COMPUTER-AIDED COMPARATIVE CHOROLOGY OF NEOTROPICAL PLANTS

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Résumé : Deux programmes informatiques (CHOROL, STATCHO) ainsi qu'une base de données d'espèces de plantes tropicales ont été développés. Basés sur une approche quantitative des motifs de répartition des espèces endémiques néotropicales, ils posent les problèmes de l'interprétation des centres d'endémisme supposés. Des fréquences de distribution aire-classes de taille à différents niveaux taxonomiques et des exemples de types chorologiques caractéristiques sont présentés. L'utilisation de motifs de répartition idéalisés mathématiquement sont illustrés par un groupe d'espèces sélectionnées.

Mots-clés : Chorologie comparative, biogéographie, néotropiques, angiospermes, espèces endémiques.

Abstract: Two computer programs (CHOROL, STATCHO) and a data base of neotropical plant species have been developed. Based on a quantitative approach to distribution patterns of neotropical endemics, problems for interpreting presumably endemic centers are pointed out. Frequency of distribution area size classes at different taxonomic levels and examples of typical chorological types are given. The use of mathematically idealized distribution patterns is illustrated for a selected group of species.

Keywords: Comparative chorology, biogeography, neotropics, angiosperms, endemics.

Introduction

The steadily increasing botanical and zoological exploration of the tropics has resulted in increasing data material, especially in regard to geographical distribution data. Therefore it appears most important to summarize and analyze these existing data to document biological diversity and to enrich our biogeographical understanding of the tropical fauna and flora. Especially to understand migration events and refuge patterns, a reinforced use of computers is an urgent need (ALLKIN & BISBY, 1984 ; ALLKIN & WHITE, 1988; BISBY, 1984 ; GOMEZ-POMPA & NEVLING, 1988 ; PANKHURST, 1988 ; REICHL, 1986).

A long-term project for computer-aided comparative chorology started some years ago, which attempts to link geographical distribution patterns with particular kinds of existing systematic, ecological and morphological data of tropical species in a special database. In the current phase, main field of interest is in neotropical plants.

The aim of this paper is to present first analyzes based on a quantitative approach in order to give new insights into (i) the distribution patterns of endemics (ii) frequency of area size classes, and (iii) chorological types. Results are obtained both by considering all species of the data base, only selected ones and single completely surveyed families and genera.

Data and methods

Two computer programs (CHOROL, STATCHO) have been developed (MORAWETZ & EBSTER, 1989, MORAWETZ *et al.*, unpubl.) to elaborate a compilation of distribution maps, to identify characteristic geographical distribution patterns, and to extract information about diversity, migration ways, vegetational zones, and systematic and evolutionary relationships.

CHOROL manages a data base of tropical (plant) taxa with their geographical range and selected annotations. The records consist of locations (latitude - longitude coordinates using a one degree grid system) and several biological and morphological characteristics (information of site, habit , leaf-, floral-, pollination-type etc.). Information used in CHOROL comes from "Flora Neotropica" monographs, other well documented taxonomic revisions and original studies. At present the database consists of more than 100,000 entries (c. 4000 neotropical species, c. 40,000 geographical localities, c. 60,000 annotations) i.e. c. 5 % of the whole angiosperm flora of the neotropics. The considered plant families, numbers of genera and species of our data base and the sources used are listed in the appendix at the end of this paper.

STATCHO is designed to analyze the distribution data in regard to similarities, distribution types, area size frequency, alpha-diversity a.o. For comparison purposes the grid maps of areas with a low collection density can be idealized to their presumably natural size. CROVELLO (1981) defined an Operational Geographic Unit (OGU) as any one unit of the whole set of geographical units to be analized in a study. An Operational Geographical Set (OGS) is the set of all OGUs in a study. Our OGS is the part of the Neotropics between 30° N and 30° S according to the Flora Neotropica base map n° 1 (published by the Institute of Systematic Botany, State University of Utrecht, the Netherlands). One degree squares are used as OGUs (1 724 squares in total).

NIMIS (1990) defined a "Chorogram" as a geographical map reporting the joint distribution of a character set within OGUs. An Operational Character Set (OCS) might be a set of taxa at any hierachic level or ecological data. Chorograms derive from matrices of characters by OGUs.

Results and Discussion

Endemics

Here, our OCS consists of neotropical plant species with narrow distribution, endemics *sensu* GOOD (1974), each occurring in maximally 3 OGUs. 2 082 species were selected from the data base, that means that more than 50% of all registered species can be regarded as endemics !

