

Uses and misuses of floras

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Summary

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Questions involving the history and evolution of groups of taxa, such as those on biogeography and speciation, are among the most commonly asked in systematics. Usually the data necessary to answer these types of questions are believed to be available only from studies of individual monophyletic groups. However, some information on biogeography and speciation can be obtained from floristic studies under certain criteria, e.g., the use of natural areas, uniform descriptions, and detailed distribution information. If these criteria are not met, detailed questions about evolution are not appropriate. However, even when evolutionary questions can not be addressed directly, it is possible to use information contained in floras, such as the numbers of species in different groups or areas, to provide interesting comparative information on species richness and areas of endemism. However, numbers alone tell us little about the value of the area in terms of biological diversity or its history and they should not be used as the sole statistic in determining the "importance" of an area.

Introduction

Early in the history of taxonomy, floras were a popular and respected form of scientific study. Recently, during the age of biosystematics, they fell into disfavor and were treated as bibliographies rather than science. Now as world concerns about biological diversity increase, floras are in the limelight once again. Systematists, conservationists, ecologists, evolutionary biologists, and many others need to be able to identify all types of living organisms. [The comments in this paper are applicable to surveys of all types of organisms.] Although floras are designed for species identification, they can provide information on a number of other topics. For example, they can be used for phylogenetic analysis to produce cladograms to study biogeography and establish patterns of speciation, to locate areas of high species richness, and to indicate areas that need further study.

There are many different types of floras, each holding different implications for those that organize and use them. Some floras are more like a series of monographs with the treatments being produced one at a time by an 'expert' in that particular group and as a result they usually contain more information, but they usually take a long time to complete. At the other extreme are manual-type floras which usually have fewer authors and are published in a few volumes over a relatively short period of time. However, every flora is unique and so anyone wishing either to make use of an existing or ongoing flora or to develop a set of guidelines for a new one must think carefully about the parameters under which the flora was, or will be, designed.

Evaluating floras

When evaluating a flora for its utility in producing information for phylogenetic analysis there are several considerations. The most important one is that the area

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encompassed by the flora should be equal to or greater than some "natural area" (floristic province); an area with historical significance. It is possible for a flora to treat an area that includes several natural areas. For instance, a flora of Brazil would describe the vegetation of several natural areas found completely within this political area such as the south-eastern coastal forest, the caatingas, campinas, and the Planalto. With the appropriate distributional information one could extract from a flora of Brazil the information one needed to produce a cladistic phylogeny to be used for evolutionary studies of these natural areas. Conversely, it is also possible to combine two or more floras to produce information on a natural area. When it is necessary to combine the information from more than one flora in order to study a natural area then either the same experts should prepare the treatments for the groups in all of the floras or discrepancies should be indicated. This type of coordination has been done successfully in the modern treatments of *Flora of tropical East Africa* and *Flora zambesiaca*. Detailed distributional information, when used in conjunction with habitat information, provides one with the ability to distinguish between what are actually sympatric taxa and those that are physically close but occupy different life zones (sympatric vs. synoptic).

The taxa used in the study should be monophyletic (when the information is available) and they must have a phylogenetic arrangement. Monophyletic groups are a reflection of evolution and the phylogenetic arrangement allows those who wish to evaluate characters for use in evolutionary studies to evaluate characters from related taxa. Alphabetical arrangements can place the *Graminae* near the *Gunneraceae* or *Goodeniaceae* and the three legume families can end up in separate volumes.

A few additional items aid the evolutionary biologist. Descriptions should be consistent and as general as possible, i.e. not diagnostic. It is especially difficult to determine what characters are apomorphic if one does not know the scope of the characters for the entire taxon. Endemic taxa should be clearly specified and overall numbers of endemic taxa in each family should be discussed. When possible, the most closely related taxon (sister group) of endemic taxa and its distribution should be indicated (also suggested by Morin & al., 1989). Any information on relationships among taxa is useful because it provides a starting point for searching for the outgroup and the outgroup allows one to evaluate the characters upon which the taxa are based. Also, literature citations provide sources for further information. Finally, information such as phenology, pollinators, and ecological life history or autecology greatly increases the utility of floras, both in providing information for studies and in pointing out interesting problems that others may investigate.

