Rev. Biol. Trop., 45 (3): 1021-10.

Distribution of Costa Rican epiphytic bromeliads and the Holdridge Life Zone System

Marta Rivas Rossi, Victor H. Mendez and Julián Monge-Nájera
Centro de Investigación General, UNED, Apartado 474-2050, San José, Costa Rica; Mailing address: Biología Tropical. Universidad de Costa Rica. 2050 Costa Rica; julianm@cariari.ucr.ac.cr

(Received. 29-XI-1996 Contcted l4-IV-1997. Accepted 8-V-l997)

Abstract: Detailed distribution maps for the major bromeliad genera native to Costa Rica were prepared based on the collections in the three largest herbaria of the country and on citations from the literature. Most records are from the montane habitats, probably reflecting the frequent need for moisture by these plants. *Vriesea* and *Guzmania* have been collected mostly in moist highlands, *Tillandsia* and *Caropsis* show abundance peaks at various altitudes and *Aechmea* is more restricted to moist lowland habitats. In 1975, Burt-Utley and Utley had hypothesized that the Holdridge Life Zone System should fit the distribution of epiphytic bromeliads because soil (a factor not considered in the System) is not important in their occurrence. However, on average, species were absent in about half of the Life Zones where they were expected to occur according to the Holdridge classification. It is hypothesized that the System failed because epiphytic bromeliad distribution reflects factor interactions rather than humidity, light or temperature individually.

Key words: Biogeography, Life Zone System, vegetation. biotic unit, bromeliad, Holdridge, Costa Rica.

For more than a century, bromeliads have been collected for the Costa Rican National Herbarium and more recently, for other collections in the country and abroad. Local and foreign collections served as bases for recent publications (e.g. Utley 1994, Luther *1995)* but their geographic distribution has not been studied in a comprehensive way *(e.g.* Burt-Utley and Utley 1975, Gómez 1986).

Burt-Utley and Utley (1975) hypothesized that the Holdridge Life Zone System should fit the distribution of epiphytic bromeliads because soil (a factor not considered in the System) is not important in their occurrence. However, their hypothesis had not been tested until now.

This paper presents, apparently for the first time, detailed distribution record maps for the major genera and includes a study of how the geographic distribution of Costa Rican epiphytic bromeliads is related with the Holdridge Life Zone System.

MATERIAL AND METHODS

Distribution records are based on examination of taxonomically identified specimens at the three largest herbaria of Costa Rica: Museo Nacional (CR, San José), Universidad de Costa Rica (USJ, San José) and Instituto Nacional de Biodiversidad (AINB, Heredia), as well as all records with enough geographic data from the literature (Holmgren *et al*. 1981, Utley 1994). Museum acronyms are according to Holmgren *et al*. (1981). Name spellings follow Luther (1995) and Utley (1994). Data were recorded with geographic coordinates to the second and plotted in, a 1:200 000 map of the Holdridge System (Tosi 1988). The number of specimens per Life Zone were tabulated by species and distribution maps were copied to smaller and simplified maps for visual examination. To assess agreement between the Holdridge Life Zone System and bromeliad occurrence, the percent of zones where each species was expected but has not been collected was calculated. A species is expected to occur in life zone “B” if it occurs in zones “A” and “C” that are immediate to it in the Holdridge classification, because zone “B” is expected to have intermediate characteristics. Here only the genus means (and related summary statistics) of those percents are presented (detailed species tables are available from the authors).

TABLE 1
Percent of Life Zones where species of five bromeliad genera were expected (according to the Holdridge Life Zone System) but were not found.

Genus	Mean	Standard deviation	Maximum	Minimum	Sample size*
Tillandsia	47	17	85	17	31
Vriesea	51	15	75	14	24
Aechmea	51	9	*67*	36	12
Catopsis	47	13	64	29	6
Guzmania	47	17	82	12	22

* Sample size *in* number of species.

RESULTS

A total of 715 valid records spanning almost a century were found (Figs. 1-34). Most records of Costa Rican epiphytic bromeliads are from the mid-altitudes along the mountainous backbone of the country (Fig.3 4). When numbers of records are pooled for genera (because not enough data are available for individual species) *Vriesea* and *Guzmania* are more frequent in moist highlands (Fig. 33), *Tillindsia* and *Catopsis* peak at various altitudes (Fig. 33) and *Aechmea* most often inhabits moist lowland habitats (Fig. 33).

The percents of Life Zones where each species was expected (see Materials and Methods) but has not been recorded had a mean of 50 % (Table 1), that is, there are no records for most species in about half the Life Zones where they should occur according to the Holdridge classification.

DISCUSSION

Biogeographic studies based on herbarium records are subject to collection bias. In this case, however, the extensive Costa Rican road % system has made all of the Life Zones accessible to collectors and an examination of Fig. 34 suggests that we have a reliable view of bromeliad occurrence across the country.

