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Research Article

A Historical Floristic Inventory of Pine Rockland Fabaceae (Leguminosae)

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ABSTRACT

The pine rocklands of southern Florida are an imperiled habitat as the higher, drier areas of land have been steadily developed over the last century. Little of the original extent of this unique ecosystem remains today, with much of it in remnant fragments affected by surrounding development. With this study, we sought to investigate temporal changes in diversity of pine rockland Fabaceae induced by anthropogenic factors. We provide a status update for Fabaceae taxa, a diverse and important group of plants in pine rocklands. Herbarium collections (1339 records) spanning 175 y (from 1830 to 2015) were used to analyze the species frequency and richness of plants collected. The results indicated temporal fluctuations in collection diversity with frequency of native species highest prior to the year 1920, and nonnative legume richness increasing with the decades. The accompanying species list resulting from the inventory included 119 Fabaceae species, in 52 genera, with an additional 18 species not previously listed for pine rocklands. Many other studies have documented the change in pine rockland cover and its extreme extent of habitat loss and fragmentation as the result of human development and population growth. The results of this study document the indirect effects of human habitation on remnant natural areas, as evidenced by collections from Miami-Dade County, with exotic invasives increasingly represented over time. The results also document the historical distributions of collections of Fabaceae species, helpful to conservation and restoration efforts in the globally imperiled pine rocklands of southern Florida.

Index terms: Fabaceae; flowers; herbaria; introduced species; legumes; native flora; pine rocklands; plant collectors

INTRODUCTION

Major issues affecting landscapes of developing countries have been the conversion of natural habitats into urban and agricultural land. According to the U.N. Food and Agriculture Organization, ~18 million acres of natural land are deforested for agricultural use every year. Urban areas, land purposed for residential and commercial use, contain 54% of the world's population (WHO); in the United States it is 80%. The resulting effects of urban development vary, with the most direct and immediate effect being habitat loss. Habitat loss resulting from urban development is considered especially harmful to natural areas, as it causes more drastic changes than land converted for agricultural use. Other documented effects of land conversion include changes to biogeochemical cycles, hydrology, changes to plant–animal interactions, and an increase of exotic species (Knapp et al. 2010). Exotic species, mainly sourced from the horticulture and landscape market (Pemberton and Liu 2009), contribute to the biotic homogenization of natural areas (Knapp et al. 2010).

The pine rocklands are a unique feature of natural southern Florida that has been a target of change and development in the region. The history of development in South Florida is relatively recent compared to elsewhere in the United States. Development occurred in a short and rapid amount of time, catalyzed by Flagler's extension of the railroad in 1896 to the bottom of the Florida peninsula (Gallagher 2003), and subsequently to Key West in the early 1900s. The region remained mostly wilderness until the late 1890s (Munroe and Gilpin 1930; Peters 1984).

Today most of the remaining and more intact pinelands are located (Figure 1) inside of protected areas in Everglades National Park (Miami-Dade County), Big Cypress (Collier County), and Key Deer National Refuge in Big Pine Key (Monroe County). Outside of protected areas, many small fragments of the pine rocklands remain, parts of a former continuum now severely fragmented due to anthropogenic habitat eradication (Shaw 2009). Despite the long-term issues brought about by urbanization and agriculture, there have not been many studies detailing these effects on local flora over long periods of time.

Here we analyze the anthropogenic effects on pine rockland Fabaceae over 100+ y. The methods involve the use of historical data stemming from herbarium specimens along with accompanying archival records. Specimens provide information and are used as reference for species verification and taxonomic studies (Lavoie 2013), serve as historical evidence of the existence of species, and may also be used to analyze biodiversity via historical floristic assessments (Chocholoušková and Pyšek 2003; Dolan et al. 2011; James et al. 2018). They have been used to study the history of colonization by exotic species, patterns of invasiveness, and climate change (Nualart et al. 2017). Fuentes et al. (2008) traced the spread of invasive species to colonization and periods of intense agriculture in Chile using herbarium collections, and changes in Boston flora induced by climate change were revealed using herbarium records dating back to 1885 (Primack et al. 2004), as well as in other parts of the world

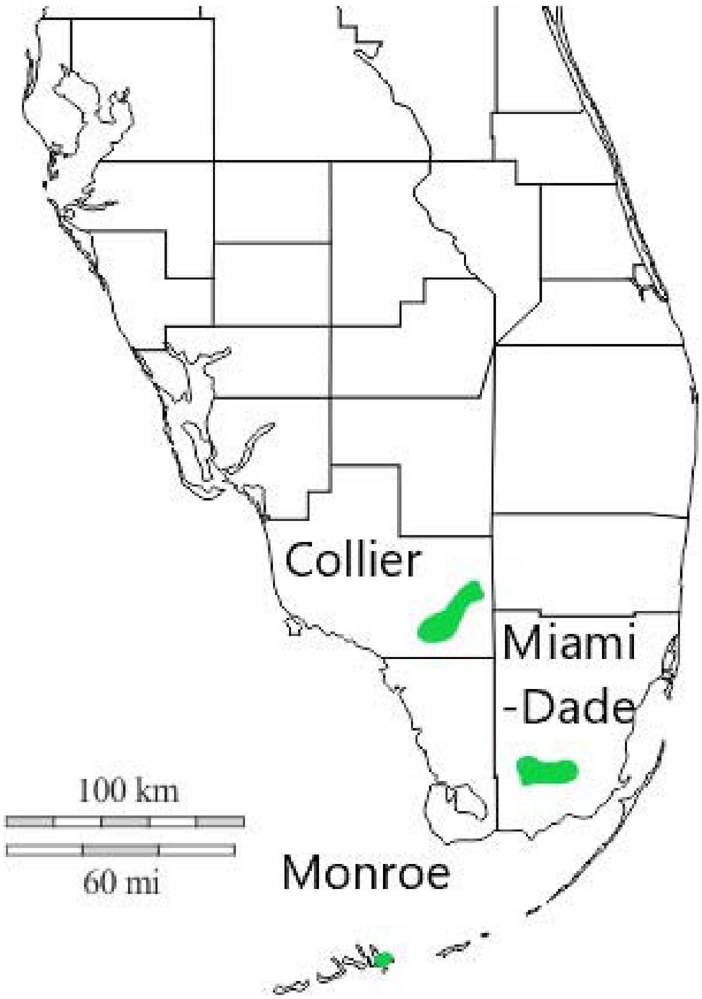

Figure 1.—Map of southern Florida with the three counties in which pine rockland is found. The shaded areas indicate the approximate areas in which pine rockland remains. (Figure after Snyder et al. 1990.)

(Willis et al. 2017). There is much untapped potential in collections for global change biology (Meineke et al. 2018).

We conducted a historical floristic inventory of pine rockland Fabaceae to examine changes in the flora due to human influences over the last centuries. We chose to focus on Fabaceae because they are a large, globally important family and are well represented in pine rocklands. We asked (1) Were native taxa represented evenly over the decades that botanists collected in pine rocklands? (2) Are extinctions and introductions detectable, and how many? (3) Did the proportion of nonnative species increase over time, and can this be correlated with human population growth? and (4) Can historical herbarium data be used to portray changes in natural habitats over time?

METHODS

Study Community

Characteristics of the pine rockland community include a rocky limestone substrate, which supports *Pinus elliotti* var. *densa* Little & Dorman (slash pine) as the dominant canopy species, along with a diverse understory (Snyder et al. 1990). Approximately 556 species are documented for the pine rocklands (Gann et al. 2001, 2019), of which 31 are endemic to Florida (Powell and Maschinski 2012). Pine rocklands are a fire-successional habitat strongly associated with rockland hammock communities, as pine rocklands can succeed into hardwood hammocks if not maintained by fire (Snyder et al. 2005). Naturally occurring transverse drainages mark the physiography of pine rocklands (Possley et al. 2018), making prairies (finger glades) and mangroves the two other associated communities bordering pine rocklands particularly within Everglades National Park (ENP) and in the Florida Keys (Snyder et al. 1990; Lodge 2010). The implication of this mosaic is some overlap in vegetation and associated species with these adjacent habitats.

