Article

The Fate of *Guzmania monostachia* in Florida Rests with Humans

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Abstract: Land use changes by humans have eliminated more than half of the wetlands in Florida over the last 200 years, and additional losses are anticipated as a consequence of climate change and ongoing development activities that will accommodate a rapidly growing human population. Both spell danger for the biodiversity and ecosystem services in Florida, and data are needed to inform conservation priorities and actions concerning threatened or endangered wetland species. We modeled the projected distribution of an endangered epiphyte native to the forested wetlands in South Florida, *Guzmania monostachia* (Bromeliaceae), in response to changing climate and sea level conditions. We constructed ecological niche models (ENMs) under the present framework by using georeferenced occurrence points and projected them into the past and future under different scenarios. Our future climate-based ENMs predicted small losses in suitable habitat for *G. monostachia* in South Florida, with expansions into higher latitudes due to the warmer climate. In contrast, the models predicted a considerable, although non-detrimental, loss of suitable habitat due to rising sea levels. The combined results suggest that human activity is and will remain the largest threat to *G. monostachia* in Florida, and conservation efforts should focus on preserving existing habitats that will remain above sea level and explore possibilities for assisted migration.

Keywords: Bromeliaceae; Florida; *Guzmania monostachia*; climate change; sea level rise; species distribution modeling; conservation

1. Introduction

The wetlands of Florida are species-rich and home to a variety of rare and charismatic plant and animal species, including the locally endangered *Guzmania monostachia* (L.) Rusby ex Mez (West Indian tufted airplant). Unfortunately, over half of the original wetlands in Florida have already been lost to dramatic land use changes made by humans, and both anthropogenic climate change and rapidly growing human populations threaten additional losses to wetland biodiversity throughout the state. Given its already significantly contracted distribution, the risk of permanently losing the genetic diversity found within a few remaining, isolated populations of *G. monostachia* in Florida is dangerously high. Thus, it is imperative that we understand the potential factors that may contribute to additional habitat losses, as well as ecological or microclimate changes within the existing habitats where *G. monostachia* persists. This information will help identify critical areas for preservation and inform meaningful policies and practices for the conservation of *G. monostachia* now and into the distant future.

1.1. Guzmania monostachia in Florida

Guzmania is a member of the Bromeliaceae, a neotropical plant clade consisting of ca. 3140 species from 8 major lineages [1]. The group is placed in the Tillandsioideae, the largest

clade within Bromeliaceae, which has an estimated stem age of 15.4 Ma and a proposed Andean origin [2,3]. In comparison to other *Guzmania*, *G. monostachia* has the broadest distribution, with populations in northern South America, Central America, the Caribbean, and South Florida [3]. Florida is home to 16 bromeliad species, all of which belong to the Tillandsioideae. Specimen records and historical observations suggest that many of these epiphytes were common throughout the forested freshwater wetlands of South Florida, where they thrived on the humid conditions and trees characterizing these habitats. However, bromeliads in South Florida have experienced rapid population declines recently due to human-related impacts such as habitat loss, poaching, and extensive damage by an invasive bromeliad-eating weevil from Mexico, *Metamasius callizona* Chevrolat, whose presence in Florida was first documented in 1989. Within its native range, *M. callizona* is known mainly as an occasional pest in shaded greenhouses, and observations of infestations on naturally occurring bromeliads are sparse [4]. In contrast, infestations on naturally occurring bromeliads in South Florida are common, and damage to individual plants is also more severe [5]. It is unclear why impacts to Floridian bromeliad populations have been so extensive, although a biological agent (e.g., a parasitoid wasp) may control populations of *M. callizona* within its native range [6].

Despite its inclusion on the Endangered and Threatened Species List for Florida, endangered conservation status, and rapidly declining plant numbers [7,8], basic research on *G. monostachia* is surprisingly lacking. Florida-based populations represent the northernmost limit of the species' distribution range, but their evolutionary origin is unknown. Also lacking is information about the genetic identity, diversity, and population structure of the remaining populations and how these characteristics compare with those of other populations in the Americas and Caribbean. Morphological and observation-based evidence, including the close proximity of the gynoecium and androecium within a largely closed corolla, muted bract coloration, and apparent lack of pollinator visitation [9], suggests that Floridian plants may be exclusively autogamous and, consequently, genetically distinct, whereas outcrossing individuals with brighter flower color and hummingbird-mediated pollination have been observed in South America [10,11]. Autogamous breeding systems lead to reduced genetic diversity through inbreeding, increasing a population's susceptibility to pests, pathogens, or environmental disturbances—for example, those resulting from climate change [12].

1.2. History of Ecosystems in Modern-Day Florida and Threats to Bromeliad Habitats

Florida is situated atop the shallow Florida Platform [13], a flat geological feature that includes the emergent portion that we currently recognize as the Florida peninsula, and a submerged portion known as the West Florida Escarpment, which extends westward by more than 160 km into the Gulf of Mexico from the modern-day coastline. The Florida Platform is composed primarily of limestone that was deposited by carbonate-producing marine organisms during the Mesozoic (190–66 Ma; [14]). During the Miocene (~23 Ma ago), a portion of the Florida platform was exposed by lower sea levels, allowing silica-based sediments from the eroding Appalachian Mountains to flow southward onto the newly exposed limestone [15]. The fluctuating sea levels that occurred from the Miocene to the present day (~23 Ma ago to present) further affected sediment deposition processes, with submerged and newly exposed areas accumulating more carbonate and sediment, respectively. Roughly one-third to one-half of the Florida Platform is above sea level today, but the extent of the emergent portion has varied through time as a result of changing climate and oceanographic events [13], shaping both its geological form and biota. The superposition of climatic events, global sea level dynamics, and changing soil composition across the Florida Platform contributed to major transitions in environments, affecting species compositions and ranges in space and time, as well as increases and decreases in the areas of suitable habitats.

