.) Hitchc.	Poaceae	LSR, TSF, MC	3	4.0	N
Lasiacis sloanei (Griseb.) Hitchc.	Poaceae	MC	1	2.0	N
Leucothrinax morrisii (H.Wendl.) C.Lewis & Zona	Arecaceae	MC	1	10.0	N
Licaria jamaicensis Kosterm. ex Leon & Alain	Lauraceae	WMF	1	5.0	Y
Lonchocarpus sericeus (Poir.) DC.	Fabaceae	WMF, LSR, TSF	4	5.0	Y
Luehea speciosa Willd.	Malvaceae	LSR	1	5.0	N
Lysiloma latisiliquum (L.) Benth.	Fabaceae	TSF	1	2.0	N
Maclura tinctoria (L.) D.Don ex Steud.	Moraceae	TSF	1	2.0	Y
Malpighia cubensis Kunth	Malpighiaceae	TSF	1	2.0	N
Malpighia sp.	Malpighiaceae	LSR	1	5.0	N
Mangifera indica L.	Anacardiaceae	LSR	1	5.0	N
Marcgravia rectiflora Triana & Planch.	Marcgraviaceae	WMF, LSR	2	2.0	N
Margaritaria nobilis L.f.	Phyllanthaceae	TSF	1	2.0	N
Matelea oblongata (Griseb.) Woodson	Apocynaceae	MC	1	2.0	N
Melicoccus bijugatus Jacq.	Sapindaceae	MC	1	2.0	N

Melothria pendula L.	Cucurbitaceae	MC	1	5.0	N
Metastelma linearifolium A.Rich	Apocynaceae	MC	1	5.0	N
Metopium brownei (Jacq.) Urb.	Anacardiaceae	MC	1	5.0	N
Miconia sp.	Melastomataceae	LSR	1	5.0	N
Microcycas calocoma (Miq.) A.DC.	Zamiaceae	MC	1	5.0	Y
Microgramma heterophylla (L.) Wherry	Polypodiaceae	MC	1	5.0	N
Momordica charantia L.	Cucurbitaceae	WMF	1	5.0	N
Morinda royoc L.	Rubiaceae	LSR, TSF, MC	6	7.5	N
Mucuna urens (L.) Medik.	Fabaceae	WMF, LSR	2	3.5	N
Nectandra coriacea (Sw.) Griseb.	Lauraceae	TSF	1	10.0	Y
Orthosia scoparia (Nutt.) Liede & Meve	Apocynaceae	MC	1	2.0	N
Ouratea elliptica (A.Rich.) M.Gomez	Ochnaceae	MC	1	2.0	Y
Oxandra lanceolata (Sw.) Baill.	Annonaceae	LSR, TSF, MC	5	12.4	Y
Pachira cubensis (A.Robyns) Fern.Alonso	Malvaceae	TSF, MC	2	2.0	Y
Parthenocissus quinquefolia (L.)Planch.	Vitaceae	TSF	1	2.0	N
Passiflora multiflora L.	Passifloraceae	MC	2	3.5	N
Passiflora suberosa L.	Passifloraceae	LSR, TSF, MC	3	5.0	N
Paullinia fuscescens Kunth.	Sapindaceae	TSF	1	2.0	Y
Peperomia rotundifolia (L.) Kunth	Piperaceae	MC	1	2.0	N
Petesiodes clusiifolium (Sw.) Kuntze	Primulaceae	WMF	1	5.0	Y
Petitia domingensis Jacq.	Lamiaceae	TSF	1	5.0	N
Philodendron consanguineum Schott	Araceae	WMF, MC	3	5.0	N
Philodendron hederaceum (Jacq.) Schott	Araceae	MC	1	2.0	N
Philodendron lacerum (Jacq.) Schott	Araceae	WMF, LSR, MC	3	5.0	N
Picramnia pentandra Sw.	Picramniaceae	TSF, MC	5	10.8	N
Pinochia corymbosa (Jacq.) M.E.Endress & B.F.Hansen	Apocynaceae	MC	1	5.0	N

Piper aduncum var. *ossanum* (C.DC.) Saralegui	Piperaceae	MC	1	5.0	N
Piper articulatum C.DC.	Piperaceae	MC	1	5.0	N
Pisonia aculeata L.	Nyctaginaceae	LSR, TSF, MC	4	9.8	Y
Platygyna hexandra (Jacq.) Müll.Arg.	Euphorbiaceae	MC, WMF	3	5.0	N
Pleopeltis polypodioides (L.) E.G.Andrews & Windham	Polypodiaceae	LSR, MC	2	2.0	N
Plumbago zeylanica L.	Plumbaginaceae	MC	1	10.0	N
Plumeria obtusa L.	Apocynaceae	LSR, TSF, MC	4	10.0	Y
Pouteria dominigensis (C.F.Gaertn.) Baehni	Sapotaceae	MC	1	2.0	N
Prockia crucis P.Browne ex L.	Salicaceae	TSF	1	2.0	N
Psidium guajava L.	Myrtaceae	TSF	1	2.0	Y
Psiguria pedata (L.) R.A.Howard	Cucurbitaceae	MC	1	5.0	N
Psychotria horizontalis Sw.	Rubiaceae	MC	1	10.0	N
Psychotria nervosa Sw.	Rubiaceae	MC	1	10.0	N
Quadrella cynophallophora (L.) Hutch.	Capparaceae	TSF, MC	2	5.0	N
Rauvolfia nitida Jacq.	Apocynaceae	TSF	1	2.0	N
Rhytidophyllum exsertum Griseb.	Gesneriaceae	MC	1	19.0	N
Rondeletia odorata Jacq.	Rubiaceae	LSR	1	5.0	N
Roystonea regia (Kunth) O.F.Cook	Arecaceae	WMF, LSR, TSF, MC	4	4.3	Y
Sabal maritima (Kunth) Burret	Arecaceae	TSF	1	5.0	N
Salix caroliniana Michx.	Salicaceae	TSF	1	2.0	N
Sapium glandulosum (L.) Morong	Euphorbiaceae	WMF	1	14.0	N
Savia sessiliflora (Sw.) Willd.	Phyllanthaceae	LSR, TSF, MC	3	12.7	Y
Securidaca elliptica Turcz.	Polygalaceae	LSR, TSF, MC	6	4.0	N
Senna spectabilis (DC.) H.S.Irwin & Barneby	Fabaceae	LSR	1	10.0	N
Serjania diversifolia (Jacq.) Radlk.	Sapindaceae	TSF	1	2.0	N
Serjania subdentata Juss. ex Poir.	Sapindaceae	LSR, MC	3	5.0	N

Sideroxylon foetidissimum Jacq.	Sapotaceae	WMF, TSF, MC	6	5.0	Y
Sideroxylon salicifolium (L.) Lam.	Sapotaceae	MC	1	5.0	N
Smilax domingensis Willd.	Smilacaceae	WMF, TSF, MC	3	5.0	N
Smilax havanensis Jacq.	Smilacaceae	LSR, TSF, MC	4	4.3	N
Solandra longiflora Tussac	Solanaceae	MC	1	2.0	N
Solanum nitidum Ruiz & Pav.	Solanaceae	MC	1	10.0	N
Spathodea campanulata P.Beauv.	Bignoniaceae	WMF	1	10.0	N
Spondias mombin L.	Anacardiaceae	LSR	1	5.0	N
Spondias purpurea L.	Anacardiaceae	TSF	1	2.0	Y
Sterculia apetala (Jacq.) H.Karst.	Malvaceae	MC	1	5.0	N
Stigmaphyllon sagraeanum A.Juss.	Malpighiaceae	LSR, MC	4	5.0	Y
Swietenia mahagoni (L.) Jacq.	Meliaceae	TSF	1	5.0	N
Syzygium jambos (L.) Alston	Myrtaceae	WMF, LSR	2	24.5	Y
Tabebuia angustata Britton	Bignoniaceae	LSR, TSF	3	5.0	Y
Tabebuia calcicola Britton	Bignoniaceae	MC	1	2.0	Y
Tabebuia leptoneura Urb.	Bignoniaceae	TSF	2	5.0	N
Tabebuia myrtifolia (Griseb.) Britton	Bignoniaceae	MC	1	2.0	N
Tabebuia shaferi Britton	Bignoniaceae	TSF	1	5.0	N
Tabernaemontana alba Mill.	Apocynaceae	TSF, MC	2	5.0	N
Talipariti elatum (Sw.) Fryxell	Malvaceae	WMF	1	14.0	Y
Tecoma stans (L.) Juss. ex Kunth	Bignoniaceae	LSR, MC	2	9.5	N
Thyana trifoliata (Poit.) Ham.	Sapindaceae	LSR, MC	3	3.0	Y
Trichilia havanensis Jacq.	Meliaceae	WMF, LSR, TSF, MC	4	7.3	N
Trichilia hirta L.	Meliaceae	LSR, TSF, MC	4	8.8	Y
Trichostigma octandrum (L.) H.Walter	Phytolaccaceae	MC	1	10.0	N
Turbina corymbosa (L.) Raf.	Convolvulaceae	LSR, MC	3	10.0	N
Turnera ulmifolia L.	Passifloraceae	MC	1	5.0	N

Unidentified Liana #1		MC	1	5.0	Y
Unidentified Liana #2		MC	1	5.0	Y
Unidentified Liana #3		MC	1	5.0	Y
Unidentified Liana #4		TSF	1	2.0	Y
Unidentified Liana #5		MC	1	5.0	Y
Unidentified Liana #6		MC	1	5.0	Y
Unidentified Liana #7		MC	1	5.0	Y
Unidentified Vine		MC	1	5.0	Y
Urena lobata L.	Malvaceae	MC	1	5.0	Y
Urera baccifera (L.) Gaudich. ex Wedd.	Urticaceae	LSR, MC	3	5.0	N
Varronia bullata L.	Boraginaceae	LSR, TSF, MC	3	6.7	N
Vernonanthura menthaefolia (Poepp. ex Spreng.) H.Rob.	Asteraceae	MC	1	5.0	N
Volkameria aculeata L.	Lamiaceae	TSF	1	10.0	Y
Wedelia rugosa Greenm.	Asteraceae	MC	1	5.0	N
Zanthoxylum caribaeum Lam.	Rutaceae	TSF	2	3.5	N
Zanthoxylum elephantiasis Macfad.	Rutaceae	TSF	1	2.0	N
Zanthoxylum fagara (L.) Sarg.	Rutaceae	TSF, MC	2	3.5	N
Zanthoxylum martinicense (Lam.) DC.	Rutaceae	WMF, LSR, MC	3	5.0	N
Zuelania guidonea (Sw.) Britton & Millsp.	Salicaceae	TSF, MC	3	2.0	N

Table 2.3: The range and average (± SD) diameter at breast height (DBH) and height of the *T. undulatum* observed was recorded for the nine 1-km transect sites across habitat types.

Site Name	**Habitat Type**	**DBH (cm)**	**Height above ground (m)**
		Average±SE	**Average±SE**
MC 1	MC	12.7^{cde} ±16.6	2.81^{f}±1.6
MC 2	MC	6.3^{e}±4.3	1.96^{eg}±1.6
TSF 1	TSF	7.7^{e}±3.8	2.94^{bcdf}±1.3
TSF 2	TSF	14.5^{cde}±10.1	2.21^{d}±1.0
TSF 3	TSF	19.9^{bcdef}±11.1	$2.29^{abcdefg}$±0.9
TSF 4	TSF	16^{cde}±9.6	2.65^{bcdf}±1.1
LSR	LSR	41.3^{a}±16.1	3.1^{cf}±2.1
WMF	WMF	20.8^{f}±11.6	2.55^{bcdf}±2.1
ENP	BH	31^{b}±18.5	1.36^{g}±0.6

