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Biodiversity: modelling angiosperms as networks

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Abstract

In the neotropics, one of the last biological frontiers, the major ecological concern should not involve local strategies, but global effects often responsible for irreparable damage. For a holistic approach, angiosperms are ideal model systems dominating most land areas of the present world in an astonishing variety of form and function. Recognition of biogeographical patterns requires new methodologies and entails several questions, such as their nature, dynamics and mechanism. Demographical patterns of families, modelled via species dominance, reveal the existence of South American angiosperm networks converging at the central Brazilian plateau. Biodiversity of habitats, measured via taxonomic uniqueness, reveal higher creative power at this point of convergence than in more peripheral regions. Compositional affinities of habitats, measured via bioconnectivity, reveal the decisive role of ecotones in the exchange or redistribution of information, energy and organisms among the ecosystems. Forming dynamic boundaries, ecotones generate and relay evolutionary novelty, and integrate all neotropical ecosystems into a single vegetation net. Connectivity in such plant webs may depend on mycorrhizal links. If sufficiently general such means of metabolic transfer will require revision of the chemical composition of many plants. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Angiosperms; Mycorrhizas; South American floristic inventories; Species dominance patterns; Habitat affinities; Taxonomic uniquenesses; Ecotones; Populational dynamics; Multicomponent networks; Plant web

1. Introduction

The greatest reservation that most scientists and philosophers have against the concept of holistic or "top down" causality is the apparent absence of a robust exposition of just how such influence might arise (Ulanowicz, 1991). Hence, in spite of its fundamental importance in the reinterpretation of the mechanisms of nature, the ecosystem/ecotone (general landscape/interfacial boundary) concept has so far been based on the observation of a few selected organisms, e.g. from the rainforest/savanna interface (Smith et al., 1997). The required holistic approach, emphasizing the totality of interactions in whole systems rather than in their individual parts (Krohne, 1997), can best be evaluated using flowering plants as models.

Angiosperms are the perceived group of living plants dominating most land areas of the present world in an astonishing variety of form (morphology) and function (metabolism). Their total number of species at more than 250,000, easily exceeds the numbers from all other groups of plants taken together. They naturally figure in most studies by botanists (systematists), and they form the basis of most pharmacology, horticulture and agriculture. Their conservation and successful exploitation closely affected the fortunes and future of humanity, and all other animals (Hughes, 1994). Brazil's 8.5 million km^2 sustain at least 55,000 species of higher plants in 10 vegetation complexes (Rizzini, 1997). Except for the very high-altitude formations, the country includes practically all possible complexes for latitudes between 4° north and 32° south (Legris et al., 1981).

It is the purpose of the present work to investigate the biogeographical distribution patterns of the South American flowering plants (here represented by dicotyledons). Recognition of these patterns entails several questions, such as their nature, dynamics and mechanism, regulating effects of secondary metabolism. The necessary holistic approach requires new methodologies. Potential applications of the results concern formulation of strategies for landscape preservation and management.

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2. Methods and results

2.1. Data base

Investigations on the spatial distribution of plants require the analysis of species registered for ecogeographically defined regions. The present work considers 76 South American inventories (Gottlieb and Borin, 1996; Pereira et al., 1996) allocated in nine habitats: six major relatively homogeneous ecosystems [Amazonian terra firme forest (AmF), Atlantic forest (AtF), caatinga (Caa), cerrado *plus* cerradão (CeC), Araucaria (Ara) and steppes (Ste)]; and bordering these ecosystems, three diverse heterogeneous ecotones [geographically related to the northern (Nor), central (Cen) and southern (Sou) neotropics] (Table 1). Subsequently, in an analysis at a finer scale, the central ecotone mosaic (Cen) was subdivided into gallery forest (Gal), montane forest (For), campo rupestre (Rup) and the remaining central ecotone complex (Cen*). Most of these ecotones lie on forest boundaries, river margins or otherwise floodable terrain.