These suggestions are best illustrated by some examples. The examples on biogeography and speciation are taken from the *Manual of the flowering plants of Hawai'i* (Wagner & al., 1990), *Flora of the Venezuelan Guayana* (Pruski, MS), and *Flora of the Guianas* (see Funk, 1991, for references). The examples of species richness and endemism are taken from the following sources: Arizona (Kearney & Peebles, 1951; Howell & McClintock, 1960), Brazilian Amazon (H. Robinson, pers. comm.), California (Munz, 1959 & 1968), Ceylon (Sri Lanka) (Grierson, 1980: 111-278), Colombia (S. Díaz, pers. comm.), Guatemala (Nash & Williams, 1976), Guianas (Funk & al., 1992), Hawai'i (Wagner & al., 1990), Intermountain area (Cronquist, MS), Marquesan Archipelago (Wagner, 1991), Missouri (Steyermark, 1963), Natal (Hilliard, 1977), Nepal (Funk, MS), New Zealand (Allan, 1961), Novo Galicia (McVaugh, 1984), Peru (Brako & Zarucchi, 1993), Pacific Northwest (Cronquist, 1955), Panama

Table 1. Data matrix for Hawaiian *Madiinae* (a = 0 & 1).

Taxon	1 1 1 1 1 1 1 1 1																		
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
<i>Madia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dubautia</i> § <i>Venoso-ret.</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
§ <i>Raillardia</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
§ <i>Dubautia</i>	0	0	0	0	0	0	0	a	0	0	0	0	0	0	0	0	0	0	a
<i>Wilkesia gymnoxyphium</i>	0	1	0	2	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0
<i>hobbyi</i>	0	1	0	2	0	0	0	1	1	0	0	1	0	0	0	1	0	0	0
<i>Argyroxiphium grayanum</i>	0	2	0	1	1	0	1	1	1	a	3	0	1	0	0	0	1	1	0
<i>virescens</i>	0	1	0	1	1	0	1	1	1	0	2	0	1	1	1	0	1	1	0
<i>kauense</i>	1	1	1	1	1	1	1	1	1	1	3	1	1	0	0	0	1	1	0
<i>caliginis</i>	1	1	1	1	0	1	1	0	2	0	1	0	0	1	1	0	1	1	0
<i>sandwicense</i>	1	1	1	1	2	1	1	1	1	0	1	0	2	0	0	0	1	1	0

(D'Arcy, 1975), Queen Charlotte Islands (Calder & Taylor, 1968: 521-552), Venezuela (Aristuegieta, 1964), and the Venezuelan Guayana (Pruski, MS).

The Hawaiian data for the analysis were extracted from the recently published *Manual of the flowering plants of Hawai'i* (Wagner & al., 1990). The Hawaiian groups studied were *Wilkesia* A. Gray and *Argyroxiphium* DC., and their outgroups *Dubautia* Gaudich. and *Madia* Molina. These data are part of a much larger study of the phylogeny of a number of Hawaiian plant genera (Funk & Wagner, MS).

Characters were polarized by outgroup comparison and the analyses were performed by the Macintosh version of PAUP 3.0q (Swofford, 1990). For a detailed

Table 2. Character list for *Wilkesia* and *Argyroxiphium*.

1. Pubescence: green = 0, gray = 1
2. Leaves: elliptic to linear = 0, narrowly swordshaped = 1, elliptically swordshaped = 2
3. Leaf cross-section: round = 0, triangular = 1
4. Leaf base: free = 0, partially connate = 1, fused and whorled = 2
5. Rachis: thin = 0, proximally fistulose = 1, fistulose = 2
6. Veins: prominent = 0, obscure = 1
7. Ray florets: absent = 0, present = 1
8. Disc florets: glandular = 0, glands absent = 1
9. Plant senescence after flowering: no = 0, monocarpic & polycarpic = 1, no evidence of monocarpy = 2
10. Decomposed leaf bases: lost = 0, retained = 1
11. Ventral pappus length: same as dorsal = 0, shorter = 1, greatly reduced = 2, absent = 3
12. Rosettes on elevated woody stems: no = 0, yes = 1
13. Number of heads per inflorescence: small = 0, medium = 1, large = 2
14. Disc floret color: white or yellow (sometimes tinged with purple) = 0, purple = 1
15. Inner involucre bract: enfolding = 0, not = 1
16. Corolla tubes: glabrous = 0, setulose = 1
17. Pectic channels in leaf: no = 0, yes = 1
18. Vascular bundles: many = 0, few = 1
19. Pappus: scales = 0, aristae = 1

explanation of cladistic methods see Wiley & al. (1991). Methods used in the biogeography and speciation studies are described in Funk & Brooks (1990). Information on speciation in the Venezuelan Guayana was taken from Funk & Brooks (1990).