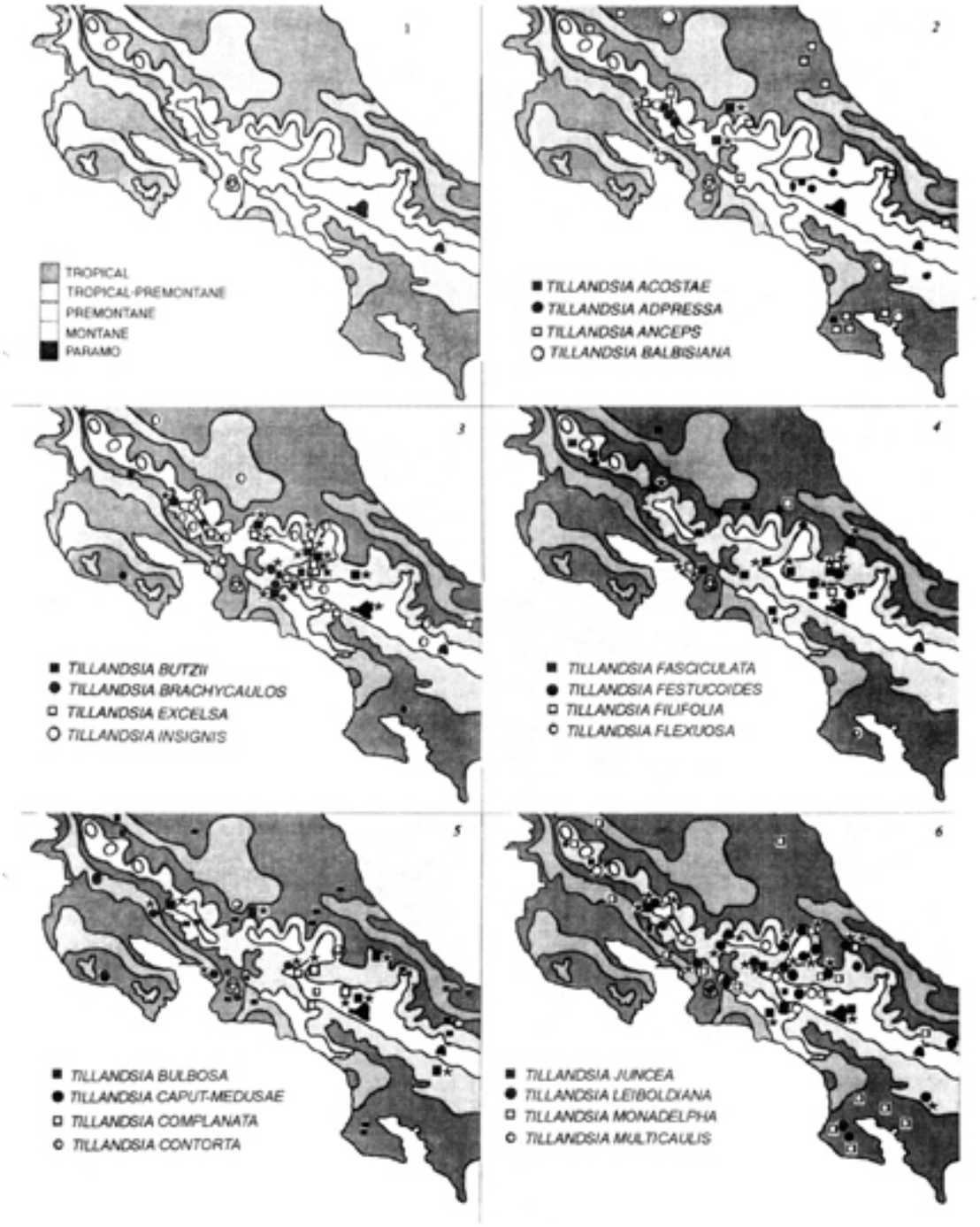
The greater number of records for montane habitats, previously noted by Gómez (1986) can be explained by the need for moisture and light that is common in epiphytic bromeliads (Picado 1911, 1913, Benzing 1994). Relatively low diversity in NW Costa Rica was reported earlier by Burt-Utley and Utley *(1975),* and attributed to the prolonged dry season there. Moisture supply strongly influences the distribution of Bromeliaceae in broad (regional) and finer (local) scales (Gómez 1986, Brown 1990, Gómez and Winkler 1991, Benzing 1994).

