

A Study of the Distribution of Several South Florida Endemic Plants in the Florida Keys

Report to the U.S. Fish and Wildlife Service

by

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INTRODUCTION:

In this Report, the results of a study of the distribution and status of five plant taxa-*Indigofera keyensis*, *Chamecrista lineata* var. *keyensis*, *Chamaesyce deltoidea* subsp. *serpyllum*, *Melanthera parvifolia*, and *Linum arenicola*-are outlined. Whereas the latter two species are known from the South Florida mainland as well as the Florida Keys, our investigation concerned only the Keys populations. The study was undertaken in order to assess the need for conservation efforts under the Federal Endangered Species Act. Prior to this investigation, what little was known about the distribution of these plants was inferred from species lists (e.g., Austin 1978), herbarium collections, and other anecdotal accounts, as well as published flora (Long and Lakela, 1978). These sources clearly indicate that *I. keyensis* is a plant of low, coastal areas, and the other four taxa are associated with pine rockland forests, but they provide little notion of the plants' extent, abundance, or habitat affinities within those broad habitat categories. Such information is a necessary initial step in the process of designing management options-particularly fire management in pine rockland forests-capable of increasing the abundance of at-risk plants. For the four pineland herbs, this study builds on results of an earlier synecological

investigation undertaken by the senior author and others (Ross et al., 1992a).

Management directed at individual plant species may include actions which modify habitat in order to make it more favorable for the species of interest, or efforts to establish plants in appropriate sites in which they do not presently occur for historical or stochastic reasons. Knowledge of species-microhabitat relationships necessary to support such activities may be derived from experimentation and/or from careful and critical analysis of spatial or temporal patterns. The latter approach is only possible if, within the range of potential habitats, equal sampling attention is accorded sites where a species does not occur as those where it does. For this reason, we chose as our sampling domain the ca 880 hectares of Lower Keys pine forest rather than known populations of *C. lineata*, *M. parvifolia*, *C. deltoidea*, and *L. arenicola*. For *I. keyensis*, on the other hand, it was necessary to limit our efforts to known populations because of the infeasibility of adequately sampling all coastal areas of the Florida Keys.

Research objectives for *I. keyensis* and for the pine rockland endemics were therefore different. For *I. keyensis*, our objective was to gain a better understanding of the plant's preferred habitat, and the status of and threats to known populations. For the pineland group, our objectives were threefold:

1. Describe the distribution of each species.
2. Determine whether within- and among-island differences in species distributions are explainable on the basis of easily measured structural variables.
3. Assess the relationship between fire history variables and species' abundances.

METHODS:

Pine rockland plants.

On the basis of vegetation maps included in Folk et al. (1991), the outlines of Florida Keys pine rockland forests more than 1 hectare in size were digitized and stored in ATLAS-GIS (Strategic Mapping, Inc., San Jose, CA). Five islands-Big Pine, No Name, Little Pine, Cudjoe, and Sugarloaf Keys-contained significant areas of pine forest ([Figure 1](#)). Within each of these islands, 1-5 transects were chosen to represent the geographical distribution of pine rocklands, depending on access and area ([Figure 2](#), [3](#), [4](#), [5](#), & [6](#)). On Big Pine Key, pine forests in the wetland complex previously sampled by Ross et al. (1992a) were not included in the present survey. Circular sample plots of 5-meter radius were arrayed at 50-meter intervals along each transect, except where those locations fell within small inclusions of different vegetation type within the pine forest matrix. Sampling intensity thus varied from 0.17% on Big Pine Key to 0.42% on No Name Key ([Table 1](#)). The latitude and longitude of each sampling station are listed in Appendix 1 (not available in HTML format).