Examples

The *Manual of the flowering plants of Hawai'i* is well suited to foster studies on speciation and biogeography. The flora encompasses a natural area (floristic province), the authors have made an attempt to recognize monophyletic groups, listed possible relationships, and cited references.

Dubautia, *Wilkesia*, and *Argyroxiphium* have long been recognized as a monophyletic group in the *Compositae* (tribe *Heliantheae*, subtribe *Madiinae*) (Hillebrand, 1888; Keck, 1936; Carr, 1985). Originally *Dubautia* was the most likely outgroup for an analysis of *Wilkesia* and *Argyroxiphium*, but after several attempts at analysing the data, no synapomorphy for *Dubautia* was found. This finding, that *Dubautia* is

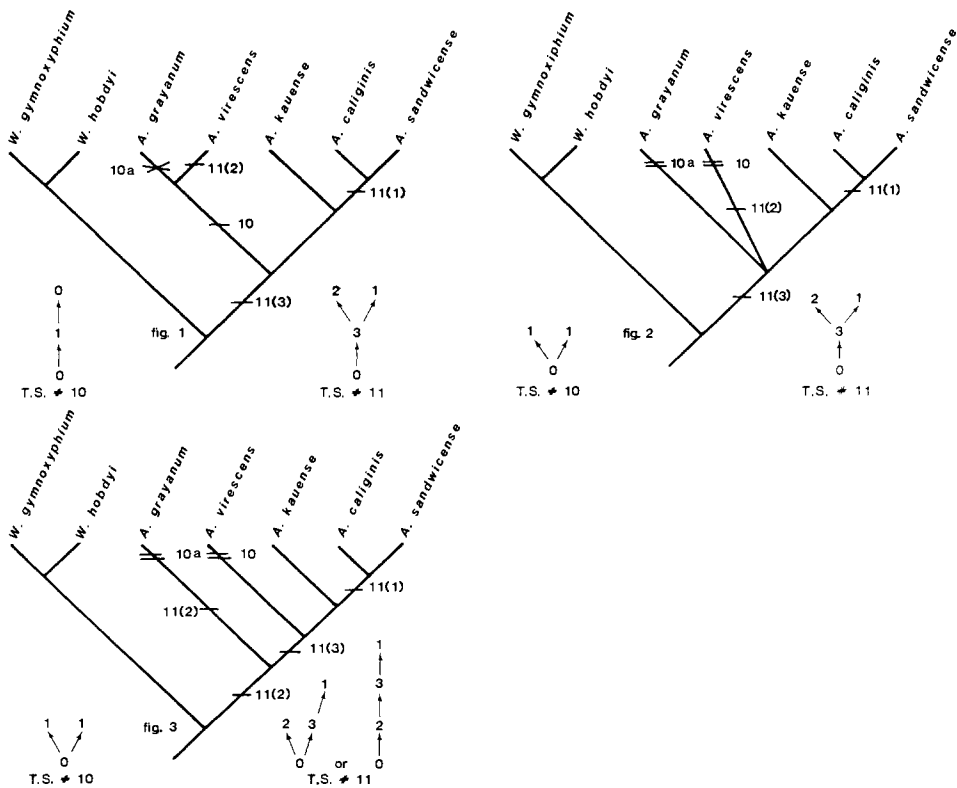


Fig. 1-3. Three most parsimonious cladograms of the ingroup *Wilkesia* and *Argyroxiphium*. 1, *A. grayanum* and *A. virescens* form a clade. 2, The relationship between *A. virescens* and *A. grayanum* is unresolved. 3, *A. grayanum* is the basal branch in *Argyroxiphium*. *Wilkesia* is the monophyletic sister group of *Argyroxiphium* in all three cladograms. 10a identifies this character as polymorphic.

Table 3: Numbers of species in the *Compositae* (see Methods section for references).