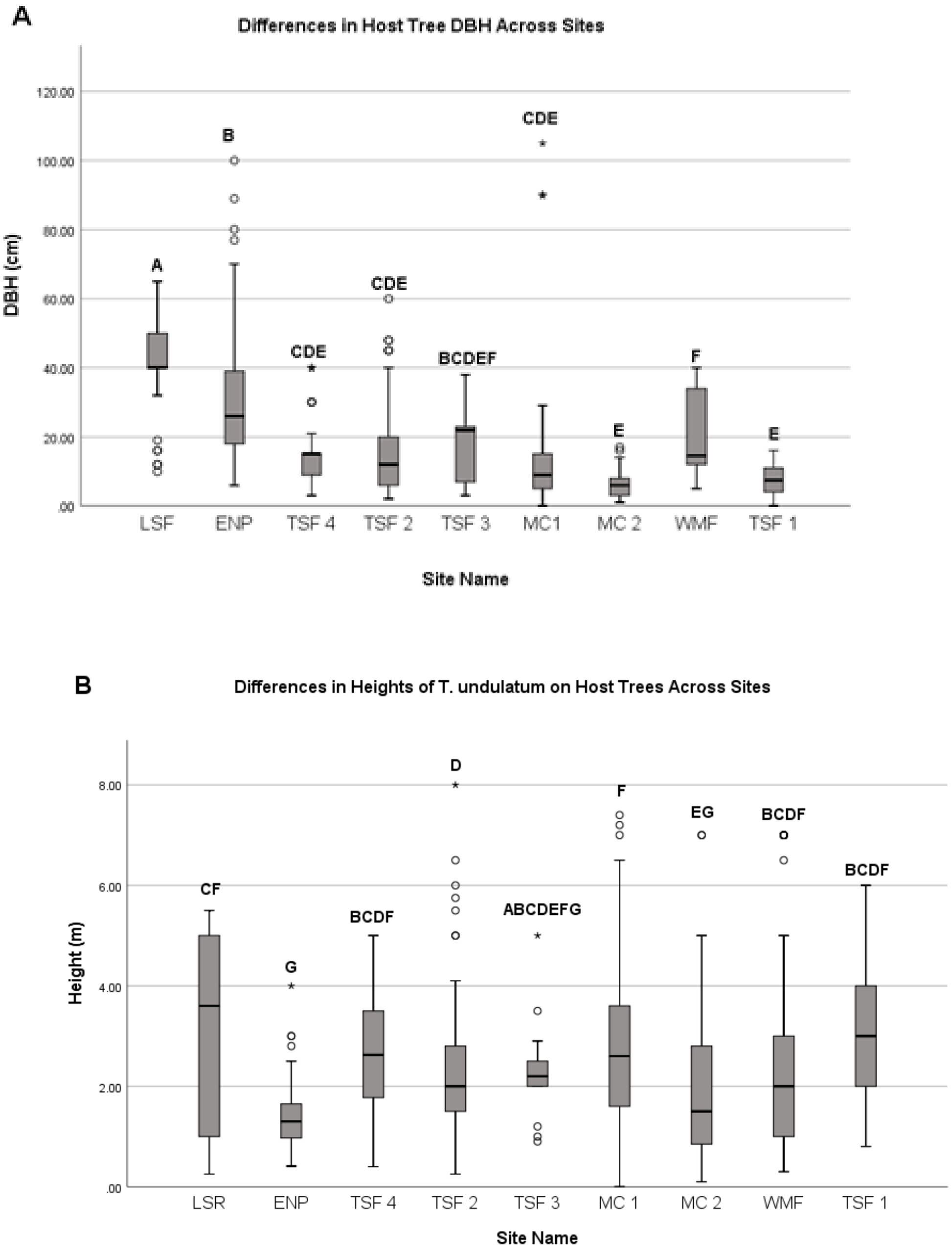


Fig 2.1 a) The range and average (± SD) diameter at breast height (DBH) and b) height of the *T. undulatum* observed was recorded for all nine 1-km transect sites across habitat types in Cuba and Florida, USA.

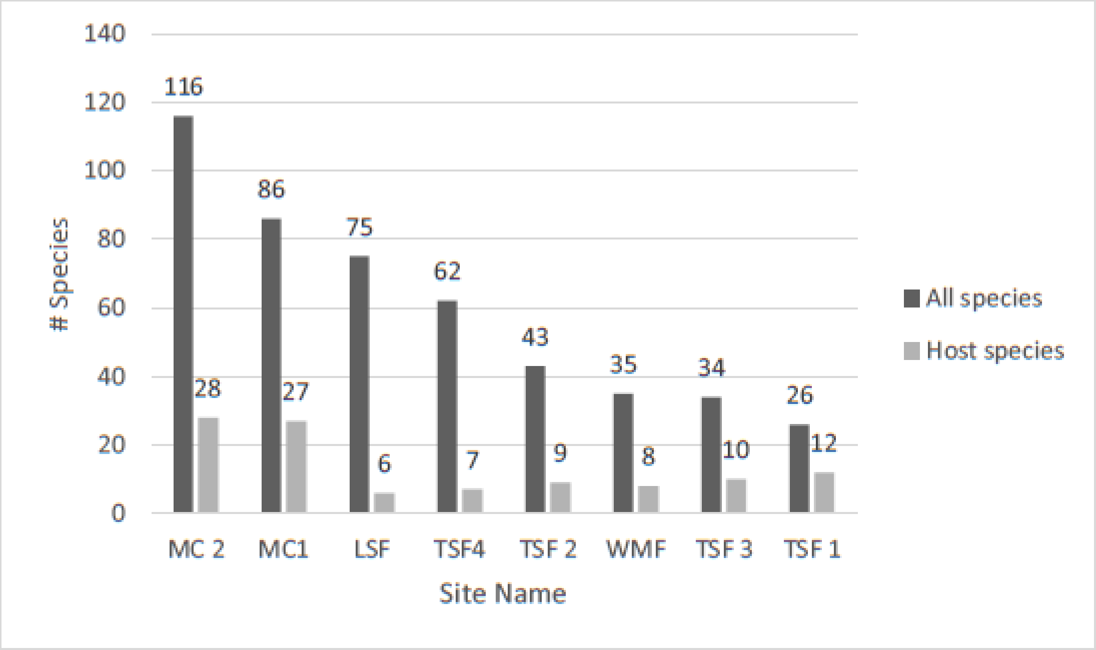
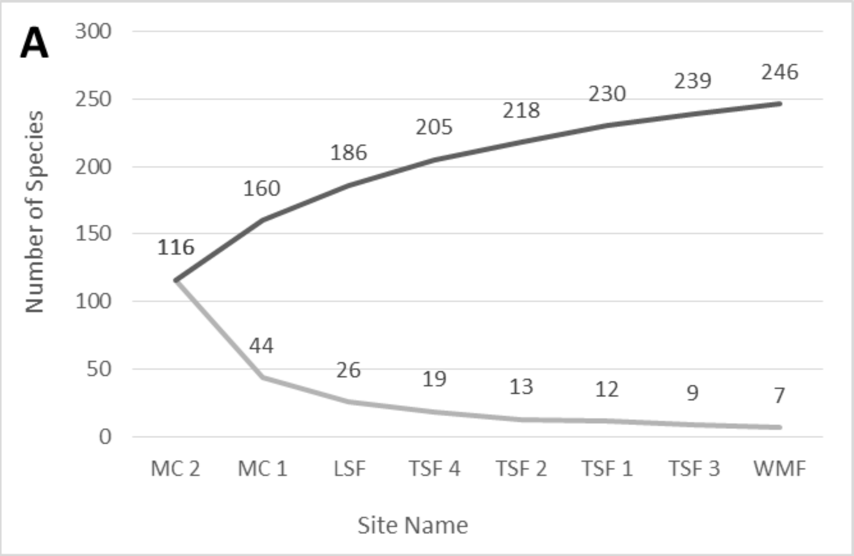


Fig 2.2 Species richness for the following **a)** total species found across eight transect sites in Cuba and **b)** *T. undulatum* host species found across eight transect sites in Cuba.



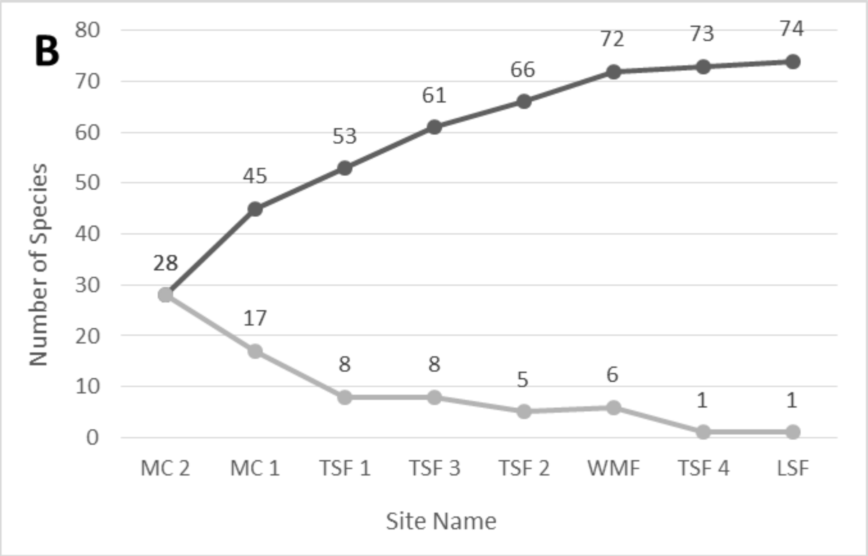
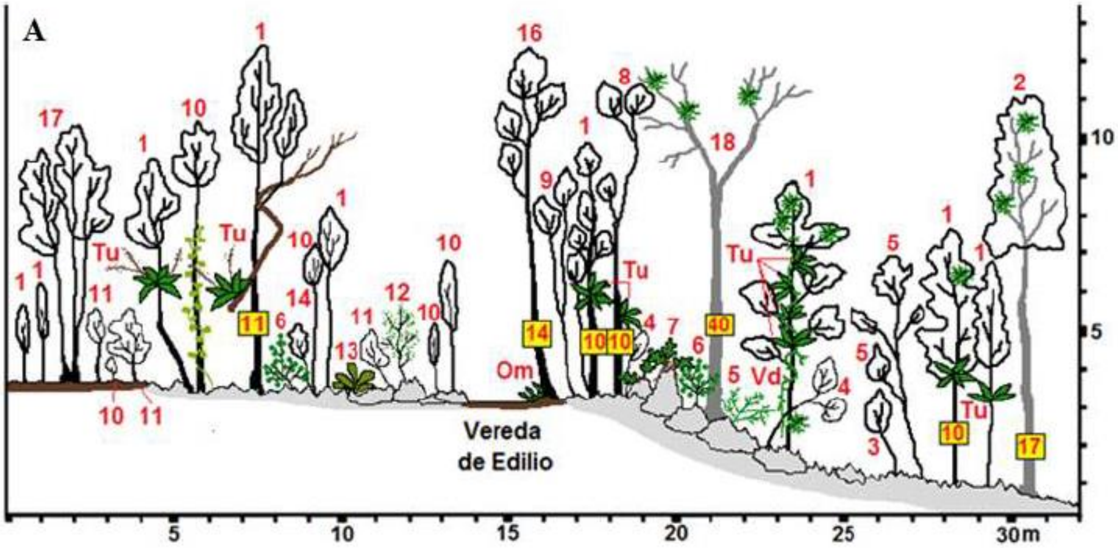


Fig 2.3 Species accumulation curves for the following a) total species found across 8 transect sites in Cuba and b) *T. undulatum* host species found across 8 transect sites in Cuba. The darker line represents the compounding total of new species and the lighter colored line represents the number of new species encountered at subsequent sites.



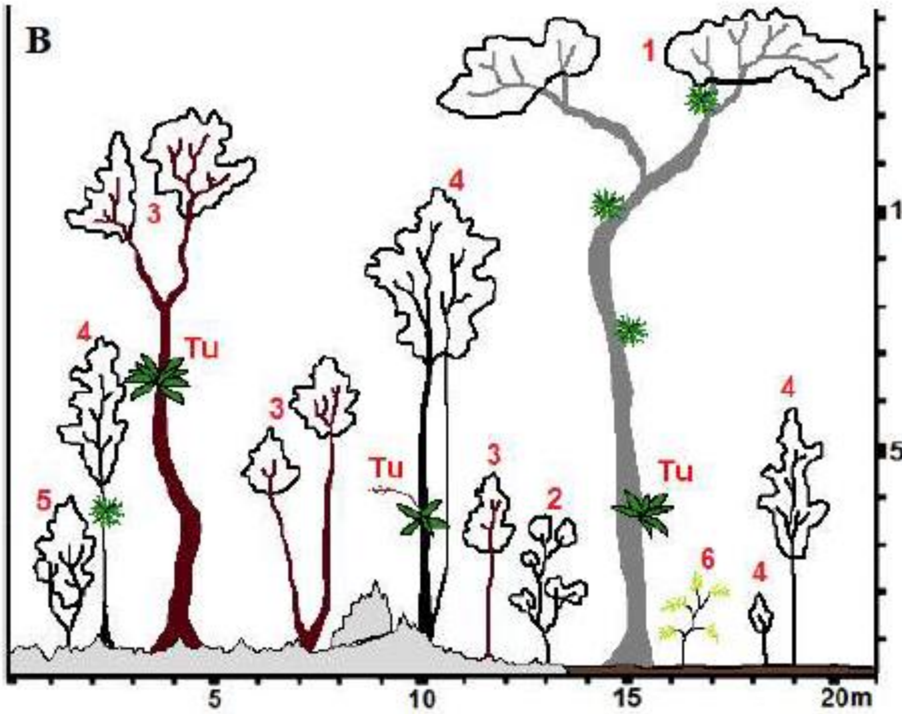


Fig 2.4 Two profiles were drawn from within transects in August of 2018 off the trail of La Vereda de Edilio, Sancti Spiritus, Cuba where demographic information was collected for *Trichocentrum undulatum* at a tropical semideciduous forest in Jobo Rosado protected area (N 22°29614 W -79°22910). *Courtesy of MSc. Armando Falcón Méndez, Biologist, Specialist of Parque Nacional Caguanes, CSASS, CITMA*. a) The woody species have numerical denominations while smaller herbaceous species are an acronym of the first letter of both genus and species: 1 - *Oxandra lanceolata*, 2 - *Zanthoxylum caribaeum*, 3 - *Adelia ricinella*, 4 - *Picramnia pentandra*, 5 - *Olyra latifolia*, 6 - *Erythroxylum havanense*, 7 - *Philodendron lacerum*, 8 - *Cupania glabra*, 9 - *Casearia aculeata*, 10 - *Eugenia axillaris*, 11 - *Amyris balsamifera*, 12 - *Eugenia ligustrina*, 13 - *Anthurium cubense*, 14 - *Cordia gerascanthus*, 15 - *Trichilia hirta*, 16 - *Exothea paniculata*, 17 - *Gossypiospermum praecox*, 18 - *Cedrela odorata*, 19 - *Bignonia diversifolia*, Tu -*Trichocentrum undulatum*, Om - *Oeceoclades maculata*, Tf - *Tillandsia fasciculata*, and Vd - *Vanilla dilloniana*. b) The woody species have numerical denominations while smaller herbaceous species are an acronym of the first letter of both genus and species: 1 - *Cedrela odorata*, 2 - *Adelia ricinella*, 3 - *Sideroxylon foetidissimum*, 4 - *Oxandra lanceolata*, 5 - *Picramnia pentandra*, 6 - *Acacia tenuifolia*, Tu -*Trichocentrum undulatum*, and Tf - *Tillandsia fasciculata*.