The following data were recorded in each plot:

1. The species and diameter at breast height of each woody stem >2.54 cm, in 5-cm diameter classes.
2. Estimated cover of shrubs, graminoids, palms (<2.54 cm DBH), and ferns, in six cover classes (0-1%, 1-4%, 4-16%, 16-33%, 33-66%, and >66%).
3. The percentage of rock exposed at the ground surface.
4. The density of small (<16 cm tall) pine seedlings within 2 meters of the plot center.
5. The density of larger pine regeneration in the plot as a whole, in four height classes (16-30 cm, 31-60 cm, 60 cm-1 m, and

>1 meter).

6. The density of *C. lineata*, *M. parvifolia*, *C. deltoidea*, and *L. arenicola* in the plot as a whole. Densities exceeding 30 individuals were estimated to the nearest 10 individuals.

For each plot, the following habitat variables were derived from these data:

1. Total tree basal area in m²/ha (**TOTBA**) and density in #/ha (**TOTDENS**).
2. Relative basal area (%) of pines (**RELPINEB**), palms (**RELPALMB**), and hardwoods (**RELHARDB**).
3. Relative density (%) of pines (**RELPINED**), palms (**RELPALMD**), and hardwoods (**RELHARDD**).
4. Average stand diameter of slash pine (**PINEASD**), i.e., the diameter of the pine tree of average basal area.
5. Total understory cover (**TUNDCOV**).
6. Relative cover (%) of shrubs (**RELSHRUB**), graminoids (**RELGRAM**), palms (**RELPALM**), and ferns (**RELFERN**).
7. %exposed rock (**ROCKCOV**).
8. Per hectare densities of large (>15 cm tall) pine regeneration (**HIREGEN**).

We also attempted to summarize the fire history of each transect on the basis of a preliminary examination of aerial photographs (1957, 1959, 1964, 1971, 1981, 1986, 1991, and 1994), fire records of the Key Deer National Wildlife Refuge, and several personal accounts. We therefore characterized each transect according to two additional habitat variables:

1. Number of years since most recent known disturbance (**FIREDATE**).
2. Number of known major disturbances in the last 40 years (**FIREFREQ**).

Where disturbance history varied clearly along a transect, we divided it into sub-units for analytical purposes. In all but one Big Pine Key sub-transect which was bulldozed, the disturbance referred to was wildfire or prescribed fire. Disturbances that affected a minority of plots along a transect or sub-transect were not included.

Data analysis was intended to describe and explain spatial variation in the abundance of the four endemic plants. First we examined patterns in the transect and sub-transect means of each plant and habitat variable throughout the study area through tabular or graphic means. We applied principal component analysis (PCA) to the habitat variables, reducing their dimensionality and creating four orthogonal, easily-interpretable composite variables. Among-island differences in the PCA factor scores were tested via MANOVA, ANOVA, and the Scheffé multiple comparison test. We also developed discriminant functions from the Big Pine Key data set alone which could be used to predict the presence or absence of the four plants, and these functions were applied to habitat data from Cudjoe, Little Pine, No Name, and Sugarloaf Keys. We set prior probabilities for each species on the latter four islands to equal those which yielded equal predicted and observed plot frequencies on Big Pine Key.

Maintenance of a pine canopy is unquestionably important for the longterm survival of pine rockland understory species. On that basis, the objectives listed in the Introduction warranted a brief examination of factors affecting pine regeneration. Plot scores in the composite habitat variables from PCA were employed as potential independent variables in regression analyses predicting the density of small (<16 cm height) pine regeneration. Separate analyses were performed on data sets from Big Pine Key and from all islands together. A forward stepwise regression procedure was used, with F-to-enter of 2.0 and

F-to-remove of 1.0.

***Indigofera keyensis*.**

Potential habitat for *I. keyensis* was unknown or poorly defined at the beginning of the study. It was therefore impossible for us to apply the same sampling methods to it as we had to the pine rockland endemics. Instead, we searched for the plant on three islands where it had been reported earlier: Long Point Key, Long Key, and Windley Key. Where we were able to relocate a local population, we qualitatively characterized its size, and recorded *I. keyensis*'s immediate plant associates.

RESULTS:

Pine rockland plants.