Area (km ²) ¹	Species number	Species per 1000 km ²	Genus number	Species per genus	Endemic species
Arizona (297,850)	523	1.76	135	3.8	few (5 %)
California (409,220)	693	1.69	143	4.8	many (40 %)
Intermountain (641,284)	600	0.94	130	4.6	few-some
Queen Charlotte Islands (9,324)	42	4.50	29	1.4	0
Missouri (154,623)	308	1.99	85	3.6	0
Pacific NW (569,800)	500	0.88	104	4.8	few (9 %)
Nueva Galicia (142,450)	750	5.27	144	5.2	very few (< 5 %)
Guatemala (108,780)	593	5.45	135	4.4	some (27 %)
Panama (77,700)	280	3.60	111	2.5	few (13 %)
Venezuela (911,680)	607	0.67	133	4.5	many (40 %)
Ven. Guayana (414,400)	260	0.63	90	2.9	many (38 %)
Colombia (1,139,600)	2500	2.19	–	–	many
Peru (1,282,050)	1433	1.12	220	6.5	many (50 %)
Guianas (448,070)	185	0.41	75	2.5	very few (< 5 %)
Brazilian Amazon (3,367,000)	150	0.04	–	–	very few (< 5 %)
Hawaii (164,465)	91	0.55	9	9.0	most (99 %)
Marquesas (1,243)	12	9.65	3	4.0	most (92 %)
New Zealand (268,583)	240	0.89	29	8.3	most (92 %)
Natal (88,060)	640	7.27	113	5.9	few (8 %)
Nepal (139,860)	390	2.79	109	3.6	few (6 %)
Ceylon (65,527)	133	2.03	60	3.6	some (19 %)

¹ The submitted version of Table 3 gave the area sizes in square miles, rounded to the nearest thousand. In typesetting they were converted to km². These values should also be considered an approximation.

(Farris, 1980) one can optimize the area cladogram (for method see Funk, 1982; Funk & Brooks, 1990) and produce a biogeographic hypothesis. According to this hypothesis (Fig. 4) the ancestor of the *Argyroxiphium-Wilkesia* clade was on Kaua'i with later colonization of Maui followed by speciation. The predominant mode of speciation appears to be dispersal followed by allopatric speciation although there are two possible instances of vicariance. The pattern is Kaua'i to Maui followed by the development of several anatomical and morphological apomorphies that define the genus *Argyroxiphium*. Some part of this ancestor on Maui developed a silvery gray color and triangular leaves and some member of this silvery gray group dispersed to south Hawai'i and developed into *A. kauense* (Rock & Neal) O. Deg. & I. Deg. The silvery gray ancestor on Maui changed slightly gaining ventral pappus and then there is an indication that either a vicariant or dispersal event took place that isolated part of it on east Maui and part on west Maui. The west Maui individuals developed into *A. caliginis* C. N. Forbes and the east Maui group into *A. sandwicense* DC. Later *A. sandwicense* dispersed to north Hawai'i and changed slightly and is now recognized at the subspecific level. During the same period the Maui species *A. grayanum* separated, either by dispersal or vicariance, into east and west populations that are now subspecies. It should be noted that east and west Maui have very different geologic histories with east Maui being approximately 1 million years younger.

Other floras can be used for similar types of studies. The *Flora of the Guianas* is monographic in nature and should be easy to use for studies of biogeography and speciation. However, the area the flora covers is not a natural one in that it occupies only part of a natural area called the Guiana Shield. The Guiana Shield covers north-eastern South America more or less east of the Orinoco River / Rio Negro and north of the Amazon River. In addition, the format of the flora does not allow much of the detailed discussion of morphological variation and distribution that occurs outside of the borders of Guyana, Surinam, and French Guiana. Part of the problem can be corrected because there is a flora of the Venezuelan Guayana in progress (Steyermark & al., 1994). This flora covers Venezuela south and east of the Orinoco River / Rio Negro up to the Guyana and Brazilian borders. However, some problems persist such as the lack of detailed information mentioned above and because part of northern Brazil is still not covered and the Venezuelan project and in contrast to the *Flora of the Guianas* it has short descriptions. Thus, the treatments are not directly equivalent even when produced by the same individual.