Florida is the only state in the continental United States (US) that is characterized by subtropical ecosystems, and 17% of its wildlife species do not occur in other states [16]. Thus,

Florida harbors unique biodiversity and habitats that are vital to conserve. In particular, the wetlands of Florida have great ecological importance, providing habitat for numerous plant and animal species, sequestering carbon, removing pollutants from flowing water, and mitigating potential flooding to surrounding areas by acting as sinks [17]. Despite their significance, these habitats have sustained considerable damage inflicted by humans. From 1780 to 1980, Florida lost 9.3 million acres of wetlands—the largest loss in the USA. Currently, Florida has only 54% of its original wetland coverage remaining [18], with losses primarily caused by the draining and filling of wetlands for agricultural land and urban development.

In addition to areas lost to human development activities, many remaining wetlands across Florida are significantly altered. The plant community composition of wetlands is heavily dependent on hydrologic regimes [19], and the draining and filling of some regions can drastically affect wetlands elsewhere in the state [20]. Climate change also has the potential to alter hydrologic regimes, perhaps with drastic consequences. For example, under various climate models, mean annual precipitation is expected to decrease in the Everglades, leading to drier conditions and a shift away from plant communities that depend on deeper and longer flooding periods [21].

In Florida, *G. monostachia* inhabits primarily two types of ecosystems: pop ash/pond apple sloughs on the west coast and tropical hardwood hammocks on the east coast (Figure 1). Pop ash/pond apple sloughs are wetland ecosystems that are unique to South Florida and dominated by *Fraxinus caroliniana* Mill. (pop ash) and *Annona glabra* (L.) (pond apple). These ecosystems are characterized by long hydroperiods of deep water and mucky soil [22]. Tropical hardwood hammocks are densely vegetated with evergreen tropical trees, including *Bursera simaruba* (L.) Sarg. (gumbo limbo), *Coccoloba diversifolia* Jacq. (pigeon plum), and *Quercus virginiana* Mill. (southern live oak), and they support a wide variety of epiphytes, including bromeliads and orchids. These hardwood hammocks are relatively small and disjunct, perched on limestone outcrops elevated by at least one meter above the surrounding valleys, and characterized by shallow soils [23]. In Florida, these hammocks are found as far north as Martin County, near Lake Okeechobee, but occur primarily in the south, from northern Miami-Dade County through the Everglades, along the Miami Rock Ridge, and the southern portion of the geological formation known as the Atlantic Coastal Ridge [24].

Currently, six distinct populations of *G. monostachia* are known from five areas in Florida, and these populations are largely fragmented and disjunct (Figure 2). The area with the largest abundance of *G. monostachia* is the Fakahatchee Strand State Preserve, which is located in Collier County in southwest Florida. This preserve encompasses numerous pop ash/pond apple sloughs that host populations of *G. monostachia.* Prior to the introduction of *M. callizona*, the total estimated number of *G. monostachia* in Fakahatchee Strand exceeded 2 million individuals. However, only half that number are estimated to exist within the preserve today. Additionally, the preference of *M. callizona* for larger plants has led to a drastic shift in population demographics; the proportion of reproductively mature individuals within the population has been reduced from roughly 50% to only 10–20% today [25]. Adjacent to and east of the Fakahatchee Strand is Big Cypress National Preserve. The latter is home to two highly disjunct populations of *G. monostachia,* which are located at the extreme north and south ends of the preserve, respectively, and with nearly 2900 km^2 of land between them. The northern population consists of roughly 200 individuals and is found within a drier pop ash/pond apple slough habitat that also contains cypress, whereas the southern population comprises approximately 1000 individuals and inhabits a more traditional pop ash/pond apple slough. A fourth area that includes *G. monostachia* is the Everglades National Park, which is home to a single population. The population is located on the east side of the park, within a tropical hardwood hammock that is only approximately 150 m in diameter. In stark contrast to the Fakahatchee Strand and Big Cypress populations, this population is currently in critical condition and includes only three individuals. The remaining populations are located in Fuchs and Meissner Hammock

Preserve. These contiguous areas are located on the outskirts of Homestead and are surrounded by agricultural land and suburban housing. The larger Fuchs Hammock, which is historically known as Sykes Hammock, includes only three individuals of *G. monostachia*, while two individuals are present in the Meissner Hammock.

(**a**)

(**b**)

(**c**)

Figure 1. *Guzmania monostachia* (**a**) in a tropical hardwood hammock habitat (**b**) and pop ash/pond apple slough (**c**).
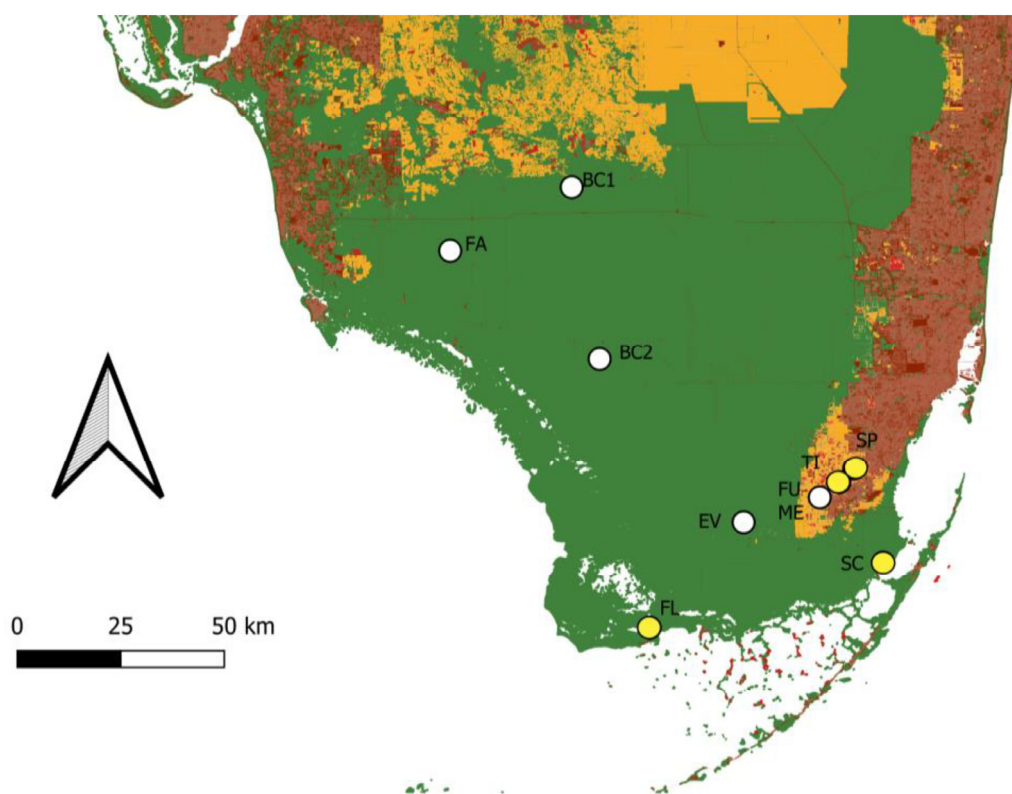
Figure 2. Land cover map of south Florida with general localities of known populations of *Guzmania monostachia*. White points are populations that are still present. Yellow points are populations that have been extirpated. Areas in green are natural lands. Areas in orange are agricultural lands. Areas in light red are rural areas. Areas in dark red are urbanized areas. Map constructed by using data from the Florida Cooperative Land Cover Map version 3.5. Population identifiers: Fakahatchee Strand (FA), Northern Big Cypress (BC1), Southern Big Cypress (BC2), Everglades (EV), Fuchs Hammock (FU), Meissner Hammock (ME), Flamingo (FL), South of Cutler (SC), Timms Hammock (TI), Silver Palm Hammock (SP).