The rockland habitat. Eighteen of the twenty transects had burned or been otherwise disturbed within the last ca forty years; two transects (BPK-2B and BPK-3A) had been affected by at least four documentable fires over the period ([Table 2](#)). As a result of difficulty in detecting low-impact fires from aerial photos, we consider the fire occurrence estimates in [Table 2](#) to be conservative. One of the two unburned transects (BPK-5) was a relatively young pine forest which probably became established in stand-replacing fires not too many years prior to our earliest photo in 1957, while the other (NN-3) has nearly succeeded to hardwood hammock.

The pine forests of the study area range in average basal area from a low of 4 m²/ha (Transects BPK-3F, SK-1) to a high of 23 m²/ha (Transect NN-2), and in stem density from about 400/ha (Transect BPK-2B) to almost 4000/ha (Transect NN-2) ([Table 3](#)). As the diameter of the average pine tree (an indicator of stand age, albeit imperfect, when applied to early-successional canopy dominants like *P. elliotii* var *densa*) increases, so does total tree basal area and density, while the relative abundance of pine in the forest canopy decreases, replaced by palm and/or hardwood species. For instance, hardwoods and palms together comprise 5 and 84% of the basal area of Transects BPK-3F and NN-2 cited above, respectively. In general, a monospecific young stand of *P. elliotii* var *densa* comprises the tree stratum in large portions of Big Pine Key, while palms and hardwoods are more important in the older pine rockland canopy on the other four islands ([Table 3](#)).

As the name "pine rockland" suggests, one of the most notable features of Lower Keys pine ecosystems is the extent of outcropped limestone bedrock and exposed calcareous rubble, especially on Big Pine Key ([Table 4](#)). The two most prominent growth forms in the forest understory are palms (*Thrinax morrissii*, *Coccothrinax argentata*, *Serenoa repens*, and *Sabal palmetto*) and broadleaved shrubs (e.g., *Byrsonima ludida*, *Psidium longipes*, *Pisonia rotundata*, and *Pithecellobium guadalupense*) ([Table 4](#)). Grasses such as *Schizachyrium rhizomatum* and *S. semiberbe*, *Muhlenbergia capillaris*, *Aristida purpurea*, and *Sorghastrum secundum* are very important on several Big Pine Key transects (BPK-1B, 3F, 4, and 5). *Pteris longifolia* and *Anemia adiantifolia* are common ferns with low coverage throughout the pine forest, while bracken (*Pteridium aquilinum*) is so dense in several recently burned areas on Big Pine, No Name, and Cudjoe Key that most other understory plants are excluded. *Conocarpus erecta* (shrub) and *Cladium jamaicensis* (graminoid) are important in the understory of the wettest rocklands sampled, but such sites were not common along our transects. Finally, several creeping or stoloniferous broadleaved herbs (e.g., *Ernodea littoralis*, *Flaveria linearis*) form a relatively continuous ground cover in many plots, but their abundance was not estimated.

Total pine regeneration ranges from zero (NN-3) to 4823 seedlings and saplings per hectare (BPK-5)

(Table 5). The absence of regeneration in Transect NN-3 is indicative of a more general regeneration failure on No Name Key (Table 5). Structurally, the dense regeneration in BPK-5 (and nearby BPK-4) grades almost seamlessly into the small, nearly monospecific upper pine canopy in those transects. Over the study area as a whole, the smallest regeneration size class (Class1 --- <16 cm height) comprises only 51% of total pine regeneration. Successively larger Classes 2-5 contain 12, 9, 10, and 18%, respectively.

