LANKESTERIANA 23(1): 81–90. 2023. doi: http://dx.doi.org/10.15517/lank.v23i1.54576

POTENTIAL DRIVERS OF SPATIAL DISTRIBUTION OF THE GHOST ORCHID, *DENDROPHYLAX LINDENII*, IN A SOUTH FLORIDA CYPRESS STRAND: A PRELIMINARY STUDY

Corrie Pieterson[1], Brenda Thomas[2], Edwin M. Everham III[2],
Brian Bovard[2,4] & Mike Owen[3]

[1]The Ohio State University, 1735 Neil Avenue, Columbus, OH 43210, USA.
[2]Florida Gulf Coast University, 10501 FGCU Blvd S, Fort Myers, FL 33965, USA.
[3]Fakahatchee Strand Preserve State Park, 137 Coast Line Dr, Copeland, FL 34137, USA.
[4]Author for correspondence: bbovard@fgcu.edu

Abstract. This study examined a population of ghost orchids (*Dendrophylax lindenii*) in Fakahatchee Strand Preserve State Park in Collier County, Florida, to determine if they exhibit host species preference, vertical stratification, substrate diameter stratification, or a distribution pattern similar to their host plants. Twenty-five ghost orchids were found on three host plant species: 20 (80%) were on pop ash (*Fraxinus caroliniana*), four (16%) on arthritis vine (*Hippocratea volubilis*), and one (4%) on pond apple (*Annona glabra*). Our analysis indicated a statistically significant occurrence of ghost orchids on pop ash relative to other woody plant species in the study area. Although most orchids were found below 3 m from the forest floor, this was not statistically significant when compared to orchids above 3 m. A weak trend (p=0.06) for increasing occurrence was observed in the next to largest (14.1 cm to 17.2 cm diameter at breast height) size class among the five size classes of pop ash in this study. The spatial analyses indicated that both the stems of pop ash and ghost orchids demonstrate non-random clumping on the landscape. In addition, the presence of an individual orchid increases the probability of multiple ghost orchids on a stem. These results further emphasize the importance of pop ash as a host species in Florida's ghost orchid populations and add to the list of hosts (arthritis vine) in the literature. Continuing to study the vertical position of ghost orchids will be important as climate change has the potential to alter humidity patterns and the occurrence of both low temperature events and hurricanes. Improved understanding of host plant preference, microhabitat requirements, spatial distribution, and continued long-term monitoring of population dynamics are critical for the conservation of the ghost orchid.

Keywords / Palabras clave: conservación de plantas, ecología de epífitas, ecología espacial, epiphyte ecology, leafless orchid, Orchidaceae, orquídea áfila, plant conservation, spatial ecology

Introduction. The ghost orchid, *Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe, is a rare epiphytic leafless orchid found in the warm, humid climate of southwest Florida and Cuba (GBIF 2023). In Florida, where it is state listed as endangered, the ghost orchid grows naturally in Lee, Collier, and Hendry Counties (http://florida.plantatlas.usf.edu) where it inhabits cypress swamps and wet hammocks (Wunderlin & Hansen 2011). In Florida, a diversity of tree species has been documented as hosts to ghost orchids including red maple (*Acer rubrum* L.), pond apple (*Annona glabra* L.), pop ash (*Fraxinus caroliniana* Mill.), oaks (*Quercus* species), royal palm (*Roystonea regia* (Kunth) O.F.Cook), and bald cypress (*Taxodium distichum* (L.) Rich.) (Brown & Folsum 2002). In Florida, despite a diversity of substrate availability, the orchids are reported to be found primarily on pop ash, and typically less than 3 m from the soil surface on trunks and main branches of all host species (Mújica *et al*. 2018).

Seed dispersal and subsequent establishment of mature individuals are important contributors to orchid distribution within habitats. Orchid seeds are typically small, produced in large numbers, and wind-dispersed (Arditti & Ghani 2000, Yoder *et al*. 2010). Fruit production by the ghost orchid is variable, including some years when no fruit is produced, and has been reported to be negatively impacted by hurricanes (Mújica *et al*. 2013, Raventós *et al*.

ORCID of the Authors: BT, EMEIII, BB
Received 12 January 2023; accepted for publication 3 March 2023. First published online: 28 March 2023.

2015a). The number of seeds per fruit in orchids can be quite high (Arditti & Ghani 2000); however, ghost orchid seed production has not been quantified. Orchid seeds typically lack endosperm (Arditti & Ghani 2000), enabling long-distance dispersal but necessitating an external nutrient source for germination (Yoder *et al.* 2010). Seeds of epiphytic orchids require a physical surface that prevents subsequent dislodging of the seed, retains sufficient moisture, and a substrate containing suitable mycorrhizal fungal species capable of providing carbon, nutrients and water (Callaway *et al*. 2002, Hoang *et al*.2017, Mújica *et al.* 2018). Different tree species likely have differing amounts of suitable microhabitat that meet the criteria for successful colonization and establishment by epiphytic orchids. Such variation in suitable microhabitat among potential host species (Mújica *et al.* 2018), along with variability in the distribution of those species on the landscape would influence and correlate with the distribution of specific epiphytic orchid species.