The populations identified above represent all known populations existing in Florida today. However, historical records identify at least four additional areas where *G. monostachia* once occurred. The plants are presumably extirpated from these areas today, highlighting the drastic range contraction that *G. monostachia* has experienced within the last hundred years [8]. Interestingly, the areas were largely unaffected by weevil activity, which points to urbanization and land conversions as the most probable causes of range contractions in this species [26]. Two of the four extirpated populations existed within what is now known as the Miami Metropolitan Area, a region of urbanized land stretching 161 km along the southeastern coast of Florida in Broward, Miami-Dade, and Palm Beach Counties. This statistical area includes several large cities, such as Miami, Fort Lauderdale, and West Palm Beach [27]. This urbanized region has expanded rapidly in recent decades and is one of the most populous human settlements in the world. From 1950 to 1995, over 2100 km^2 of natural land within Broward, Miami-Dade, and Palm Beach counties was converted to urban use [28]. This urban expansion has continued in recent decades, albeit at a slower rate. For example, the Miami Metropolitan Area gained only 860 km^2 of urban area between 1992 and 2016 [27]. While several hammocks that historically supported populations of *G. monostachia* remain as preserved and protected natural lands within the Miami Metropolitan Area today, their hydrology and microclimates have likely changed considerably as a consequence of increasing urbanization in the areas surrounding them. Development activities by humans are likely to have disrupted historical patterns of hy-

drological flow within these areas, and the hammocks no longer offer suitable habitat conditions for *G. monostachia*.

1.3. Conserving Bromeliads in Florida

The conservation of native bromeliads is critical, in part because of the important ecosystem services they provide. Water collected in the leaf bases of tank bromeliads such as *G. monostachia*, which are known as a "phytotelmata", sustains life for a variety of organisms, including some invertebrates that exist solely on these plants. Thus, it may be appropriate to view individual bromeliads as ecosystems within ecosystems [29], and the loss of these plants could have cascading negative effects on the biodiversity within a given area. Additionally, Florida populations of *G. monostachia* represent the northernmost edge of an extensive distribution range, which is the most extensive of any *Guzmania*, and may harbor genetic diversity that is potentially important to the long-term survival of the species. Numerous studies show that populations occupying the periphery of species ranges are often genetically distinct from those closer to the center [e.g., [30,31]]. As global temperatures rise and species ranges shift toward the poles, these leading-edge gene pools could prove critical for the evolutionary or adaptive potential of the species [32]. Thus, the genetic diversity of *G. monostachia* in Florida is critical to investigate, ultimately to be able to generate meaningful conservation strategies.

Ecological niche models (ENM) make use of known species occurrence data, as well as data about the environments in which they occur, to reconstruct past and future distribution ranges [33]. By using data from paleoclimatic and future climate projections, ENMs can help generate species distribution models (SDMs) that hypothesize historical and future geographic species ranges. ENMs have become an important tool for conservation, enabling researchers to make predictions about the impacts of climate change on the geographic ranges of imperiled species [34,35]. Predictions about the future range and distribution of *G. monostachia* in Florida can inform effective conservation strategies, priorities, and actions that ensure the persistence of *G. monostachia* in Florida by pinpointing populations at risk of extirpation, areas that should be preserved as potential future habitats for the species, and other important elements in their associated plant communities. Paleohistorical projections of the distribution of *G. monostachia* can provide both insights into the historical interactions between climate changes and distribution ranges and context for interpretations of current range and distribution patterns. Studies show that climate and distribution range interactions are generally conserved over paleohistorical time, with periods of warmer climate shifting distribution ranges toward the pole, and periods of cooler climate shifting distribution ranges toward the equator [36].

In this study, we use ecological niche modeling to infer past and future distribution ranges of Florida *G. monostachia* based on paleohistorical, current, and projected climate data, as well as sea level changes. We analyze the extent to which these processes have affected the past ecosystem and examine how they may potentially impact *G. monostachia* populations in the future. The present study has three goals: (1) to infer the past and present ranges of *G. monostachia* in Florida and broadly determine the amount of suitable habitat, (2) to project climate data into the future under various climate change scenarios and determine their effects on areas of suitable habitat, and (3) to determine the potential impacts of projected sea level changes and their effects on areas of suitable habitat in the future.

2. Materials and Methods

2.1. Occurrence Data Compilation

We utilized a combination of GPS co-ordinates from field observations and georeferences from detailed locality information or historical maps on expert-vetted herbarium specimens (Table S1). The latter were made by using GEOLocate version 3.22 [37]. Because some occurrences (points) comprising the compiled dataset were within 1 km (30 s) of one another and exceeded the resolution of our chosen ecological variables (see below), we

filtered the dataset with the "gridSample" function of the dismo R package [38] and retained only one point per 1 km grid cell. The filtering rarefied points to 1 km/30 arcsecond, producing a final set of occurrence co-ordinates for our analyses.