The Study Organisms: Family Fabaceae

Fabaceae are the third largest family of flowering plants, encompassing 770 genera and ~19,500 species worldwide (Azani et al. 2017; Christenhusz et al. 2017).Traditionally, the family was split into 3 subfamilies: Caesalpinioideae, Mimosoideae, and Faboideae (Papilionoideae), based on floral morphology. At the writing of this paper, the latest phylogenetic updates have now split the family into six subfamilies (Azani et al. 2017), based on molecular data and morphological characteristics. In terms of South Florida pine rocklands, only *Bauhinia* and *Tamarindus*, both exotic genera, fall into the new Cercidoideae and Detarioideae, respectively. All native pine rockland genera currently belong to either Caesalpinioideae (including the mimosoid clade) or Faboideae.

Data Collection

We compiled a preliminary list of Fabaceae species (Figure 2) previously recorded for the pine rocklands using several sources: *Vascular Flora of the Southeastern United States: Leguminosae* (Isley 1990), *Guide to the Vascular Plants of Florida, 3rd Edition* (Wunderlin and Hansen 2011), and The Floristic Inventory of South Florida Database Online (http://www.regionalconservation.org/ircs/database/database.asp). Next, we conducted an inventory targeting Fabaceae collections originating in the geographic areas of known historical distribution of pine rocklands: Miami-Dade, Monroe, and Collier counties (Appendix A), using both physical and online databases (Appendix B). Data recorded for each specimen were species name, habitat, county, year collected, and collector, using the label data included with each specimen. Locality and habitat data on the labels were assumed to be correct, so our data included only those specimens originating from the historical distribution of pine rocklands, collectors who identified the habitat as pine rockland, or those who included a general habitat description along with a known locality (Figure 3). Species nomenclature was determined using Wunderlin and Hansen (2011), The Plant List (http://www.theplantlist.org), International Legume Database Information System (https://www.ildis.org), and the Integrated Taxonomic Information System (https://www.itis.gov).

The Florida Exotic Pest Plant Council's invasive species list was used to verify invasive status. The Endangered Species Act (ESA), published by the U.S. Fish and Wildlife Service, was used to determine federal and state conservation status, and the International Union for Conservation of Nature (IUCN) for Red

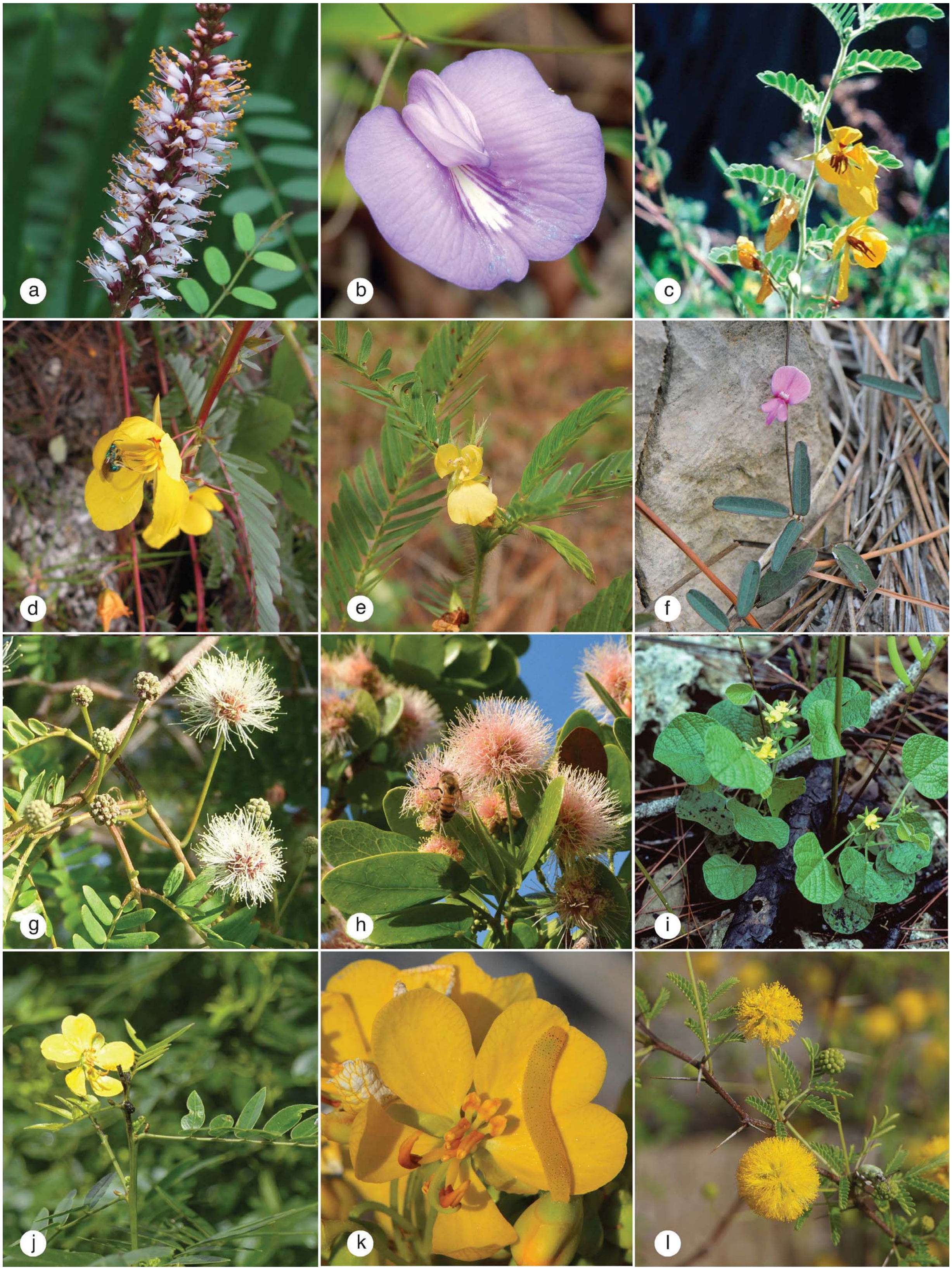

Figure 2.—Some Fabaceae of pine rocklands: (a) *Amorpha crenulata*, (b) *Centrosema virginiana*, (c) *Chamaecrista lineata* var. *keyensis*, (d) *C. deeringiana*, (e) *C. nictitans*, (f) *Galactia parvifolia*, (g) *Lysiloma latisiliquum*, (h) *Pithecellobium keyense*, (i) *Rhynchosia reniformis*, (j) *Senna ligustrina*, (k) *S. mexicana* var. *chapmannii*, (l) *Vachellia pinetorum*. (Photo credits: Brittany M. Harris – f, h, k; Hipolito Paulino Neto – d; Maria Cleopatra Pimienta – b; James R. Snyder e, g, i; A. Peña – l; S. Koptur – a, c, j.)

Figure 3.—Representative herbarium specimens of some pine rockland Fabaceae (location abbreviations from Index Herbariorum): (a) *Centrosema virginiana* specimen collected by J.K. Small and P. Wilson 1904; (b) *Chamaecrista deeringiana* collected by J.K. Small and P. Wilson 1904; (c) *Galactia parvifolia* collected by A.H. Curtiss 1896; (d) *Lysiloma latisiliquum* collected by D.B. Ward with R.K. Godfrey and D. Burch, 1964; (e) *Rhynchosia reniformis* collected by J.K. Small and C.A. Mosier, 1915; (f) *Vachellia farnesiana* var. *pinetorum* collected by J.K. Small and P. Wilson, 1904. These images belong to the C.V. Starr Virtual Herbarium (a, b, e, f) (http://sciweb.nybg.org/VirtualHerbarium.asp); the Digital Collection of the Harvard University Herbaria (c); and the University of Florida Herbarium (FLAS), Florida Museum of Natural History (d), image by Kathy M. Davis. All are reproduced here with permission.