Compared to animals, plants receive relatively little attention when it comes to conservation and protection. This is likely a function of several factors, such as plant blindness, and conservation efforts focused on charismatic megafauna species (Balding & Williams 2016). Orchids are a plant group analogous to charismatic megafauna and one could argue that ghost orchids could be the "charismatic megaflora" poster child. All plants, including orchids, perform important ecosystem functions and services that are often ignored, such as serving as an energy source for pollinators, and in the case of ghost orchids, serving as recreational and tourism resources. Human activities have significantly impacted orchid populations such as ghost orchids (Wraith & Pickering 2018). Historically, this species has been heavily affected due to poaching by orchid enthusiasts, logging of old growth cypress forests, land use change, and altered hydrology and fire regimes in southern Florida. Looking into the future, it will be further impacted by changes resulting from anthropogenic climate change. Ghost orchids will unlikely be able to sustain their populations given all these pressures from human activities. If they are to remain on the landscape, there is a strong need for conservation efforts focused on protecting and enhancing their populations.

To promote successful conservation and/or recovery of this and other orchid species, the integration of multiple areas of research - genetic diversity, propagation science, pollination biology, mycology, ecology and distribution, and reintroduction - are required (Stewart 2007). While work has been done on the biology of the ghost orchid - exodermis structure and its relationship to mycorrhizal fungi (Chomicki *et al*. 2014), desiccation tolerance (Coopman & Kane 2019), greenhouse acclimatization methods (Coopman & Kane 2018), and germination and seedling development (Hoang *et al*. 2017) - until recently little was known about its ecology (but see Mújica *et al*. 2018, Ray *et al.* 2012, Zettler *et al.* 2011, 2019). Recent ecological studies have primarily focused on the orchid's population biology and pollinator ecology (Danaher *et al*. 2020, Houlihan *et al*. 2019, Mújica *et al*. 2021, Sadler *et al*. 2011, Zettler *et al*. 2019). This work examined a population of ghost orchids in Fakahatchee Strand Preserve State Park (FSPSP) in Collier County in southwest Florida to determine if ghost orchids in FSPSP exhibit host preference, vertical stratification, substrate diameter stratification, and a distribution pattern similar to that of their host plants. The data presented here will aid in the long-term quantification of both spatial and temporal changes in this orchid population (Zotz *et al.* 1999) and afford a better understanding of this orchid's population ecology, providing valuable information to those making management and conservation decisions.

Materials and methods

Study site.— Fakahatchee Strand Preserve State Park (FSPSP), located in Collier County in southwest Florida (Fig. 1), experiences a humid, subtropical climate with a mild winter dry season and hot summer rainy season. Mean annual temperature is 23°C, ranging from a mean January temperature of 14°C to a mean August temperature of 28°C (Duever 1986). Most of the region's mean annual rainfall of 136 cm falls during the summer (Duever 1986).

FSPSP comprises a complex mosaic of ecosystems, including a cypress strand that runs north to south through the center of the Preserve. The strand, regrown after extensive logging in the mid-20th century and characterized by a 6 to 9-month hydroperiod (Ewel 1990), is dotted with deep sloughs with a second growth bald cypress canopy and an understory dominated by pond apple and pop ash. Humidity from the deep waters of the central strand and the ponds within provide insulation for tropical epiphytic orchids during the infrequent cold events that occur in south Florida (Lodge 2016, Mújica *et al.* 2018).

Data collection.— A line-transect of 90 m was established in a mixed bald cypress/pond apple/pop ash slough within FSPSP with a known population of ghost orchids. The geographic coordinates of this population are not described here due to the risk of poaching associated with the study species. Woody plant species within 15 m of the transect and with a dbh (diameter at breast height or 1.3 m) greater than 4 cm were identified, dbh recorded, and their locations mapped. The vertical stems of multi-stemmed trees, such as pond apple and pop ash were mapped individually, to provide a better indicator of habitat availability (Bennett 1986). All ghost orchids were recorded, and orchid heights were quantified as above or below 3 m, based on a previous study (unpublished data) indicating the slough's standing water provided thermal protection up to 3 m above the ground during irregular frost events. Ghost orchids co-occur with the leafless ribbon orchid, *Campylocentrum pachyrrhizum* (Rchb.f.) Rolfe, at this study site but were distinguishable by their significantly less compressed roots which have short white dashes that parallel the direction of growth.

Data analysis.— Likelihood Ratio χ^2 tests were conducted to determine if ghost orchids were randomly distributed among tree species, or at different heights, and on host plant stems of varying dbh. Pearson χ^2 tests were used when data were sparse (Sall *et al.* 2017). We limited our diameter preference analysis to pop ash because most individual ghost orchids in this study were found on this host tree species. Because of its increased power compared to other indices (Goodall & West 1979), the Hopkins Index of Aggregation (A) was computed for pop ash trees, individual pop ash vertical stems, and ghost orchids to determine whether their distributions on the landscape were significantly clumped (A greater than 1) compared to random (A equal to 1) and whether the dispersion pattern of the two species was different (Hopkins & Skellam 1954). The Hopkins Index of Aggregation was computed in Microsoft Excel. All other statistics were conducted in R using package "RVAideMemoire" (Hervé 2019) and in SAS-JMP® Version *14.0* (SAS Institute Inc., Cary, NC).