2.2. Ecological Variables Assembly

We obtained bioclimatic data from Worldclim V.2 at 30 arcsec ($\approx$1 km^2) resolution [39]. Additionally, we obtained 5 soil variables at 30 arcsec resolution from ISRC SoilGrids API, which we averaged in QGIS across 5 core depths [40,41]. The inclusion of soil data prevents the overestimation of suitable habitat based solely on climatological data [42]. Additionally, soil variables help reflect various land-cover and forest properties that are important to modeling epiphyte ranges, especially in areas where the climate is relatively homogeneous and the focal group is a substrate generalist [43–45]. We tested all 19 Bioclim and 5 SoilGrid variable layers for correlation in the training area of the model and used a Pearson's correlation coefficient cutoff of $\pm$0.8 to identify non-correlated layers for use in our analyses. For layers that were correlated with one another, we chose those that best captured climatic and edaphic factors relevant to *G. monostachia* [46].

We compiled eight variable layers capturing facets of climate and soil for the Mid-Holocene, present, 2050, and 2090. These comprised five Bioclim temperature and precipitation variables: bio1 (mean annual temperature), bio5 (maximum temperature of warmest month), bio9 (mean temperature of driest quarter), bio12 (annual precipitation), bio13 (precipitation of wettest month); and the three soil layers: clay percentage, pH, and organic carbon content. For the remainder of this paper, "environmental variables" will refer to both climatic and edaphic variables. We also obtained projected climatic data for 2050 and 2090 at Shared Socio-economic Pathways (SSP) 2-4.5 from Worldclim. We selected SSP 2-4.5 because it was determined to be the most plausible by the United Nations Intergovernmental Panel on Climate Change, given current moderate mitigation efforts and global policies regarding CO_2 emissions, plus future advances in carbon-zero technologies [47]. Sea level rise (SLR) masks at one and two meters that were used in post-processing for SDM maps and range size calculations were from the Sea Level Scenario tool from the University of Florida Geoplan Center [48,49].

2.3. Ecological Niche Models

To establish the range and training area for our species of interest, we used a 1 km buffer around every point in our processed locality dataset by using the "gBuffer" function of the "rgeos" R package [50]. Short seed dispersal distances of ca. 80 cm have been documented for *Guzmania monostachia* [10]. Thus, the size of the buffer around each point was based on the dispersal potential and accessible area for a species with limited dispersal [51,52]. We edited these shapefiles to form continuous areas and produce the final shapefile [35,53].

Studies on SDMs for narrow-range species that utilize real and simulated data have indicated that the sum of environmental variables included for model creation is not a factor that increases the so-called "minimum required sample size", which, in species with narrow ranges, may be as low as three to five unique points (also referred to as the "absolute minimum sample size"; [54]). Therefore, we followed McPherson et al. [55] for choosing a model training area that is comparative to the confirmed presence area of the assessed species so that at least 10% of the training area cells contain a locality point. We checked locality prevalence for our species of interest with the virtualspecies R package [56].

We produced ENMs by using the R package ENMeval V0.3.0 [57] in conjunction with MaxEnt V3.4.1k [58]. We selected ENMeval because it (1) allows for the partitioning of occurrence data by creating datasets for *k*-fold cross-validation, (2) builds an ensemble of models by using MaxEnt under different user-defined settings, and (3) simplifies selecting optimal model settings by providing multiple evaluation metrics. R random *k*-folds (=bins) were used for partitioning locality data and calculated four metrics to evaluate and select the best model: the area under the curve of the receiver-operating characteristic for test

localities (AUC$_{\text{TEST}}$), the difference between training and testing AUC (AUC$_{\text{DIFF}}$), the delta-Akaike information criterion adjusted for small sample sizes (ΔAICc), and the Continuous Boyce Index (CBI) calculated by using Ecospat V3.1. [59]. The resulting models were projected onto the training region or onto the whole of Florida to see if a suitable habitat hypothetically occurs north of the species' current range. To determine the extent of model extrapolation and uncertainty, we ran a Multivariate Environmental Similarity Surfaces analysis (MESS; [60]) to find areas in our projections where extrapolation may occur for predicting areas of suitable habitat. SLR masks at one and two meters were applied after model creation and projection.

2.4. Identifying Areas of Suitable Habitat

We compared the predicted geographical ranges under both present and future conditions to evaluate changes in suitable habitat for *G. monostachia*. Overlap between the two scenarios was calculated by (1) comparing differences in size of suitable geographic area (km^2), and (2) analyzing raster extent overlap between the present and future areas of suitable habitat by using Schoener's *D*, a measure for which 0 indicates no similarity and 1 represents complete similarity [61]. We calculated the 5th and 10th percentile training presence (90 pct, 95 pct) and minimum training presence (MTP) to remove all areas with suitability lower than the suitability values for the 5%, 10%, and lowest predicted suitability value for an occurrence point. This means that 5% or 10% of the occurrence records found in the least suitable habitat do not occur in regions that are representative of the overall habitat of a species and, therefore, should be omitted [62]. The MTP calculation ensures that all locality points are found within the boundaries of the thresholded model because it assumes that the least suitable habitat in which the species is known to occur is the minimum suitability value [63]. By using these binary models, the area and zonal functions of the Raster package in R [64] were used to sum the area of each cell of the prediction raster that was considered suitable habitat. The cells were split into three groups: total suitable area currently, total suitable area in the future, and the ratio of suitable area in the present to the future. We divided the total area of projected suitable habitat in the future by the total area of suitable habitat in the present to quantify how much habitat a species is predicted to gain or lose under a climate change scenario. We then determined if our species was gaining (ratio > 1) or losing (ratio < 1) habitat. A recent report by The United States Geological Survey and National Oceanographic and Atmospheric Administration [48], which details SLR projections for the entire US coastline, states that the Southern Florida coastline can expect up to 7.08 feet (2.16 m) of SLR by the end of the century. Thus, to calculate range size changes while also considering future SLR, we used the above approach while incorporating two scenarios: an intermediate SLR of 1 m and the projected 2 m.