Previous studies of the biogeography and speciation of the *Compositae* of the Guiana Shield (Funk & Brooks, 1990) analysed data from a combination of descriptions from the *Flora of the Guianas* (Funk, 1991; Funk, MS) and ongoing work on the Venezuelan Guayana (Pruski, MS). The Guiana group studied in detail was *Stenopadus* Blake and the preliminary results have been published (Funk & Brooks, 1990) along with less extensive information on other composite genera. (Because the treatments from the two floras are not yet published data on additional groups are not yet available.) These preliminary studies indicate that, while some groups show a vicariant pattern of allopatric speciation, other species are clearly the result of four different dispersal patterns followed by allopatric speciation.

Both the *Manual of the flowering plants of Hawai'i* and the *Flora of the Guianas - Flora of the Venezuelan Guayana* have proven to be useful for asking questions about speciation and biogeography, primarily because they satisfy some of the criteria listed in this paper which are necessary for such investigations.

Species richness and biological diversity

When the information needed to ask questions about biogeography and speciation in the manner suggested above is not available, other types of questions can be asked. Data from floras and florulas have been the basis of many papers (e.g., Balslev & al., 1987; Gentry, 1986) using numbers of species to make estimates on species richness, family importance and the relative importance of one area over another. However, numbers alone can be misleading.

In analysing floras and florulas one must work at the species level. Because of the differences in the size of various taxa and due to different taxonomic treatments, higher level categories are impossible to compare (Signor, 1985). Table 3 evaluates the ability of numbers of species to impart information about an area using the *Compositae* as an example. Although this is only one family, it is a good one to study because it is cosmopolitan in its distribution, common in both temperate and tropical areas, and large, having approximately 23,000 species.

Table 3 shows that when the number of species has been corrected for size of the area of the flora (number of species per 1000 km²) there is a big difference in the numbers ranging from the higher numbers such as 9.65 in the Marqueses, 7.27 in the Natal and 5.45 in Guatemala to low numbers of 0.55 in Hawai'i, 0.41 in the Guianas and 0.04 in the Brazilian Amazon. Some of these differences might be predicted because it is now known that the *Compositae* in the Guianas and the Brazilian Amazon are a depauperate flora and that Guatemala and Natal are relatively rich. However Hawai'i and the Venezuelan Guayana have rich and interesting *Compositae* floras and they have ratios of 0.55 and 0.63, respectively. In contrast, Panama has a predominately weedy and relatively uninteresting *Compositae* flora and it has a ratio of 3.6, probably because elements from the northern Central American and South American floras come together in this area. The number of species per genus also is not particularly informative; Panama and the Venezuelan Guayana both have low numbers. Finally, even the number of endemic species is not reliable. The *Flora novo-galiciana* covers a very interesting area of the Sierra Madre del Sur, but it has a very low level of endemism because, even though many of the genera and species have the heart of their distribution in this area, they also range elsewhere.

If one tries to control one of the variables there is still no obvious pattern. For instance, one can look at all areas that have 600-650 species and compare their size which ranges from large, such as the Intermountain area and Venezuela (641,284 and 911,680 km²) to small, such as Natal and Guatemala (88,060 and 108,780 km²). Likewise one can control the area size and investigate species number. For areas between 388,500 and 518,000 km² one can have many species, such as California with 693, or few species, such as the Guianas with 185.

The same type of results were obtained from species-area curves using species vs. log/area (MacArthur & Wilson, 1967; Williamson, 1981). A regression analysis of species on the log area found that the amount of variation explained was only approximately 16 % (adjusted squared multiple $r = 0.155$) indicating that there is minimal, if any, predictability in this data set (Wilkinson, 1990).

Numbers such as those found in Table 3 are frequently used in discussions of biodiversity. Recently teams have been set up to perform quick surveys of areas and make estimates of diversity based on species richness (Conniff, 1991), and often family importance values (FIV) are assigned to areas based on numbers alone (Mori

& Boom, 1987). However, biodiversity is a much more complex concept and cannot be defined by numbers alone. Very different explanations can exist for the same number (similar observations have been made by Vane-Wright & al., 1991). Fig. 5 shows a clade with five species in an area, but the knowledge of the total range of the species is necessary to help evaluate the importance of that number. Area A has five widespread species, typical of *Compositae* in the Guianas, area B has five endemics, typical of the *Compositae* in Hawai'i and some of the *Compositae* of the tepui area of the Guayana, and area C is an example of a mixed pattern of distribution typical of some Andean *Compositae*. Certainly, knowing the ranges of the species involved greatly increases our ability to evaluate the biodiversity of an area.