CHAPTER III

POPULATION DYNAMICS OF *TRICHOCENTRUM UNDULATUM* (ORCHIDACEAE): THE EFFECTS OF HURRICANES, HERBIVORY, AND LOGGING ACROSS CUBA AND IN SOUTH FLORIDA

3.1 ABSTRACT

In a time of global change, endangered species management should be a priority to prevent extinctions. Unfortunately, detailed ecological information on a per-species basis is often difficult to attain due to the complexities of life histories, inter-species interactions, and the roles of stochastic events. This is especially true for tropical and epiphytic species due to lack of research resources. The Florida state-listed endangered mule-ear orchid, *Trichocentrum undulatum,* is found across the island of Cuba, the species' core range as well as in southern Florida, USA, its northern-most distribution. Through repeated censuses of marked plants at five populations, including the sole population in southern Florida, I was able to calculate plant survival, growth, and seedling recruitment rates and contrasted these vital rates among populations and related them to herbivory intensity, hurricane and logging events. All populations experienced inflorescence-crippling herbivory, at various degrees. The northern peripheral population in Florida experienced higher herbivory pressure overall by (1) having more intense attack by an inflorescence-crippling herbivore, *Melanagromyza miamensis*, prior to Hurricane Irma, and (2) experiencing mortality-triggered leaf herbivory by the invasive scale insect *Diaspis boisduvalii*. Nevertheless, the Florida population had episodic high recruitment events during the study period.

Using demographic matrix modeling and stochastic simulations I investigate the impacts of herbivory, hurricanes, and logging (in Cuba) on population growth rates. Matrices covering the hurricane event and the years following high leaf herbivory attacks had the lowest finite population growth rates (λ) for the sole Florida population. Life table response experiments suggest the differences in population growth rates (λ)

between the Florida population and the growing Cuban population is due to the difference in adult survival. It is particularly concerning that the invasive leaf herbivore and hurricanes cause adult mortality. However, population growth increases following hurricane events and all types of herbivory decreases. Population growth rates of the Cuban populations are less variable, with declining population growth rates in three of the four sites. A Hurricane event also preceded the lowest λ seen among Cuban populations. Logging simulations in Cuba show that the orchid population can continue to grow if selective logging occurs at low frequency.

This study indicates that the Florida population is under high extinction risk and most populations in the core range while more stable, are also in decline. The invasive scale affecting the Florida population is particularly troubling since the insects cause adult mortality. Active restoration in southern Florida, the species' northern peripheral habitat, is needed to ameliorate the threats from sea-level rise (to host habitat) and invasive herbivorous insects.

3.2 INTRODUCTION

The mechanisms of species range expansion is a complicated yet increasingly significant research topic as landscapes rapidly change (Parmesan 2006, HilleRisLambers et al. 2013, Cassini 2013, Louthan et al. 2015). When conditions for sustaining a population in the long-term are no longer viable it would be ideal for a species to be able to move and expand into available habitats that are within the bounds of their ecological limitations. Although populations located on the edge of distributions are usually marginal or constrained due to a variety of reasons such as climate, predation, and geographic barriers, the very same peripheral populations can be sources for future range expansions with their leading “head start” and adaptive genetics (Durka 1999, Parmesan et al. 1999, Parmesan & Yohe 2003, Hampe & Petit 2005, Gibson et al. 2009). Studying the nature of biotic and abiotic factors that drive a population’s dynamics throughout a species’ distribution is valuable to improve the success of conservation and management of the species (Light & MacConaill, Seddon et al. 2013, Römer et al. 2021).

Stochastic events such as hurricanes, drought, and wildfires are main drivers in population dynamics (Ehrlén et al. 2014) and may become more frequent or powerful due to climate change (IPCC 2021). For example, the changes in total frequency of tropical cyclones (TC) due to climate change, be it a maintenance of historical numbers, decreases, or increases, is still in debate; yet the number of TCs that intensify into hurricanes has been modeled to increase (Lin et al. 2021, Murakami et al. 2018, Holland & Bruyere 2014, Bender et al. 2010, Emanuel 2005). The climate and stochastic disturbance regimes of a site is important in determining its of suitability for a given species as well as the presence of interacting species such as herbivores, pollinators, and other symbiosis partners (Morris et al. 2020). If a species were to depend on specialized interspecies interactions, then the distribution of the species can be even more confined than species that were not. In general, specialized interactions have a high sensitivity to environmental changes and theoretically are at their most vulnerable at peripheral habitats because these interactions are expected to be the first of interaction types to become compromised and the most susceptible to disruption (Barman & Devadas 2013, Theobald et al. 2016). An understanding of the differences in ecological conditions between the core of a species range and their peripheral areas will be a needed component in adequately conserving and managing populations of species threatened by global change.

Epiphytic plants, such as orchids and bromeliads, make up a significant portion of the biodiversity in tropical forests (Kress 1985, Gentry & Dodson 1987a). A high sensitivity to wind disturbances, such as tropical storms and hurricanes, makes epiphyte populations and communities often ephemeral (Migenis & Ackerman 1993, Tremblay 2008, Mondragon & Ticktin 2011). Logging can also be devastating to epiphytes due to the potential for direct mortality of plants when a tree is felled as well as the reduction of recruits on potential host trees (Barthlott et al. 2001). Epiphytes inherently depend on other species as host plants and are often specialized to particular sites due to host characteristics, e.g. bark rughosity, trunk diameter or mycorrhizal associations (Callaway et al. 2002, Sayago et al. 2013, McCormick & Jacquemyn 2014, Yang et al. 2017; Zarate-Garcia et al. 2020). Not only can host characteristics of many orchids be narrow in suitability, but other species interactions, e.g. pollinator dependence can be limiting (Raventos et al. 2015, Houlihan et al. 2019). Epiphytes, orchids in particular, are sensitive to changes and can be considered as dynamic due to their climate sensitive physical positions that are prone to disturbance, i.e. above ground with exposed roots (Huston 1994, Zuleta et al. 2016). This sensitivity, together with their dependence on biotic interactions, makes epiphytic orchids quite indicative of tropical ecosystem health (Benzing 1998, Zotz et al. 2009).

Southern Florida has a sub-tropical climate with occasional frost events that are tolerable to some tropical species (Obeysekera et al. 1999, Downing et al. 2016). Both natural and human-led northward-bound expansion of species from the Caribbean and tropical America to southern Florida have already been documented, creating the source populations for these species to expand further north in the North America land (Paulson 2001, Skov & Wiley 2005, Pemberton & Liu 2007, Pemberton & Liu 2008a,b).

The South Florida region is the northern latitudinal limit for 59 orchid species, 44 of which are listed as endangered in the state of Florida. Tailored management strategies are needed for these endangered and threatened populations, to ameliorate threats to population decline and extinction (Martin 2001, Munzbergova et al. 2004, Liu et al. 2012, Borrero et al. 2022). To this end, I studied the ecology and dynamics of several populations of an epiphytic orchid, *Trichocentrum undulatum* (Sw.) Ackerman & M. W. Chase across its distribution range, i.e. in Cuba the presumptive distribution core and in southern Florida, the northernmost edge. I addressed the following questions: (1) Is the Florida population expected to persist? (2) What are the major differences between populations in the core versus edge distribution in terms of growth, fecundity, and overall long-term persistence? (3) What are the impacts of current threats and disturbances to the orchids' populations? In this study I observe and evaluate the effects of leaf and inflorescence herbivory, a major hurricane, and different logging scenarios.

3.3 METHODOLOGY

Study species and area

Trichocentrum undulatum is a tropical epiphytic orchid found in the Greater and Lesser Antilles and southeastern United States (Cetzal-Ix et al. 2016, Ackerman 2014). The orchid is not host specific across its range, but is only known to grow on one species, *Conocarpus erectus* in Florida (Borrero et al. 2022). The orchid experiences flower-crippling herbivory on the inflorescence stalks by the fly *Melanagromyza miamensis* Spencer (Diptera: Agromyzidae) (Hammer 2001, Gann et al. 2007). The fly is suspected to be a specialist herbivore because it is only known to attack the flowering stalks of *T. undulatum* (Borrero et al. 2018). In Florida, the orchid is also severely affected by an invasive scale insect, *Diaspis boisduvalii* Signoret (Hemiptera: Diaspididae).

Historical anthropogenic threats to *T. undulatum* populations include unregulated collection and deforestation, especially in Florida. Records show that the local South Florida distribution of *T. undulatum* was larger prior to logging and extraction, which had occurred in the early 20th century (Gann 2009). While these two threats have greatly diminished in Florida, they are still impacting Cuba and other Caribbean populations to various degrees (personal observations). Natural stochastic events such as hurricanes are expected to be a main driver of population dynamics as they often impact plant communities where populations of *T. undulatum* occur, such as the coastal buttonwood forest of the Everglades National Park (ENP) (Hammer 2001, Gann et al. 2007, Borrero et al. 2018).

Cuba is the largest Caribbean island with over 312 native orchid species which readily disperse to nearby islands and southern Florida, the south-eastern tip of the mainland North America (Ackerman 2014). I studied the demography of four populations of *T. undulatum* in Cuba, each occurring in different vegetation types using classification from Borhidi 1991: Semi-Deciduous Tropical Forest (TSF), Lowland Seasonal Forest (LSF), Wet Montane Forest (WMF), and Mogote Complex (MC). The orchid grew epiphytically on many tree species, as well as epilithically on limestone in MC habitats (Borrero et al. 2022). Only one population exists in Florida and it occurs in Everglades

National Park (ENP) making it a part of the northern limit of the species' distribution. It occurs in the southern coastal Buttonwood (*Conocarpus erectus*) Hammock (BH) habitat and is found growing only on *C. erectus*.

Field methods

Censuses took place between 2013 and 2021. The longest census period was that of the ENP population with a total of nine years (2013-2021). All four populations in Cuba used in demography that were censused more than once: Mogote Complex site 1 (2016-2019, four years), MC site 2 (2018-2019, two years), Tropical Semi-Deciduous Forest site 1 (2016 and 2018 two years), and TSF 2 (2018-2019, two years) (Appendix A). In November 2017, Hurricane Irma hit parts of Cuba and southern Florida, impacting the ENP population.

Four additional populations in Cuba were visited only once, LSF, WMF, TSF 3, and TSF 4. Sites with one census were not included in the life history and matrix model analyses of this paper due to the lack of population transition information, but they were included in the analysis on the correlation between herbivory and fruit rate. All Cuban sites were located between Western and Central Cuba, spanning four provinces: Matanzas (TSF 1 and TSF 4), Mayabeque (MC 1), Sancti Spiritus (TSF 2, WMF, LSF) Pinar del Rio (MC 2 and TSF 3).

At each population of *T. undulatum* presented in this study, individuals were studied within ~1-km strips where *T. undulatum* occurrence was deemed representative of the site, mostly occurring along informal forest trails (Borrero et al. 2022). Once an individual of *T. undulatum* was located, all trees within a 5-m radius were searched for additional individuals. Since tagging was not permitted, we used a combination of information to track individual plants for the repeated censuses. These include the host species, height of the orchid, DBH of the host tree were, and hand drawn maps. Individual plants were also marked by GPS at the ENP site. If a host tree was found bearing more than one *T. undulatum,* then I systematically recorded the orchids in order from the lowest to highest as well as used the previous years' observations in future censuses for individualized notes and size records. I recorded plant size and reproductive variables during each census including: the number of leaves, length of the longest leaf (cm), number of inflorescence stalks, number of flowers, and the number of mature fruits. I also noted any presence of herbivory, such as signs of being bored by *M. miamensis*, and whether an inflorescence was partially or completely affected by the fly, and whether there was other herbivory, such as *D. boisduvalii* on leaves.

I used logistic regression analysis to examine the effects of year (at the ENP site) and sites (all sites) on the presence or absence of inflorescence herbivory at all the sites. Cross tabulation and chi-square analysis were done to examine the associations between whether a plant was able to fruit and the presence of floral herbivory by *M. miamensis.* The herbivory was scored as either complete or partial.

During the orchid population scouting expeditions I came across a small population in the Matanazas province (TSF 4, within 10 km of TSF 1 Site) and recorded the demographic information. Although the sampled population was small (N = 17), I was able to observe logging impacts at the site and recorded logging associated mortality on the subsequent return to the site.