The approach outlined above calculates the probable distribution of suitable range for a species in the future while also considering the impacts of SLR on suitable habitat size. We measured how much of the present projected habitat will remain habitable, despite predicted climate change and SLR, and quantified how much of the current suitable habitat overlaps with the future projected suitability at several different scenarios. The area where both overlap represents habitat that will remain habitable from the present into the future. Additional new habitat may also become available in the future, allowing a species such as *G. monostachia* to expand its range northward in the Florida peninsula. However, even with the availability of a new suitable habitat in the future, a species may not be able to effectively disperse and establish there. Therefore, the appearance of new habitat in the future does not guarantee that a species will be present in the area.

3. Results

3.1. Occurrence Data

A total of 80 occurrence records were compiled for *Guzmania monostachia* in Florida (Table S1). After occurrences were filtered within each 1 km^2 grid cell, 15 points were retained and used for our analyses. Due to the endangered status of *G. monostachia* and the

potential for poaching-related threats to natural populations, only generalized locality data are provided in Table S1.

3.2. Ecological Niche Models

We used ΔAICc, CBI, and AUC scores to determine model performance. We used CBI specifically because of its ability to provide predicted-to-expected ratio curves that offer insights into model quality, specifically model robustness, habitat suitability resolution, and deviation from randomness [35]. CBI performs particularly well for presence-only based predictions and complements the typical methods of evaluation of presence/absence models [65]. The index ranges from −1 to 1. Values > 0 indicate that the model's output is positively correlated with the true probability of presence. Values < 0 indicate that it is negatively correlated with the true probability of presence. ΔAICc differentiates between the AICc of a given model and the AICc of the model with the lowest AICc, allowing for ensemble model comparisons.

An ENM is determined to have performed well if its AUC > 0.7, ΔAICc < 2, and CBI is close to 1. We used CBI and ΔAICc to select the best model (Table S2). The CBI of the highest-scoring model was 0.917. Only two models had CBI scores lower than 0.7. The median ΔAICc was 7.64. The median training AUC was 0.8 ± 0.11. Regarding AUC scores, they should be interpreted together with other measures because sampling bias can negatively affect model quality by inflating model accuracy (by erroneously calculating higher AUC scores; [66]). MESS outputs for our species indicate that the future climates within the projection region are mostly within the parameters of the present training region, signifying sufficient reliability for model transferability between different scenarios (Figures S1–S3), with extrapolation affecting projections only in the northernmost part of the range of *G. monostachia*.

3.3. Changes in Suitable Habitat

The area of suitable habitat increased by 7% between the Mid-Holocene and the present day (Table 1; Figure 3). Gains occurred primarily in the central portion of southern Florida, and small amounts of suitable habitat were lost in the southeast portion of Florida in the Everglades. According to our 90 and 95% threshold analyses (Table 1), *G. monostachia* is predicted to lose suitable habitat as a result of climate change and sea level rise between the present day and 2090. Although losses affect primarily the southwest coastline and lower lying areas of the Everglades, they are almost exclusively due to sea level rise, rather than changes in climate (Figure 4).
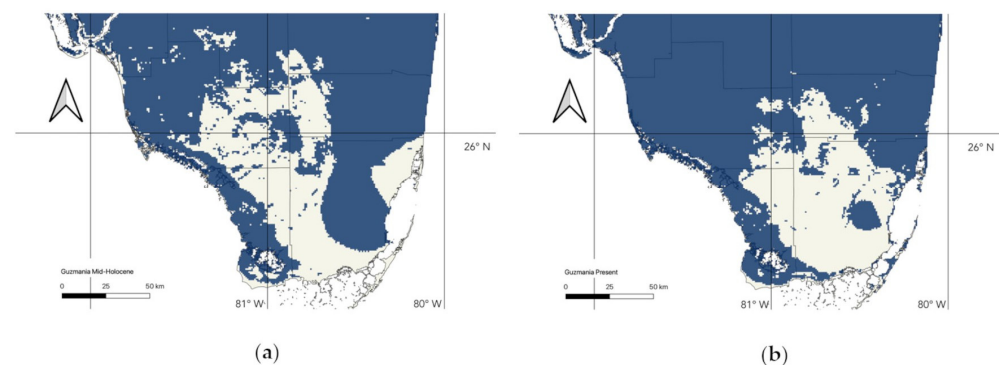

(a)   (b)

Figure 3. Representation of 90% thresholded species distribution models of *Guzmania monostachia* in Florida during the Mid-Holocene (**a**) and for the present day (**b**). Areas in blue represent areas that contain habitat which is at least 90% suitable.

Table 1. Results from Species Distribution Models (SDMs) comparing past/present and present/future models with differing future sea level rise (SLR) projections for *Guzmania monostachia*, which are calculated with a 90 and 95% threshold.