2.2. Demographical patterns via species dominance (SD)

In order to quantify the relative importance of each family (f) per inventory (i), the percentages of their species (SD_i) were calculated:

$$SD_\mathrm{i} = 100x_\mathrm{f}/z$$

x_f = number of species of family f in inventory i

z = total number of species in inventory i

This procedure, which compares the importance of families not by the absolute number, but by the relative diversity of species, aims to minimize the scale-effect due to the different sizes of the particular inventoried regions.

Thus, the demographical patterns (SD_i) of each one of the 162 dicotyledon families were established for each one of the 76 floristic inventories (e.g. Lauraceae, Fig. 1A). Since the habitat types of all inventories are known (Table 1), the means of SD_i values for each habitat (h) can be calculated for each one of the 162 dicotyledon families:

$$SD_\mathrm{h} = \sum_{1}^{y} SD_\mathrm{i}/y$$

y = number of inventories per habitat.

These mean values (SD_h) express species dominance patterns per habitat for each family (e.g. Lauraceae; Fig. 1B).

2.3. Habitat assembly via bioconnectivity

The SD_h values of all 162 dicotyledon families for each habitat (e.g. 162 SD_h values for AmF) were correlated with the SD_h values of all other habitats, either pairwise (e.g. 162 SD_h values for AmF with 162 SD_h values for Nor) or in combination (e.g. 162 SD_h values for AmF with 162 SD_h values for all habitats). In the former case, the respective correlation coefficient (r) was taken to indicate the demographical affinity for each pair of habitats (Table 2). In the latter case, SD_h values were combined through multiple regression analysis. The corresponding multiple correlation coefficient (R) was taken to indicate bioconnectivity of each habitat within the system (Table 3).

Table 1
Characterization of 76 inventoried neotropical regions

Code	Habitat	Latitude S	Longitude W	No. of invent.	Area number[b]
AmF	Amazonian Terra Firme Forest	1°50′–11°45′	57°37′–66°35′	14	1, 2, 10, 12, 13, 15–19, 27, 28, 30, 31
AtF	Atlantic Forest	22°21′–25°18′	42°15′–48°5′	5	52–54, 61, 64
Caa	Caatinga	6°-12°	35°-45°	1	26
CeC	Cerrado *plus* Cerradão	15°21′–22°16′	46°25′–55°49′	10	34, 36–38, 40, 41, 43, 49, 50,[c]
Ara	Araucaria Forest	25°–25°25′	49°17′–50°	2	62, 65
Ste	Steppe	40°–46°	72°–73°	2	79, 80
Nor	Northern Neotropics	2°35′–10°11′	49°53′–64°55′	13	3–7, 9, 11, 14, 21–24, 29
Cen	Central Neotropics	12°49′–23°35′	42°55′–55°49′	19	32, 33, 35, 42, 44–48, 51, 56–60,[c]
Sou	Southern Neotropics	30°02′–30°21′	51°01′–51°12′	10	69–78
Cen*[a]	Central Neotropics*	12°49′–23°35′	47°50′–53°45′	3	32, 58,[c]
Gal	Galery Forest	15°21′–23°35′	47°50′–55°49′	4	33, 35, 59,[c]
For	Montane Forest	15°30′–23°35′	44°-53°45′	8	47, 48, 51, 56, 57, 60,[c]
Rup	Campo Rupestre	18°03′–20°10′	42°55′–43°50′	4	42, 44–46

[a] Cen* = Cen without Gal, For and Rup.

[b] Numbers refer to areas listed in Table 1 of Gottlieb and Borin (1996).

[c] See additionally Pereira et al. (1996).

Comparison of habitat compositions per family through correlation coefficients may become of considerable value for the orientation of preservation and management efforts. Indeed for each habitat, the greater the number of significantly high *r*-values the stronger the relative pressure of its species dominance pattern.