List status. South Florida human population data were obtained from records published by the U.S. Census Bureau.

Collectors create biases in plant collections, over-sampling rare things and under-sampling common ones. These tendencies may have changed over time, but we hypothesize that a temporal comparison of collections over the decades will be informative in answering the questions posed.

Data Analysis

For each of the first-named collectors, we totaled the number of specimens they collected and the number of species represented in their collections, and plotted one against the other to see if a correlation exists between collection size and number of species collected. For each decade, we compared the number of specimens collected of native species vs. nonnative species. As the numbers of specimens differed over the decades, we also plotted the percent of nonnative vs. native specimens collected. We also compared the number of species (native and nonnative) collected each decade. We performed correlations and regression analyses to detect any significant relationships between human population size and these data.

To compare collection richness over the decades, we used EstimateS (Colwell 2013), including only the decades that had more than 10 specimens collected. Though some decades had collections in excess of 200 specimens (Supplemental Appendix C), we plot only 200 individuals for comparison of the number of individuals vs. the number of species collected. As the confidence intervals of all decades overlapped, we only plot the estimates so they can be more clearly discerned.

We also compared diversity measures of collections made each decade to determine species richness (S) of the collections made for each of the areas (counties) considered. Shannon's diversity index was calculated for each decade using the formula

$$H = \sum_{i=1}^{S} (P_i * \ln P_i)$$

where H is Shannon's diversity index, S is the total number of species in the community, and P_i is the proportion of S made up of the *i*th species.

Shannon's equitability index was calculated using the formula

$$E_H = H/H_{max} = H/\ln S$$

where E_H is the index of evenness or equitability, determined by dividing H by H_{max} (here assumed to be the natural log of the total number of species, lnS).

We consider proportional collection frequency (PCF) for each species: the number of specimens collected in a decade in proportion to all collected specimens in that time period. PCF = number of specimens of species *x* / number of specimens of all species collected.

Data, analyses, and Appendices not included here will be archived in the FIU Research Data Portal (https://doi.org/10.34703/gzx1-9v95/8E8CL1).

RESULTS

A total of 1339 records were used in our analysis, with specimens spanning years from 1830 through 2015. Collections made in Miami-Dade County comprised 73% of the specimens, Monroe County 26%, and Collier County less than 1%. These differences correspond, in relative order, to the original extent of pine rockland in each of those counties (Figure 1). The number of collectors was large, but most of them collected only one or a few specimens of pine rockland Fabaceae (Figure 4a). Similarly, most collectors collected relatively few of the Fabaceae species (Figure 4b). A collector who collected a single specimen collected only one species, but the number of species per collector was correlated with the number of specimens collected ($r^2 = 0.8407$; Figure 4c).

The number of specimens collected each decade can be divided into native and nonnative taxa (Figure 5a). While collection numbers differed widely among decades, the proportion of nonnative plants collected increased over time (Figure 5b), as did human population in the area (Figure 5c). Rarefaction of the collection data by decade shows that the more specimens collected, the more species collected (Figure 6). As the confidence intervals of all decades overlapped substantially, we conclude that although collecting effort differed among the decades, collection species diversity was similar over the decades (Figure 6a, 6b).

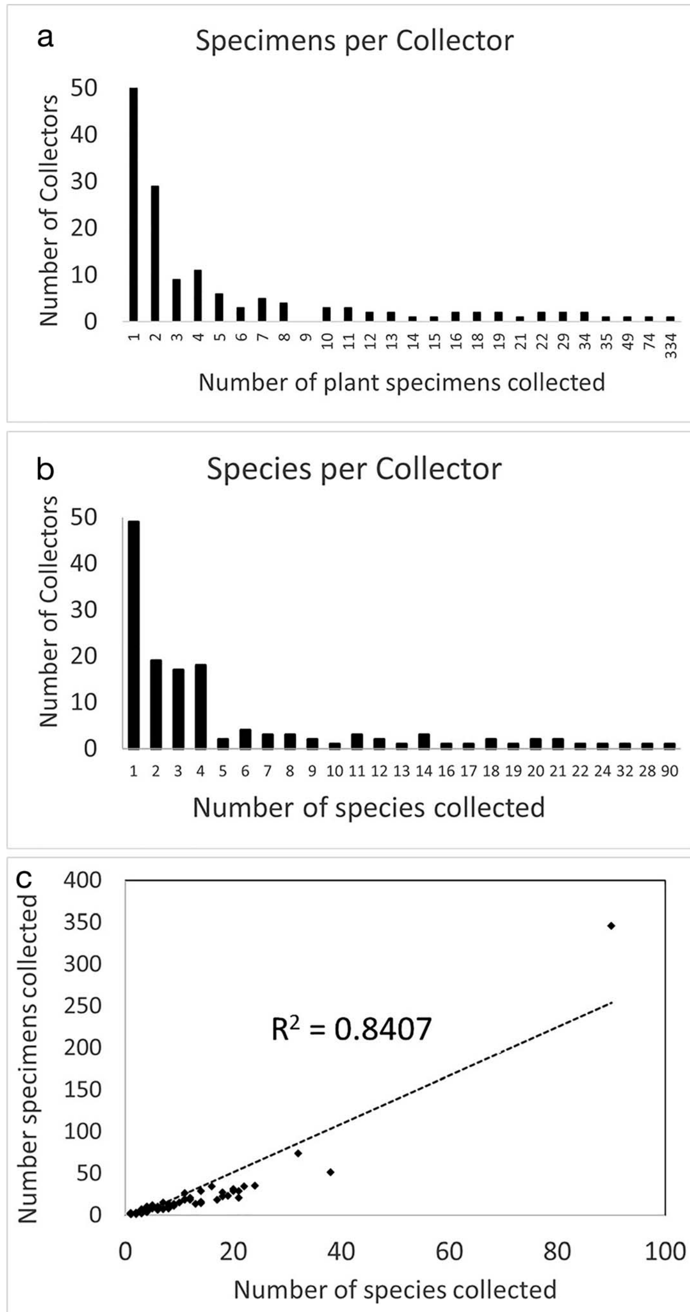

Figure 4.—Collectors and their collections: (a) number of collectors that collected each number of species of pine rockland Fabaceae over the decades in this study; (b) number of collectors that collected each number of total specimens, as above; (c) correlation of number of specimens collected and number of species collected for each collector.