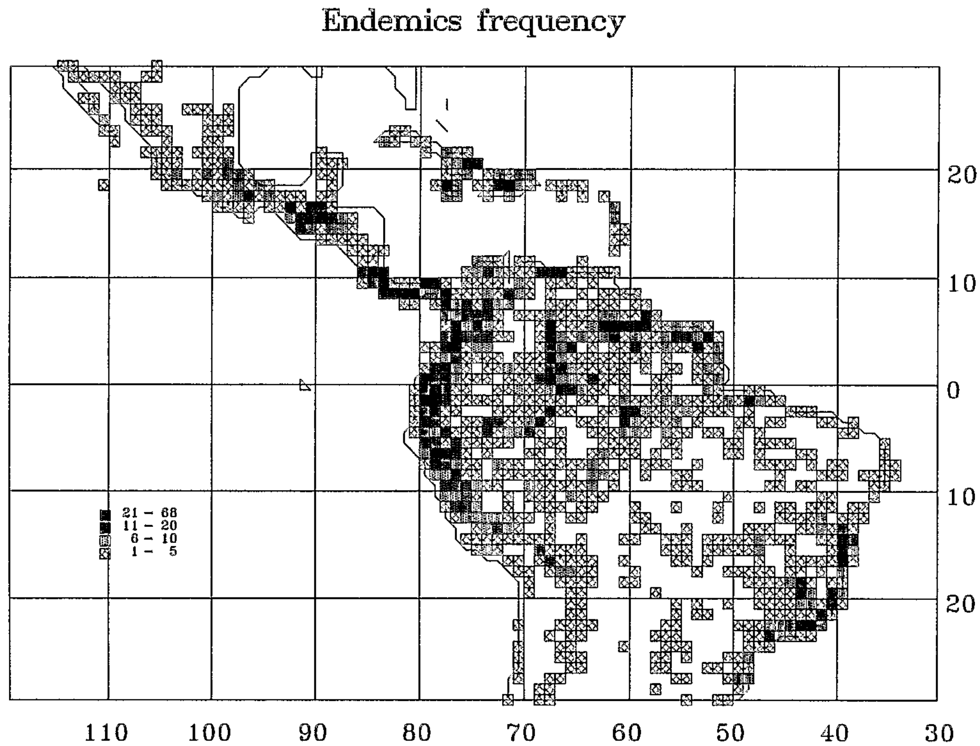

Figure 1

Chorogram of neotropical endemics. The dot maps of 2082 species with 1-3 OGUs are overlayed. The darkness of the grids corresponds to endemics richness per OGU. It is demonstrated by a self-defined, nonlinear 4-class scale (1-5spp. cross hatched, 6-10, 11-20 and more than 20 spp, black).

An overlay of all those (chorogram fig.1) shows their distribution and species richness occurring in each OGU. Regarding the relatively low sample number (5% of neotrop. Angiosperms) one can state that almost every part of the plant mosaic covering the Neotropics contains a large number of endemics. These results relativize the importance of endemism centres and refuge areas to a certain degree.

Nevertheless the here presented map indicates also a certain concentration of endemics in some localities. However, such centers are frequently located at places with high collection density (Rio de Janeiro, Panama, Manaus etc.) similarly stated by Nelson *et al.* (1990). In part they correspond with the possible geographic location of former forest refuges postulated by Haffer (1969). From 10 endemism centres from the Amazon basin reported by Nelson *et al.* (1990) we found a complete correspondence with 5 of our centres, a correspondence in part in 4 cases and one completely different centre, possibly due to a geographical mismatch of data. A more detailed analysis of endemism and "almost endemism" certainly will give a good base for areas of highest biological priority for conservation and certainly will extend and reinforce the data already published by Prance (1990).

Frequency classes

The frequence of size classes (5%, 10%, 15% etc. of the OGS size) was elaborated for all species available in the data base (Fig. 2) in comparison with selected families and genera (Fig. 2, 3). A general pattern could be shown for almost all groups : 70 to 90% of the species of each group had an area size smaller than 5% according to our OGS. All the other size classes had a significantly lower frequence, thus forming a steep exponential function. Only in the Annonaceae (Fig. 2) the distribution is slightly different with relatively many species with large areas. Nevertheless, the high similarity of frequency distribution between the different groups suggests a general pattern valid for many of the larger neotropical plant groups. Of special interest is, that the neotropical flora does not differ essentially from the temperate one in regard to this pattern (Haeupler, 1974). Finally this general regularity seems to confirm the suitability of the selection and the size of our data set.

Chorograms and chorological types

The ability of the program to establish chorograms by the modes of selection, comparison and overlay may lead in the future to well established chorological types ("Arealtypen") sensu Meusel *et al.* (1978). That would mean that species of different genera and families may exhibit the same geographic distribution as well as more or less similar ecological behaviour. This pattern then can be related to historical factors, soil types, climatic conditions and may help to define vegetation types or subunits of otherwise uniform plant communities.