Application of principal component analysis (PCA) to the 18 habitat variables defined in the Methods yielded four orthogonal, easily-interpretable factors which together explain 62% of the total variance (Table 6). Factor 1 ("Lacking Hardwoods") includes high negative (<-.35) loadings for hardwood tree variables, shrub cover, overall tree density and total basal area. It also includes strong positive loadings (>+.35) for pine tree density, rock cover, graminoid cover, and fern cover. Sites with high Factor 1 scores are therefore open, grassy, rocky pine forests lacking hardwoods. Factor 2 ("Pine No Palm") loads positively for pine tree variables and negatively for overstory palms. Factor 3 ("Recently Unburned") has strong negative loadings for number of historical fires and understory palms, and strong positive loadings for time since last fire, graminoid cover, and large pine regeneration. Negative associations of fire with grasses and pine regeneration are at least superficially counterintuitive, and will be discussed later. Factor 4 ("Stand Maturity") features high positive loadings for pine average diameter, total basal area, and fern cover, and high negative loadings for rock and grass cover.

Application of MANOVA to plot PCA factor scores indicated a rejection ($p < .00001$) of the null hypothesis of no difference in habitat among islands. Among-island differences in individual factors were all significant ($p < .0001$ for each). These differences are examined further in Table 7. Big Pine Key is highest in both Factor 1 ("Lacking Hardwoods") and Factor 2 ("Pine No Palm"). Relatively high scores in Factor 3 ("Recently Unburned") and low scores in Factor 4 ("Stand Maturity") on Big Pine derive from a number of young pine stands on the southern end of the island that have not burned for several decades or more. The large pines and high bracken cover on Cudjoe Key and No Name Keys lead to high scores on "Stand Maturity". Cudjoe, whose canopy includes many palm trees but few hardwoods, scores high for Factor 1 habitat and very low for Factor 2. Factor 3 scores are lowest on Little Pine Key, a remote island whose small pineland has abundant large regeneration and has burned three times during the last 25 years. The low Factor 1 scores for Sugarloaf, No Name, and Little Pine Keys are indicative of extensive hardwood invasion on those islands.

The four rockland endemics.

C. lineata occurred in all Big Pine Key transects (Table 8). It was present in 130 (89%) of the 145 plots sampled on the island (Figure 7), and in densities that sometimes exceeded 1 plant/m² averaged over an entire transect (Table 8). Maximum densities occurred in the northern end of the island (Transects 2B-2C and 3A-3E). *C. lineata* was relatively uncommon in Transect 3F, an area which had been bulldozed in 1969, and in Transects 1A and 1B along the western edge of the island (Table 8). The discriminant analysis (Table 9) associates the presence of *C. lineata* with forest canopies in which hardwoods are relatively unimportant, and in which palms are important in both the overstory and understory. *C. lineata* density appears to be unaffected by longterm fire frequency, but is low (<0.5/m²) in Big Pine Key stands unburned for more than a decade, and quite variable in more recently burned forests (Figure 8).

M. parvifolia occurred in only 22 sample plots on Big Pine Key, distributed among five transects in the northern half of the island (Figure 9). Where it occurred, *M. parvifolia* was found in low densities, never exceeding 1 plant per 50 m² averaged over an entire transect (Table 8). The discriminant functions for *M. parvifolia* indicate that the plant tends to be absent from sites in which the understory is dominated by broadleaved shrubs, as well as sites with high overall tree density (Table 9). The species

was absent where burning has not occurred in over a decade ([Figure 10](#)).

C. deltoidea was present in 32 plots in eight transects on Big Pine Key ([Figure 11](#)). Like *M. parvifolia*, it was not found in western or southern transects. Unlike that species, however, *C. deltoidea* was frequently found in dense colonies. Average densities which exceeded 2 plants per m² were observed in two transects, 3B and 3F ([Table 8](#)), while densities in several individual plots were much higher. *C. deltoidea* was present in all 11 plots in Transect 3F. The discriminant analysis associates extensive exposed rock substrate, low total understory cover, and low hardwood density with the presence of this species ([Table 9](#)). The distributional pattern of *C. deltoidea* did not appear to be strongly related to time since fire or fire frequency ([Figure 12](#)).