Matrix modeling

Definition of size-stage classes

To assess the life stage transitions and population structures for each plant for each population’s census period we first defined the stage classes for the species. The categorization for each plant’s stage class depended on both its size and reproductive capabilities, a method deemed appropriate for plants (Lefkovitch 1965, Harper 1977). A size index score was calculated for each plant based on the number of observed leaves plus the length of the longest leaf, an indication of accumulated biomass (Emeterio-Lara et al. 2021). The smallest plant size index that attempted to produce an inflorescence is considered the minimum size for an adult plant. Plants were classified by stage based on their size index, flowering capacity and age (a minimum age based on return censuses) as the following: (1) seedlings (or new recruits), i.e. new and small plants with a size index score of less than 6, (2) juveniles, i.e. plants with a size index score of less than 15 with no observed history of flowering or a minimum of three years of age, (3) adults, plants with size index scores of 15 or greater. Adult plants of this size or larger are capable of flowering but may not produce an inflorescence in a given year. The orchid’s population matrix models were constructed based on these stages.

In general, orchid seedlings are notoriously difficult to observe and easily overlooked in the field due to the small size of protocorms. A newly found juvenile on a subsequent site visit (not the first year) may therefore be considered having previously been a seedling in the preceding year. In this study, I use the discovered “seedlings” as indicatory of recruitment for the populations. Adult plants are able to shrink or transition into the smaller juvenile stage class, but a juvenile cannot shrink to the seedling stage.

Matrix elements and population vital rates calculations

Annual transition probabilities for every stage class were calculated. A total of 16 site and year specific matrices were constructed. When seedling or juvenile sample sizes were < 9, the transitions were estimated using the nearest year or site matrix elements as proxy. Due to the length of the study and variety of vegetation types with a generally large population size at each site, transition substitutions were made with the average stage transition from all years at the site as priors. If the sample size of the averaged stage was still too small, the averaged transition from a different population located at the same vegetation type was used. I avoided using transition values from populations found in different vegetation types to conserve potential environmental differences. A total of 20% (27/135) of the matrix elements were estimated in this fashion, the majority being seedling stage transitions (19/27) and noted in the Appendices alongside population size (Appendix A). The fertility element transitions from reproducing adults to seedlings were calculated by the number of seedlings produced per adult plant.

Deterministic modeling analysis

I used integral projection models (IPM) to project the long-term population growth rates for each time period and population. The finite population growth rate (λ), stochastic long-term growth rate (λ_s), and the elasticity were projected for each matrices using R Popbio Package 2.4.4 (Stubben & Milligan 2007, Caswell 2001). The elasticity matrices were summarized by placing each element into one of three categories: fecundity (transition from reproductive adults to seedling stage), growth (all transitions to new and more advanced stage, excluding the fecundity), and stasis (plants that transitioned into the same or a less advanced stage on subsequent census) (Liu et al.

2005). Life table response experiments (LTREs) were conducted to identify the stage transitions that had the greatest effects on observed differences in population growth between select sites and years (i.e. pre-post hurricane impact and site comparisons of same vegetation type).

Due to the frequent disturbances that epiphytes in general experience as well as our species' distribution in hurricane prone areas, we ran transient dynamic models that assumes the populations censused were not at stable stage distributions (Stott et al. 2011). I calculated three indices for short-term transient dynamics to capture the variation during 15-year transition period: reactivity, maximum amplification and amplified inertia. Reactivity measures a population's growth in a single measured timestep relative to the stable-stage growth, during the simulated transition period. Maximum amplification and amplified inertia is the maximum of *future population density* and the maximum *long-term population density*, respectively, relative to a stable-stage population that began at the same initial density (Stott et al. 2011). I used a mean matrix for TSF 1, TSF 2, MC 1, and MC 2 sites and the population structure of their last census. For the ENP site, I averaged the last three matrices post-hurricane disturbance and used the most-recent population structure. I standardized the indices across sites with the assumption of initial population density equal to 1 (Stott et al. 2011). Analysis was done using R Popdemo version 1.3-0 (Stott et al. 2012b).

Stochastic simulation

I created matrices to simulate the effects of episodic recruitment, hurricane impacts, herbivory, and logging (Appendix B). The ENP site is the longest running site with nine years of censuses (eight transitions) which I used to select matrix elements that contained the years that experienced episodic recruitments, direct impact from Hurricane Irma (category 3, a major hurricane), as well as leaf herbivory impacts from scale insects. *Trichocentrum undulatum* experiences infrequent recruitment, but I captured episodes of high recruitment at the ENP site during the first and sixth monitoring years.

Specifically, an episodic recruitment simulation matrix for one of the Cuban field sites with the longest running census period (MC1 Site) was created to calculate the probability of episodic recruitment that the population will need in order to reach a stable $\lambda_s = 1$ (Appendix B). The simulated matrix for MC 1 was created using the average transitions for the real-time site censuses and substituting the transition elements of fecundity, seedling survival, and seedling growth transition from the episodic recruitment event at the ENP.

To simulate the impact of the lethal *D. boisduvalii* attacks, I removed the plants that were observed as dead due to scale infestation during the third and fourth census and constructed a new matrix to calculate λ_s (Appendix B). Similarly, to infer the impact of Hurricane Irma, I excluded mortality caused by the hurricane (2017) at the ENP site, i.e. deaths attributed to the hurricane for each stage class documented in the fifth census and generated a non-hurricane affected matrix to calculate λ_s.

To project the effects of hurricanes at the ENP site, positions of hurricanes passing through a 100 km circle centered at the site between the years 1970 and 2020 were extracted from National Oceanic and Atmospheric Administration (NOAA) and the National Hurricane Center's HURDAT2 climatology (Landsea and Franklin 2013). I used the historical hurricane frequency at the ENP site (one hurricane per decade) to calculate the λ_s under the same hurricane regime. In an abundance of caution for the potential increase in TC intensification into hurricanes at the site, I also carried out a simulation using a scenario with more frequent hurricane episodes (an increase in hurricane frequency of 50%) in order to see the effect on the projected long-term population growth of the population. I created a Markovian chain (adapted code from S. Elsner 2008) with four major transition phases: (1) phase I, the hurricane year (census 5); (2) phase II, first year post-hurricane (census 6); (3) phase III, second and third year post hurricane (7 and 8); (4) phase IV, non-hurricane affected years (census 1, 2, 3, and 4) (Table 3.3; Appendix A).

The probability of a hurricane happening on any given year was 0.1. If a hurricane did occur, then Phase II was followed by Phase III, unless another hurricane. The two matrices in phase III occurred at equal probability on the second and third year post-hurricane. On the fourth year after a hurricane and until the next hurricane occurs, the four matrices in phase IV occurred at equal probability. To project the effects of an increase in hurricane frequency, we applied changes to the yearly hurricane probability to 0.15 (an increase of 50%). The remaining probabilities for the above post-hurricane stayed the same.

The TSF 1 site is one of the largest populations censused in this study and is found in a coastal forest that experiences periodic flooding similarly to the ENP site. Hurricane Irma swept over the northern coast of Cuba and did not affect TSF 1. I used the mortality for each stage class observed at the ENP from hurricane damage and created a hurricane matrix for the TSF 1 population. I simulated different hurricane year probabilities alongside the other empirical-data based matrices for the TSF 1 censuses until a stable stochastic long-term growth rate ($\lambda_s = 1$).

Logging and its impact was documented near the TSF 1 site in the same regional coastal forest. I used data on the species identification and DBH of the logged host species to simulate the effects of two types of logging regimes on *T. undulatum*. Specifically, *T. undulatum* that were growing on species targeted by loggers were marked as dead, no matter the DBH of the host plants. The targeted species are *Bucida buceras*, *Tabebuia angustata*, and *Annona glabra*. A second matrix was created that used both host species and a minimum DBH measure from the nearby field observations to attribute mortality to the *T. undulatum*. I used the following minimum DBH sizes per logged host species: *B. buceras* = 18 cm, *T. angustata* 22 cm, *A. glabra* = 23 cm. The λ_s was calculated for both logging scenarios to determine the frequency of logging under both regimes that would allow projected long-term persistence ($\lambda_s = 1$).

3.4 RESULTS

Population Descriptions

i. Population structure

In total, 278 individuals of *T. undulatum* were recorded at the ENP population for all censuses. On average across the censuses at ENP, approximately two-thirds (63%) of *T. undulatum* was comprised of adults, a fifth of which flowered. A little more than a quarter (27%) made up the juvenile stage class with the rest (11%) of seedling stage. The census year with the least adults observed in proportion to the other stage classes was in 2014 and 2019, where approximately half of the population was comprised of adult plants (Figure 3.1). The 2013 and 2014 census years had the highest percentage of seedlings making up the population at 17 and 22% respectively (Figure 3.1).

For the Cuban populations, on average both MC 1 (N = 193) and TSF 2 (N = 53) had a dominant stage class of adults exceeding 90% (96% and 97% respectively) (Figure 3.1). Approximately half of the adults at each site flowered, 52% at MC 1 and 45% at TSF 2. There was a small portion of the populations that comprised of juveniles (4% and 2%) and less than 1% of seedlings (Figure 3.1). About three-quarters of the plants at sites MC 2 (N = 104) and TSF 1 (N = 290) were adults, 82% and 72% respectively, with 26% and 43% of the plants being reproductive adults. Thirteen percent of the plants at MC 2 and approximately a quarter to a third of plants at TSF 1 were juvenile. Less than 5% of the plants were categorized as seedlings at both sites, 5% at MC2 and 2% at TSF 1 (Figure 3.1).

The LSF (N = 34) and TSF 3 (N = 17) populations had no seedlings observed during census years, juvenile stage classes were between 0-20% of the population at TSF 3 and 11% at LSF. At both sites the adults made up between 88 and 100% of the population with the majority of the total plants being reproductive adults at TSF 3 (73-80%) and the vegetative (71%) at LSF (Figure 3.1). The WMF (N = 66) and TSF 4 (N = 76) had less than 6% of the population made up of seedlings (Figure 3.1). The juvenile stage comprised of 35% at both sites. Vegetative adults made up the largest cohort at TSF 4 of 33% with reproductive adults making up the largest stage group at the WMF site (44%) (Figure 3.1).

Fruit set varied from year to year at the ENP site with sporadic fruiting occurrence, 14 or more fruit, in 2013 (four plants fruited), 2014 (four plants fruited), and 2019 (three plants fruited). No fruit were observed on all other ENP censuses (Table 3.1). There were three populations in Cuba that were reproductive on every censuses year with a minimum of one fruit and maximum of five observed, they were: MC 1 (between one and two plants fruiting per year), MC 2 (between one and three plants fruiting per year), and TSF 1 (one fruit per year) (Table 3.1). The TSF 3, TSF 4, LSF, and WMF populations were not found to have fruit on any survey year.

ii. Survival at Everglades National Park, Florida

At the ENP site, 23.9% of the plants recorded in 2013 survived until 2021 (N = 184). The ENP site experienced two significant declines of over 40% in annual survival during the 2015-2017 year observation period as well as the 2017-2019 years.

iii. Presence and effects of herbivory on leaves and fruiting

The plant's ability to set fruit was significantly affected by the herbivore *M. miamensis* attack on the inflorescence (N = 599) ($\chi 2 = 7.524$, df = 1, $P < 0.006$). Herbivory observations differed between census years, yet *M. miamensis* was found in every census and affected all populations of *T. undulatum* over the course of this study (Table 3.1). The probability of inflorescence herbivory varied across years at the ENP population ($\chi 2 = 56.832$, df = 6, $P < 0.001$). Inflorescence herbivory rates in the ENP were above 80% between 2013 and 2015, with 100% of flowering plants affected in 2015. During this period there was a combination of complete and partial herbivory (Fig. 3.8). Rates of complete herbivory exceeded 91% of flowering plants in 2015, rendering them completely affected incapable of flowering (Table 3.1). The lowest rates of inflorescence herbivory recorded at ENP was post-hurricane Irma in 2019 and 2021 at 14.3% and 13.3% respectively (Table 3.1). All of the flowering plants that were affected by *M. miamensis* between 2017 and 2019 were unable to produce flowers due to complete inflorescence herbivory (Table 3.1).

Herbivory intensity varied significantly across sites ($\chi2 = 73.11$, df = 8, $P < 0.001$). All inflorescences of three Cuban populations were affected by *M. miamensis*; MC 2 and TSF 2 in 2019, and TSF 3 in 2018. I documented inflorescence herbivory exceeding 88% during other census years, as well for TSF 1 and LSF in 2018 (Table 1). Both TSF 2 and TSF 3 had at least 90% of their flowering stalks completely affected by the fly. The remaining populations, MC 1 and WMF, experienced between 25-65% fly herbivory on their flowering plants.

The ENP site had rates of general leaf herbivory by a *D. boisduvalii* across plants exceeding 17% in 2013 (N = 132) and 2021 (N = 59) (Table 3.2).

Deterministic modeling

Declining finite population growth rates occurred across the majority of sites and years. Positive growth was projected for the first ($\lambda = 1.09$) and sixth ($\lambda = 1.04$) matrices at the ENP site and on both censuses' at TSF 1 site ($\lambda = 1.07$ and 1.04) (Figure 3.3). The lowest finite population growth rate ($\lambda = 0.698$) was the hurricane year matrix (2017-2018) in ENP. Other sites and years with the low finite population growth rate was ENP from the second to fourth censuses (ranging from $\lambda = 0.856$ to 0.871) and TSF 2 site ($\lambda = 0.86$) (Figure 3.3). Across all of the sites, the stasis of adults had the highest elasticity to long-term population growth rates and fecundity had the lowest (Figure 3.4, Figure 3.5).