Some *Vriesea* are known to require high humidity, low light levels and thin phorophyte - branches (Brown 1990, Fontoura 1995) which agrees with the over-representation of the genus in moist Costa Rican highlands (the same may apply to *Guzmania).*

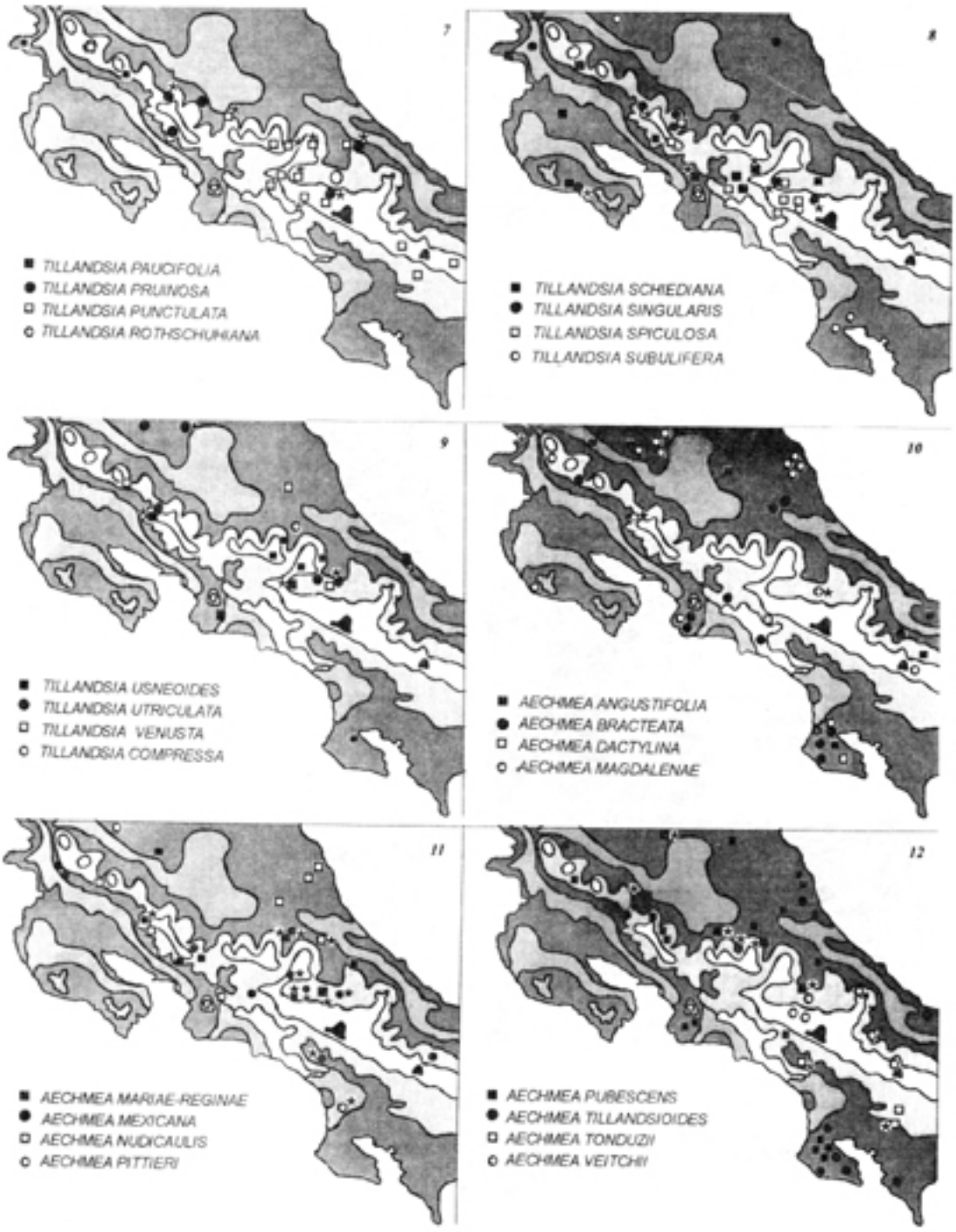
The need for high humidity characterizes many species of *Tillandsia,* but this ecophysiologically diverse genus has species with very contrasting habitat requirements (GarcIa-Franco and Peters 1987, Brown 1990) which may explain why abundance varied greatly with Life Zone in this study. Finally, the apparent exclusion of most *Aechmea* from open habitats (Brown 1990) is also consistent with our results, except for species such as *Aechmea mexicana.*

Individual species were absent in about half of the expected Life Zones: light, humidity and temperature, *i.e.* the factors used by the Holdridge life System, fail to fully predict bromeliad occurrence. Assuming that sampling is consistent across Life Zones, this study rejects the hypothesis proposed by Burt-Utley and Utley (1975), even for *Vriesea,* which in their opinion followed the Life Zone classification System closely (Burt-Utley and Utley 1975).