L. arenicola was found in only 16 plots in five Big Pine Key transects, none of which were west of Key Deer Blvd ([Figure 13](#)). *L. arenicola* occasionally occurred in high abundance; its highest plot density was slightly more than 0.5 individuals per m². It differed from the other three species in reaching maximum abundance in transects toward the southern end of Big Pine Key ([Table 8](#)). Both of the stands in which *L. arenicola* was most abundant (Transects 4 and 3F) were young forests which had not burned for several decades; however, appropriate fire history and developmental stage do not guarantee its presence on Big Pine Key (cf Transects 2A and 5 in [Figure 14](#)). According to the discriminant functions for this species, sites most likely to support *L. arenicola* have a high relative representation of graminoids in the understory, abundant pine regeneration, and high cover of exposed rock ([Table 9](#)).

Neither *C. lineata*, *M. parvifolia*, *C. deltoidea*, nor *L. arenicola* were observed in sample plots, between plots along the transects, or along the roadsides on any island except Big Pine Key ([Table 8](#)). Moreover, the discriminant functions developed from the Big Pine Key data set suggest that habitat variables for the four plants are not as frequently favorable on Cudjoe, Little Pine, No Name, and Sugarloaf Key as on Big Pine ([Table 10](#)). Nevertheless, the models do indicate that appropriate habitat occurs at many locations on all islands for *C. lineata*, at multiple locations on Cudjoe Key for *M. parvifolia*, and at scattered locations on Little Pine and Sugarloaf Key for *C. deltoidea* and *L. arenicola* ([Table 10](#)).

Pine Regeneration.

Equations analyzing sources of variation in the density of small (<16 cm height) pine regeneration from the entire 232-plot data set and from the 145-plot Big Pine Key data set were very similar ([Table 11](#)). In both cases Factor 3 ("Recently Unburned") and Factor 4 ("Stand Maturity") were identified as the best combination of independent variables. However, these equations explained only about 10% of the total variance in the dependent variable. The significant positive association of young regeneration with recently unburned stands ([Table 11](#)) is visually apparent in [Figure 15](#). This relationship is stronger when pine regeneration of all sizes is considered ([Figure 16](#)). The association of pine regeneration with stand development is likewise highly significant and in the negative direction ([Table 11](#)).

Indigofera keyensis

I. keyensis was encountered in two of the three locations in which it had previously been observed, on Long Point and Long Keys. We were unable to relocate a third population on Windley Key, possibly because of the lack of specific location information in the collection notes.

The population on Long Point Key consisted of 3-4 individuals in a small (ca 15-meter diameter) opening on privately-owned land (Lat 24045'7.32", Lon 80059'9.22"). The property (owned, we are

told, by the Switlik family), occupies the distal end of a peninsula extending into Florida Bay, and abutting the Curry Hammock property recently acquired by the State of Florida through the CARL program. The habitat is categorized as Buttonwood Woodland with graminoid understory (ESU-5) in the ecosystem classification system of Ross et al. (1992). Associated plants listed in [Table 12](#) include a number of other vines (e.g., *Urechites lutea*, *Cynanchum bahamense*, *Jacquemontia pentantha*, and *Rhynchosia minima*) twining through low *Conocarpus erecta* and *Pithecellobium guadalupense* shrubs. Encroaching Brazilian pepper (*Schinus terebinthifolius*) threatens to close over the small opening. For this reason, we consider it unlikely that the small *I. keyensis* population will survive another decade under current conditions.

The Long Key population of *I. keyensis* is scattered through a ca 0.5 hectare area north of U.S. 1 in Long Key State Recreation Area (Lat.24° 48'38.20", Lon.80°49'49.84"), and consists of perhaps 100 individuals or more. The plant's habitat classification here (Buttonwood woodland with graminoid understory) is identical to that on Long Point Key, and many of the same associates are present ([Table 12](#)). Species diversity is relatively high, including the rare and declining cactus *Opuntia triacantha*. *I. keyensis* is prominent among a number of vines clambering through shrubby openings, which are interspersed with small groups of trees. Prospects for *I. keyensis* survival here in the near future are not nearly as grim as on Long Point Key, because of the population size, the amount of available habitat, the ownership characteristics, and the relative scarcity of *Schinus terebinthifolius*.