The LTRE experiments showed that the vital rates with the largest contributions to the difference of λ between the ENP and TSF 1 populations were both the lower adult survival and reproduction at the ENP site (Figure 3.6). The shrinkage of adults and increased juvenile growth were the highest contributors to the lower λ observed on the hurricane impacted year versus the preceding non-hurricane impacted year, high fecundity and adult mortality were also contributors (Figure 3.6). Comparisons between both TSF sites show that lower stage shrinking, lower growth and lower fecundity were the largest contributors to TSF 2's lower λ (Figure 3.6). The largest contributors to the difference in TSF 1's λ when compared to MC 1 is the lower fecundity and seedling growth at MC 1 (Figure 3.6). For MC 2, lower adult survival and seedling growth contributed the lower λ when compared to TSF 1. Comparing both MC sites show that lower adult survival and higher adult shrinkage at MC 1 were the main contributors to its lower λ (Figure 3.6).

The transient indices for the ENP, MC 1, TSF 1 and TSF 2 populations show that the population density is higher than the stable stage distribution or in amplification prior to stabilization (Figure 3.7). The indices for the MC 2 population show a lower and decreasing density than the stable stage distribution prior to stabilization. The TSF 2 population increases sharply followed by a decreasing density than the stable stage distribution prior to stabilization.

Stochastic modeling and simulations

The stochastic growth rate for all sites is <1, indicating projected population decline, except for TSF 1 (Figure 3.4). Growth rate for ENP site is below 1 ($\lambda_s = 0.91$) and remained so even if the effects of leaf herbivory and hurricane mortality ($\lambda_s = 0.95$) are removed. The hurricane simulations projected $\lambda_s = 0.899$ for the historical probability of a hurricane and a slightly smaller $\lambda_s = 0.898$ under the assumption of hurricanes becoming 50% more frequent.

To reach a stable stochastic growth rate ($\lambda_s = 1.0$), the peripheral ENP site would need an average 0.65 seedlings per adult produced each year. The λ_s at MC 1 with no manipulations to the matrices was 0.974. The introduction of episodic recruitment at MC 1 site increased the λ_s to 1.0 if it occurred with an average of 0.30 seedling per adult per year.

3.5 DISCUSSION

Conventionally, core populations are defined geographically or by population densities, yet there are limitations due to spatial complexities and that of a species' life history (Sagarin & Gaines 2002, Barnett et al. 2021). A species' core range can be determined ecologically based on habitat quality and diversity, where a setting that is harboring better and more diverse habitats make up a species' core range. This study illustrates that the peripheral population of *T. undulatum* observed in this study is located in a marginal habitat due to contrasting threats and a lower projected long-term persistence when compared to core populations. The results of this study provides insight into the population dynamics spanning a species' distribution.

While there have been several studies on the impacts of hurricanes on epiphytic orchids (Rodriguez-Robles et al. 1990, Oberbauer et al. 1996, Ackerman & Moya 1996, Wiegand et al. 2013, Raventos et al. 2015), this study is one of the very few that conducted census on a population several years before and several years after the impact of a hurricane, and the first to examine interaction effects of hurricane and insect herbivory on an orchid species. In addition, very few orchid studies have focused on the impacts of herbivory and differences of ecosystems on population dynamics (Light & MacConaill 2011, Mondragon & Dutra 2013).

Site differences: peripheral vs. core range

The majority of the monitored populations of *T. undulatum* are projected to decline over the long-term during the study period, which may not be so different from other epiphytic orchid species that often experience long-term persistence $\lambda < 1$ (Mondragon et al. 2015, Ackerman et al. 2020). The population growth rates of the northern peripheral population in ENP varied more widely than that of the core populations in Cuba, and the only population showing long term growth ($\lambda > 1$) was TSF 1, a Cuban population. The transient analysis does provide insight into the short-term (15 year) population density related to stable stage and show that four out of the five populations are in an upwards trajectory, the exclusion is MC 2 which is shown to have a slightly smaller population density than λ projects.

The major differences between the ENP site and most Cuban sites (excluding hurricane affected TSF 2 with a low λ_s) is the higher survival rates of adult plants and the higher transition from juveniles to adults in Cuba. The rate of population decline in Cuba is slower than that of the ENP site, except for TSF 1 which is the only population in this study projected to increase. Similarly to ENP, the TSF 1 site is coastal and experiences flooding, yet adult survival is higher at TSF 1. In general, core populations are host to more diverse set of mutualistic partners as well as ideal habitat characteristics than the potentially more marginal peripheral populations (Martin 2001, Sexton et al 2009). In the growing core population of TSF 1 there is a higher diversity of host tree species when compared to the ENP site (Borrero et al. 2022). A higher richness of pollinators in the core range is also likely. Due to *T. undulatum*'s core range being located in the tropics, there may be a dependence on tropical bee species found in Cuba, i.e. the Hymenopteran genus *Centris*, whereas only one species is present in southern Florida and five species in

Cuba (Pascarella et al. 1999, Genaro 2008). The larger diameter of host trees in Cuba may also support the concept of less branch breakage from wind damage caused mortality at ENP (Mondragon & Dutra 2013, Borrero et al. 2022). There are no publications on mycorrhizal associations of *T. undulatum*. Mycorrhizal associations may differ between countries as well as host tree species, yet a lack of sufficient recruits is not the drive for a declining population in Florida; unlike in populations of *Dendrophylax lindenii* across its range (Mujica et al. 2018). Similarly to work conducted on small island populations of *Brassavola culcullata* in the Caribbean, with general long-term decline it seems that adult survival alongside moderate rates of recruitment is needed to maintain population persistence over the long-term (Mondragon et al. 2015, Ackerman et al. 2020). The elasticity values for both seedlings and juveniles were also found to be small, reflecting that variation in their numbers may not affect the main conclusions found here and supports the decision in substituting select matrix elements for small sample sizes in certain sites and years, although the use of a Dirichlet distribution is otherwise an ideal alternative (Tremblay et al. 2021).

Herbivory impacts: inflorescence and leaf herbivory

There were two significant mortality events during the study period at the ENP site. The first in the 2015-2017 period was preceded by relatively high leaf herbivory observations, the majority of which was scale insect infestation by *D. boisduvalii*. The leaf herbivory, having only been observed at the ENP population, might have both increased the likelihood of pathogen infection and deaths among plants, which may be responsible for the second lowest finite population growth rate over the nine-year study period. The simulated removal of the leaf herbivory impacts led to an increase in the long term growth rate, suggesting direct deleterious effects from the herbivory pressure of *D. boisduvalii* at the peripheral population. The largest mortality event for the peripheral site was that of the hurricane impact year period of 2017-2018, which was followed by both an increase in plant growth as well as a reduction in leaf and inflorescence herbivory.

Noticeably different herbivory rates and fruit sets were recorded across the different populations and habitat types of *T. undulatum*. Although the ENP site exhibited sporadic fruit set with certain years making no fruit whatsoever, there was at times a dramatically large number of fruits although the population experienced high inflorescence herbivory exceeding 80% of the flowering plants. The dampening of recruitment numbers by floral herbivory can be nebulous to quantify (Leavitt & Robertson 2005, McCall & Irwin 2006, Recart et al. 2013), yet it seems for *T. undulatum* that as long as the inflorescence herbivory by *M. miamensis* is partial and does not completely hinder flowering, then the recruitment may not be of too much consequence and pollination may still take place. The Cuban populations with no fruit recorded during the course of this study exhibited high *M. miamensis* herbivory of greater than 88% (TSF 3 and LSF sites). The likelihood of successful pollination is lowered when there are fewer flowers available, although possible like in the case of ENP or of TSF 1 that experienced over 96% fly herbivory in 2018 yet was able to produce fruits.

Non-rewarding orchids, such as *T. undulatum*, in general have been observed to have low fruit set, especially when pollinator limited (Ackerman et al. 1996, Turnbull et al. 2000, Tremblay et al. 2005). Generally, a peripheral population lacks certain ecological characteristics that make the site less than adequate or less than the ideal core range location (Lawton 1993). It seems that although the ENP population is in a precarious position on a coastal buttonwood hammock forest that is in danger of both sea-level rise (that may impact the survival of host trees), more intense pressure from the native inflorescence herbivore than the Cuban populations, and an addition of an exotic herbivore impact, there was more fruit set and recruiting events observed in the single population than in the core populations in Cuba. This of course is under the assumption that there are occasional low herbivory years by the specialist inflorescence herbivore that would allow *T. undulatum* to flower unimpeded or at least with partial success. Simulating an increase in episodic recruitment to the same degree as observed at ENP was shown to benefit the Cuban site MC 1, though it would need to occur at a high annual probability of 0.30 to stabilize the population and may be unlikely since no such episodic recruitment was observed in any of our censuses populations in Cuba.

Small populations of non-rewarding orchids composed of a small number of flowering adults have been shown to have higher fruit sets when compared to larger populations (Tremblay et al. 2005), this may partially explain the higher fruit set in ENP when compared to the other populations with a higher proportion of flowering individuals in the population structure. The pollinator richness and visitation frequencies among sites may also explain the variation in fruit set, with some species being more effective than others (Robertson & Wyatt 1990) or occurring in a higher abundance (Ackerman et al. 1997, Nilsson 1983c, Tremblay et al. 2005).

The simulated removal of scale insect mortality for a two year period at the ENP improved the simulated long-term population growth. It is concerning that adult plant survival is both affected by *D. boisduvalii* and are the same plants that if dead, are expected to have the largest relative impact to the projected long-term population growth.

There is also the possibility that future *D. boisduvalii* infestations can occur at higher rates, particularly without the dampening effects from a hurricane. Observations of *D. boisduvalii* herbivory affecting rare and endangered orchids in the greater Everglades region have been documented at various rates (between 8-54.5%) and our reporting of its presence in the southern extent of the Everglades National Park is significant to not only the single population of *T. undulatum*, but to other orchid taxa (Ray et al. 2012, Zettler et al. 2015).

Hurricane impact

The largest population decline recorded at the ENP population was in the 2017-2019 period and coincided with the landfall of Hurricane Irma, a category three storm that caused widespread mangrove die-offs and high storm surge across the southern Everglades coastal regions, including the buttonwood hammocks of our ENP study site.

Observations of both *M. miamensis* as well as the invasive *D. boisduvalii* insect sharply declined post-hurricane impact of 2017. Hurricanes and large storms can provided respite from the deleterious effects of herbivores (Koptur et al. 2002), i.e. scale induced mortality and inflorescence stalk herbivory. Although there is less inflorescence stalk damage, one can assume that insect pollinators will have also declined decline post-storm event causing still a limited fruit set as seen at the ENP population. Projecting the assumptions of leaf herbivory decline and the maintenance of historical hurricane frequency, the ENP population continues to decline.

Logging impact

The logging simulations at the TSF 1 site show how damaging the removal of host tree species can be for *T. undulatum*. Both of the logging scenarios present a reduction in the long-term growth rate, with the selective logging of host species above a minimum DBH size of 18 cm for *B. buceras*, 22 cm for *T. angustata*, and 23 cm *A. glabra* being a more sustainable option. The elasticity analysis indicate that adult survival can have a large contribution to changes in λ. The culling of host tree species will not only remove potential recruitment sites of newly dispersed seeds, but directly cause the death or removal of adult plants from the population which can negatively impact the resilience of the population. The dependence of epiphytes to their host trees render them susceptible to logging activities. Epiphyte assemblages has been shown to decrease in areas affected by logging (Turner et al. 1994, Barthlott et al. 2001). The untargeted tree species of logging activities may not necessarily be ideal host trees due to their smaller sizes as well as the potential for a mismatch of epiphyte-host interactions (Borrero et al. 2022). Once a forest is disturbed it may take time to regenerate the richness and abundance that was lost, especially when considering that epiphytes have been shown to recover due to their slow growth (Zotz 1995, Barthlott et al. 2001, Gradstein et al. 2008).

Implications for management at the Everglades National Park and in Cuba

Overall the coastal populations at ENP and TSF 2 are the sites with the highest rates of long-term decline. The TSF 2 population had a limited census period with visits occurring after Hurricane Irma impacts. The ENP site periodically exhibits sporadic and heavy fruiting events that provides an influx in recruitment for the population, yet not to a degree that stabilizes the population over the long-term. Removing the effects of hurricanes and scale herbivory from the ENP site did stabilize the population in simulations. There is another factor at play that is as of yet unknown, with the possibility of differing evapotranspiration rates across the vegetation types (Zuleta et al. 2016). Yet the continued monitoring of the pestiferous scale is important to determine if in-situ control may be warranted on years with high rates of herbivory, especially if rates exceed what has been observed in this study. Extending the monitoring of *D. boisduvalii* to other orchid species in the lower Everglades National Park would be wise, particularly with deleterious effects having been observed on various native orchid species in the region by Zettler et al. 2015.