When at all possible, knowledge of the phylogeny for some of the groups found in an area can aid in interpreting the numbers. Fig. 6 shows that even when all five species in a group in a certain area are endemic there can be three different phylogenetic patterns. Area A shows allopatric speciation from five different clades, a pattern common in the Guianas. Area B has one introduction (either vicariant or dispersed) followed by radiation, a pattern common on the individual islands in Hawai'i. Finally, area C shows that sometimes the scenario in area B is followed by movement out of the area, a pattern common for some *Compositae* groups in the Guayana.

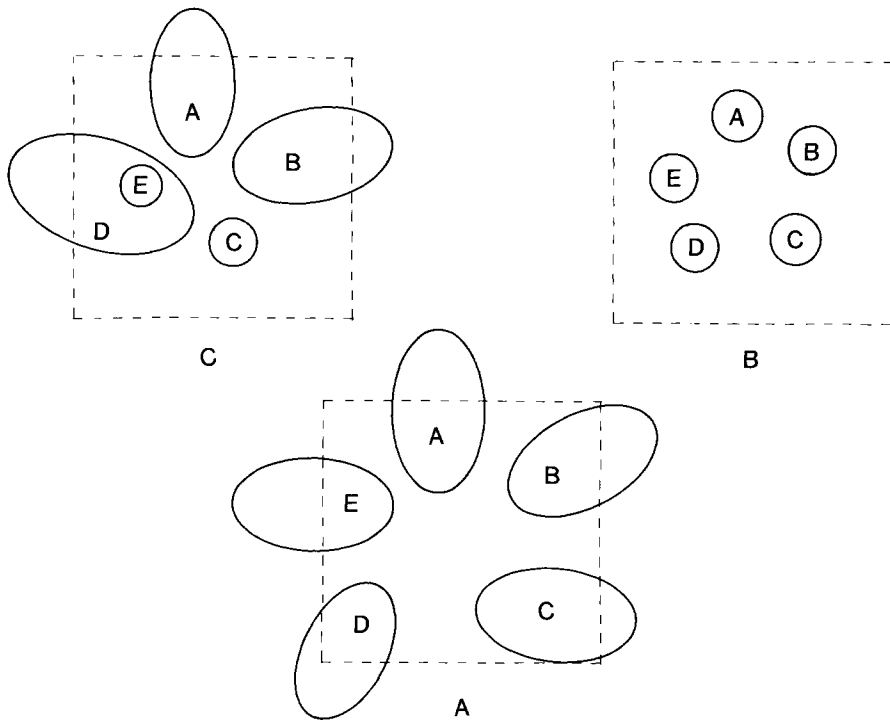


Fig. 5. Species distributions. Area A has five species that are broadly distributed. Area B has five species that are endemic. Area C has five species two of which are endemic and three are broadly distributed.

The observations made from Table 3 and Fig. 5-6 are important when one considers that numbers such as these are taken from floras and faunas are used to make decisions about which areas are 'important' and worthy of protection and which ones are 'less important'. The only way to really determine how interesting an area is to combine a knowledge of the history of the area with some knowledge about the total distribution and phylogeny of some or all of the groups of organisms involved.

Conclusions

Flora projects should be structured around natural areas. If this is not possible then a flora should encompass an area that contains more than one natural area along with the detailed distributional data required to extract the necessary information. Statistics on the amount or level of endemism and numbers of species should be based on natural areas within the flora and not on the flora as a whole. Species that are outside the flora area but part of an otherwise endemic group should be included in the totals, otherwise statistics will have little value for estimating the level of endemism of an area. Each natural area of the flora should have a short introductory chapter that includes the number of species, amounts of endemism and a discussion of the distribution patterns, and a short evaluation of the flora of the area. Each family should contain the same type of information. In addition, any information available on total