|	Mid-Holocene Suitable Area (in km²)	Current Suitable Area (in km²)	Schoener's *D*	Present Area/Past Area
G. monostachia (90 and 95 pct)	16,559.87	17,723.16	0.83	1.07
G. monostachia (90 pct)	**2090 Suitable Area (in km²)**	**Current Suitable Area (in km²)**	**Schoener's *D***	**Future Area/Present Area**
0 m SLR	17,206.83	17,723.16	0.93	0.97
1 m SLR	13,180.92	N/A	0.93	0.74
2 m SLR	10,861.82	N/A	0.95	0.61
G. monostachia (95 pct)	**2090 Suitable Area (in km²)**	**Current Suitable Area (in km²)**	**Schoener's *D***	**Future Area/Present Area**
0 m SLR	20,877.974	17,723.16	0.84	1.17
1 m SLR	15,552.71	N/A	0.87	0.87
2 m SLR	11,776.39	N/A	0.95	0.66
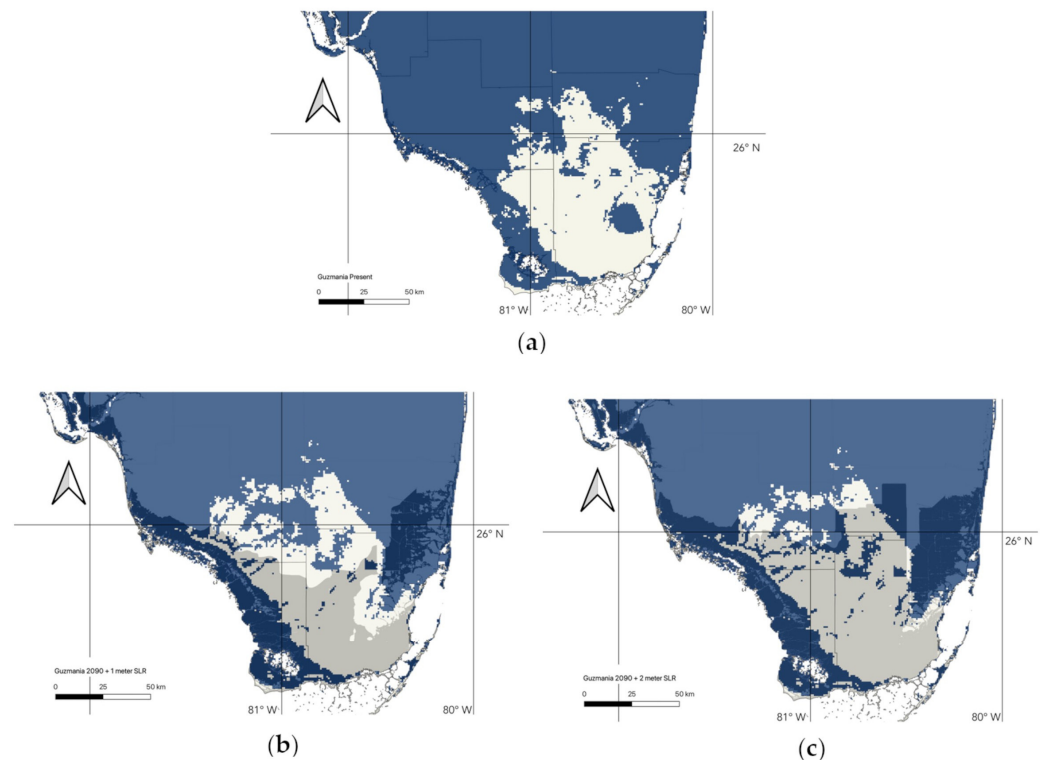
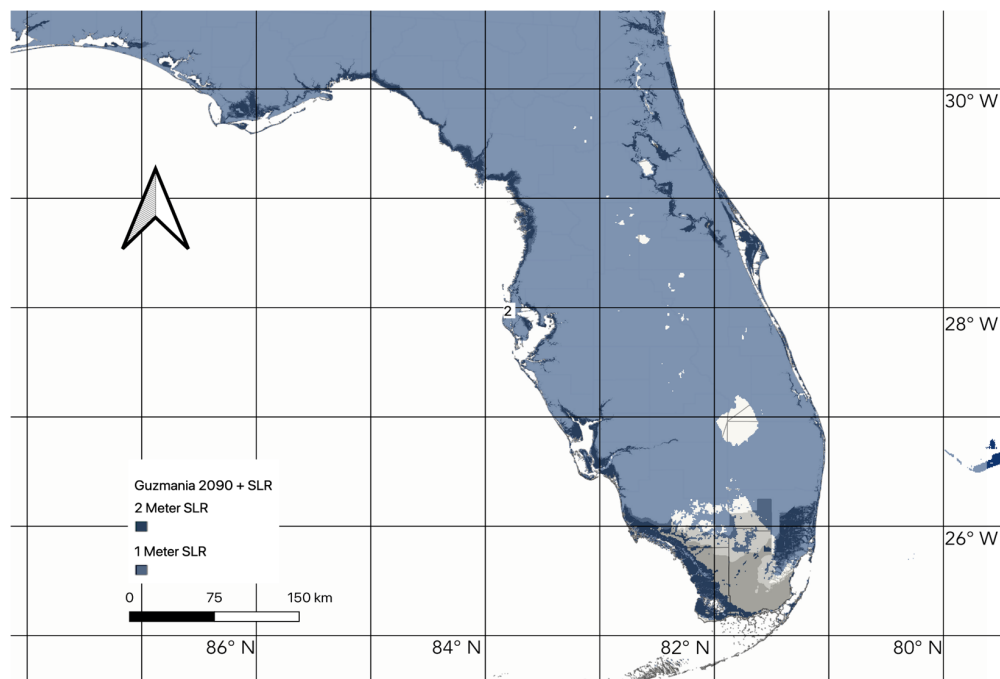**Figure 4.** Representation of 90% thresholded species distribution models of *Guzmania monostachia* and sea level rise model in Florida for the present day (**a**), 2090 with 1 m of sea level rise (**b**), and 2090 with 2 m of sea level rise (**c**). Areas in blue represent areas that contain habitat which is at least 90% suitable. Areas submerged by 1 m sea level rise are represented by the overlying darker color (dark blue over suitable habitat).

Without accounting for sea level rise, our models predict that *G. monostachia* would lose only 3% of its suitable habitat in South Florida (516.33 km² of habitat with at least 90% suitability) between the present day and 2090. These habitat losses are projected to occur mostly along the southwest coast. However, under a projected sea level rise of 1 m for

the same time period, *G. monostachia* is expected to lose roughly 25% of its suitable habitat (4542.24 km^2 of habitat with at least 90% suitability, Figure 4b), which is focused along mainly the southwestern Florida coast and areas west of the Miami Rock Ridge. With 2 m of sea level rise, the projected loss of suitable habitat increases to almost 40% (6861.34 km^2 of habitat with at least 90% suitability, Figure 4c), with almost the entirety of the Southern tip of Florida submerged. When we extend the area of our model to include all of Florida (Figure 5), rather than just the southern portion where *G. monostachia* currently occurs, we project that nearly all of Florida would be expected to harbor a suitable habitat by 2090, with a northward expansion.

Figure 5. Representation of 90% thresholded species distribution models of *Guzmania monostachia* and sea level rise model for 2090 with the model area expanded to cover all of Florida. Areas in blue represent areas that contain habitat which is at least 90% suitable. Areas submerged by 1 and 2 m sea level rise are represented by the overlying darker color (progressively darker blue over suitable habitat).