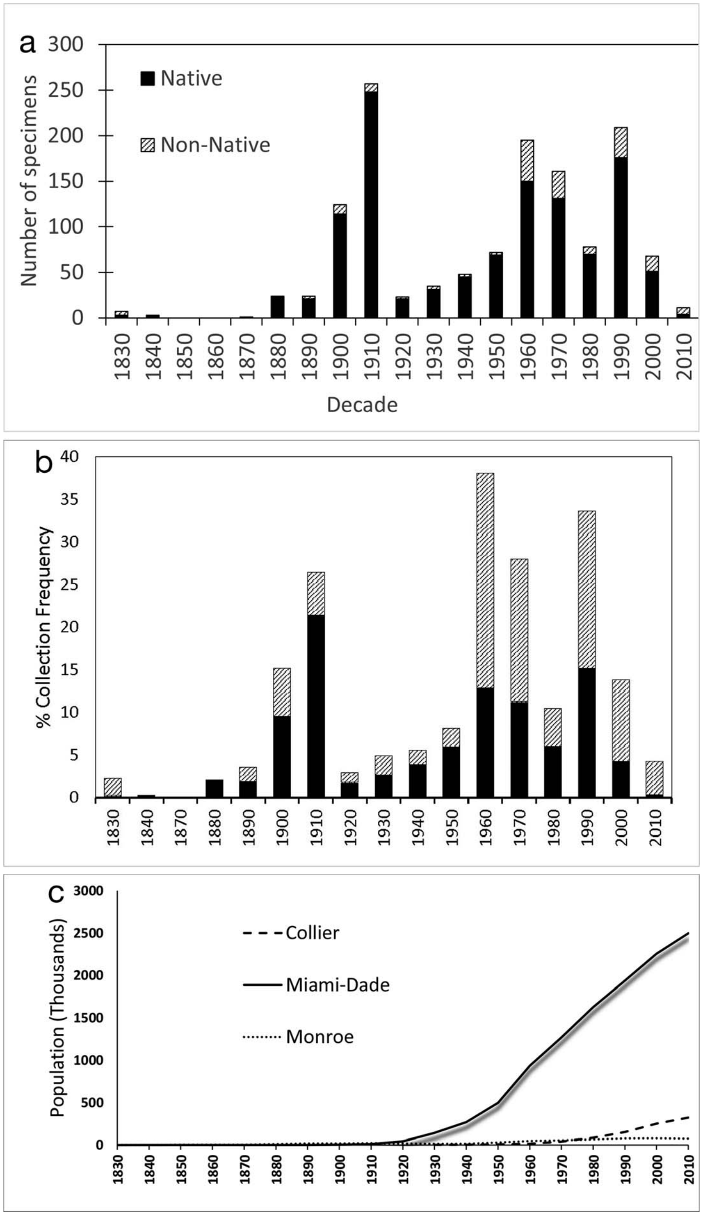

Figure 5.—Numbers of specimens and species collected each decade. (a) Number of specimens collected for all species for the decades of 1830–2010. Lower part of each bar is the specimens of native species; upper part of each bar, specimens of the nonnative. (b) Proportional Collection Frequency (PCF) for native and nonnative species for the decades of 1830–2010. (c) Human population increase for Miami-Dade, Monroe, and Collier counties for the decades of 1830–2010.

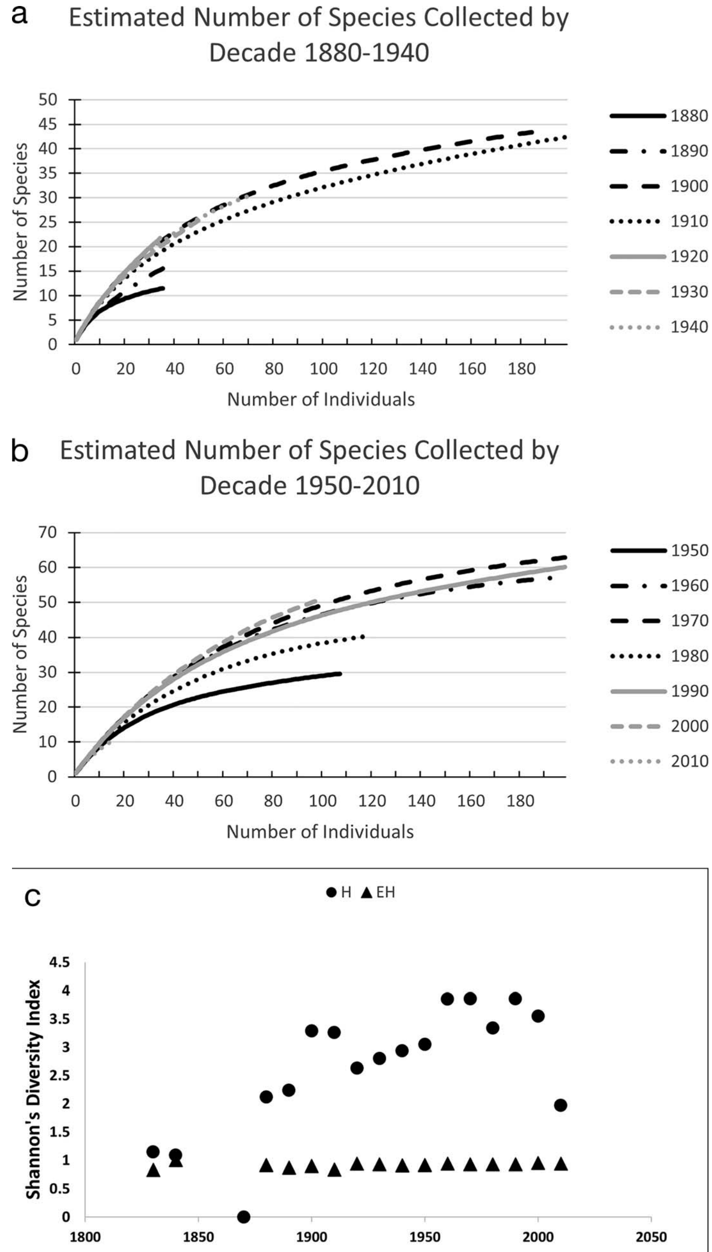

Figure 6.—Rarefaction curves for estimated number of species collected by decade (estimates of species numbers if collection sizes were equivalent over the decades) and diversity measures. (a) Decades of 1880–1940; (b) Decades of 1950–2010. Presented as two graphs so that lines may be discerned. Actual number of specimens collected each decade is shown in Table 2. (c) Diversity (H) and evenness (E_H) of collections over the decades.

The overall collection diversity, measured by Shannon's H, increases over time (Figure 6c), and is correlated with increasing human population in the three-county area in southern Florida ($P < 0.001$). The equitability index, E_H, remains constant (Figure 6c), showing relatively even collections, spread evenly over many species with respect to the number collected, over the decades, and is not related to population size ($P = 0.51$).

Major Collectors

The major collectors of specimens were mainly involved in making records of flora composition. The botanist collecting the most Fabaceae specimens from the period 1900–1920 was John K. Small, coauthor of *Flora of the Southeastern United States* (Small and Rydberg 1913), revised in 1933. Most of the 1960s specimens were collected by Olga K. Lakela of the USF herbarium, where she coauthored the *Flora of Tropical Florida* (Long and Lakela 1971). Donovan S. Correll collected the most pine rockland Fabaceae in the 1970s. In the 1990s, Keith Bradley was the major collector while he contributed to the Institute for Regional Conservation (IRC) Floristic Inventory.

Table 1.—Summary of the overall collection patterns for native species. The most collected species have the LARGEST total number of specimens. Species collected 10 decades or more have collection records of 100 y or more.

Most collected	Collected ≥10 decades	Decreasing PCF	Increasing PCF
Chamaecrista lineata var. *keyensis*	*Chamaecrista fasciculata*	*Dalea carthagenensis* var. *floridana*	*Crotolaria pumila*
		Indigofera miniata	*Desmodium lineatum*
Crotalaria rotundifolia	*Chamaecrista lineata* var. *keyensis*	*Neptunia pubescens*	*Stylosanthes hamata*
Indigofera miniata	*Chamaecrista nictitans* var. *aspera*	*Rhyncosia reniformis*	*Galactii smallii*
Rhynchosia reniformis	*Crotalaria pumila*	*Senna ligustrina*	
	Crotalaria rotundifolia	*Neptunia pubescens*	
	Neptunia pubescens		
	Rhynchosia cinera		
	Rhynchosia minima		
	Rhynchosia reniformis		
	Senna mexicana var. *chapmanii*		

Collection Frequency

The proportional collection frequencies (PCFs) were highest for all species (Supplemental Appendix D) in the decades beginning in 1910, 1960, 1970, and 1990. PCF for native plant collections was highest in 1910 and nonnative PCF was highest in 1960 (Figure 5b). The most collected species (those represented by the greatest number of specimens) and the most consistently collected (10 or more decades of collections) are a relatively small subset of all the species in the family. The species with the highest frequency of collections overall was the distinctive *Rhynchosia reniformis* DC. (Table 1, Figures 2i, 3e). Six species decreased in collection frequency over the decades of collections and four species increased in frequency (Table 1).