Ideally, the conservation efforts on threatened orchid populations would do well to establish new populations. Orchids can be slow growing and a new population establishing itself can take decades, and has been observed to take upwards of 80 years to occur (Pedersen et al. 2012, Rasmussen et al. 2015). In cultivation, *T. undulatum* has been shown to reach an adult size with the capability of flowering at four years of age (personal communications, Fairchild Tropical Botanic Gardens, Dr. Jason Downing). The use of theoretical population viability and ecological studies such as LTREs to shed light on prominent life stages for use in focusing the conservation efforts of threatened species can improve project success (Albrecht & Maschinski 2012). The relatively quick-paced ex-situ propagation of *T. undulatum* alongside the LTREs in this study indicating that adult plants have the greatest effect on λ, lead me to recommend the out-planting of adult plants. The selection of more host species diverse, non-buttonwood hammock sites for out-planting and seeding of new populations may maintain long-term stability and growth. Site selection for conservation efforts would do well to emulate the healthiest sites in the core range of Cuba, namely TSF 1 to secure *T. undulatum* at its northern range margin (Borrero et al. 2022). Furthermore, long-term seed storage and banking throughout the species range would be appropriate in addition to any out-planting efforts at *T. undulatum's* northern range.

The TSF 2 population had a limited census period with visits occurring after Hurricane Irma impacts. There is a need to continue to survey the TSF 2 population for a more accurate measure of the life history for the population. Attention must be paid to the logging activities in mature forests in Cuba, due to the detrimental effects that the removal of host tree species may have on the epiphyte assemblages of an area. Prior to logging taking place it is recommended for management to enforce restrictions or selective logging of tree species of a minimum size or trees with no orchid presence.

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Table 3.1 Inflorescence herbivory rates by the fly, *Melanagromyza miamensis*, across nine populations of *Trichocentrum undulatum*. Distinctions were made on whether a portion or the entire inflorescence stalk was affected by herbivore. The number of fruit produced on the census year is documented as well as the percentage of the flowering plants that were successful in fruit production. The “Ψ” marks the census year following Hurricane Irma, a category 3 hurricane that directly impacted the orchid population. The “*” marks gaps in the data due to a lack of censuses. Fruit observations from the gap year was collected on the subsequent census where ripe or dehisced fruit were visible

Site	Year	Total no. plants that flowered	Total no. inflorescences (n)	% of total with infl. herbivory	% of affected plants with partial herbivory	% of affected plants with complete herbivory	No. fruit on survey year	% of flowering plants that fruited
ENP	2013	17	23	82.61%	50.00%	50.00%	16	23.53%
ENP	2014	10	15	93.33%	22.22%	77.78%	14	40.00%
ENP	2015	24	39	100.00%	8.33%	91.67%	0	0.00%
ENP	2016	*	*	*	*	*	0	0.00%
ENP	2017	6	6	33.33%	0.00%	100.00%	0	0.00%
ENP	2018 Ψ	14	16	25.00%	0.00%	100.00%	0	0.00%
ENP	2019	12	14	14.29%	0.00%	100.00%	15	25.00%
ENP	2020	*	*	*	*	*	0	0.00%
ENP	2021	13	15	13.33%	100.00%	0.00%	0	0.00%
MC 1	2016	43	64	25.00%	46.15%	61.54%	1	2.33%
MC 1	2017	64	79	48.10%	71.88%	28.13%	1	1.56%
MC 1	2018	67	91	64.84%	72.09%	27.91%	2	2.99%
MC 1	2019	95	165	56.97%	85.25%	14.75%	3	2.11%
MC 2	2018	23	25	88.00%	30.00%	70.00%	1	4.35%
MC 2	2019	27	36	100.00%	50.00%	50.00%	5	11.1%
TSF 1	2016	23	33	72.73%	68.42%	31.58%	1	4.35%

TSF 1	2018	93	159	96.23%	28.89%	71.11%	4	1.08%
TSF 2	2018	22	45	97.78%	45.45%	54.55%	0	0.00%
TSF 2	2019	20	27	100.00%	10.00%	85.00%	0	0.00%
TSF 3	2016	8	9	88.89%	85.71%	14.29%	0	0.00%
TSF 3	2018	4	5	100.00%	0.00%	100.00%	0	0.00%
TSF 4	2018	5	7	57.14%	33.33%	66.67%	0	0.00%
WMF	2018	9	10	50.00%	60.00%	40.00%	0	0.00%
LSF	2018	15	26	96.15%	26.67%	73.33%	0	0.00%

* No census data. Fruit information collected on subsequent census where dehisced fruit may have been visible

Ψ Post-hurricane Irma census

Table 3.2 The rate of leaf herbivory by the scale insect *Diaspis boisduvalii* observed on *Trichocentrum undulatum* at the Everglades National Park population. The "Ψ" marks the census year following Hurricane Irma, a category 3 hurricane that directly impacted the orchid population. No censuses were conducted in 2016 and 2020.

Year	**Percentage of plants with leaf herbivory**	**Total No. plants observed**
2013	17.42%	132
2014	9.49%	158
2015	6.02%	133
2017	8.93%	56
2018 Ψ	0.00%	45
2019	10.00%	70
2021	18.64%	59

Table 3.3 Matrix functions for stochastic simulation of hurricane induced population decline probabilities for *Trichocentrum undulatum* at the Everglades National Park site.

Phase	Time since hurricane (yr)	No. time steps	No. matrices
I	0	1	1
II	1	1	1
III	2 - 3	2	2
IV	4 - 10	4	4

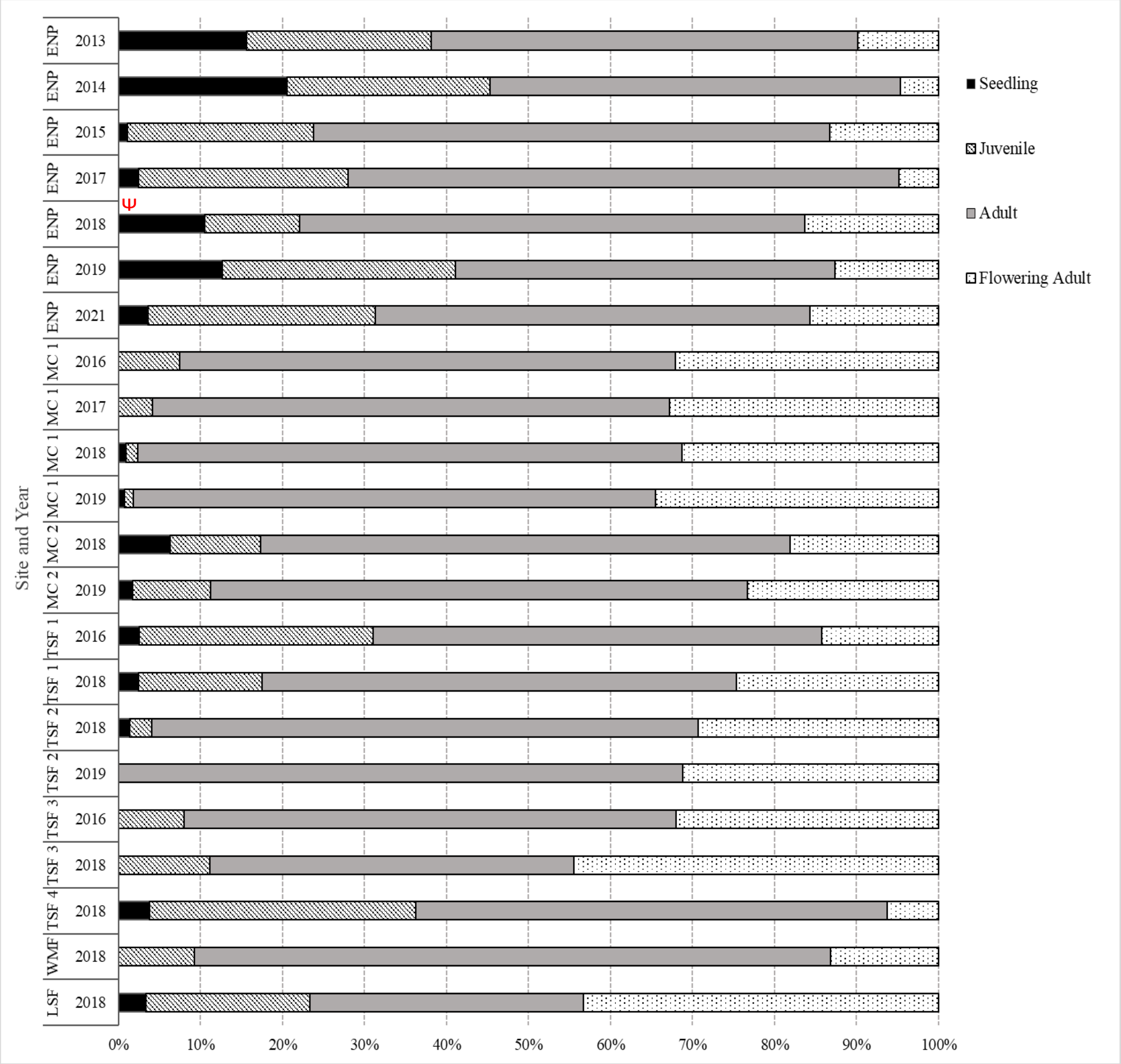

Fig 3.1 The percentage of each stage class (seedling, juvenile, vegetative adult, and reproductive adult) on each census for every *Trichocentrum undulatum* populations censused over the course of this study: Everglades National Park (ENP), Mogote Complex 1 (MC), Mogote Complex 2 (MC2), Tropical Semi-deciduous Forest 1 (TSF 1) and Tropical Semi-deciduous Forest 2 (TSF 2), Tropical Semi-deciduous Forest 3 (TSF 3), Lowland Seasonal Forest (LSF), and Wet Montane Forest (WMF). The "Ψ" marks the year that Hurricane Irma impacted the site.

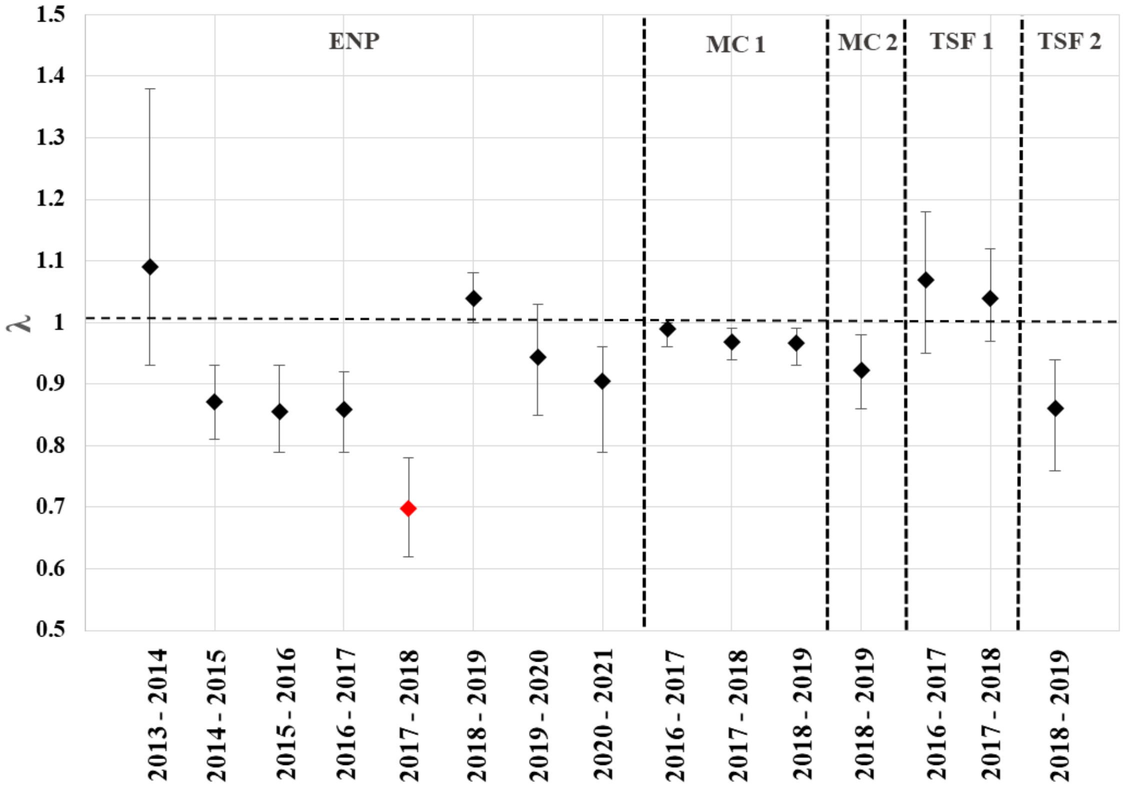

Fig 3.2 Finite population growth rate (λ) plotted for populations of *Trichocentrum undulatum* at the Everglades National Park (ENP), Mogote Complex 1 (MC), Mogote Complex 2 (MC2), Tropical Semi-deciduous Forest 1 (TSF 1) and Tropical Semi-deciduous Forest 2 (TSF 2), error bars represent a 95% confidence interval. A value great than 1 indicates long-term population growth. The red marker at the ENP population is to note that the census was conducted post-Hurricane Irma.