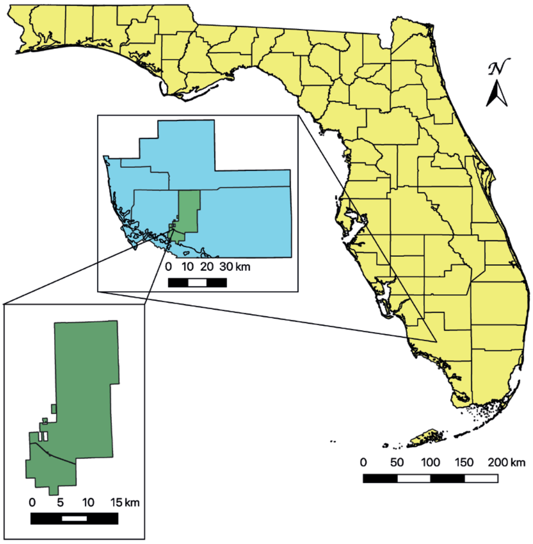

Figure 1. Location of Fakahatchee Strand Preserve State Park in Collier County, Florida (Thomas 2009). The state of Florida is in yellow with county boundaries in black. The insets are of Collier County, Florida in blue and the Fakahatchee Strand Preserve State Park in green.

Results. A total of 695 stems were recorded among 13 woody plant species. *Fraxinus caroliniana* stems totaled 33.5% of all stems measured, bald cypress totaled 25.6%, and pond apple totaled 20.3% (Table 1). Laurel oak exhibited the highest mean dbh (28.7 cm) of all woody plant species while arthritis vine (*Hippocratea volubilis* L.), a woody vine, had the lowest (4.6 cm) (Table 1).

Host species preference.— Twenty-five ghost orchids were found on three host plant species - 20 (80%) on pop ash, four (16%) on arthritis vine, and one (4%) on pond apple (Table 2). Although the sample size is small, by some estimates, it could represent over 1% of the entire Florida population (Zettler *et al*. 2019). Given that most ghost orchids occurred on pop ash (20), we used a likelihood ratio χ^2 to determine whether this frequency was statistically greater on pop ash than other species based upon the host plant species com-

Table 1. Composition of the forested study site, including the number of stems, percentage of all stems, and mean dbh for all woody plant species greater than 4 cm dbh.

Species	Number of stems	% of all stems	Mean dbh (cm)
Pop ash (*Fraxinus caroliniana)*	233	33.5	13.6
Bald cypress (*Taxodium distichum*)	178	25.6	27.7
Pond apple (*Annona glabra*)	141	20.3	7.9
Arthritis vine (*Hippocratea volubilis*)	60	8.6	4.6
Strangler fig (*Ficus aurea*)	29	4.2	9
Dahoon holly (*Ilex cassine*)	22	3.2	8.5
Myrsine (*Myrsine cubana*)	10	1.4	4.9
Red Maple (*Acer rubrum*)	9	1.3	26.1
Sabal palm (*Sabal palmetto*)	7	1.0	*
Gumbo limbo (*Bursera simaruba*)	2	0.3	7
Laurel oak (*Quercus laurifolia*)	2	0.3	28.7
Marlberry (*Ardisia escallonioides*)	1	0.1	5.1
Royal palm (*Roystonea regia*)	1	0.1	*

Table 2. Woody plant species hosting ghost orchids, including stem dbh and the number of orchids found 3 m above and below ground level.

Species	dbh	<3m	>3m
Pond apple	7.7	0	1
Pop ash	5.0	1	0
Pop ash	8.2	1	0
Pop ash	8.4	1	0
Pop ash	8.6	0	1
Pop ash	9.6	1	0
Pop ash	12.1	1	0
Pop ash	13.5	1	1
Pop ash	14.0	0	1
Pop ash	14.3	1	0
Pop ash	14.6	3	0
Pop ash	16.5	0	1
Pop ash	17.2	0	3
Pop ash	23.0	0	1
Pop ash	27.1	1	0
Pop ash	31.9	1	0
Arthritis vine	2.8	0	1
Arthritis vine	2.9	1	0
Arthritis vine	4.0	1	0
Arthritis vine	6.0	1	0

position of the forest (Fig. 2). This analysis indicated a statistically significant occurrence of ghost orchids on pop ash relative to all of the other species in the study area ($\chi^2 = 30.3$, $p<0.01$).

To determine if the distribution on pop ash was greater than expected for just the species it occurred on in this study, the frequencies of *D. lindenii* were compared against the relative frequencies of only pond apple, pop ash, and arthritis vine. The Pearson χ^2 test indicated significantly more ghost orchids on pop ash and less on pond apple compared to what would be expected given their relative frequencies in the study area ($\chi^2 = 9.9$, $p<0.01$). However, comparing the frequencies of ghost orchids against the relative basal areas of the host plant species on which it occurred, arthritis vine, representing only 2% of the relative basal area of host species, accounted for significantly more of the ghost orchid occurrences (16%) than would be expected ($\chi^2 = 14.6$, $p<0.001$). Pond apple accounted for fewer than expected ghost orchids compared to its relative basal area contribution of 17.5% and pop ash accounted for 80% of the ghost orchids, matching its 80% contribution to the relative basal area of the species upon which ghost orchids were growing.