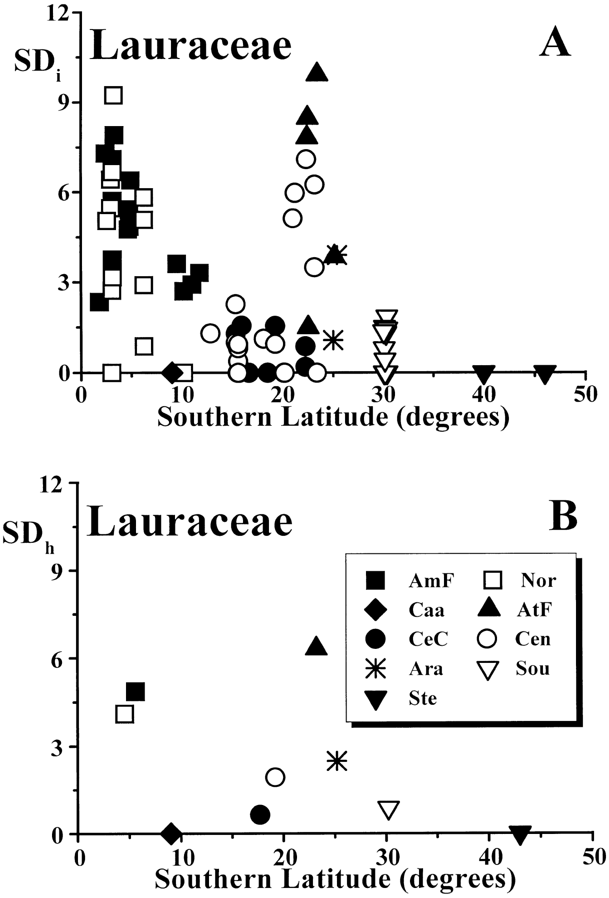

Fig. 1. Species dominance patterns for Lauraceae in: (A) 76 floristic inventories (SD_i), (B) nine habitats (SD_h).

Gradual loss of affinity, as inferred by *r*-values for pairs of regions, diminishes from north (AmF/Nor, $r = 0.86$) to south (AmF/Ste, $r = -0.01$); and from south (Ste/Sou, $r = 0.85$) to north (Ste/AmF, $r = -0.01$). On the other hand, central regions show significant positive correlations with north (Cen/AmF, $r = 0.51$), east (Cen/AtF, $r = 0.80$) and south (Cen/Ste, $r = 0.45$) (Table 2).

Table 3
Connectivity of each habitat within the plant network, given by multiple correlation coefficients (*R*) obtained by comparisons among SD_h values of 162 dicotyledon families in each habitat[a]

Missing variables		Dependent variables								
		AmF	Nor	Caa	AtF	CeC	Cen	Ara	Sou	Ste
—		0.89	0.96	0.78	0.93	0.84	0.95	0.94	0.94	0.91
AmF		–	0.91	0.77	0.93	0.84	0.95	0.94	0.94	0.91
	Δ[b]	–	**0.05**	**0.01**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Nor		0.72	–	0.68	0.88	0.84	0.95	0.94	0.94	0.91
	Δ	**0.17**	–	**0.10**	**0.05**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Caa		0.89	0.95	–	0.91	0.84	0.95	0.94	0.94	0.91
	Δ	**0.00**	**0.00**	–	**0.02**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
AtF		0.88	0.94	0.69	–	0.84	0.94	0.94	0.94	0.90
	Δ	**0.01**	**0.02**	**0.09**	–	**0.00**	**0.01**	**0.00**	**0.00**	**0.01**
CeC		0.89	0.96	0.78	0.93	–	0.92	0.94	0.94	0.91
	Δ	**0.00**	**0.00**	**0.00**	**0.00**	–	**0.03**	**0.00**	**0.00**	**0.00**
Cen		0.89	0.96	0.78	0.92	0.75	–	0.93	0.94	0.91
	Δ	**0.00**	**0.00**	**0.00**	**0.01**	**0.09**	–	**0.01**	**0.00**	**0.00**
Ara		0.89	0.96	0.78	0.93	0.83	0.94	–	0.94	0.90
	Δ	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**	**0.01**	–	**0.00**	**0.01**
Sou		0.89	0.96	0.78	0.93	0.84	0.95	0.93	–	0.88
	Δ	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**	–	**0.03**
Ste		0.89	0.96	0.78	0.92	0.84	0.95	0.93	0.92	–
	Δ	**0.00**	**0.00**	**0.00**	**0.01**	**0.00**	**0.00**	**0.01**	**0.02**	–

[a] The impact of each habitat on the network is simulated by its omission from the processes.