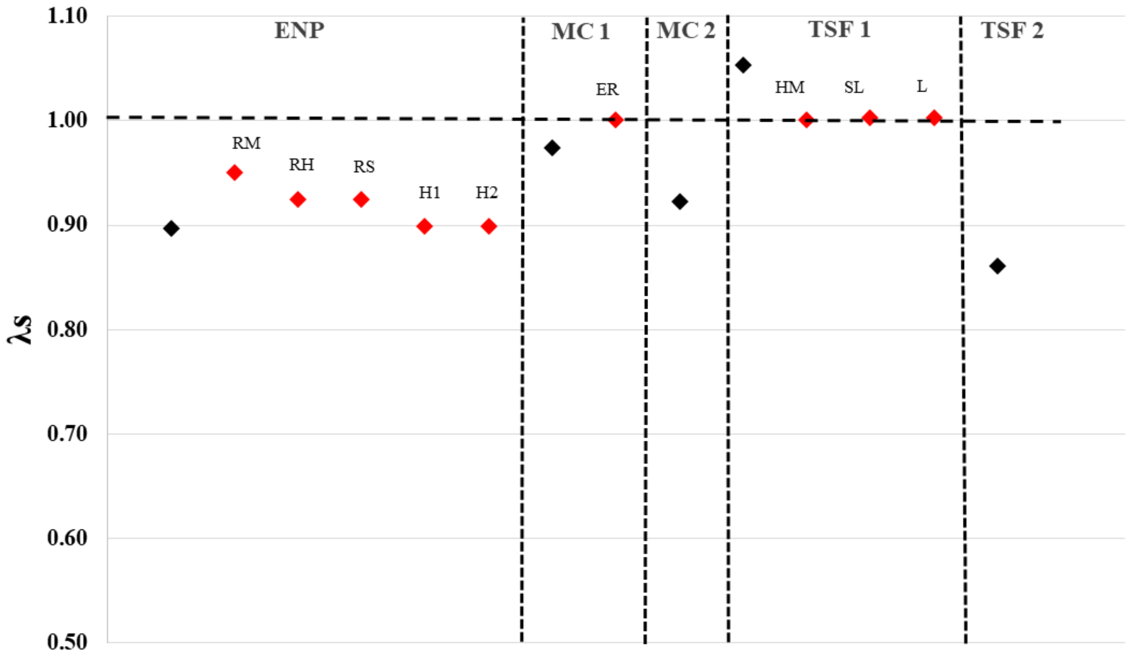

Fig 3.3 Stochastic population growth rate (λ_s) plotted for populations of *Trichocentrum undulatum* at the Everglades National Park (ENP), Mogote Complex 1 (MC), Mogote Complex 2 (MC2), Tropical Semi-deciduous Forest 1 (TSF 1) and Tropical Semi-deciduous Forest 2 (TSF 2), error bars represent a 95% confidence interval are too small to see represented in this figure. The black markers indicate un-manipulated matrices (Appendix A) with MC 2 and TSF 2 exhibiting the same value of (λ) due to a single transition matrix. The red markers indicate the use of a simulated matrices under wither one of the following conditions: "RM" = reduced mortality from leaf herbivory and hurricane, "RS" = removal of scale attributed mortality, "RH" = removal of hurricane event, "ER" = episodic recruitment introduction at 0.3 probability of occurrence, "H1" = historical hurricane probability projection, "H2" = 50% increase in hurricane probability, "HM" = hurricane mortality introduction at 0.085 probability of occurrence, "SL" = selective logging of host tree species with a minimum DBH at 0.17 probability of occurrence, and "L" = clear cut logging of host tree species of all sizes at 0.085 probability of occurrence (Appendix B).

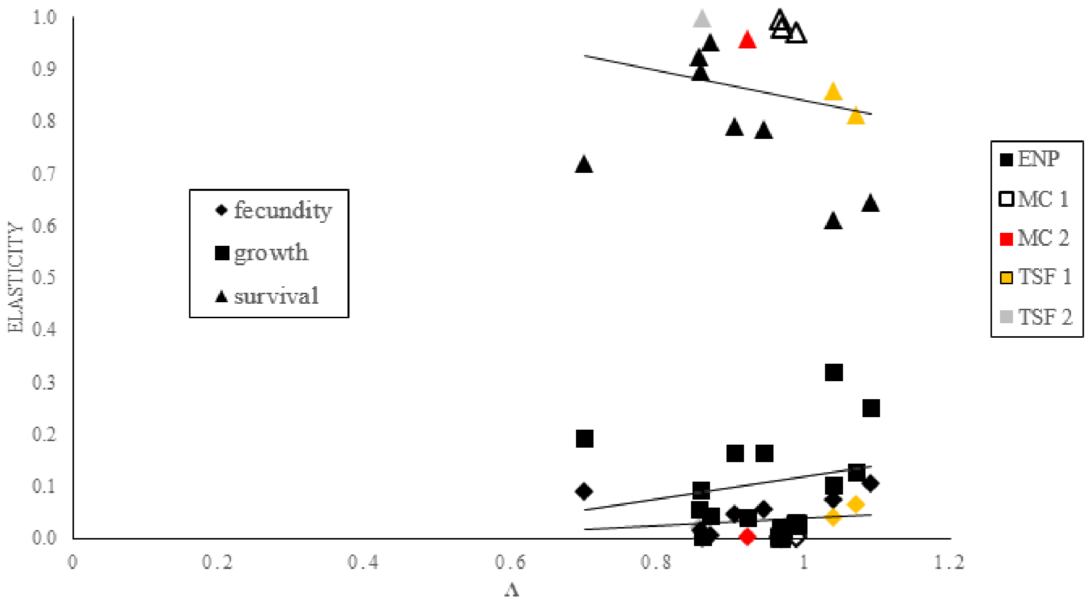

Fig 3.4 Elasticities of fecundity, growth, survival of *Trichocentrum undulatum* as a function of finite population growth rate (λ) at the Everglades National Park (ENP), Mogote Complex 1 (MC), Mogote Complex 2 (MC2), Tropical Semi-deciduous Forest 1 (TSF 1) and Tropical Semi-deciduous Forest 2 (TSF 2) populations.

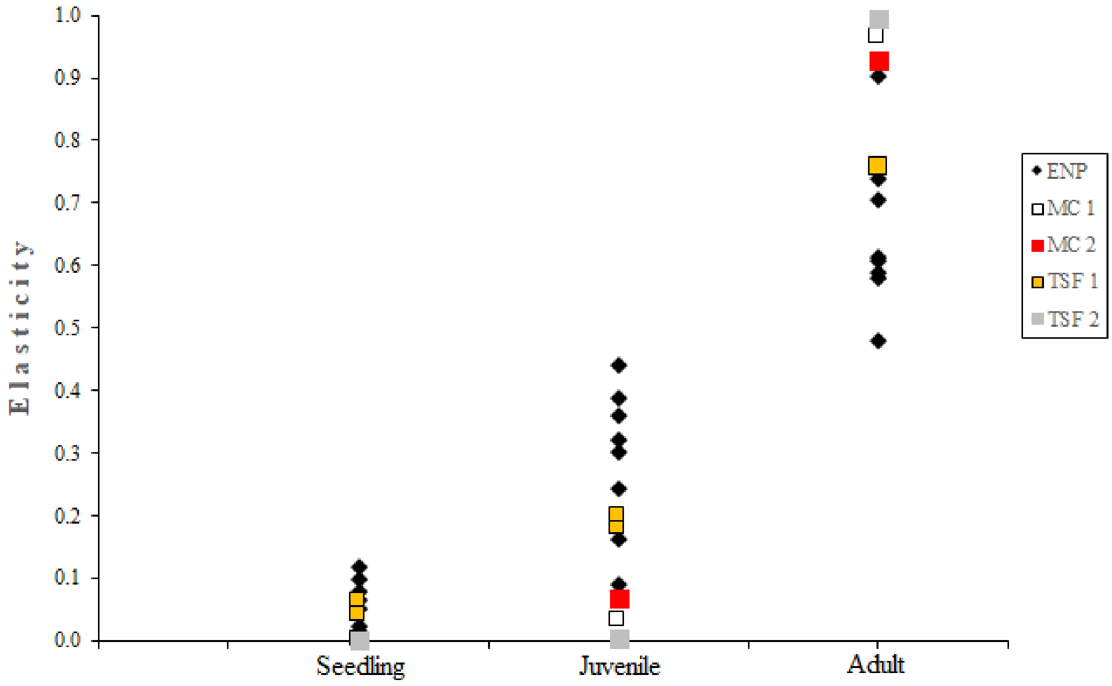

Fig 3.5 Elasticities of different life history stages of *Trichocentrum undulatum* at the Everglades National Park (ENP), Mogote Complex 1 (MC), Mogote Complex 2 (MC2), Tropical Semi-deciduous Forest 1 (TSF 1) and Tropical Semi-deciduous Forest 2 (TSF 2) populations: seedling, juvenile, and adult.

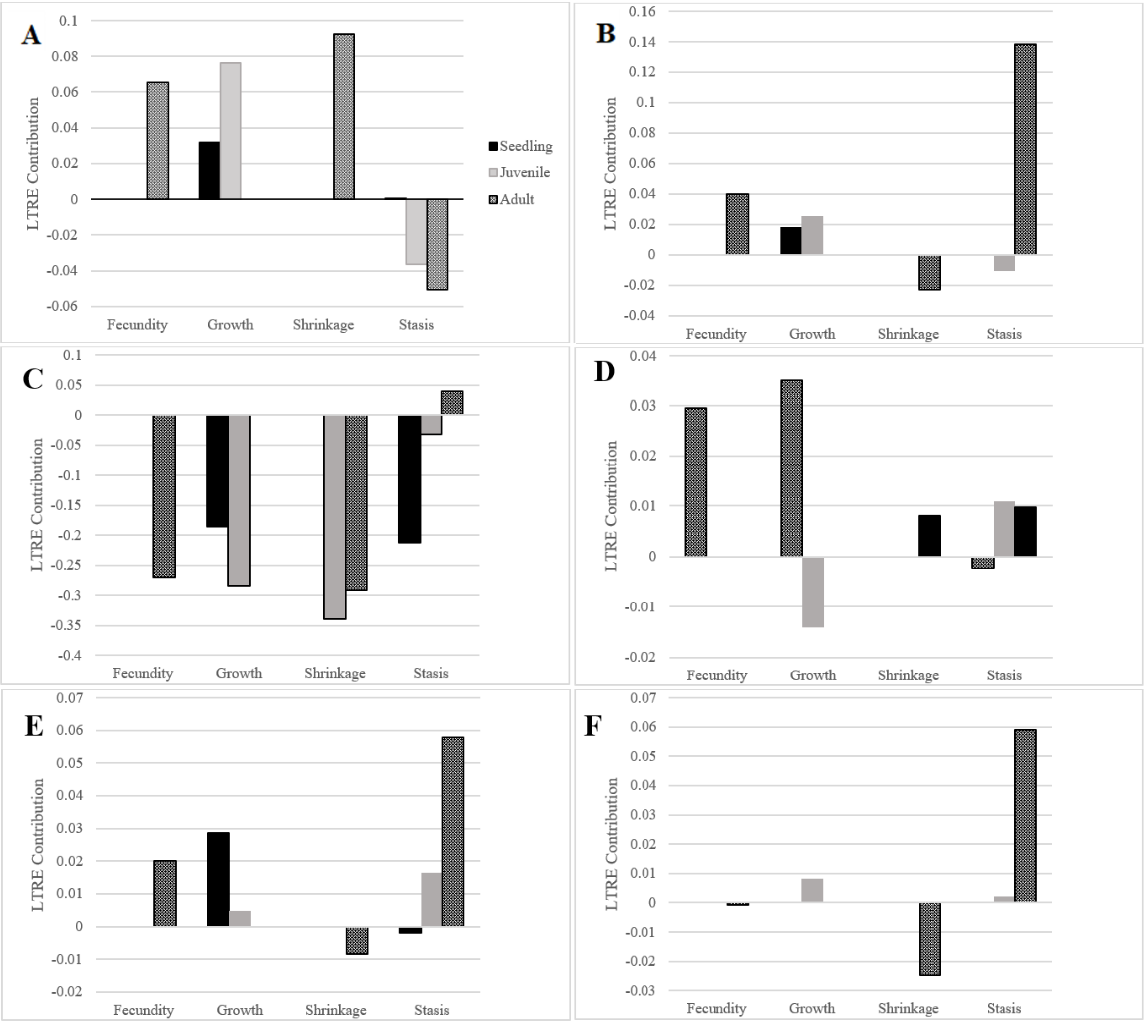

Fig. 3.6 Life Table Response Experiment (LTRE) comparing select years and populations of *Trichocentrum undulatum* **a)** Everglades National Park population (ENP) hurricane year compared to pre-hurricane year **b)** ENP compared to Tropical Semi-deciduous Forest population 1 (TSF 1) on survey Year 4 (2016-2017) **c)** TSF 1 survey Year 5 compared to Tropical Semi-deciduous Forest population 2 (TSF 2) survey Year 6 **d)** TSF 1 compared to Mogote Complex population 1 (MC 1) on survey Year 4 **e)** TSF 1 survey Year 5 (2017-2018) compared to Mogote Complex population 2 (MC 2) survey Year 6 (2018-2019) **f)** MC 1 compared to MC 2 on survey Year 6 (2018-2019)