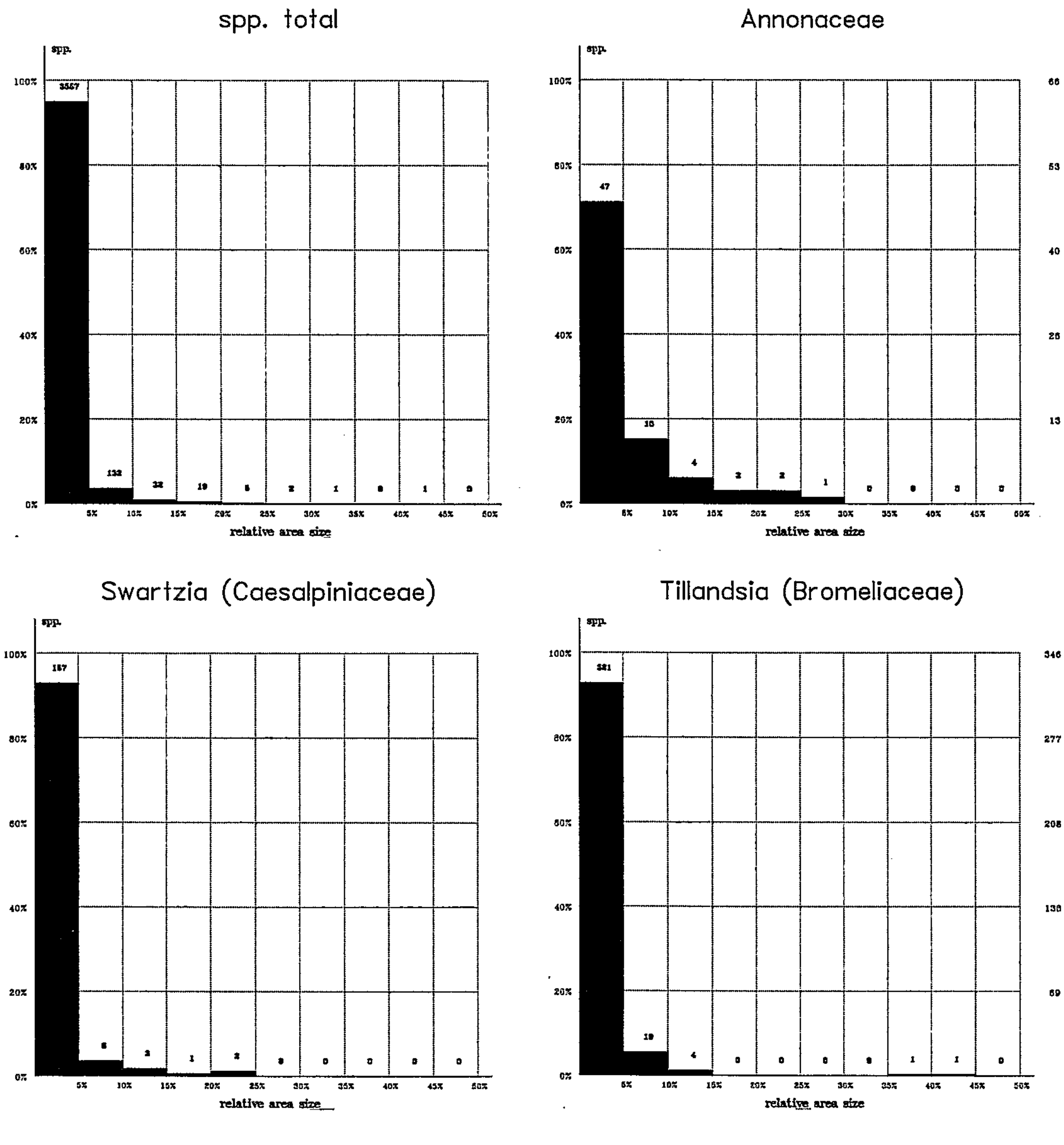

Figure 2

Distribution of frequency classes at different taxonomic levels. Angiosperms, all listed species (top left), Annonaceae (top right), *Swartzia* (Caesalpiniaceae) and *Tillandsia* (Bromeliaceae). Abscissa: Relative area size (100% = 1724 grids, bars represent 5% steps). Ordinate : 100% of species investigated.

We are aware that at the present stage the definition of chorological types still is based also on subjective interpretation such as personal knowledge of certain regions or families and former data from literature. A selection of chorological types based only on mathematical calculations failed so far, partly due to the hardware, partly due to the lack of appropriate algorithms. Nevertheless, the here used method is highly reproducible.