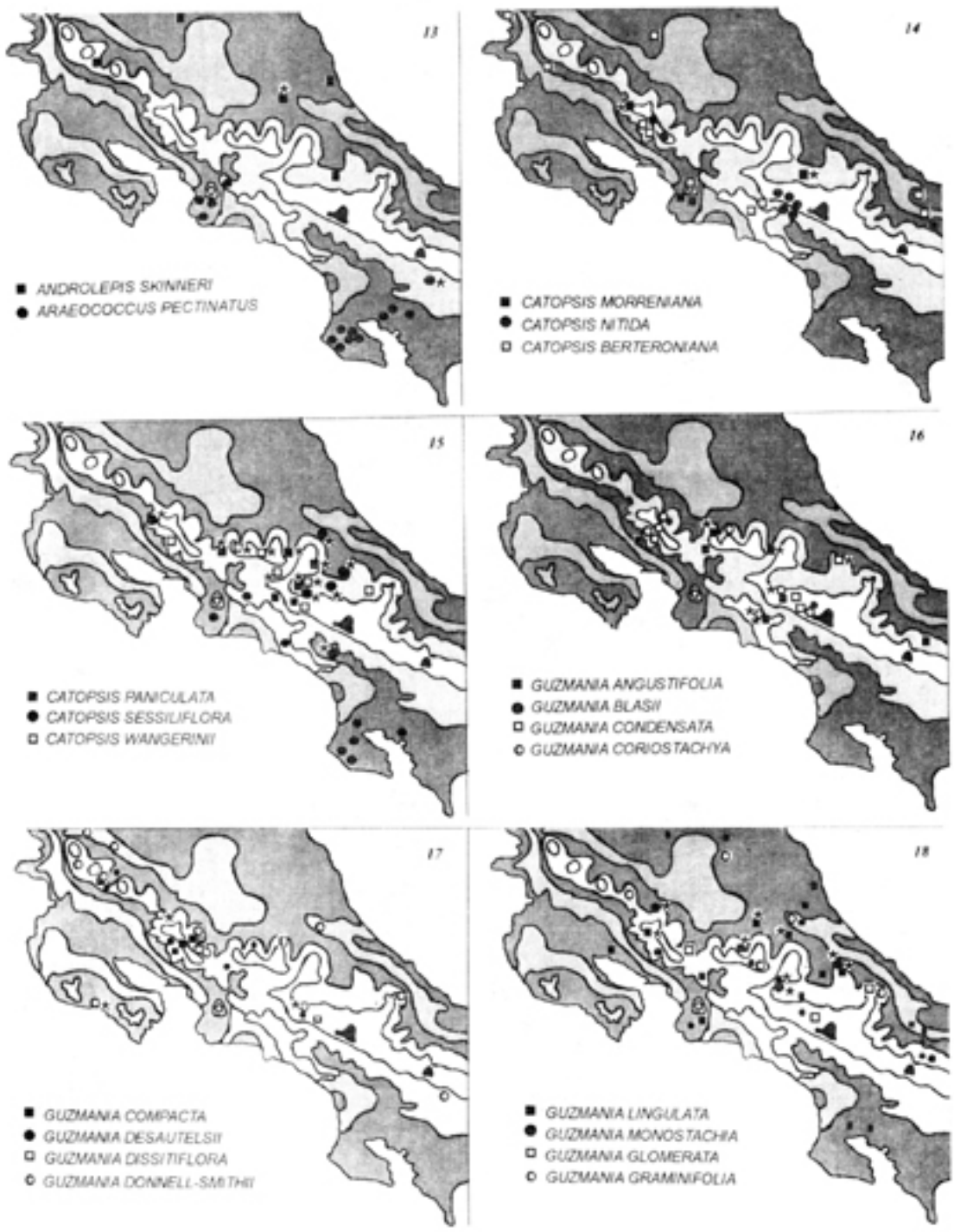
Gómez (1989) stated that Holdridge's Life Zone Ecology map of Costa Rica was not intended to be a vegetation map but this fact does not justify the System's failure because bromeliads are known to depend on environmental factors considered by the system (Burt-Utley and Utley 1975). Future workers may test the hypothesis that epiphytic bromeliad distribution reflects factor interactions rather than humidity, light or temperature individually.