Human Population Growth

Human population statistics from the U.S. Census Bureau showed population for Miami-Dade and Collier counties increasing steadily over time, although Monroe county population fluctuated (Figure 5c). Miami-Dade County experienced exponential rates of change in population beginning with the 1880s and Monroe County's population increased drastically in the 1840s, declining later after major hurricanes. Human population in Collier County was very small before 1930 but has increased steadily as development has proceeded in southwest Florida.

Linear regression reveals a significant correlation between total human population size over the decades and the total number of species ($F = 7.1$, $P = 0.03$, $R^2 = 0.81$). The correlation is also significant with the number of native species collected ($F = 9.9$, $P = 0.015$), but not with the number of nonnative species ($F = 3.44$, $P = 0.11$). When we consider instead the increases and decreases of those species that are nonnative, there is a significant correlation with total human population size over the decades ($P = 0.006$), significant also for both Miami Dade ($P = 0.007$) and Monroe ($P < 0.001$) counties, but not Collier County ($P = 0.903$).

Table 2.—Post-inventory species list summary.

Total species	119
Genera	52
Native species	69
Exotic species	41
Invasive species	9
Extinct taxa	5
IUCN listed taxa	3
ESA listed taxa	5
Florida listed taxa	12

Species Summary

The resulting list from our inventory contained 119 species in 52 genera (Table 2; taxa are listed in Appendix A). This was 18 additional native and 32 additional nonnative species over what we originally anticipated (Supplemental Appendix E). Of specimens collected in Miami-Dade County, 87% were of nonnative species; for Monroe County, 12% were nonnatives species. No exotics were represented in specimens collected in Collier County. Miami-Dade County clearly displayed the majority of the invasive species from the collected specimens.

Fabaceae exotics found in pine rocklands originate from all over the globe, but most of the invasive legumes are from Asia. The first exotic Fabaceae was recorded in 1903 for Miami (*Crotolaria incana* L.), while for Monroe County it was in 1830 (*Caesalpinia pulcherrima* (L.) Sw.). Most were introduced from the horticultural market (Pemberton and Liu 2009). Two invasives come from the genus *Albizia*, and several from the genus *Crotalaria*.

Five legume species are currently listed as extinct or extirpated in the wild. *Chamaecrista deeringiana* Small and Pennell and *Galactia elliottii* Nutt. are no longer found in Monroe County; *Desmodium floridanum* Chapm. has disappeared from Collier County, and *Phaseolus polystachyus* var. *sinautus* (Nutt. ex Torr. & A. Gray) R. Marechal, J.M. Mascherpa & F. Stainier, and *Tephrosia angustissima* Shuttlew. ex Chapm. are gone from Miami-Dade County. Most of these extirpated taxa are Faboideae and were last recorded in the 1960s. As part of a reintroduction program, *T. angustissima* was introduced to Ludlam pineland preserve in 2003 and 2013, and as of 2016 a small population remains (Lange et al. 2017). Comments on additional species have been included in Supplemental Appendix F.

DISCUSSION

This study attempted to gauge temporal changes in biodiversity of pine rockland Fabaceae using herbarium data from 1330 specimens collected from 1830 to 2015. There were gaps in the collection, as no specimens were encountered from the decades of 1850 to 1870, and there were few collections from 1920 to 1960.

Overall, we found that the herbarium data displayed a positive relationship between legume species collection richness and human population size, significant also for the richness of native species, but not for nonnative species. However, the proportion of nonnative plant species in the collections increased with human population size. Patterns in richness are likely more indicative of collection effort, as the number of specimens and number of species are correlated. Specimen counts, as used in our study, have been found to be moderately accurate and specific in determining which species are not threatened, but less useful in predicting which species are threatened (Lughadha et al. 2018).

While results of this study are strongly related to collection effort, analyzing collection frequencies mitigates some bias in the data. Collection frequency can be correlated to frequency in nature, by highlighting gaps or patterns occurring over time (Hedenäs et al. 2002). In this study, some patterns emerge, with some species either increasing or decreasing in collections over time. Whether or not a species is collected is influenced by accessibility, while those species more difficult to collect are therefore underrepresented (Moerman and Estabrook 2006; Stolar and Nielsen 2015). It is widely accepted in ecology that habitat fragmentation leads to more edge habitat, and some species are more commonly found in such situations. For example, *Chamaecrista nicititans* var. *aspera* grows in somewhat disturbed sites, and so could be more common as a result of habitat fragmentation. *Crotolaria* spp. are often observed along pineland edges, and both *C. pumila* and *C. rotundifolia* are common species, as are most species belonging to the Faboideae subfamily. However, many of the most frequently collected species are not only found in many fragments around Miami-Dade (Gann et al. 2019), but also occur in various terrestrial habitats outside of pine rocklands and are widely distributed throughout the southern United States (Isley 1990; Wunderlin and Hansen 2011). Studies show there is an association between distribution and abundance (Brown 1984), which may also contribute to collection frequency for widespread species.

There are also characteristics that imply greater plant fitness and perhaps abundance. Some *Crotalaria* spp. have projectile seeds that are secondarily dispersed by ants (Stamp and Lucas 1990). Many pine rockland Fabaceae bear extrafloral nectaries (Koptur 1992) that may help increase reproductive fitness by attracting ants and other beneficial insects (Jones and Koptur 2015; Koptur et al. 2015). These characteristics may have contributed to the abundance and persistence of these species over time.

When a few individuals collect the majority of the specimens, their own interests and proclivities may also bias the collection (Daru et al. 2018; Panchen et al. 2019). The endangered *G. smallii* and *C. lineata* var. *keyensis* are currently listed but may have been more common in previous years. Herbarium-based studies indicate botanists tend to emphasize and over-collect rare flora (Garcillán and Ezcurra 2011; Lavoie 2013). In addition, *G. smallii* has been found to have a broad distribution in Miami-Dade pine rockland fragments (O'Brien 1998; Possley et al. 2008), in large part due to efficient conservation efforts on the part of local managers (Possley et al. 2018). There were, however, species whose collection frequency decreased over time. From this category, only *R. reniformis* and *D. carthagenensis* var. *floridana* are federally and state listed species (Appendix A). *Rhynchosia reniformis* occurs in pristine habitats, and so habitat change may explain its decrease in PCF over time.

Tephrosia chrysophylla (Appendix A) was not present in the collected data. According to Gann et al. (2002), *T. chrysophylla* was collected by Roy Woodbury in the Cutler and Ludlam pinelands in the 1940s but has not otherwise been found or listed for Miami-Dade. Perhaps *T. chrysophylla* may be a threatened species that has not been assessed as such or may be an example of spurious collections that complicate species status or historical presence when using herbarium specimens. Such a species, not already listed for conservation, would need to be examined further and surveyed in field sites to assess whether the decline in PCF, or absence in the herbarium data, is due to the species becoming increasingly rare or some taxonomic mistake.

The most striking pattern observed is the increased presence of nonnative species in the second half of the twentieth century (Supplemental Appendix E). While the earliest exotic recorded in the collection is from 1830, they increase with time, especially for Miami-Dade County. An increase in human population growth of 89%, almost doubling numbers of inhabitants from the previous decade in the county, was accompanied by an increase in development for agriculture, businesses, and housing. Human habitation has landscaping, and most exotics are a product of the horticulture industry, which brings in many nonnative species that escape cultivation (Reichard and White 2001; Pemberton and Liu 2009). Planted landscapes can provide connections among remnant natural habitat patches and facilitate spread of nonnative species (Angold et al. 2006; Haddad et al. 2014; Resasco et al. 2014). They may, however, serve as corridors for native plants and pollinators to move among remnant habitat patches (Damschen et al. 2019). There may also have been a concerted effort to collect exotic species during the later 1900s, although a study of collections from California found exotics to be under-collected in both Fabaceae and Asteraceae (Williams and Pearson 2019). Our inventory found George N. Avery to be the biggest collector of exotic Fabaceae, followed by Olga Lakela, and Keith Bradley. All these collectors compiled checklists of South Florida flora, and although we found no information about specific expeditions for the collection of nonnative species, it is possible that exotics are overrepresented because of collectors focusing on new occurrences. The increased collection frequencies of exotics may, however, be a result of the species spreading in natural and disturbed areas over time. Some studies suggest a lag time from introduction to invasion for woody species of 130–147 y (Niinemets and Peñuelas 2008). This theory is consistent with the time of introduction for most of the woody Fabaceae introduced before 1900 that have in turn become invasive.