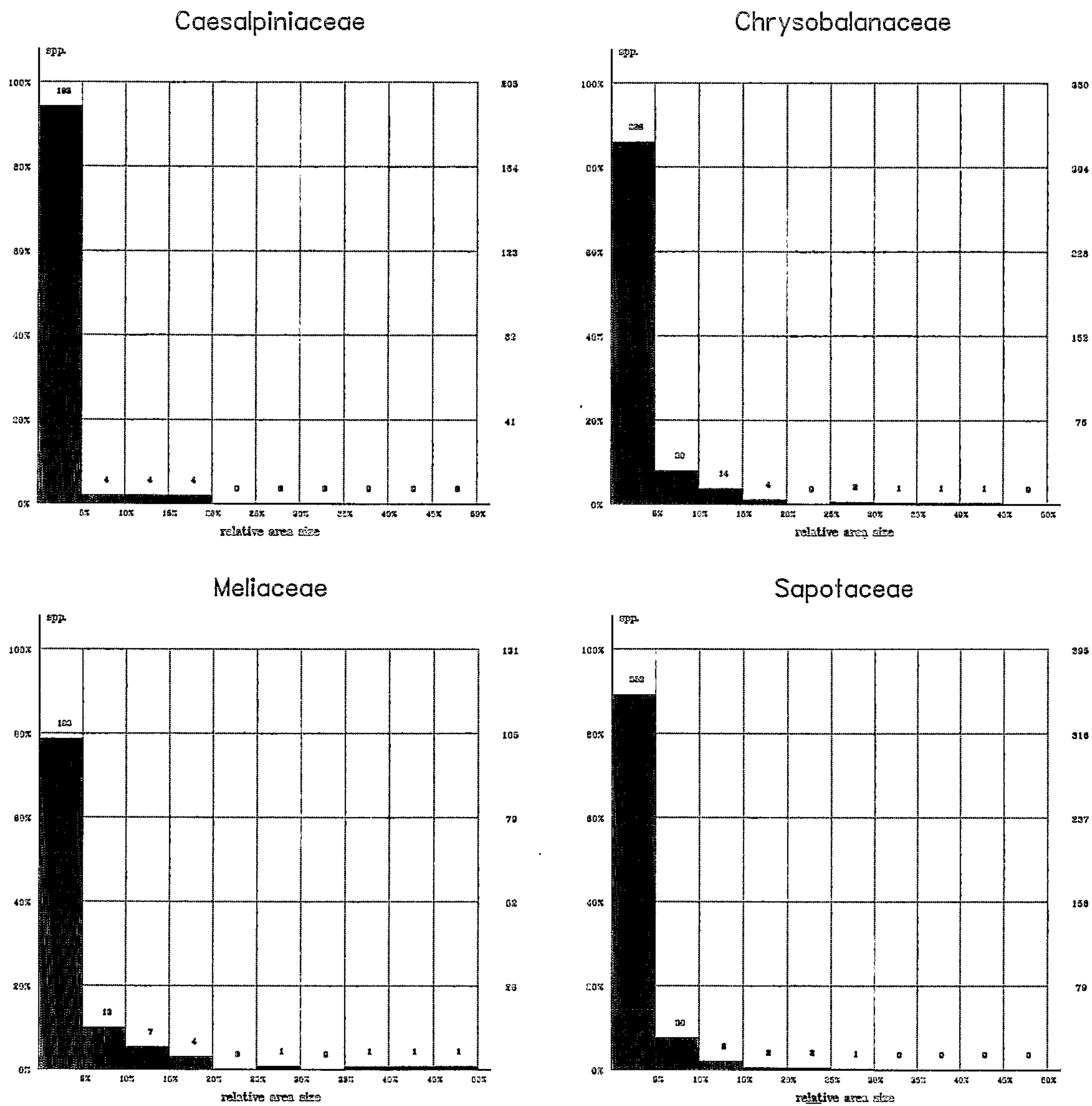

Figure 3
Distribution of frequency classes in different plant families. See also Fig. 2.

1) Our first example (Fig. 4, a), representing a limited mesoamerican rain forest distribution, is based on *Guarea rhopalocarpa* (Meliaceae), a small tree occurring from the lowland to montane rain forests in the isthmus region of Central America (PENNINGTON *et al.*, 1981).

18 further species of different families share this quite limited distribution type. Some of them are pure lowland rain forest plants such as *Amphitecna isthmica* (Bignoniaceae) or the undergrowth herb *Renealmia pluriplicata* (Zingiberaceae), the latter with a further W-amazonian disjunct occurrence. The similarily disjunct *Piper subsessile* (Piperaceae) exhibits an additional grid in N. Venezuela.

Most of the selected species occupy both lowlands and uplands such as *Palicourea purpurea* (Rubiaceae), *Parmentiera macrophylla* (Bignoniaceae) or *Calyptrogyne brachystachys* (Areacaceae), sometimes specialized to secondary growth like *Piper fimbriulatum* (Piperaceae).