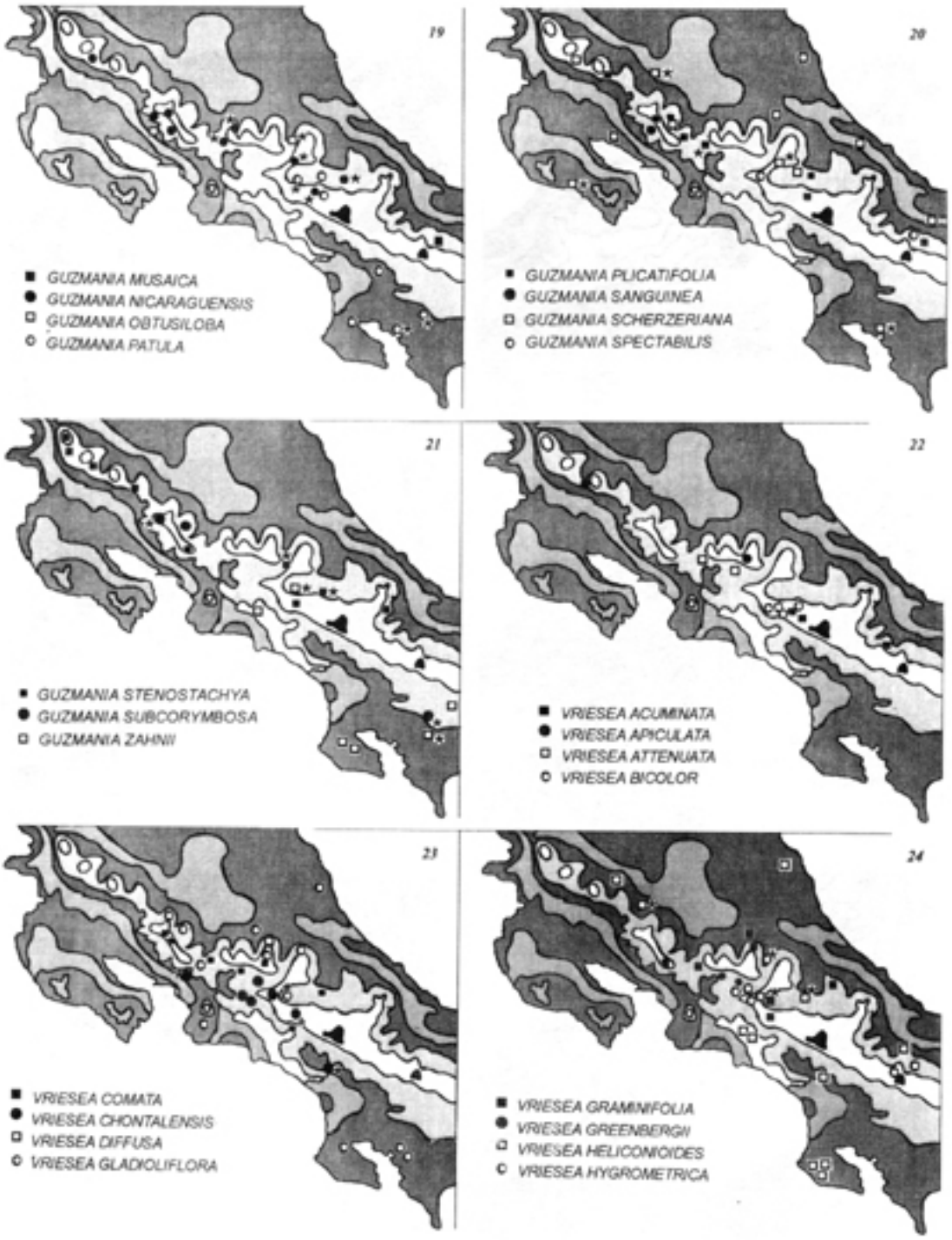
Figs. 1-6. Costa Rica: General Life Zone (1) and localities where several species of *Tillandsia* have been collected (2-6). In this and following figures asterisks indicate data from the literature (see main text)