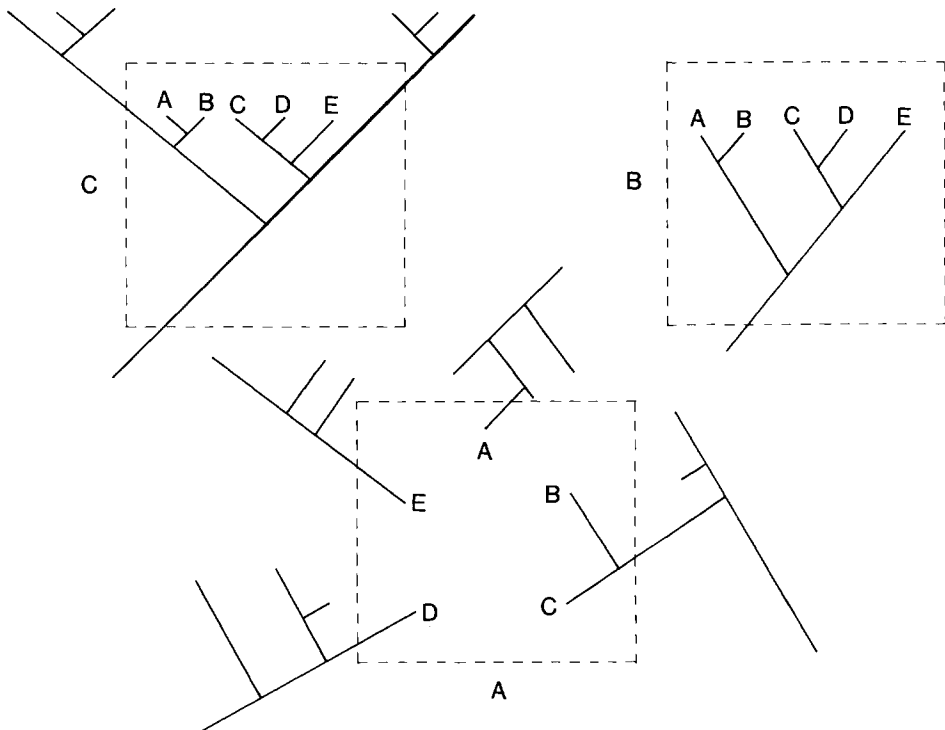


Fig. 6. Species relationships. Area A has five species from four different clades. Area B has five species that form a monophyletic group. Area C has two endemic clades that form a paraphyletic group.

distributions, morphological variation and relationships should be included. Taxa should be monophyletic and should be treated in phylogenetic order.

Interpreting the numbers of species from a flora to make estimates of species richness and biodiversity can lead to errors. All such information must be evaluated in conjunction with knowledge of the history of the area and the phylogeny and evolution of the groups involved.

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Literature cited

- Allan, H. H. 1961. *Flora of New Zealand*, 1. Wellington.
- Aristuegieta, L. 1964. *Flora of Venezuela* [Compositae]. 10(1,2). Edicion especial del Instituto Botanico, Ministerio de Agricultura y cria, Caracas.
- Baldwin, B. G., Kyhos, D. W. & Dvorak, J. 1990. Chloroplast DNA evolution and adaptive radiation in the Hawaiian silversword alliance (*Asteraceae*-*Madiinae*). *Ann. Missouri Bot. Gard.* 77: 96-109.
- Balslev, H., Luteyn, J., Øllgaard, B. & Holm-Nielsen, S. B. 1987. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* 92: 37-57.
- Brako, L. & Zarucchi, J. 1993. Catalogue of the flowering plants and gymnosperms of Peru. *Monogr. Syst. Bot. Missouri Bot. Gard.* 45: 103-189.
- Calder, J. A. & Taylor, R. L. 1968. *Flora of the Queen Charlotte Islands*, 1. Ottawa.
- Carr, G. D. 1985. Monograph of the Hawaiian *Madiinae* (*Asteraceae*): *Argyroxiphium*, *Dubautia*, and *Wilkesia*. *Allertonia* 4: 1-123.
- Conniff, R. 1991. RAP: on the fast track in Ecuador's tropical forest. *Smithsonian Mag.*, June: 36-49.
- Cronquist, A. 1955. *Compositae*. Pp. 1-343 in: Hitchcock, C. L., Cronquist, A., Ownbey, M. & Thompson, J. W. (ed.), *Vascular plants of the Pacific Northwest*, 5. Seattle.
- D'Arcy, W. G. 1975. Flora of Panama, 9. *Ann. Missouri Bot. Gard.* 62.
- Farris, J. S. 1980. Methods for computing Wagner trees. *Syst. Zool.* 19: 83-92.
- Funk, V. A. 1982. Systematics of *Montanoa* (*Asteraceae*: *Heliantheae*). *Mem. New York Bot. Gard.* 36: 1-135.
- 1991. The *Compositae* of the Guianas, I: *Heliantheae* (*Heliantheae*, *Tageteae*, *Coreopsi-deae*). *Rhodora* 93: 256-267.
- & Brooks, D. R. 1990. *Phylogenetic systematics as the basis of comparative biology*. Washington & London.
- , Robinson, H. & Pruski, J. 1992. *Asteraceae*. Pp. 81-88 in: Boggan, J., Funk, V., Kelloff, C., Hoff, M., Cremers, G. & Feuillet, C. (ed.), *Checklist of the plants of the Guianas* (*Guyana, Surinam, French Guiana*). Washington.
- Gentry, A. H. 1986. Species richness and floristic composition of Choco region plant communities. *Caldasia* 15: 71-91.
- Grierson, A. J. C. 1980. *Compositae*. Pp. 111-278 in: Dassanayake, M. D. & Fosberg, F. R. (ed.), *A revised handbook to the flora of Ceylon*, 1. New Delhi & Washington.
- Hillebrand, W. 1888. *Flora of the Hawaiian Islands: a description of their phanerogams and vascular cryptogams*. Heidelberg, London & New York.
- Hilliard, O. M. 1977. *Compositae in Natal*. Pietermaritzburg.