2) A second example is provided by a typical patchy central Brazilian distribution (Fig. 4, b) as shown by the still little understood distribution patterns of *cerrado* and *campo rupestre* plants we can

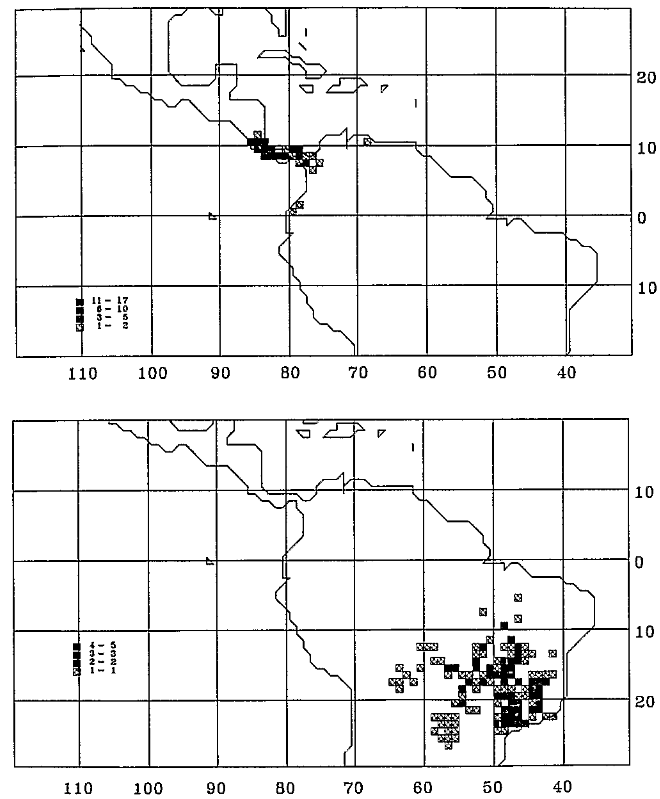

Figure 4

Two different chorological patterns. a. A narrow mesoamerican one based on the geographic distribution of *Guarea rhopalocarpa* and 18 further species which are overlayed in this chorogram. b. A patchy c. Brazilian distribution based on *Banisteriopsis argyrophylla* and 4

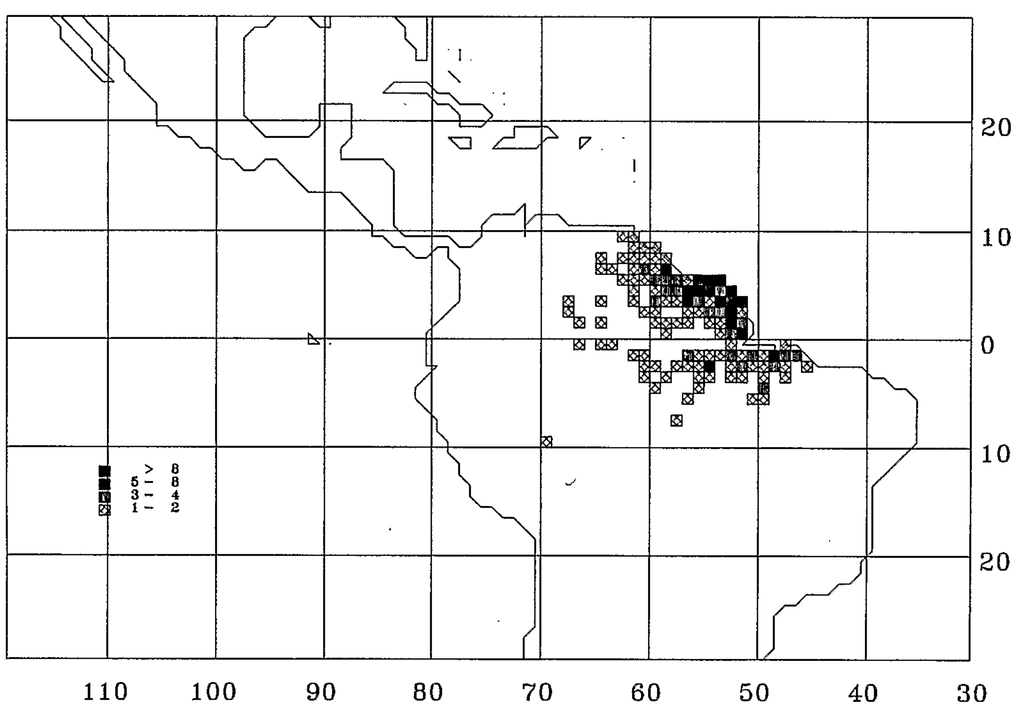

Figure 5

A coastal Guayana-E. Amazon distribution is revealed clearly by *Jacaranda copaia* ssp. *copaia* and 12 further species. In contrast the pattern of *Guarea kunthiana* and 3 further similarly distributed species gives here no clear impression of the chorological type which is outlined in Fig. 6.