DISCUSSION:

Pine Forest Endemics

The most fundamental result of our survey was the complete absence of the four rockland herbs in pine forests outside Big Pine Key. For *L. arenicola* and *C. deltoidea*, it is possible (though not necessarily likely) that this absence is attributable to structural variables subject to habitat management, including prescribed fire. However, *C. lineata* and *M. parvifolia* are confined to Big Pine Key despite significant areas with seemingly appropriate structural characteristics on other islands. To speculate more knowledgeably regarding the possible significance of such patterns for the conservation of these endemic South Florida plants, we must first examine limitations in our data set, then consider what the current data indicate about the longterm (centuries) and shortterm (decades) development of Florida Keys pine forests, and the place of these species in it.

Variation in community structure and composition in the Florida Keys is strongly associated with physical variables, most prominently the proximity of the water table to the ground surface and its salinity (Davis 1942, Dickson 1955, Craighead 1971, Ross et al. 1992b). For instance, the species composition of pine rockland communities on high- and low-elevation sites in central Big Pine Key are strongly differentiated (Ross et al. 1992a). Edaphic characteristics vary predictably with these differences in topographic/hydrologic setting, and also may affect plant life history processes directly. These important physical variables could not be measured with available resources, and alternative approaches (e.g., using plant community composition as an indicator of the physical variables based on known species-environment relationships) were also impossible given time constraints and the large area to be sampled. Thus, much of the spatial variation observed in the current study may result from unmeasured within- and among-island differences in hydrologic or edaphic variables.

Some of our conclusions are also limited by the quality of the fire record, which was estimated from aerial photographs, supplemented by written and oral communications of the KDNWR. Aerial photo coverage is limited in historical reach. The earliest photo we considered useful for mapping purposes was taken only 39 years ago, in 1957. Furthermore, existing photo coverage within the four-decade

period is somewhat uneven among islands, with the most complete record available for Big Pine Key. Similar limitations apply to the written and oral accounts. The written record for recent fires has been relatively complete and detailed, while earlier communications are often vague with regard to fire location and conditions. Most importantly, differences in fire intensity and speed are difficult or impossible to surmise from either the KDNWR records or aerial photos, constraining us to lump an heterogeneous group of fires into our FIREDATE and FIREFREQ variables. Such limitations in our data will allow only the strongest fire-vegetation relationships to emerge.

Given the above limitations, the following sequence of pine forest development is consistent with the structural patterns we observed, and which are summarized in Tables 3, 6, and 7. The canopy in Lower Florida Keys' pine rocklands exist in one of three conditions: (1) Type 1-nearly monospecific stands of *Pinus elliottii* var *densa*, (2) Type 2-stands in which pines and palms share dominance, the former emergent from the relatively continuous subcanopy of the latter, and (3) Type 3-mixtures of pine, palm, and hardwoods, with pines again emergent from the mixed lower canopy. Following Robertson (1952), Alexander and Dickson (1972), Carlson (1989), and others, we suggest that these structural types are associated with early, medium, and late stages in pine stand development following a single catastrophic fire or a series of fires in which a significant proportion of the forest canopy is killed. Fires of lesser impact halt this developmental process for a short while, but only very intense or recurrent fires remove hardwoods or palms once they are established in the forest canopy, reestablishing the Type 1 forest structure. Big Pine Key is typified by Type 1 pine forests, Cudjoe Key by forests of Type 2, and No Name Key by Type 3 forests (Tables 3 and 7). However, since fires do not usually burn through all uplands on an island, or with equal intensity throughout, Florida Keys pine forests are in reality mosaics of stands in different developmental stages.