Species Designated as Extirpated

Of the six legume species currently listed as extinct or extirpated in the wild, most are Faboideae. All were last seen or recorded in the 1960s.

Vachellia choriophylla (Benth.) Seigler & Ebinger (Mimosoideae) is considered extirpated in its native range in the Florida Keys. One record places it in ENP pine rocklands. IRC records claim the occurrence in Miami-Dade is the result of it being naturalized from cultivation. It was last collected in the 1960s.

Chamaecrista deeringiana (Caesalpinioideae) is listed as possibly extirpated in Monroe County. One historical specimen exists from Monroe from 1912 (Small), the only time it was recorded in that county. Both historical and modern records exist for the other counties, and it is still widespread in ENP.

Galactia elliottii (Faboideae) is presumed extirpated in Monroe-Keys and Collier, but not listed for Miami-Dade. We found a 1973 inventory record from Monroe. Assuming it was correctly identified, it could have potentially disappeared after that point.

Desmodium floridanum (Faboideae) is presumed extirpated in Collier County. There are both historical and recent records from Miami-Dade but none from Collier. While there are records of the species in other habitats in Collier in the 1960s and earlier, no records were found in rocky pinelands for Collier.

Phaseolus polystachyus var. *sinautus* (Faboideae) is assumed extirpated, last collected in 1913. All records for this taxon are historical.

Tephrosia angustissima (Faboideae) is now extinct in Miami-Dade. Listed as one of Florida's rare species endemic to pine rockland, it was last collected in 1968 (Avery) (Supplemental Appendix F).

CONCLUSION

This inventory provided a 175 y history of floristic exploration of pine rockland Fabaceae. We fully expected to see a decrease in plant species diversity in the collections accompanied by an increase in human population numbers, but this was not the case, as collecting activities were not consistent through time, and we saw only that the proportion of nonnative species increased with human population size. The size of pine rocklands in Miami-Dade County before major development was estimated at 185,000 acres, and by the 1990s only ~4400 acres remained (Maguire 1995). In 1955 surveys of the lower Florida Keys (Monroe County), pine rocklands covered 2592 acres of Big Pine Key, but by 1989 they covered only 1732 acres (Folk et al. 1991). Anthropogenic development was likely the major determinant of habitat loss for pine rocklands; in Miami-Dade County this occurred rapidly, in less than 100 y. This extreme reduction in the extent of pine rocklands is very likely responsible for the increase in nonnative taxa, as well as the listing of pine rockland taxa restricted to part of the extent of the original rocklands.

Habitat loss has large, negative effects on biodiversity (Fahrig 2003), and although many studies have been undertaken to measure the negative effects of habitat fragmentation on the diversity of biota, when considered at the landscape level ("per se," that is, the same amount of habitat in many pieces vs. larger chunks) fragmentation is not necessarily a bad thing (Fahrig 2017). A recent meta-analysis found that most landscape-level studies have shown no significant ill effects on species conservation (Fahrig et al. 2019), and those that were significant were mostly positive regarding species richness, occurrence, and abundance. However, a large group of prominent scientists have warned that those conclusions may be biased and should be interpreted with caution (Fletcher et al. 2018). Many species now live in degraded patches of fragmented habitat following habitat loss (Koper et al. 2010; Haddad et al. 2014); pine rockland fragments are often neglected and degraded, with exotic invasive plants encroaching from the edges and understory hardwoods taking over with lack of periodic fires (O'Brien 1998; Jones and Koptur 2017).

Smaller fragments are more likely to be invaded by nonnative species that results in decline in habitat quality (Koper et al. 2010). Some taxa show marked population declines and absence in smaller habitat fragments, especially if the matrix around remaining fragments is inhospitable to their dispersal and movements (Laurence et al. 2011). However, small reserves may be better, or appropriate, for certain targets (Schwartz 1999), and native plant populations in compromised landscapes can still contribute to biodiversity conservation, as well as make the public aware of imperiled flora and habitats (Lawson et al. 2008). As pine rocklands in south Florida were naturally somewhat fragmented, divided by transverse glades due to small differences in topography, some species may have been accustomed to persisting in relatively isolated populations in certain areas. Plants may persist in the absence of their animal mutualists for some time, as they grow from seed that may be present in the seed bank, and many have adaptations for self-pollination with or without pollinators. However, too many years without adequate gene exchange may lead to eventual decline of the populations as the fragmentation incurs an "extinction debt" (Tilman et al. 1994; Hanski and Ovaskainen 2002; Jamin et al. 2020; Loeffler et al. 2020), although a recent experiment has shown little ill effects of habitat fragmentation on select plants (Brudvig et al. 2015). Our findings that diversity of native species of pine rocklands did not decline is perhaps good news that demonstrates the maintenance of intact pine rockland habitat, even in mostly small fragments, has so far preserved most species endemic to this imperiled ecosystem.

The key findings of this study were that exotic invasive plants increased with time, as human population increased and pine rockland habitat disappeared beneath human development and agricultural land. While exotic invasives are harmful to local biodiversity and are an important threat to pine rocklands, they are a distant second to the drastic habitat loss and fragmentation that pine rocklands experienced over the last century. We found records of 18 native species not previously listed for the pine rocklands, providing evidence for species presence and the historical distribution of Fabaceae. The accompanying species list resulting from the inventory also contributes a needed review and status update for the Fabaceae of the region. We found that the overall frequency of collections fluctuated over time with some species exhibiting patterns that merit further examination through field surveys.

Herbaria are very useful for research if one is cognizant of the limitations, specifically when it comes to surveys. Researchers should be careful when using online databases and files as some may be incomplete or incorrectly catalogued, as we found to be the case in many instances. These errors were only revealed through physical inventory.

Conservation of pine rocklands and their rare endemic species remains an important current issue in environmental concerns of Florida. While natural areas managers improve habitats for rare pine rockland endemics in the remaining sites, without enough pine rockland habitat the persistence of these endemic taxa is precarious. Conservation of individual species is also important as habitat conservation becomes increasingly difficult. There are some *ex situ* efforts already underway with the help of local institutions, such as Fairchild Tropical Botanic Garden's "Connect to Protect" program. As South Florida has many green spaces outside natural areas, the exotic homogenization can also be mitigated on a local level by promoting landscaping with native plants from local gardens and native plant nurseries. Programs now exist to distribute native plants to residents and businesses in local neighborhoods (Powell and Maschinski 2012), and public education initiatives (Feinsinger et al. 1997; Caro et al. 2003) are using native plants to create schoolyard habitats and even restore pine rocklands on some school grounds. Future conservation efforts should focus on buying disturbed lots occurring in areas previously occupied by pine rocklands for restoration (PRWG 2020).

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Pine rockland art by Sandy Koi - skoi001@fiu.edu

APPENDIX A.—Species check list.