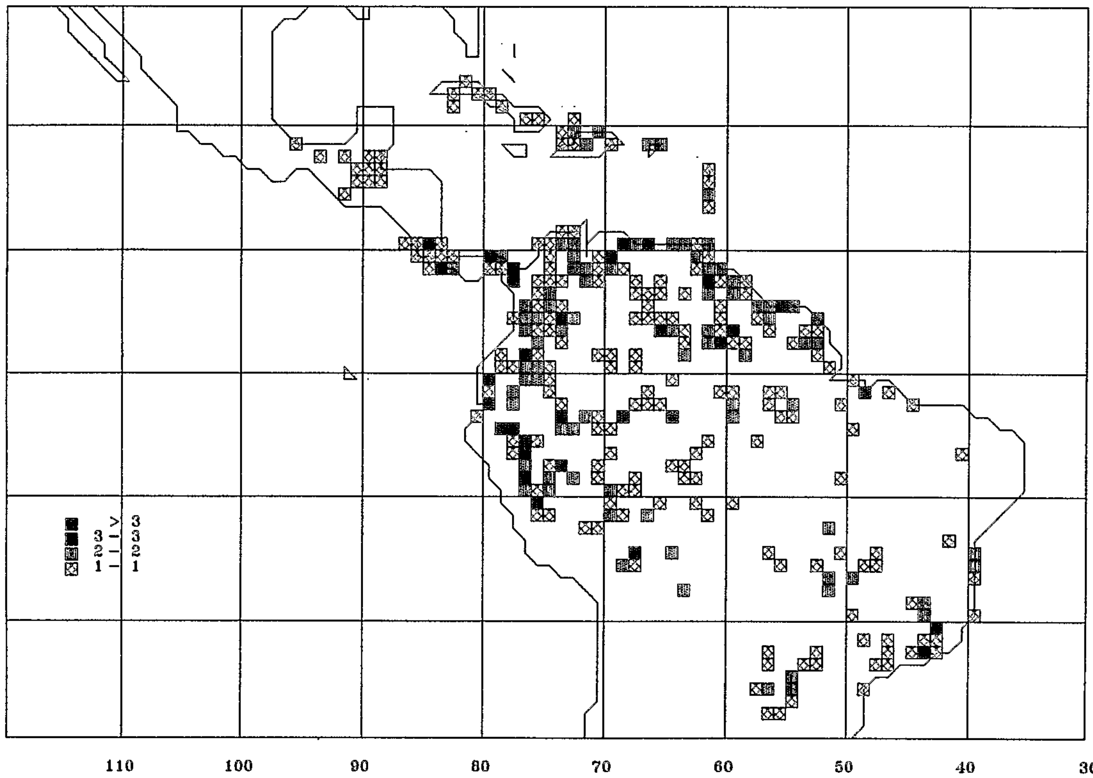

Figure 6

The mathematically idealized geographical distribution of 4 species with a typical widespread disjunct pattern. The black grids are well documented collection areas, the white grids are the presumable natural distribution.