Vertical stratification.— Fifteen ghost orchids (60%) were found growing below 3 m and 10 (40%) were growing above 3 m (Table 2). A likelihood ratio χ^2 was used to determine if this differed significantly from a

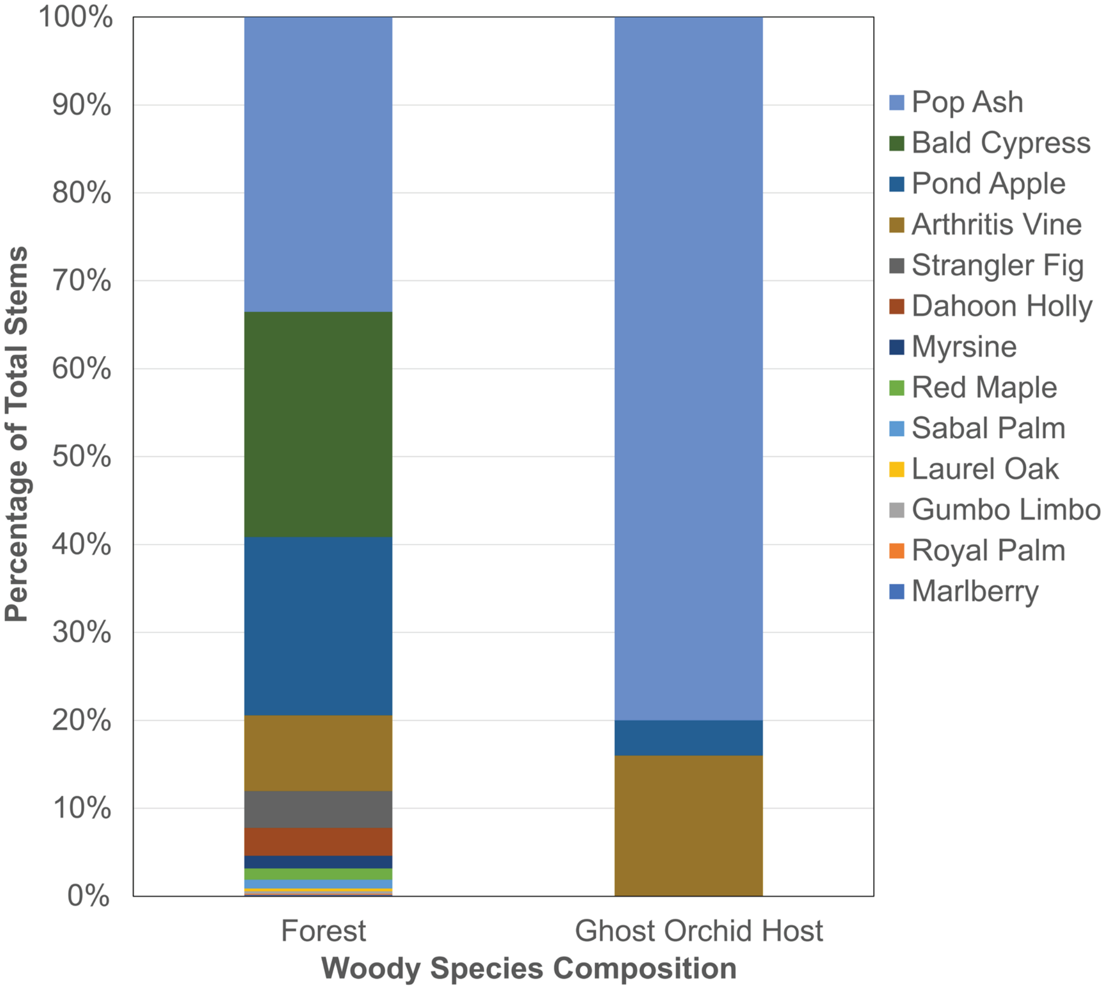

Figure 2. Woody plant species composition of the forested study site and the composition of the ghost orchid host species, calculated as a percentage of all stems.

50:50 ratio. The data in this study do not indicate a statistically greater number of ghost orchids occurring <3m from the forest floor compared to above that height (χ^2=1.0, p=0.32).

Substrate diameter stratification.— To assess host plant diameter preference, we divided all pop ash stems into five dbh classes, each containing approximately equal numbers of stems (Table 3). Most ghost orchids growing on pop ash were found on stems between 14.1 cm and 17.2 cm dbh (Table 3). The χ^2 test indicated a weakly significant deviation from a random distribution of ghost orchids across the five dbh categories (χ^2 =9.07, p=0.06).

Dispersal.— The spatial distribution of individuals of both ghost orchids and pop ash were assessed in two separate ways. First, the Hopkins Index of Aggregation (A') was computed for the locations of the pop ash trees, the individual pop ash stems, and the ghost orchids. The data in this study indicate the trees and stems of pop ash and the epiphytic ghost orchids demonstrate departures from random dispersal on the landscape (Table 4) with all of them being significantly clumped (p<0.01). The pop ash trees showed the lowest Index of Aggregation (3.0), and ghost orchids had the highest (9.0).

Additionally, we tested whether the presence of ghost orchids on a host plant significantly increased the

Table 3. Number of ghost orchids per dbh class of pop ash used to assess host diameter preference. All stems greater than 4 cm dbh were categorized into the classes below so that each class contains nearly equal numbers of stems.

F. caroliniana **dbh class (cm)**	**Number of stems per class**	**Number of** ***D. lindenii*** **per class**
<9.2	49	4
9.2–11.8	49	1
11.9–14.0	50	3
14.1–17.2	49	9
>17.2	49	3

Table 4. Hopkins index of aggregation A' and associated t-statistics and p-values for pop ash and ghost orchids observed in this study. A random dispersion pattern on the landscape is indicated if A'=1, A'<1 indicates a uniform or regular pattern and A'>1 signifies clumping.