Name	Nativity	Common name	Synonyms	Status
Abrus precatorius L.	Invasive	Rosary pea	*Abrus abrus* (Linnaeus) W. Wight	
Acacia auriculiformis A. Cunn. ex Benth.	Invasive	Earleaf acacia	*Racosperma auriculiforme* A. Cunn. ex Benth	
Acacia angustissima (Mill.) Kuntze	Native	Prairie acacia	*Acaciella angustissima* (Mill.) Britton & Rose	FLA-E
Aeschynomene pratensis Small	Native	Meadow jointvetch	None	ESA-C, FLA-E
Aeschynomene viscidula Michx.	Native	Sticky jointvetch	*Secula viscidula* (Michaux) Small	
Albizia julibrissin Durazz.	Invasive	Silktree	*Acacia julibrissin* (Durazz.) Willd	
Albizia lebbeck (L.) Benth	Invasive	Woman's tongue	*Acacia lebbeck* (L.) Willdenow	
Albizia lebbekoides (DC.) Benth.	Exotic	Indian albizia	*Acacia lebbekoides* DC.	
Albizia procera (Roxb.) Benth.	Exotic	Tall albizia	*Acacia procera* (Roxb.) Willd	
Alysicarpus vaginalis (L.) DC.	Exotic	White moneywort	*Alysicarpus vaginalis* (L.) DC. var. *typicus* King	
Amorpha fruticosa L.	Native	Bastard false indigo	*Amorpha curtissii* Rydb.	
Amorpha herbacea var. *crenulata* (Rydb.) Isley	Endemic	Miami lead plant	*Amorpha crenulata* Rydb.	IUCN-CE, ESA-E, FLA-E
Bauhinia variegata L.	Invasive	Orchid tree	*Phanera variegata* (L.) Benth	
Caesalpinia pulcherrima (L.) Sw.	Exotic	Dwarf poinciana	*Poinciana pulcherrima* L.	
Cajanus cajan (L.) Huth	Exotic	Pigeonpea	*Cajanus flavus* DC.	
Canavalia brasiliensis Mart. ex Benth.	Exotic	Brazilian jackbean	*Canavalia caribaea* Urb.	
Canavalia rosea (Sw.) DC.	Native	Baybean	*Canavalia maritima* Thouars	
Cassia fistula L.	Exotic	Golden shower	*Bactyrilobium fistulum* Willd.	
Centrosema virginianum (L.) Benth.	Native	Spurred butterfly pea	*Bradburya virginiana* (L.) Kuntze	
Ceratonia siliqua L.	Exotic	Carob	None	
Chamaecrista deeringiana Small & Pennell	Native	Deering partridge pea	*Cassia deeringiana* (Pennell) J.F. Macbr.	
Chamaecrista fasciculata (Michx.) Greene	Native	Partridge pea	*Cassia chamaecrista* L.	
Chamaecrista lineata (Sw.) Greene var. *keyensis* (Pennell) H.S. Irwin & Barneby	Endemic	Keys partridge pea	*Cassia keyensis* (Pennell) J.F. Macbr.	ESA-E, FLA-E
Chamaecrista nictitans var. *aspera* (Muhl. ex Elliott) H.S. Irwin & Barneby	Native	Hairy sensitive pea	*Cassia simpsonii* Pollard	
Clitoria mariana L.	Native	Atlantic pigeonwings	*Clitoria mariana* (L.) var. *pubescentia* Fantz.	
Clitoria ternatea var. *ternatea* L.	Exotic	Asian pigeonwings	*Clitoria ternatea* L.	
Crotalaria incana L.	Exotic	Shakeshake	*Crotalaria pubescens* Moench	
Crotalaria pallida var. *obovata* (G. Don) Polhill	Exotic	Smooth rattlebox	*Crotolaria striata* DC.	
Crotalaria pumila Ortega	Native	Low rattlebox	*Crotalaria elliptica* Roxb.	
Crotalaria retusa L.	Exotic	Rattleweed	*Crotalaria retusa* var. *maritima* Trimen	
Crotalaria rotundifolia J.F. Gmel.	Native	Rabbitbells	*Crotalaria linaria* Small	
Crotalaria spectabilis Roth	Exotic	Showy rattlebox	*Crotalaria sericea* Retz.	
Crotalaria verrucosa L.	Exotic	Blue rattlebox	*Crotalaria flexuosa* Moench	
Dalbergia sissoo Roxb. ex DC.	Invasive	Indian rosewood	*Amerimnom sissoo* (Roxb.) Kuntze	
Dalea carnea (Michx.) Poir.	Native	Whitetassels	*Kuhnistera carnea* (Michx.) Kuntze	
Dalea carthagenensis var. *floridana* (Rydb.) Barneby	Endemic	Florida prairieclover	*Parosela floridana* Rydb.	ESA-C, FLA-E
Dalea feayi (Chapm.) Barneby	Native	Feay's prairieclover	*Kuhnishtera feayi* (Chapman) Nash	
Delonix regia (Bojer) Raf.	Exotic	Royal poinciana	*Poinciana regia* Bojer	
Denisophytum pauciflorum (Griseb.) Gagnon & G.P. Lewis	Native	Fewflower holdback	*Caesalpinia pauciflora* (Griseb.) C. Wright	FLA-E
Desmanthus virgatus (L.) Willd.	Native	Wild tantan	*Acacia agustisiliqua* (Lam.) Desf.	
Desmodium ciliare (Muhl. ex Willd.) DC.	Native	Hairy small-leaf ticktrefoil	*Meibomia ciliare* (Willd.) S.F. Blake	
Desmodium floridanum Chapm.	Native	Florida ticktrefoil	*Meibomia floridana* (Chapm.) Kuntze	
Desmodium incanum DC.	Native	Zarzabacoa	*Aeschynomene incana* (Sw.) G. Mey.	
Desmodium lineatum DC.	Native	Sand ticktrefoil	*Meibomia arenicola* Vail	
Desmodium marilandicum (L.) DC.	Native	Smooth ticktrefoil	*Meibomia marilandicum* (L.) DC.	
Desmodium rigidum (Elliott) DC.	Native	Stiff ticktrefoil	*Desmodium obtusum* (Muhl. ex Willd.) DC.	
Desmodium scorpiurus (Sw.) Desv.	Exotic	Scorpion ticktrefoil	*Hedysarum scorpiurus* Sw.	
Desmodium strictum (Pursh) DC.	Native	Pinebarren ticktrefoil	*Meibomia stricta* (Pursh) Kuntze	
Desmodium tortuosum (Sw.) DC.	Exotic	Dixie ticktrefoil	*Meibomia tortuosa* (Sw.) Kuntze	
Desmodium triflorum (L.) DC.	Exotic	Threeflower ticktrefoil	*Meibomia triflora* (L.) Kuntze	
Erythrina herbacea (L.)	Native	Coralbean	*Erythrina arborea* Small	
Galactia elliottii Nutt.	Native	Elliott's milkpea	None	
Galactia floridana Torr. & A. Gray	Native	Hairy milkpea	*Galactia fasciculata* Vail	
Galactia parvifolia A. Rich.	Native	Small leaf milkpea	*Galactia grisebachii* Urb.	
Galactia pinetorum Small	Endemic	Pinerockland milkpea	None	
Galactia regularis (L.) Britton, Sterns & Poggenb.	Native	Eastern milkpea	*Dolichos regularis* L.	
Galactia smallii H.J. Rogers ex Herndon	Endemic	Small's milkpea	*Galactia prostrata* Small	ESA-E, FLA-E
Galactia striata (Jacq.) Urb.	Native	Florida hammock milkpea	*Galactia spiciformis* Torrey & A. Gray	
Galactia volubilis (L.) Britton	Native	Downy mikpea	*Galactia macreei* M.A. Curtis	

APPENDIX A.—Continued.