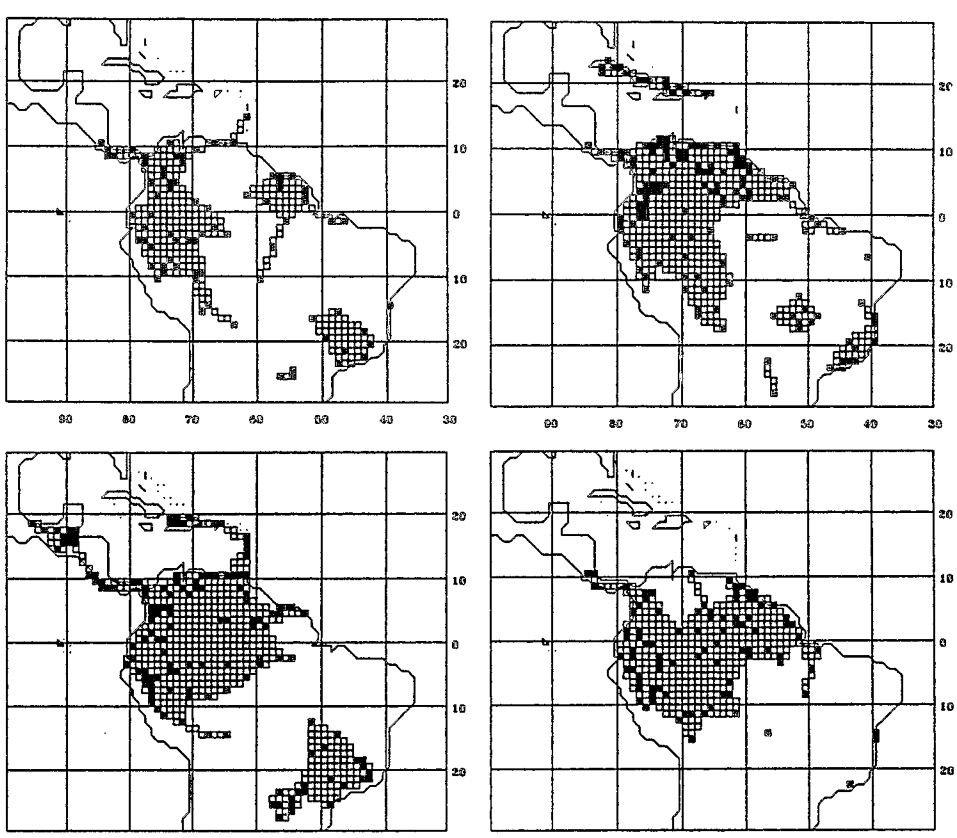

Figure 7

The mathemathoically idealized geographical distribution of 4 species of Meliaceae (see also Fig. 6) with a typical widespread disjunct pattern. The black grids are well documented collection areas, the white grids are the presumable natural distribution calculated by STATCHO with resolution factor 5° (see Data and methods).

demonstrate a typical patchy C. Brazilian distribution (Fig. 4). On the basis of *Banisteriopsis argyrophylla* (Malpighiaceae) four further species share the same pattern, all adapted to the special soils and regular burning, i.e. *B. campestris* and *Couepia grandiflora* (Chrysobalanaceae). Nevertheless we may expect especially within the *campos* areas several smaller and well delimited distribution types.

3) A third chorological type corresponds with the eastern Amazon lowland rain forests (Fig. 5) with a preference to moist or swampy areas as exemplified by *Jacaranda copaia* ssp. *copaia* (MORAWETZ 1982). 12 further species with overall similar ecology were selected by the program STATCHO such as *Rinorea riana* (Violaceae), *Licania majuscula* (Chrysobalanaceae) or *Anaxagorea prinoides* (Annonaceae). Characteristic of this type is the high concentration of different species per grid next to the mouth of the river Amazon which contains several swampy and overflood areas without having true *igapós* and *várzeas*.

4) In contrast with these clear cut distribution types an overlay of the grid maps of *Guarea kunthiana* and 3 further species gives little information (Fig. 6). In this case a comparison of idealized distribution patterns is more helpful (black areas: collection localities; white grids idealized area) and reveals a disjuction between the wider Amazonian area and the coastal rain forest. To a certain extent one can also recognize within these about a disjunction between the Guyanas, the Amazon basin and the Serra do Mar.

Conclusion

It is shown that for an understanding of the biogeography of the Neotropics, there is a need for thorough and computer-aided analysis. According to our first results, we can expect that many of the phytogeographic conclusions drawn up must now be overthought newly.

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BIBLIOGRAPHY

ALLKIN R. & BISBY, F.A. - 1984 - Data bases in systematics. *Systematics Association Special Volume* 26, Academic Press, New York.

ALLKIN R. & WHITE, R.J. - 1988 - Data management models for biological classification. Classification and related methods of data analysis - ed. H.H. BOCK -. North Holland, Amsterdam.

BISB, F.A. - 1984 - Automated taxonomic information systems. Current concepts in plant taxonomy - ed. by V.H. HEYWOOD and D.M. MOORE -, pp. 301-322. *Systematics Association Special Volume* 25, Academic Press, New York.

CROVELLO T.J. - 1981 - Quantitative biogeography: an overview. *Taxon*, 30, 563-575.

GOMEZ-POMPA, A. & NEVLING L.I. Jr. - 1988 - Some reflections on floristic data bases. *Taxon* 37- 3 -, 764-775.

GOOD R. - 1974 - The Geography of Flowering Plants. London: Longman - 4th ed. -.

HAFFER J. - 1969 - Speciation in Amazonian forest birds. *Science* 165, 131-137.

HAEUPLER H. - 1974 - Statistische Auswertung von Punktrasterkarten der GefÑ·pflanzen SÅd-Niedersachsens. *Scripta Geobotanica* 8, p. 141. Verlag E. Goltze KG, Göttingen.

MEUSEL H., JAEGER E., RAUSCHERT S. & WEINERT E. - 1978 - Vergleichende Chorologie der zentraleuropeaischen Flora. Gustav Fischer, Jena.

MORAWETZ W. - 1982 - Morphologisch-îkologische Differenzierung, Biologie, Systematik und Evolution der neotropischen Gattung Jacaranda - Bignoniaceae -. ôsterr. Akad. Wiss. Denkschriften 123.

MORAWETZ W. & EBSTER D. - 1989 - CHOROL und STATCHO, zwei neue Computerprogramme zur Darstellung und vergleichenden Analyse von chorologischen Daten fÅr die Neotropen. *Flora* 182, 419-434.

NIMIS P. J. - 1990 - The use of chorograms in quantitative phytogeography and in phytosociological syntaxonomy. *Fitosociologia*. 25, 69-87.

PANKHURST R. J. - 1988 - Data base design for monographs and floras. *Taxon* 37, 733-746.

PENNINGTON T. D., STYLES B. T., TAYLOR D. A., - 1981 - A monograph of Neotropical Meliaceae. *Flora Neotropica*. 28.