Species	**A'**	**t-statistic**	**p-value**
Pop ash trees	3.0	5.04	<0.01
Pop ash stems	4.2	6.21	<0.01
Ghost orchids	9.0	8.03	<0.01

probability of having multiple ghost orchids (13.0%) present on the same host compared to the probability of any stem in the study being host to at least one ghost orchids (2.9%) or not (97.1%). The Pearson χ^2 test on these data indicates a significantly increased probability of multiple individuals of ghost orchids occurring on a host plant if there is at least one individual present (p=0.004). This test is further evidence of increased clumping in ghost orchids compared to its host plants.

Discussion

Host species preference.— Pop ash served as the primary host for ghost orchids growing in a mixed cypress strand in FSPSP, as has been reported in nearby Florida Panther National Wildlife Refuge (Coopman & Kane 2019, Mújica *et al*. 2018). Alternatively, Sadler *et al.* (2011) reported pond apple as the predominant host species in another ghost orchid population in Collier County. This work documents a greater utilization of pop ash than previously reported (Mújica *et al.* 2018) and describes arthritis vine, a woody vine, as a new host species for ghost orchids in south Florida. Further, this work examined the distribution of ghost orchids in relation to the relative proportion of the woody plant species in the forested transect.

Although there were more pop ash stems within the transect than the other woody species, ghost orchids were not randomly distributed among all species, or randomly distributed among the stems of host species at the site. For example, pond apple made up 20.3% of all stems, but only one ghost orchid (4% of total individuals) was found on this species. In contrast, bald cypress made up 25.6% of all stems, but hosted no ghost orchids. The orchid's distribution is likely explained by the synergy of several factors influencing host preference in epiphytes. However, as suggested by Zettler *et al.* (2019) this preference for pop ash by the ghost orchid must also be considered in the context of the invasion of the exotic emerald ash borer as a threat to this preferred host.

Pop ash and pond apple are similar in architecture, often producing multiple stems per tree, while the other woody species in the study site tend to produce one main stem per tree. Multiple stems from the same root system would create proximal suitable habitat for wind-dispersed orchid seeds from parent plants. Although similar numbers of stems existed for pop ash and pond apple (Table 1), pond apple only served as host to one ghost orchid.

Age of the host tree may also influence host preference (Benzing 1980). Successful pollination of ghost orchids is rare (Luer 1972) as is successful seed germination (Zettler *et al*. 2011). In addition, epiphytic orchids are slow-growing due to the resource-limited environments in which they live (Laube & Zotz 2006). Therefore, an older substrate may have an increased probability of hosting ghost orchids than a younger substrate. For example, Thomas (2009) found that pop ash growing in another slough in FSPSP were older than bald cypress in the same slough by 30-40 years, likely due to successional processes during recovery following logging in the 1940s and 1950s.

No data were collected on bark roughness for this work, although bark texture is known to affect host preference in epiphytes (Benzing 1990) and is suggested as critical to ghost orchids (Zettler *et al*. 2019). A rough surface creates cracks and fissures where moisture can potentially be retained and seeds lodge until conditions are right for germination (Callaway *et al*. 2002, Hoang *et al*. 2017, Mújica *et al*. 2018). Zarate-García *et al.* (2020) more specifically suggest bark water storage linked to microrelief characteristics influences phorophyte preferences of orchids. Mújica *et al.* (2018) characterize pop ash and pond apple bark as corrugated, with crevices between 0.5 and 2.0 cm deep, and suggest bald cypress has "smoother bark" than these species. Brown (1984, p.18) describes bald cypress bark as "…an interwoven pattern of narrow flat ridges and narrow furrows," which may suggest bald cypress as a suitable substrate for ghost orchid seeds. However, unlike pop ash and pond apple, bald cypress sheds its bark, perhaps explaining why no ghost orchids were found on this potential host species.

Recent research emphasizes the role of mycorrhizal fungi in the life cycle of epiphytic orchids. Orchids require these fungi to stimulate germination (Yoder 2000). Rasmussen (2002) and Gowland *et al*. (2011) suggest host preference may be related to the mycobiont found on a host species. A strain of *Ceratobasidium* grows symbiotically with adult ghost orchids in Florida (Mújica *et al*. 2018) and improves germination and seedling development (Hoang *et al.* 2017). The presence of this strain or other fungal symbionts may be necessary for establishment of ghost orchids (Mújica *et al.* 2018, Hoang *et al*. 2017). Suitability of host plants for ghost orchid establishment therefore may be determined partially by the fungal species present on the hosts. The endophytic fungal strains studied by Hoang *et al*. (2017) were collected from a ghost orchid population in the Florida Panther National Wildlife Refuge in Southwest Florida. Hoang *et al*. (2017) did not specify the host plants supporting the individual ghost orchids that they sampled but reported that most epiphytic orchids in their study area grew on pop ash and pond apple. While explored to some extent by Johnson (2019), the importance of fungal symbionts to the establishment of ghost orchids and other epiphytic orchids warrants further investigation into the spatial distribution and potential host plant preference of these fungal species.