Name	Nativity	Common name	Synonyms	Status
Guilandina bonduc L.	Native	Gray nicker	*Caesalpinia bonduc* (L.) Roxb.	
Indigofera caroliniana Mill.	Native	Carolina indigo	*Indigofera disperma* L.	
Indigofera hirsuta L.	Exotic	Hairy indigo	*Anila hirsuta* (L.) Kuntze	
Indigofera miniata Ortega	Native	Coastal indigo	*Indigofera miniata* var. *florida* Isely	
Indigofera spicata Forssk.	Exotic	Trailing indigo	*Anila spicata* (Forsskål) Kuntze	
Indigofera suffruticosa Mill.	Exotic	Anilde pasto	*Indigofera anil* L.	
Kummerowia striata (Thunb.) Schindl.	Exotic	Japanese clover	*Desmodium striatum* (Thunb.) DC.	
Leucaena leucocephala (Lam.) de Wit	Invasive	White leadtree	*Acacia leucocephala* (Lam.) Link	
Lysiloma latisiliquum (L.) Benth.	Native	Wild tamarind	*Acacia bahamensis* (Bentham) Grisebach	
Lysiloma sabicu Benth.	Exotic	Horseflesh mahogany	*Acacia formosa* Kunth	
Macroptilium gibbosifolium (Ortega) A. Delgado	Exotic	Wild bushbean	*Phaseolus heterophyllus* Willd.	
Macroptilium lathyroides (L.) Urb.	Invasive	Wild bushbean	*Phaseolus lathyroides* L.	
Melilotus albus Medik.	Exotic	White sweetclover	*Medicago alba* (Medikus) Krause	
Mimosa pudica L.	Exotic	Sensitive plant		
Mimosa quadrivalvis var. *angustata* (Torr. & A. Gray) Barneby	Native	Sensitive brier	*Mimosa horridula* Michx.	
Mucuna pruriens (L.) DC.	Exotic	Velvetbean	*Dolichos pruriens* L.	
Neptunia pubescens Benth.	Native	Tropical puff	*Neptunia floridana* Small	
Pachyrhizus erosus (L.) Urb.	Exotic	Yam bean	*Cacara erosa* L.	
Parkinsonia aculeata L.	Exotic	Jerusalem thorn	*Parkinsonia spinosa* Kunth	
Phaseolus lunatus L.	Exotic	Lima bean		
Phaseolus polystachios var. *sinuatus* (Nutt. ex Torr. & A. Gray) R. Marechal, J.M. Mascherpa & F. Stainier	Native	Thicket bean	*Phaseolus sinuatus* Nutt. ex Torr. & A. Gray	
Phaseolus vulgaris L.	Exotic	Kidney bean		
Piscidia piscipula (L.) Sarg.	Native	Fishpoison tree	*Piscidia erythrina* L.	
Pithecellobium bahamense Northrop	Native	Bahama blackbead	None	
Pithecellobium dulce (Roxb.) Benth.	Exotic	Monkeypod	*Mimosa dulcis* Roxb.	
Pithecellobium keyense Britton ex Britton & Rose	Native	Florida Keys blackbead	*Pithecellobium guadalupense* (Pers.) Chapm.	
Pueraria montana var. *lobata* (Willd.) Maesen & S.M. Almeida ex Sanjappa & Predeep	Invasive	Kudzu	*Dolichos lobatus* Willd.	
Rhynchosia cinerea Nash	Native	Brownhair snoutbean	*Dolicholus cinereus* (Nash) Vail	
Rhynchosia michauxii Vail	Native	Michaux's snoutbean	*Dolicholus michauxii* (Vail) Vail	
Rhynchosia minima (L.) DC.	Native	Least snoutbean	*Dolicholus minimus* (L.) Medikus	IUCN-LC
Rhynchosia parvifolia DC.	Native	Small leaf snoutbean	*Dolicholus parvifolium* (DC) Vail	
Rhynchosia reniformis DC.	Native	Dollarleaf	*Dolicholus simplicifolius* (Walter) Vail	FLA-T
Senna ligustrina (L.) H.S. Irwin & Barneby	Native	Privet wild sensitive plant	*Cassia bahamensis* Mill.	
Senna mexicana var. *chapmanii* (Isely) H.S. Irwin & Barneby	Native	Chapman's wild sensitive plant	*Cassia chapmanii* Isely	FLA-T
Senna obtusifolia (L.) H.S. Irwin & Barneby	Native	Coffeeweed	*Cassia obtusifolia* L.	
Senna occidentalis (L.) Link	Exotic	Septicweed	*Cassia occidentalis* (L.)	
Senna pendula var. *glabrata* (Vogel) H.S. Irwin & Barneby	Invasive	Valamuerto	*Cassia coluteoides* Collad.	
Senna surattensis (Burm.f.) H.S. Irwin & Barneby	Exotic	Glossy shower	*Cassia surattensis* Burman f.	
Sesbania herbacea (Mill.) McVaugh	Native	Danglepod	*Sesbania emerus* (Aubl.) Urb.	
Sesbania vesicaria (Jacq.) Elliott	Native	Bagpod	*Glottidium floridanum* (Willd.) DC.	
Sophora tomentosa L. var. *truncata* Torr. & A. Gray	Native	Yellow necklacepod	*Sophora tomentosa* L. subsp. *bahamensis* Yakovlev	
Stylosanthes biflora (L.) Britton et al.	Native	Sidebeak pencilflower	*Trifolium biflorum* L.	
Stylosanthes calcicola Small	Native	Everglades Key pencilflower	None	FLA-E
Stylosanthes hamata (L.) Taub.	Native	Cheesytoes	*Stylosanthes procumbens* Swartz	
Tamarindus indica L.	Exotic	Tamarind	*Tamarindus officinalis* Hooker	
Tephrosia angustissima Shuttlew. ex Chapm.	Endemic	Narrowleaf hoarypea	*Cracca angustissima* (Shuttleworth ex Chap.) Kuntze	IUCN-E, FLA-E
Tephrosia florida (F. Dietr.) C.E. Wood	Native	Florida hoarypea	*Cracca angustissima* (Shuttleworth ex Chapm.) Kuntze	
Tephrosia spicata (Walter) Torr. & A. Gray	Native	Spike hoarypea	*Cracca ambigua* (M.A. Curtis) Kuntze	
Trifolium hybridum L.	Exotic	Alsike clover	*Trifolium bicolor* Moench	
Trifolium repens L.	Exotic	White clover	*Amoria hybrida* (L.) C. Presl	
Vachellia choriophylla (Benth.) Seigler & Ebinger	Native	Cinnecord	*Acacia choriophylla* Bentham	FLA-E
Vachellia cornigera (L.) Seigler & Ebinger	Exotic	Bullhorn acacia	*Acacia cornigera* (L.)	
Vachellia farnesiana (L.) Wight & Arn. var. *farnesiana*	Native	Sweet acacia	*Acacia farnesiana* (L.) Willd.	

APPENDIX A.—Continued.

Name	Nativity	Common name	Synonyms	Status
Vachellia farnesiana (L.) Wight & Arn. var. *pinetorum* (F.J. Herm.) Seigler & Ebinger	Native	Pineland acacia	*Acacia pinetorum* F.J. Hermann	
Vachellia sphaerocephala (Schltdl. & Cham.) Seigler & Ebinger	Exotic	Bee wattle	*Acacia sphaerocephala* Schltdl. & Cham.	
Vicia acutifolia Elliott	Native	Fourleaf vetch	*Cracca acutifolia* (Elliott) Alefeld	
Vigna adenantha (G. Mey.) Maréchal, Mascherpa & Stainier	Exotic	Wild pea	*Leptospron adenanthum* (G. Mey.) A. Delgado	
Vigna luteola (Jacq.) Benth.	Native	Hairypod cowpea	*Vigna repens* (L.) Kuntze	
Vigna speciosa (Kunth) Verdc.	Exotic	Prairie vetch	*Sigmoidotropis speciosa* (Kunth) A. Delgado	
Zornia bracteata J.F. Gmel	Native	Viperina	*Hedysarum tetraphyllum* Poiret	

APPENDIX B.—Institution collections inventoried. Codes from Index Herbariorum (Thiers 2016).

Herbaria inventoried	Code	Online databases used	Code
New York Botanic Garden Steere Herbarium	NY	South Florida Collections Management Center at Everglades National Park	SFCMC
Brooklyn Museum Herbarium	BKL	Robert K. Godfrey Herbarium at Florida State University	FSU
Harvard University Herbaria	GH	National Herbarium at Smithsonian	US
Fairchild Tropical Botanic Garden Herbarium	FTG	University of Florida Herbarium online Plant Atlas	FLAS
Florida Atlantic University Herbarium	FAU	Herbarium at the Royal Botanic Gardens Kew	K