4. Discussion

4.1. Habitat Suitability in the Future under Climate Change

The amount of suitable habitat for *Guzmania monostachia* in Florida has changed, and it will continue to shift over time with future changes in climate. However, climate-related transitions and habitat losses may be inconsequential relative to other anthropogenic factors.

The only overall gain of habitat in Florida occurred between the Mid-Holocene and present day, with suitable habitat gained primarily in the central portion of southern Florida, with small amounts of suitable habitat lost in the Everglades (Figure 3). In comparison with changes that occurred in the past, the total amount of suitable habitat is projected to decrease small amounts from the present day to 2090, although the Everglades remain a distinct area marked by substantial habitat loss in both. Currently, the small suitable area in the Everglades is disjunct from the remainder of the available *G. monostachia* habitat, and the population there is already struggling, consisting of only three individuals. According to our projections, this disjunct habitat may be reduced to roughly half its current area by 2090, although it is expected to become less isolated as areas of additional suitable habitat become available in Southeast Florida (Figure 4). Alterations to hydrology are likely to drive major losses in the Everglades. The region is expected to experience decreases in

mean annual precipitation, which will have a profound negative impact on its wetland vegetative communities [21]. However, based on climate alone, large amounts of suitable habitat for *G. monostachia* are expected to remain throughout South Florida.

When sea level rise is incorporated into our predictions, the scenarios for *G. monostachia* become bleaker. Under a prediction of 1 m of sea level rise, large areas of suitable habitat, especially on the west coast, are expected to retreat under water by 2090 (Figure 4b), making this region, which currently harbors 3 of the 6 known populations, inhospitable for *G. monostachia.* Under our worst-case scenario prediction of 2 m of sea level rise, nearly all of the southern tip of Florida will be submerged by 2090, resulting in a 40% reduction of suitable habitat (Figure 4c) and the loss of 5 of the 6 populations known today, the habitats of which will become submerged.

Based on our ENM that considers the entirety of Florida (Figure 5), nearly all of the state is predicted to harbor suitable habitat by 2090. This extensive northward range expansion suggests that a warmer climate will not negatively impact the persistence of *G. monostachia* in Florida. Conversely, it may facilitate northern migration. It is important to temper expectations on this front, however, especially since projecting an ENM onto geographic areas distant from the occurrence point data used in training the model could result in an overestimation of habitat suitability [67]. Our MESS analysis shows some moderate levels of model extrapolation in northern areas of the Florida peninsula (Figures S2 and S3), indicating that the model over-projects the likelihood of suitable habitat in some of this large area.

Our ENM for the current distribution shows large continuous areas of suitable habitat for *G. monostachia* in South Florida (Figure 4a), while known populations currently occupy only a few small, disjunct areas in this region (Figure 2). Our results demonstrate that, while ENMs are useful forecasting tools, they often fail to account for additional factors that impact habitat suitability, especially those related to regional human activity [68,69]. Despite the presence of suitable soil and climatic conditions, many areas of suitable habitat in Florida identified by our ENMs are unlikely to represent suitable habitats currently or in the future. For example, our 2090 projections show a hotspot of suitable habitat aligning with the existing Miami Metropolitan area. While *G. monostachia* currently exists in at least one preserve and formerly occurred in others within this large, densely populated urban area, there are seemingly no (or at least very few) truly suitable habitats remaining outside of the existing protected areas. Given population declines within these small preserves, it may be unreasonable to assume that any suitable habitat will remain in the Miami Metropolitan area into the foreseeable future. Thus, we caution against direct interpretations of ENM results concerning already urbanized or rapidly developing areas; other factors such as rates of population growth and land use changes impacting the area must be considered for a realistic view of habitat suitability (Figure 6).

In Figure 6a, areas in blue represent areas that contain habitat which is at least 90% suitable. Areas submerged by 1 m sea level rise are represented by the overlying darker color (dark blue over suitable habitat). In Figure 6b, white points are populations that are still present. Yellow points are populations that have been extirpated. Areas in green are natural lands. Areas in orange are agricultural lands. Areas in light red are rural areas. Areas in dark red are urbanized areas. Map constructed by using data from the Florida Cooperative Land Cover Map version 3.5. Population identifiers: Fuchs Hammock (FU), Meissner Hammock (ME), Timms Hammock (TI), Silver Palm Hammock (SP).
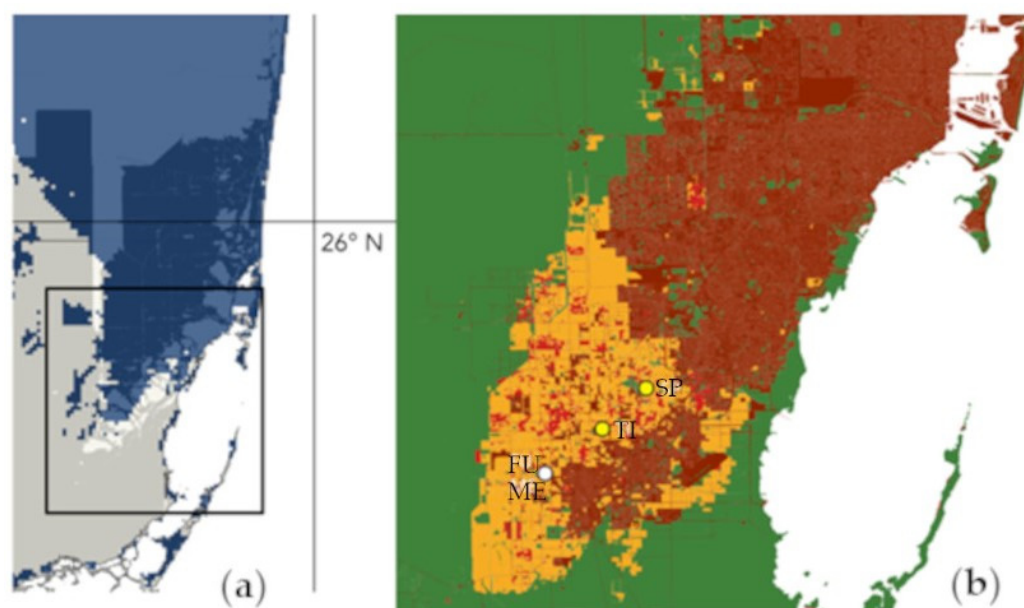
Figure 6. A comparison projected suitable habitat in 2090 for *Guzmania monostachia* in SE Florida assuming a 2 m sea level rise (**a**) versus where populations of the species have currently and previously been found in Miami-Dade County (**b**).