Vertical stratification.— We anticipated a significant tendency for the orchid to occur below 3 m, as has been reported (Mújica *et al*. 2018). Although most of the individuals we located were below 3 m (15 of 25), the trend was not significantly different from a random distribution above and below 3 m. Canopy height was not assessed in this study but may significantly impact vertical stratification of ghost orchids because of differences in solar radiation and vapor pressure deficit. Future investigation of the role of canopy height on orchid vertical stratification across populations from different locations would provide valuable insights into the observed differences across studies. It is difficult to quantify the available space for potential colonization, given the variable stem diameter and height of potential host species and the complex surfaces of these stems at greater height with numerous branches. It is possible that ghost orchid occurrence at higher positions in the canopy may be underreported as seeing this leafless orchid in upper canopy levels would be difficult when not in flower. Alternatively, many epiphytes are sensitive to higher light levels found in higher positions in the canopy (Laube & Zotz 2006). In addition, a pilot study indicated standing water in the swamp provides thermal protection of up to 2°C as high as 3 m above the ground surface from irregular frost events (unpublished data). It may be that historical vertical distributions were driven in part by cold events, but these events are likely to decrease in the future due to climate change. Mújica *et al*. (2013) found no differences in the mean height of surviving and non-surviving ghost orchid individuals following Hurricane Ivan in Cuba, suggesting that hurricane damage may not differentially affect individuals based on vertical position on the host plant. However, continuing to study the vertical position of ghost orchids in the canopy will be important as climate change can alter the occurrence of both low temperature events and hurricanes, particularly in landscapes impacted by human activities that alter hydrology.

Substrate diameter stratification.— The distribution of ghost orchids among pop ash stems of varying diameter was not random. Rather, ghost orchids exhibited a weak preference for larger stems, specifically those between 14.1 and 17.2 cm dbh. Abe *et al*. (2018) found a similar trend among the Okinawa dendrobium (*Dendrobium okinawense*)*,* an epiphytic orchid from Japan. Larger, and hence older, trees often have rougher bark, creating crevices for orchid seeds, symbiotic fungi, and sufficient moisture to support them both. In addition, older trees would give the slow-growing orchids a longer opportunity to establish and grow.

We did not collect data on the size of the ghost orchid individuals. However, individuals were found on the smallest size class of pop ash (<9.2 cm dbh) suggesting relatively recent establishment, possibly indicating this population is not 'senile' (Zettler *et al.* 2019) but may be actively recruiting.

Dispersal.— In terms of aggregation of ghost orchids, the data from this study indicated individuals of their primary host species, pop ash, have a clumped spatial arrangement on the landscape. As would be expected, the stems of pop ash with ghost orchids appear to be even more clumped. Such a spatial arrangement on the landscape may be a function of dispersal (e.g. Trapnell *et al*. 2013) or appropriate microhabitat conditions during establishment. The clumped arrangement of pop ash likely is contributing to the clumping observed in ghost orchids. However, our analysis suggests additional dispersal and/or microhabitat limitations on ghost orchids may be further influencing its dispersion pattern. Many variables determine the suitability of a host plant species, including bark stability and texture, age and architecture, and bark chemistry (Migenis & Ackerman 1993, Zettler *et al*. 2019). In addition, abiotic and biotic factors including fungal associations, temperature, irradiance, relative humidity, water availability, wind speed and direction during seed dispersal events, may collectively contribute to the clumping patterns observed in this species, and all warrant further investigation.

Establishment of new populations may be driven primarily by a few founding individuals who later reproduce, with nearby establishment of offspring, or by the concurrent arrival and establishment of many founding individuals. Trapnell *et al*. (2013) inferred the former pattern in the epiphytic Lady of the Night orchid, *Brassavola nodosa* (L.) Lindl. It is not known which pattern is typical of ghost orchid populations. However, the population dynamics of ghost orchids suggest that recruitment of new individuals, along with reproductive success, is especially important in maintaining a stable population (Raventós *et al.* 2015b). Population decline has been reported in ghost orchid populations affected by hurricanes (Mújica *et al*. 2013, Raventós *et al*. 2015a), which are predicted to become more intense under climate change projections (Knutson *et al*. 2010). Hurricane events may negatively impact host plants, and they can influence orchid-pollinator species interactions (Ackerman & Moya 1996, Mújica *et al*., 2018, Zettler *et al*. 2019). However, unpublished data from Fakahatchee Strand Preserve State Park suggests increased seed capsule production following hurricane disturbance. This dichotomy may suggest the response of this species varies according to hurricane intensity and ecosystem structure. Therefore, an improved understanding of host plant preference, microhabitat requirements, disturbance impacts and distribution of ghost orchids is crucial for the conservation of this charismatic epiphytic orchid.

Conclusion. Conservation of the ghost orchid in southern Florida must include both protection and additional research to better understand its ecology. This work adds to the understanding of ghost orchid spatial distribution and suggests potential drivers of that distribution. Long-term monitoring of this population should be continued to quantify spatial and temporal changes, particularly in a time of changing climate. However, due to the risk of poaching, this should be done with the utmost of discretion. At the time of this writing, several of the orchids within this population have been removed by humans since the fieldwork was completed.

Acknowledgements. The authors would like to thank Fakahatchee Strand Preserve State Park for access to the study site. Thank you to Karen Relish for assistance with fieldwork, particularly with the sometimes-difficult plant identification. We thank the Florida Gulf Coast University Inland Ecology Research Group for invaluable assistance with fieldwork. Finally, we thank the editors and anonymous reviewers for their helpful suggestions in improving the manuscript.