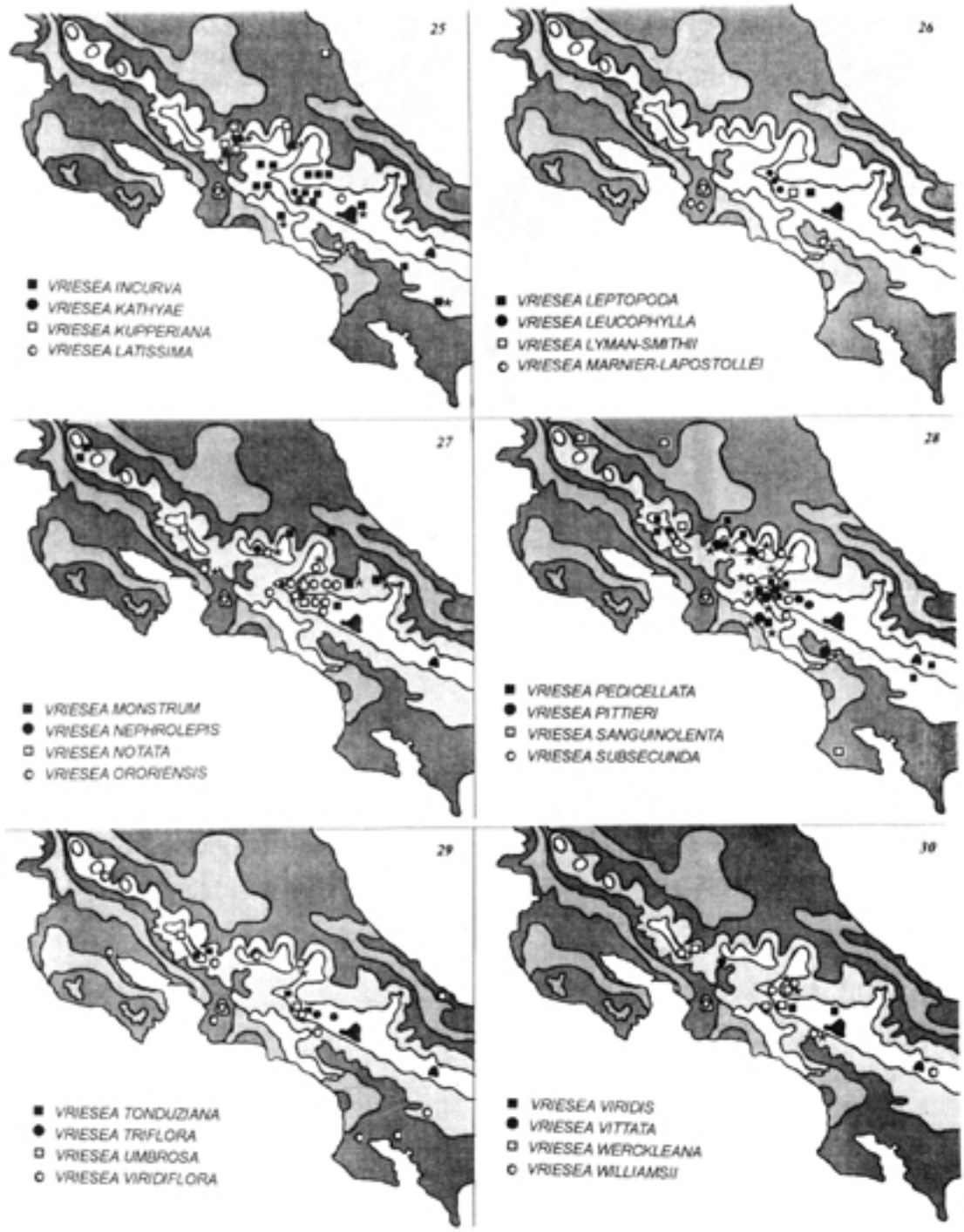
Figs. 7-12. Localities where several species of *Tillandsia* and *Aechmea* have been collected



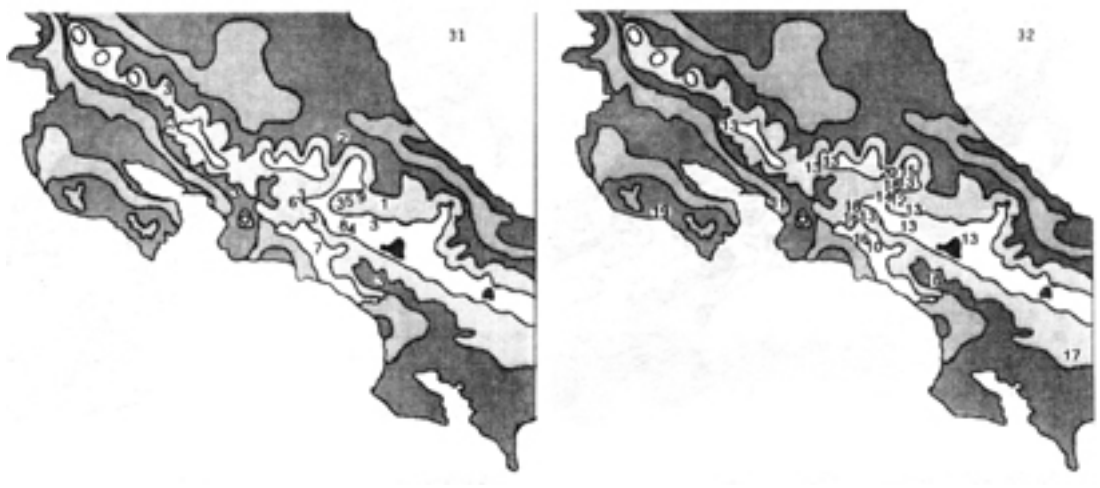
Figs. 13-18. Localities where several species of *Androlepis, Araeococcus, Catopsis* and *Guzmania* have been collected.



Figs. 19-24. Localities where several species of *Guzmania* and *Vriesea* have been collected.