Another challenge in modeling *G. monostachia* is its epiphytic habit. Variables such as soil composition, which are frequently incorporated into ENMs for terrestrial plants, do not directly determine suitable habitat for epiphytes, but rather reflect the suitable habitats of their host plant species. Many epiphytic species, including *G. monostachia*, show some degree of host and environmental specificity [46,70]. While host species data may (in certain cases) prove informative for epiphyte-focused ENMs, studies have been successfully performed without them [71]. In our case, host tree species data were not included because of dramatic differences in host tree species distribution ranges relative to that of *G. monostachia*. For example, one preferred host, *Fraxinus caroliniana* Mill., occurs throughout the southeastern United States and as far north as southern Virginia [72], while *G. monostachia* does not occur outside of South Florida. In this case, inclusion of this host tree distribution data would contribute to an overestimation of suitable habitats for the focal species, which is notably less tolerant of temperate climatic conditions.

4.2. Implications for Conservation and Future Steps

Projecting ENMs onto future climate scenarios provides useful information for conservation efforts, particularly in the face of climate change. Investing considerable effort and resources into preservation activities in areas that may not support species in the future could prove counterproductive and wasteful. Based on the use of ENMs and the predicted impacts of climate change, conservationists can instead focus on preserving areas and populations that are likely to persist into the foreseeable future. For example, the ENMs shown here for *G. monostachia* can inform future conservation efforts by highlighting specific populations and areas of suitable habitat that will persist above sea level as climate change progresses over the next century. Additionally, future research might also consider species interactions between *M. callizona* and *G. monostachia* and utilize a joint SDM to identify potential areas where their projected distributions do not overlap. These non-overlapping areas may represent future safe havens for *G. monostachia*, particularly if they are also unaffected by SLR, and their preservation may prove beneficial to bromeliad-focused conservation efforts. In addition to climate change, anthropogenic impacts on environments must be taken into account when planning conservation efforts. The ongoing urban expansion in South Florida is likely to reduce or negatively impact remaining wetland environments throughout the region, but this variable is difficult to incorporate in

an ENM. Within the Miami Metropolitan Complex, many of the disjunct rockland hammocks along the Miami Rock Ridge exist today as preserved lands. Records indicate that *G. monostachia* historically occurred in four of these preserved areas; however, despite their protected status, populations are reportedly extirpated from two. The remaining hammocks, Fuchs Hammock and Meissner Hammock, are contiguous preserves that form a single small area, but populations of *G. monostachia* in both are in steep decline. Dwindling plant numbers in these small forest fragments suggest that the preservation of small pockets of habitat is an ineffective conservation strategy for *G. monostachia*. Small forest fragments are known to suffer from edge effects that can negatively affect the microclimate or host-related requirements of many epiphytes, resulting in biodiversity loss [73]. Large preserves are more resilient to edge effects, particularly with increasing distance into their interiors. Perhaps this is why the largest and most robust populations of *G. monostachia* are found within Fakahatchee Strand and Big Cypress Preserves, which have large contiguous areas of suitable habitat. This could also explain the dismal state of the population within Everglades National Park. While the park itself is a large preserve, the rockland hammocks that provide suitable habitat for *G. monostachia* are small and fragmented. The hammock that holds the only known population of *G. monostachia* in the Everglades is only 140 m in diameter and is surrounded by dry, sparsely forested pine rockland and prairie ecosystems [74].

Our ENM results suggest *G. monostachia* will not be further imperiled by the changing climate in Florida. Instead, sea level rise and human urban expansion represent the main threats to remaining populations, and conservationists should carefully consider both as part of future strategies, plans, or actions. In situ conservation efforts should focus on surviving populations occurring at elevations greater than 2 m above sea level, while ex situ conservation should be undertaken for both populations at lower elevations and those threatened by urban encroachment. The Fairchild Tropical Botanic Garden (FTBG) has already begun ex situ conservation efforts for *G. monostachia* from Fuchs and Meissner Hammock Preserves, respectively, due to the marked decline of these populations [75,76], and other botanical gardens and institutions in South Florida have been encouraged to implement a similar approach. Other opportunities for ex situ conservation might be undertaken by hobby bromeliad growers and collectors. Bromeliads are charismatic and visually striking plants that are coveted by a large community of growers and collectors worldwide, particularly in Florida, where production by the ornamental bromeliad industry generates an estimated $20 million annually [77]. Furthermore, private gardens represent additional venues for ex situ conservation [78]. For example, efforts such as the FTBG-led Million Orchid Project [79] include re-introducing imperiled native orchids into public and private landscapes in population-dense areas of South Florida, and this initiative may serve as a programmatic model for the community-driven conservation of *G. monostachia* and other bromeliads native to Florida.

Our ENMs show that suitable habitat for *G. monostachia* will extend northward beyond its current range; therefore, a future conservation measure might involve transplanting individuals within preserved areas in Central or even North Florida, where they would be less affected by sea level rise and urban development. This conservation strategy is known as assisted migration, and it has been a contentious subject among conservationists [80,81]. General arguments against assisted migration focus on the possible unintended consequences of translocating species—for example, the possibility for invasiveness, impacts to native organisms in areas of introduction, or loss of genetic diversity. However, cases cited in the debate involve translocation over long or even intercontinental ranges [82,83]. *Guzmania monostachia* could be a model candidate for assisted migration based on available implementation guidelines [84–86]. Its current population fragmentation pattern, large area of existing suitable habitat outside its current range, potential for short-distance translocation, and potentially high transplantation success rate [84] suggest that assisted migration may be a viable conservation approach for *G. monostachia*, pending financial feasibility.

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