Literature Cited

Abe, S., Kotaka, N., Takashima, A., Abe, T., Saito, K. & Masaki, T. (2018). Host selection and distribution of *Dendrobium okinawense*, an endangered epiphytic orchid in Yambaru, Japan. *Ecological Research*, 33(5), 1069–1073.

Ackerman, J. D. & Moya, S. (1996). Hurricane aftermath: resiliency of an orchid-pollinator interaction in Puerto Rico. *Caribbean Journal of Science*, 32, 369–374.

Arditti, J. & Ghani, A. K. A. (2000). Numerical and physical properties of orchid seeds and their biological implications. *New Phytologist*, 145(3), 367–421.

Balding, M. & Williams, K. J. (2016). Plant blindness and the implications for plant conservation. *Conservation Biology*, 30(6), 1192–1199.

Bennett, B. C. (1986). Patchiness, diversity, and abundance relationships of vascular epiphytes. *Selbyana*, 9(1), 70–75.

Benzing, D. H. (1980). *The biology of bromeliads*. Eureka, California, USA: Mad River.

Benzing, D. H. (1990). *Vascular epiphytes*. New York, USA: Cambridge University Press.

Brown, C. A. (1984). Morphology and biology of cypress trees. In: K. Ewel & H. Odum (Eds.), *Cypress swamps*. Gainesville, FL: University of Florida Press.

Brown, P. M. & Folsom, S. (2002). *Wild orchids of Florida: with references to the Atlantic and Gulf Coastal Plains*. Gainesville, FL: University of Florida Press.

Callaway, R. M., Reinhart, K. O., Moore, G. W., Moore, D. J. & Pennings, S. C. (2002). Epiphyte host preferences and host traits: mechanisms for species-specific interactions. *Oecologia*, 132(2), 221–230.

Chomicki, G., Bidel, L. P. & Jay-Allemand, C. (2014). Exodermis structure controls fungal invasion in the leafless epiphytic orchid *Dendrophylax lindenii* (Lindl.) Benth. ex Rolfe. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 209(2), 88–94.

Coopman, J. & Kane, M. E. (2018). Greenhouse acclimatization methods for field establishment of *in vitro*-derived ghost orchid (*Dendrophylax lindenii*) plants. *Native Plants Journal*, 19(2), 100–108.

Coopman, J. C., & Kane, M. E. (2019). *In vitro* desiccation tolerance of the epiphytic Ghost Orchid, *Dendrophylax lindenii* (Lindl.) Benth x. Rolfe. *In Vitro Cellular & Developmental Biology-Plant*, 55(1), 60–70.

Danaher, M. W., Ward, C., Zettler, L. W. & Covell, C. V. (2020). Pollinia removal and suspected pollination of the endangered ghost orchid, *Dendrophylax lindenii* (Orchidaceae) by various hawk moths (Lepidoptera: Sphingidae): Another mystery dispelled. *Florida Entomologist*, 102, 671–683.

Duever, M. J. (1986). *The Big Cypress National Preserve (Research report no. 8 of the National Audubon Society)*. USA: Natl Audubon Society.

Ewel, K. C. (1990). Swamps. In R.L. Myers & J.J. Ewel (Eds), *Ecosystems of Florida* (pp. 281–317). USA: University of Central Florida Press.

GBIF (2023). Global Biodiversity Information Facility Occurrence. Retrieved from https://doi.org/10.15468/dl.yqxzbd [Accessed 17 February 2023]

Goodall, D. W. & West, N. E. (1979). A comparison of techniques for assessing dispersion patterns. *Vegetatio*, 40(1), 15–27.

Gowland, K. M., Wood, J., Clements, M. A. & Nicotra, A. B. (2011). Significant phorophyte (substrate) bias is not explained by fitness benefits in three epiphytic orchid species. *American Journal of Botany*, 98(2), 197–206.

Hervé, M. (2019). RVAideMemoire: Testing and plotting procedures for biostatistics. Version 0.9-73. Retrieved from https://cran.r-project.org/web/packages/RVAideMemoire/index.html

Hoang, N. H., Kane, M. E., Radcliffe, E. N., Zettler, L. W. & Richardson, L. W. (2017). Comparative seed germination and seedling development of the ghost orchid, *Dendrophylax lindenii* (Orchidaceae), and molecular identification of its mycorrhizal fungus from South Florida. *Annals of Botany*, 119(3), 379–393.

Hopkins, B. & Skellam, J. G. (1954). A new method for determining the type of distribution of plant individuals. *Annals of Botany*, 18(2), 213–227.

Houlihan, P. R., Stone, M., Clem, S. E., Owen, M. & Emmel, T. C. (2019). Pollination ecology of the ghost orchid (*Dendrophylax lindenii*): A first description with new hypotheses for Darwin's orchids. *Scientific Reports*, 9(1), 12850.

Johnson, L. J. (2019). Investigating specificity and diversity of orchid mycorrhizal fungi of *Vanilla planifolia* and *Dendrophylax lindenii* (Doctoral dissertation, Northwestern University).

Knutson, T. R., McBride, J. L., Chan, J., Emanuel, K., Holland, G., Landsea, C., Held, I., Kossin, J. P., Srivastava, A. K. & Sugi, M. (2010). Tropical cyclones and climate change. *Nature Geoscience*, 3(3), 157–163.

Laube, S. & Zotz, G. (2006). Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany*, 97(6), 1103–1114.