PRANCE G. T. - 1990 - Consensus for conservation. *Nature*. 345, 384.

REICHL E.R. - 1986 - Computers in Biogeography. *Schriftenreihe für Informatik*. Universitaetsverlag R. Trauner, Linz.

APPENDIX

Overview about the families, genera, and species (brackets) used in this study. Authors are only recorded in part of the references.

Acanthaceae (1/3), Daniel 1988 ;
Annonaceae (5/66), Maas & Westra 1985, Morawetz 1985 ;
Arecaceae (9/100), Wessels Boer 1968, Kubitzki 1987, Moraes & Henderson 1990, Henderson 1990 ;
Asteraceae (2/29), Powell 1965, Bolick 1991 ;
Alzateaceae (1/2), Silverstone & Graham 1986 ;
Bignoniaceae (5/85), Gentry 1980,1989 ;
Boraginaceae (1/3), Todzia 1989 ;
Bromeliaceae (1/284), Till 1984 ;
Burmanniaceae (11/52), Maas *et al.* 1986 ;
Caesalpiniaceae (5/205), Da Silva 1986, Kubitzki 1987, Cowan 1968 ;
Campanulaceae (2/11), Ayers 1990 ;
Cecropiaceae (2/198), Berg *et al.* 1990 ;
Chloranthaceae (1/40), Todzia 1988 ;
Chrysobalanaceae (8/386), Prance 1989 ;
Clusiaceae (1/3), Kubitzki 1987 ;
Cochlospermaceae (2/9), Poppendieck 1981 ;
Combretaceae (2/6), Kubitzki 1987 ;
Connaraceae (6/96), Forero 1976, 1983 ;
Convolvulaceae (1/2), Eckenwalder 1989 ;
Cyperaceae (2/19), Thomas 1984, Wheeler 1990 ;
Caryocaraceae (1/17), Prance & Da Silva 1973 ;
Dichapetalaceae (2/12), Prance 1972 ;
Dryopteridaceae (1/16), Moran 1991 ;
Elaeocarpaceae (1/4), Bricker 1991 ;
Ericaceae (3/119), Luteyn 1983, 1984 ;
Euphorbiaceae (2/7), Breckon 1979, Webster 1984 ;
Fabaceae (4/81), Da Silva 1976, Grear 1978, Lee *et al.* 1989 ;
Gentianaceae (2/20), Maas & Ruyters 1986 ;
Gesneriaceae (1/4), Clark 1990 ;
Humiriaceae (1/1), Kubitzki 1987 ;
Lauraceae (3/56), Kubitzki & Renner 1982, Kubitzki 1987 ;
Lecythidaceae (7/84), Prance & Mori 1979, Mori & Prance 1981 ;
Loasaceae (1/2), Clark 1990 ;
Malpighiaceae (6/112), Anderson 1982, Gates 1982, Kubitzki 1987 ;
Maranthaceae (4/39), Anderson 1977 ;
Melastomataceae (6/64), Judd & Beaman 1988, Renner 1989, 1990, 1991 ;
Meliaceae (9/132), Pennington et *al.* 1981 ;
Mimosaceae (1/16), Hopkins 1986 ;
Moraceae (10/67), Berg 1972 ;
Musaceae (1/50), Anderson 1985 ;
Myristicaceae (1/35), Rodrigues 1980 ;
Myrtaceae (7/49), Landrum 1986 ;
Ochnaceae (1/1), Kubitzki 1987 ;
Olacaceae (6/12), Sleumer 1984 ;
Orchidaceae (2/12), Dressler 1965, Barringer 1991 ;
Piperaceae (1/54), Tebbs 1990 ;
Poaceae (3/17), Clark 1990, Zuloaga & Judziewic 1991 ;
Proteaceae (2/2), Kubitzki 1987 ;
Rubiaceae (7/88), Kirkbride Jr. 1976, Rogers 1984, Taylor 1989 ;
Rutaceae (4/56), Kaastra 1982 ;
Rhabdodendraceae (1/2), Prance 1972 ;
Sapotaceae (11/395), Penn 1990 ;
Scrophulariaceae (3/257), Molau 1988, 1990 ;
Simaroubaceae (1/1), Kubitzki 1987 ;

Solanaceae (1/23), Roe 1967, Knapp 1989, 1992 ;
Styracaceae (1/3) ;
Trigoniaceae (1/29), Lleras 1978, Penn 1990 ;
Triuridaceae (4/14), Maas & RÀbsamen 1986 ;
Theophrastaceae (1/43), Stahl 1991 ;
Ulmaceae (1/9), Todzia 1989 ;
Violaceae (1/50), Hekking 1988 ;
Vochysiaceae (1/1), Kubitzki 1987 ;
Winteraceae (1/2), Ehrendorfer 1979 ;
Zingiberaceae (2/69), Maas 1977.