Results summarized in Tables 6, 7, 8, 9, 10, 11, & 12 demonstrate that the composition of the pine rockland understory over the five islands is influenced by variation in overstory structure associated with developmental stage. For instance, understories in Type 1 pine forests frequently contain a strong graminoid component, while graminoids are most often of low abundance in the shrub/palm understories of Types 2 and 3. Interestingly enough, the same data suggest that graminoids are not favored by non-catastrophic fire in pine forests of late developmental stage; such fires have resulted instead in the dense bracken thickets that characterize portions of No Name, Cudjoe, and Big Pine Key.

The four understory plants of particular interest in this study differ considerably in their association with various developmental stages or affinity with fire in Big Pine Key pine forests (Table 8 and 9, Figures 8, 10, 12, 14). *C. lineata*, the most abundant and widely distributed of the four, reaches its maximum density in Transects 3B and 3D. These Type 2 stands feature relatively large pines and a heavy component of palms, and have each experienced recent fires. In contrast, *L. arenicola* is narrowly distributed in Transects 3F and 4. These dense, monospecific Type 1 stands have not burned for several decades, perhaps since stand establishment. *C. deltoidea* is found in very dense colonies in Transects 3B and 3F. The very open conditions and rock exposures required by this plant apparently may be satisfied in young, unburned stands or in recently-burned mid-developmental pine forests. *M. parvifolia* is found in low densities under recently-burned, sparse pine or pine-palm canopies. None of the plants are abundant in Transects 1A and 2A, which are the only sampled Big Pine stands with a significant hardwood subcanopy (Type 3).

Whereas canopy-understory interactions or fire-understory interactions may contribute to the distributional patterns of the four taxa on Big Pine Key, our discriminant analysis (Tables 10 & 11) indicates that they are not sufficient to explain the plants' complete absence from other Lower Keys islands. This applies especially to *C. lineata*, which is most abundant in recently burned pine-palm forests, a common environment on all islands. At least two reasonable hypotheses can be advanced, each of which incorporates the unverified assumption that the current Big Pine Key populations of all four

plants are relicts of more extensive populations. The first hypothesis is a variant of the biogeographic principle that populations on smaller islands are more prone to extirpation from a number of sources, including demographic and environmental stochasticity. The variant proposed here is that local extinctions were the endpoint of species responses to canopy conditions, where canopy closure resulted from low fire recurrence rates on small islands. The second hypothesis suggests that population responses were to intrinsic differences in ecologically significant environmental factors among islands, in this case in edaphic/hydrologic correlates of salt-water intrusion associated with sea level-rise.

The first hypothesis is derived from a discussion by Carlson (1989), who viewed among- island differences in Keys pine forest structure to be relatively permanent features attributable to differences in historical fire frequency. By chance alone, lightning was more likely to strike somewhere on a larger island than a smaller one. Because individual ignitions on large islands have the sometimes-realized potential to burn larger acreages, fire recurrence ought to be greatest on the largest in a chain of islands, e.g., Big Pine Key in the Lower Florida Keys. Now, assume the pine to pine-palm to pine-palm-hardwood developmental sequence described earlier, and assume some compositional "memory" after fire, i.e., the amount of hardwood or palm from the pre-burn forest that survives a fire is proportional to its initial abundance, and these survivors hasten invasion into the developing Type 1 pine forest. It is not difficult to imagine how this island-size effect, maintained over multiple sequences of stand development, could contribute to more-or-less stable variations in subcanopy structure among islands, and ultimately to the extirpation of local populations of shade-intolerant pine rockland herbs on small islands. From a management perspective, strong evidence in support of the fire frequency mechanism would suggest that species restoration is possible, via a reintroduction program in conjunction with manipulation of canopy structure through fire.