Lodge, T. E. (2016). *The Everglades handbook: understanding the ecosystem*. Boca Raton, FL: CRC Press.

Luer, C. A. (1972). *The native orchids of Florida* (No. 584.15 L8). New York Botanical Garden.

Migenis, L. E. & Ackerman, J. D. (1993). Orchid—phorophyte relationships in a forest watershed in Puerto Rico. *Journal of Tropical Ecology*, 9(2), 231–240.

Mújica, E. B., Herdman, A. R., Danaher, M. W., González, E. H. & Zettler, L. W. (2021). Projected status of the ghost orchid (*Dendrophylax lindenii*) in Florida during the next decade based on temporal dynamic studies spanning six years. *Plants*, 10, 1579.

Mújica, E. B., Mably, J. J., Skarha, S. M., Corey, L. L., Richardson, L. W., Danaher, M. W., Danaher, M. W., Gonzalez, G. H. & Zettler, L. W. (2018). A comparison of ghost orchid (*Dendrophylax lindenii*) habitats in Florida and Cuba, with particular reference to seedling recruitment and mycorrhizal fungi. *Botanical Journal of the Linnean Society*, 186(4), 572–586.

Mújica, E., Raventós, J., González, E. & Bonet, A. (2013). Long-term hurricane effects on populations of two epiphytic orchid species from Guanahacabibes Peninsula, Cuba. *Lankesteriana*, 13(1–2), 47–55.

Rasmussen, H. N. (2002). Recent developments in the study of orchid mycorrhiza. *Plant and Soil*, 244(1), 149–163.

Raventós, J., González, E., Mújica, E. & Bonet, A. (2015a). Transient population dynamics of two epiphytic orchid species after Hurricane Ivan: implications for management. *Biotropica*, 47(4), 441–448.

Raventós, J., González, E., Mújica, E. & Doak, D. F. (2015b). Population Viability Analysis of the Epiphytic Ghost Orchid (*Dendrophylax lindeni*i) in Cuba. *Biotropica*, 47(2), 179–189.

Ray, H. A., McCormick, J. P., Stice, A. L., Stocks, I. C. & Zettler, L. W. (2012). Occurrence of boisduval scale, *Diaspis boisduvalii* (Hemiptera: diaspididae), on native epiphytic orchids in Collier Co., Florida, including Fakahatchee Strand State Preserve. *Florida Entomologist*, 95(2), 312–318.

Sadler, J. J., Smith, J. M., Zettler, L. W., Alborn, H. T. & Richardson, L. W. (2011). Fragrance composition of *Dendrophylax lindenii* (Orchidaceae) using a novel technique applied *in situ*. *European Journal of Environmental Sciences*, 1(2), 137–141.

Sall, J., Stephens, M. L., Lehman, A. & Loring, S. (2017). *JMP start statistics: a guide to statistics and data analysis using JMP*. SAS Institute.

Stewart, S. L. (2007). *Integrated conservation of Florida Orchidaceae in the genera Habenaria and Spiranthes model orchid conservation systems for the Americas*. PhD dissertation, University of Florida.

Thomas, B. L. (2009). *Succession of the plant communities of Fakahatchee strand following anthropogenic disturbances* (MS Thesis). Florida Gulf Coast University.

Trapnell, D. W., Hamrick, J. L., Ishibashi, C. D. & Kartzinel, T. R. (2013). Genetic inference of epiphytic orchid colonization; it may only take one. *Molecular Ecology*, 22(14), 3680–3692.

Wraith, J. & Pickering, C. (2018). Quantifying anthropogenic threats to orchids using the IUCN Red List. *Ambio*, 47(3), 307–317.

Wunderlin, R. P. & Hansen, B. F. (2011). *Guide to the vascular plants of Florida*. University Press of Florida.

Yoder, J. A., Imfeld, S. M., Heydinger, D. J., Hart, C. E., Collier, M. H., Gribbins, K. M. & Zettler, L. W. (2010). Comparative water balance profiles of Orchidaceae seeds for epiphytic and terrestrial taxa endemic to North America. *Plant Ecology*, 211(1), 7–17.

Zarate-García, A. M., Noguera-Savelli, E., Andrade-Canto, S. B., Zavaleta-Mancera, H. A., Gauthier, A. & Alatorre-Cobos, F. (2020). Bark water storage capacity influences epiphytic orchid preference for host trees. *American Journal of Botany*, 107(5), 726–734.

Zettler, L. W., Corey, L. L., Richardson, L. W., Ross, A. Y. & Moller-Jacobs, L. (2011). Protocorms of an epiphytic orchid (*Epidendrum amphistomum* A. Richard) recovered in situ, and subsequent identification of associated mycorrhizal fungi using molecular markers. *European Journal of Environmental Sciences*, 1(2), 108–114.

Zettler, L. W., Kane, M. E., Mújica, E. B., Corey, L. L. & Richardson, L. W. (2019). The ghost orchid demystified: biology, ecology and conservation of *Dendrophylax lindenii* in Florida and Cuba. In *Proceedings, 22nd World Orchid Conference. Asociación Ecuatoriana de Orquideologia, Guayaquil, Ecuador* (pp. 136–148).

Zotz, G., Bermejo, P., & Dietz, H. (1999). The epiphyte vegetation of *Annona glabra* on Barro Colorado Island, Panama. *Journal of Biogeography*, 26(4), 761–776.