- Howell, J. T. & McClintock, E. 1960. *Supplement to the Arizona Flora*. Berkeley, Los Angeles & London.
- Kearney, T. H. & Peebles, R. H. 1951. *Arizona Flora*. Berkeley, Los Angeles & London.
- Keck, D. D. 1936. The silverswords: systematics, affinities, and phytogeographic problems of the genus *Argyroxiphium*. *Occas. Pap. Bernice Pauahi Bishop Mus.* 11: 1-38.
- MacArthur, R. H. & Wilson, E. O. 1967. *The theory of island biogeography*. Princeton.
- McVaugh, R. 1984. *Flora novo-galiciana*, 12. Ann Arbor.
- Mori, S. & Boom, B. 1987. The forest. *Mem. New York Bot. Gard.* 44: 9-29.
- Morin, N. R., Whetstone, R. D., Wilken, D. & Tomlinson, K. L. 1989. Floristics for the 21st century. *Monogr. Syst. Bot. Missouri Bot. Gard.* 28: 1-163.
- Munz, P. A. 1959. *A California flora*. Berkeley, Los Angeles & London.
- 1968. *Supplement to A California flora*. Berkeley, Los Angeles & London.
- Nash, D. L. & Williams, L. O. 1976. Flora of Guatemala, 12. *Fieldiana, Bot.* 24: 1-603.
- Signor, P. W. 1985. Real and apparent trends in species richness through time. Pp. 129-150 in: Valentine, J. W. (ed.), *Phanerozoic diversity patterns*. Princeton.
- Steyermark, J. A. 1963. *Flora of Missouri*. Ames.
- , Berry, P. & Holst, B. 1994. *Flora of the Venezuelan Guayana*. Portland (in press).
- Swofford, D. L. 1990. *PAUP: Phylogenetic analysis using parsimony. Version 3.0*. Champaign.
- Vane-Wright, R. I., Humphries, C. J. & Williams, P. H. 1991. What to protect? Systematics and the Agony of Choice. *Biol. Conservation* 55: 235-254.
- Wagner, W. L. 1991. Evolution of waif floras: A comparison of the Hawaiian and Marquesan Archipelagoes. Pp. 267-284 in: Dudley, E. C. (ed.), *The unity of evolutionary biology*, 1. Portland.
- , Herbst, D. R. & Sohmer, S. H. 1990. *Manual of the flowering plants of Hawai'i*. Honolulu.
- Wiley, E. O. 1982. *Phylogenetics*. New York, Chichester, Brisbane & Toronto.
- , Segal-Causey, D., Brooks, D. R. & Funk, V. A. 1991. *The compleat cladist*. Lawrence.
- Wilkinson, L. 1990. *SYSTAT: The system for statistics*. Evanston.
- Williamson, M. 1981. *Island populations*. Oxford.