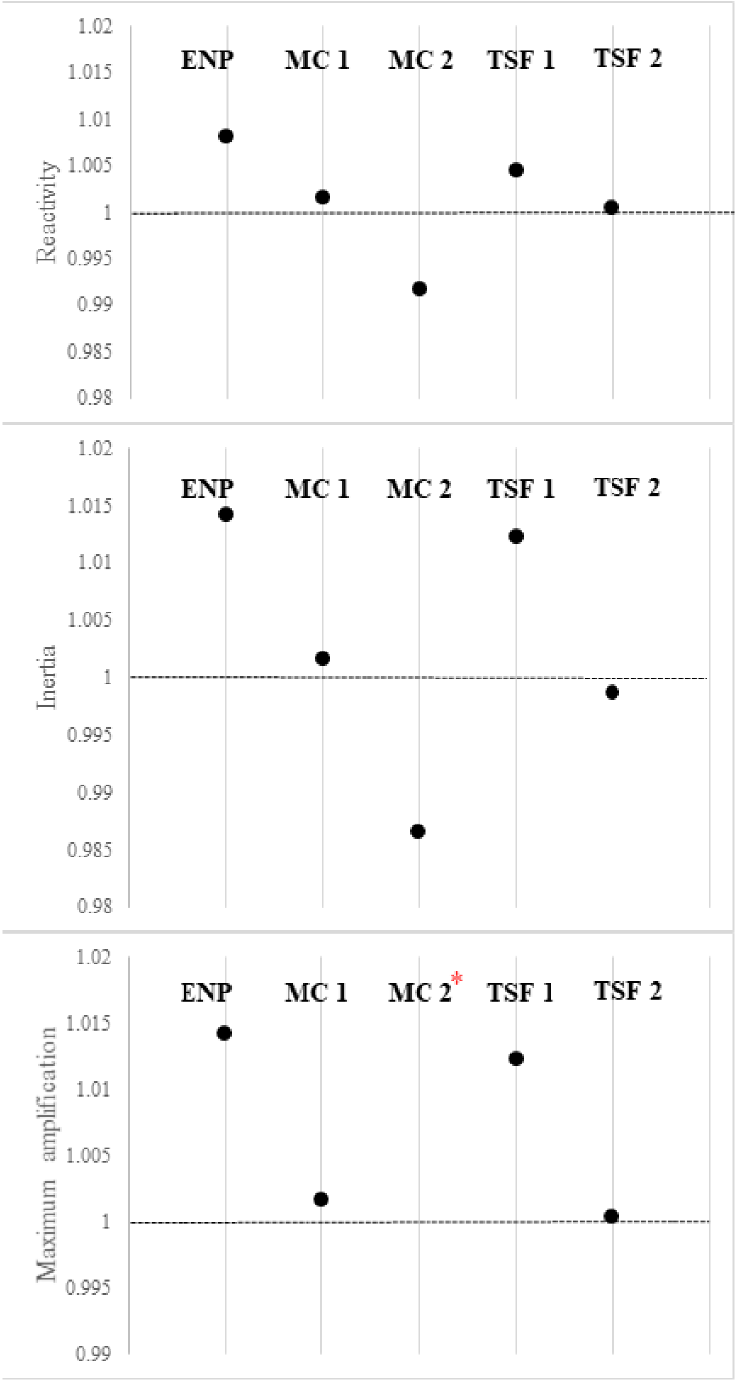

Fig 3.7 Transient dynamic indices for *Trichocentrum undulatum* at the Everglades National Park (ENP), Mogote Complex 1 (MC), Mogote Complex 2 (MC2), Tropical Semi-deciduous Forest 1 (TSF 1) and Tropical Semi-deciduous Forest 2 (TSF 2) populations. *Reactivity* is the population growth within the first time step compared to that of a stable state. *Inertia* is the largest long-term population density when compared to stable state. *Maximum amplification* is the largest future population density that can be

reached when compared to stable state. Mean matrices for all populations were used for the transient analysis as well as the most recent population structure (see Methods).

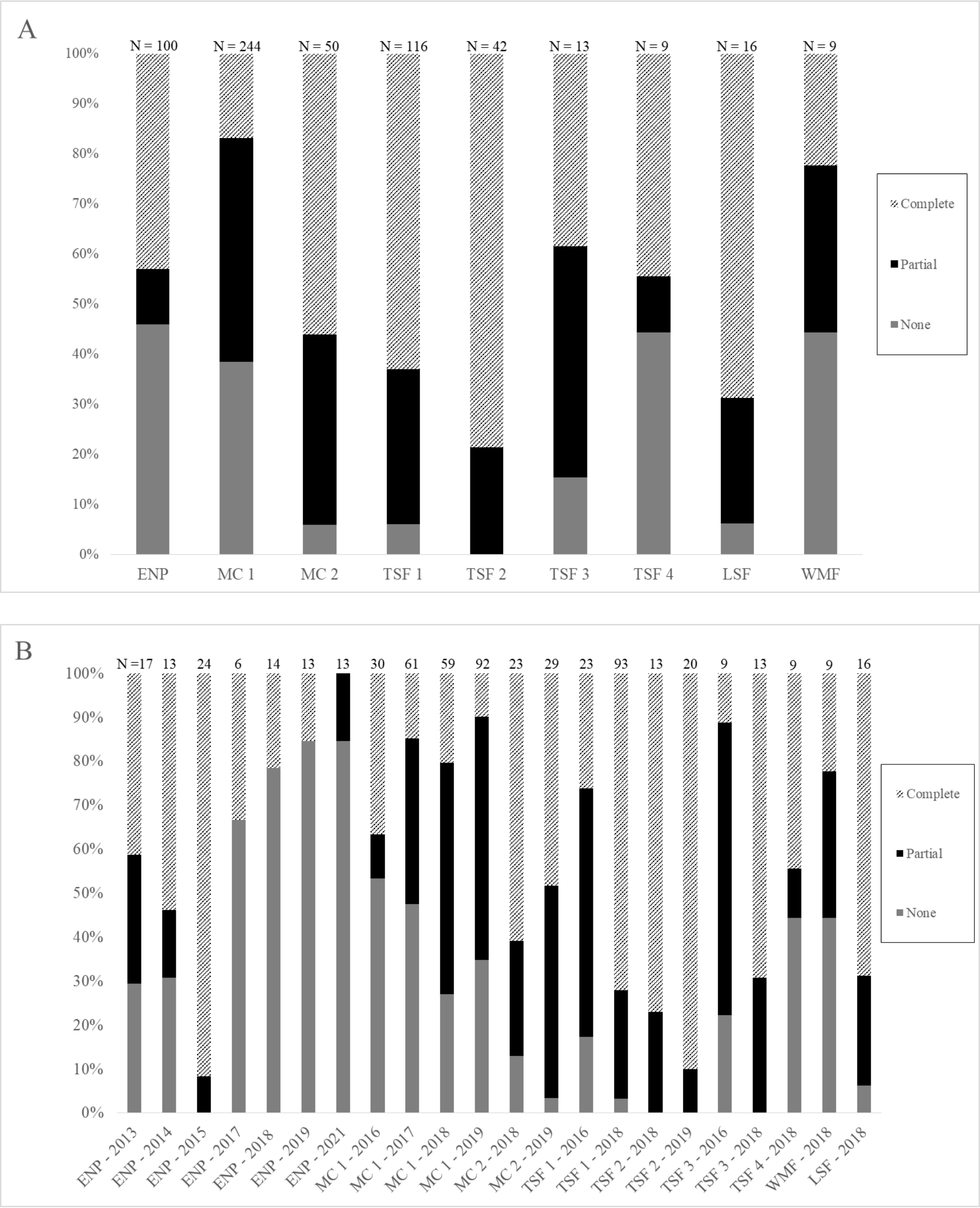

Fig. 3.8 a) *Melanagromyza miamensis* herbivory rates on inflorescences of *T. undulatum* among populations, distinguishing whether the fly affected the stalks completely (no

flowers), partially (partially flowered), or none (not affected by fly). **b)** The herbivory rates of *M. miamensis* among populations and census year.

Appendix A Transition matrices for populations of *Trichocentrum undulatum* arranged by site and year transition. Bold indicates fertility elements that were estimated using pooled data (see in text Methods).

Site		Seedling	Juvenile	Adult
A) Everglades National Park, FL, USA				
Number of individuals monitored: 278				
Most recent population structure: (3, 30, 40)				
Year 1 - 2, 2013-2014				
	Seedling	0.11111111	0	0.467556
	Juvenile	0.81481481	0.64102564	0.066667
	Adult	0	0.23076923	0.855556
Year 2 -3 , 2014-2015				
	Seedling	0.02272727	0	0.018868
	Juvenile	**0.3536585**	0.66666667	0.018692
	Adult	0	0.15686275	0.850467
Year 3 - 4, 2015-2016				
	Seedling	**0.0731707**	0	0.052632
	Juvenile	**0.3536585**	0.79487179	0.008772
	Adult	0	0.07692308	0.815789
Year 4 -5, 2016-2017				
	Seedling	**0.0731707**	0	0.030612
	Juvenile	**0.3536585**	0.75	0.030612
	Adult	0	0.15625	0.795918
Year 5 -6, 2017-2018 Ψ Hurricane Year				
	Seedling	**0.0769231**	0	0.107143
	Juvenile	**0.7692308**	0.28125	0.011905
	Adult	0	0.26315789	0.607143
Year 6 -7, 2018-2019				
	Seedling	0.07692308	0	0.226415
	Juvenile	0.76923077	0.66666667	0.207547
	Adult	0	0.33333333	0.698113
Year 7 - 8, 2019-2020				
	Seedling	0.16666667	0	0.157343
	Juvenile	0.66666667	0.7037037	0.068182
	Adult	0	0.14814815	0.818182
Year 8 - 9, 2020-2021				
	Seedling	**0.0769231**	0	0.075
	Juvenile	**0.7692308**	0.6	0.05
	Adult	0	0.26666667	0.8
B) Mogote Complex 1, Mayabeque, Cuba				

Number of individuals monitored: 193
Most recent population structure: (2, 4, 136)
Year 4 -5, 2016-2017

Seedling	**0.1**	0	0.012658
Juvenile	**0.1**	0.77777778	0.012658
Adult	0	0.22222222	0.974684

Year 5 - 6, 2017-2018

Seedling	**0.1**	0	0.016667
Juvenile	**0.1**	**0.6842105**	0.008333
Adult	0	**0.2631579**	0.958333

Year 6 -7, 2018-2019

Seedling	**0.1**	0	0.014184
Juvenile	**0.1**	**0.6842105**	0
Adult	0	**0.2631579**	0.964539

C) Mogote Complex 2, Pinar del Rio, Cuba

Number of individuals monitored: 104
Most recent population structure: (3, 12, 76)
Year 6 -7, 2018-2019

Seedling	**0.1**	0	0.024691
Juvenile	**0.1**	0.64285714	0.036585
Adult	0	0.14285714	0.902439

D) Tropical Semi-deciduous Forest 1, Matanzas, Cuba

Number of individuals monitored: 290
Most recent population structure: (9, 30, 102)
Year 4 -5, 2016-2017

Seedling	0	0	0.125
Juvenile	1	0.69565217	0
Adult	0	0.2826087	0.977273

Year 5 - 6, 2017-2018

Seedling	0	0	0.090909
Juvenile	1	0.77777778	0.020202
Adult	0	0.16666667	0.969697

E) Tropical Semi-Deciduous Forest 2, Sancti Spiritus, Cuba

Number of individuals monitored: 53
Most recent population structure: (0, 0, 44)
Year 5 - 6, 2017-2018

Seedling	**0.0666667**	0	**0.001**
Juvenile	**0.3333333**	**0.7142857**	0
Adult	0	**0.2380952**	0.86

Appendix B Transition matrices for simulated populations of *Trichocentrum undulatum* arranged by simulation type and site. Modified matrices for the simulations are identified in "Status."

Site	Seedling	Juvenile	Adult
A) Everglades National Park, Florida, USA			
Status: Removal of mortality from leaf herbivory			
Year 1 transition			
Seedling	0.0731707	0	0.0526316
Juvenile	0.3536585	0.8857143	0.009434
Adult	0	0.0857143	0.8773585
Year 2 transition			
Seedling	0.0731707	0	0.0306122
Juvenile	0.3536585	0.7741935	0.0315789
Adult	0	0.1612903	0.8210526
B) Mogote Complex 2, Mayabeque, Cuba			
Status: Episodic recruitment introduction			
Seedling	0.2222222	0	0.4675556
Juvenile	0.5555556	0.6842105	0.0058824
Adult	0	0.2631579	0.9647059
C) Tropical Semi-deciduous Forest Site 1, Matanzas, Cuba			
Status: Introduction of hurricane induced mortality			
Seedling	0	0	0.1283422
Juvenile	0	0.2790698	0.0106383
Adult	0	0.0697674	0.606383
Status: Logging induced mortality based on host species			
Seedling	0	0	0.1709402
Juvenile	0.9090909	0.3076923	0.025641
Adult	0	0.0512821	0.4273504
Status: Logging induced mortality based on host species & DBH			
Seedling	0	0	0.1709402
Juvenile	0.6363636	0.4102564	0.025641
Adult	0	0.1282051	0.7008547

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PUBLICATIONS

Borrero, H., Alvarez, J.C., Prieto, R.O., & Liu, H. (2022). Comparisons of habitat types and host tree species across a threatened Caribbean orchid's core and edge distribution. *Journal of Tropical Ecology*.

Borrero, H., Richards, M., Giardina, D., Alvarez, J.C., Prieto, R.O., Coffey, E.D., & Liu, H. (2019). The shared natural heritage of southern Florida and Cuba: Orchid conservation across borders. *FIU Hemisphere Magazine*. *28*: 11-13.

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