Evidence for the alternative hypothesis was first advanced by Alexander (1953, 1976). He identified rising sea level as the ultimate cause of directional shifts among forest types in the upper Florida Keys, specifically changes from pine forest to mangrove. Ross et al. (1994) extended these observations to Sugarloaf Key and to intermediate habitat types, by documenting a continuous shift from pine forest to more salt-tolerant upland and wetland community types during this century. In the Sugarloaf study, these vegetation changes were associated with increases in porewater and groundwater salinity, and decreases in depth to the water table. Well-known hydrogeologic relationships suggest that during a period of rising ocean levels, such physical changes will occur first on lower and smaller islands, which is at least in part consistent with the distributional patterns observed. Local extinctions among understory plants might occur directly by salinity stress, or indirectly by salinity-mediated alterations in the balance among keystone species in the upper forest strata. In contrast to the fire frequency hypothesis, evidence favoring the salt water intrusion hypothesis would indicate that the combination of reintroduction and fire management would be insufficient for successful reestablishment of the four species outside of Big Pine Key, because the ultimate cause of the plants' decline would not have been treated.

Results of the current study do not favor one or the other alternative outlined above. On the surface, the lack of association between fire variables and the abundance of *C. deltoidea* and *L. arenicola* (Figures 12 and 14) appears to conflict with the fire frequency hypothesis. However, this is a false conflict, because periodic fire is necessary for the perpetuation of each of these early-to mid-successional species, as well as that of *C. lineata*. The question is what kind, how often, and at what stage of stand development, because the later (hardwood) stages of succession are inimical to all four. Thus evidence regarding the mechanism for the truncated distributions we have observed must be sought anew. Such evidence might consist on the one hand of paleoecologic information showing more frequent fires on Big Pine than the other Keys, and on the other of greenhouse and/or field demonstrations that observed soil or groundwater salinities on those islands elicited adverse effects in the species of interest, given otherwise favorable conditions. Finally, the proposed mechanisms may not

be mutually exclusive at all, and both may be contributing or interactive forces.

Regeneration of *Pinus elliottii* var *densa*

We touch briefly here on the issue of pine regeneration because of the demonstrated influence of forest canopy characteristics on the distribution of the four plants of interest, and because of singular effects that pine litter may have on significant factors in the life history of such herbs, including fire intensity, seed bed characteristics, and nutrient availability. Our data present a great paradox: fire is clearly responsible for the open condition which allows slash pine to regenerate, yet at the same time fire is a primary agent of mortality among young pines. It is hoped that fire may be used to manipulate pine population structure, and with it the suite of herbaceous plants that distinguish the pine rocklands. Several results of our survey may be of relevance:

1. Newly-established seedlings continue to accumulate over a long period of time, perhaps 3-4 decades, in developing young pine stands.
2. Regeneration in most older stands is low, especially when widely-spaced adult pine trees are interspersed with hardwoods and palm trees.
3. Over the forest as a whole, regeneration density is distributed very unevenly, and neither the structural variables that we measured, nor recency/frequency of fire are effective predictors of this distribution.

Clearly, episodes of abundant slash pine regeneration occur rarely, probably in years in which a number of fortuitous conditions are met, while low levels of seedling establishment occur in most years. The research attention this important process has received in pine rockland ecosystems is still inadequate to support the development of a suitable fire management system.

***I. keyensis*.**

This endemic vine is apparently quite restricted in distribution within its range in the Florida Keys. However, our investigation was designed to determine the general nature of the plant's habitat, not its complete distribution. The two locations where we found *I. keyensis* were very similar in plant species composition and community structure, i.e., a variant of the Buttonwood woodland with graminoid understory ecosystem type described in Ross et al. (1992b). This is a brackish-water wetland environment with elevations of 0.5 to 1 meter above sea level, inundated during very high tides, especially when these occur in combination with rainy periods. In comparison to most sites in this Ecological Site Unit, the two locations in which *I. keyensis* was found had high plant species diversity, a species composition weighted more heavily than normal toward upland taxa, and an open canopy structure. Both sites were in the Middle Keys. Future efforts might concentrate on identifying new populations, using the above site characteristics as a sampling guide, and on studying/monitoring population processes within the Long Key population.

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