Figs. 25-30. Localities where several species of *Vriesea* have been collected.



Figs. 31-32. Additional localities where several species of *Vriesea* have been collected (all from the literature) *Aechmea*1 *castelnavii*, 2 *penduliflora; Catopsis* 3 *mutans*, 4 *werkleana*, 5 *Guzmania mitis*; *Tillandsia* 6 *abdita*, 7 *biflora*, 8 *cauliflora*, 9 *lampropoda*, 10 *longofolia*, 11 *makoyana*, 12 *oerstediana*, 13 *tricolor*, *Vriesea* 14 *ampla*, 15 *balanophora*, 16 *brunei*, 17 *burgeri*, 18 *picta*, 19 *ringens*, 20 *stenphyla*.

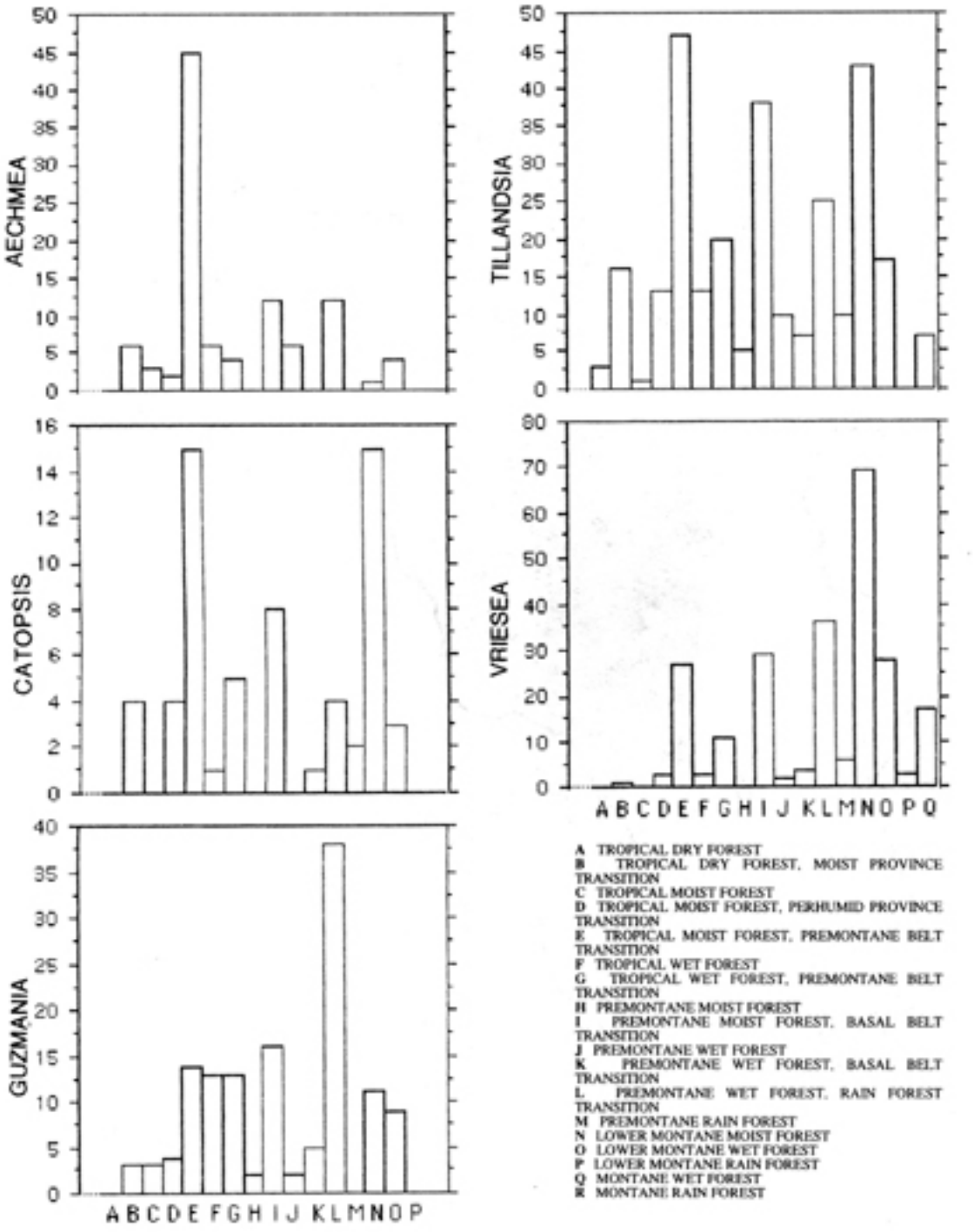


Fig. 33. Number of herbarium specimens versus life zone (from lowlands on the left to highlands on the right) representing several genera of Costa Rican bromeliads

Fig. 34. Summary of Costa Rican bromeliad locality records considered in this study

ACKNOWLEDGMENTS

This project was financed by Centro de Investigación General, UNED. We thank Mariela Bermtidez, Luis D. Gómez and B. Hammel for authorizing study of their institutional collections, Luis Fourmer 0., Luis

D. Gómez P. and two anonymous reviewers for valuable suggestions to improve an earlier draft, and Martin Law Romero for his assistance.

RESUMEN

Se preparó mapas detallados de distribución para los principales géneros de bromelias epifitas nativos de Costa Rica, con base en las colecciones de los tres principales herbarios del país y de informes en la literatura. La mayoría de los registros corresponde a los habitats montañosos, lo cual probablemente refleja la necesidad de humedad que tienen estas plantas. *Yriesea* y *Guznwnia* han sido recolectadas principalmente en regiones altas y húmedas; *Tillandsia* y *Catopsis* muestran picos de abundancia en varias altitudes y *Aechmea* está mas restringido a los habitats húmedos de bajura. En 1975, Burt-Utley y Utley habían sugerido la hipótesis de que el Sistema de Zonas de Vida de Holdridge deberla calzar con la distribución de las bromelias epifitas porque el suelo (un factor no considerado por el sistema) no es importante en su presencia. Sin embargo, en promedio, las especies estuvieron ausentes en aproximadamente la mitad de las zonas de vidas en las cuales se les esperaba según la clasificación de Holdridge. Se presenta la hipótesis de que el sistema falló porque la distribución de las bromelias epifitas depende de las interacciones entre factores, más que de humedad, luz o temperatura individualmente.

REFERENCES

Benzing, D.H. 1994. How much is known about Bromeliaceae in 1994? Selbyana 15: 1-7.

Brown, A.D. 1990. El epifitismo en las selvas montañas del Parque Nacional “El Rey”, Argentina: Composicidn fioristica y patrón de distribución. Rev. Biol. Trop. 38: 155-166.

Burt-Utley, K. & J.F. Utley. (1975). Supplementary notes: Phytogeography, physiological ecology and the Costa Rican genera of Bromeliaceae. Historia Natural Costa Rica 1: 9-29.

Fontoura, T. 1995. Distribution patterns of five Bromeliaceae genera in Atlantic rainforest, Rio de Janeiro State, Brazil. Selbyana 16: 79-93.

Garcfa-Franco, ***3.0.*** & C.M. Peters. 1987. Patrdn espacial y abundancia de ***Tillandsia*** spp. a través de un gradiente altitudinal en los altos de Chiapas, Mexico. Brenesia 27: 35-45.

Gómez, MA. & S. Winkler. 1991. Bromeias en manglares del Pacffico de Guatemala. Rev. Biol. Trop. 39: 207-214.

Gómez P., L.D. 1986. Vegetacidn de Costa Rica. Apuntes pars una biogeograffa costarricense, p. 1-328. ***In*** L.D. G6mez P. (ed.). Vegetación y china de Costa Rica. vol. 1. Universidad Estatal a Distancia, San Jose, Costa Rica.

Gómez P., L.D. 1989. Costa Rica, p. 305-308. In D.G. Campbell & D. Hammond (eds.). Floristic inventory of tropical countries. NY Botanical Gardens, New York.

Herrera, S.W. & L.D. Gômez. 1993. Mapa de unidades bióticas de Costa Rica. Incafo, San José, Costa Rica. 1:685 000.

Holdridge, R.L. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica. 206 p.

Holmgren, **P.K., W.** Keuken & B. K. Schofield. 1981. Index herbariorum. I. **W.** Junlc The Hague. 417 p.

Luther, H.E. 1995. An annotated checklist of Bromeliaceae of Costa Rica. Selbyana 16: 230-234.

Picado, C.. 1911. Les bromCliacées épiphytes comme milieu biologique. Compt. Rend. Acad. Sci. 153: 960-963.

Picado, C.. 1913. Les broméliacées Cpiphytes considérées comme milieu biologique. Bull. Sci. France Belgique 47:1-398.

Tosi, J.A. 1967. Mapa ecológico: Republica de Costa Rica según la clasificaciôn de zonas de vida del mundo de L.R. Holdridge. Centro Científico Tropical, San José, Costa Rica (map).

Tosi, J.A. 1988. Mapa de las zonas de vida de Costa Rica. Centre Cientffico Tropical, San José, Costa Rica (map, 1:200 000).

Utley, J.F. 1994. Bromeiaceae, p. 89-156. ***In*** **G.** Davidse (ed.). Flora mesoamericana, vol. 6. Universidad Nacional Autónoma de Mexico, Mexico, D.F.