[b] Δ: Differences between *R*-values considering all habitats (1st line) and *R*-values with one omitted habitat. For all correlations $P < 0.000001$.

Table 2
Demographical affinities for each pair of habitats, given by correlation[a] coefficients (*r*) obtained by comparisons between SD_h values of 162 neotropical dicotyledon families in each habitat

	AmF	Caa	AtF	CeC	Ara	Ste	Nor	Cen	Sou	Cen[b]	Gal	For	Rup
AmF	—												
Caa	0.51a	—											
AtF	0.60a	0.38a	—										
CeC	0.47a	0.59a	0.59a	—									
Ara	0.12	0.23a	0.48a	0.43a	—								
Ste	−0.01	0.12	0.15	0.29a	0.82a	—							
Nor	0.86a	0.65a	0.80a	0.66a	0.27a	0.04	—						
Cen	0.51a	0.54a	0.80a	0.79a	0.71a	0.45a	0.71a	—					
Sou	0.12	0.24a	0.47a	0.44a	0.92a	0.85a	0.26a	0.70a	—				
Cen*[,b]	0.41a	0.52a	0.55a	0.81a	0.54a	0.38a	0.53a	0.85a	0.54a	—			
Gal	0.62a	0.49a	0.68a	0.61a	0.40a	0.15	0.70a	0.83a	0.42a	0.66a	—		
For	0.52a	0.54a	0.88a	0.71a	0.61a	0.29a	0.77a	0.93a	0.57a	0.68a	0.74a	—	
Rup	0.18b	0.28a	0.44a	0.60a	0.84a	0.79a	0.31a	0.78a	0.86a	0.73a	0.48a	0.56a	—

[a] Correlation is significant at the (a) 0.01 or (b) 0.05 level, determined by ANOVA (*F*-test) and *t*-test.

[b] Cen* = Cen without Gal, For and Rup.

However, our circumscription of Cen encompasses several different types of vegetation. In order to evaluate the influence of this fact on the conclusions, we separated from the Cen complex three types of communities, Gal, For and Rup, maintaining in Cen* the further, consistently heterogeneous, inventories (Table 1). The quantitative data reveal the affinities of Gal, For and Rup with northern, eastern (AtF) and southern regions, respectively (Table 2), confirming the influences of these three regions on the vegetations of the central Brazilian plateau. Furthermore, the linear correlation coefficients for Cen* and Cen are practically identical (Table 2), justifying our initial inclusion of the diverse central habitats in a unique type.

Two general observations revealed by the plot of all linear regression values for correlations between habitats merit attention (Fig. 2). First, the decreasing influences of the Amazonian-pattern toward the south and the Patagonian-pattern toward the north, form an "X" figure with the mid-point representing the central Brazilian plateau. Second, the number of results possessing $r \geqslant 0.65$ ($P < 0.00001$) to be 5 for Nor and Cen, and 3 for Sou ecotones; but with exception of Ara, less than 3 for ecosystems; or even better, in the case of subdivision of the Cen-mosaic, 6 for Nor, 5 for For, 4 for Cen*, Gal and Rup and 3 for Sou ecotones, but only 3 or less for all ecosystems. The analysis involving pairs of ecogeographically close habitats (e.g. Nor/AmF, Cen/CeC and Sou/Ste) demonstrates the ecotones, rather than the ecosystems, to display greater affinities with all the remaining habitats (Fig. 3). Thus, in an adjacent ecotone/ecosystem pair, the former component is usually more strongly correlated with other biomes than the latter component. This is confirmed by the consistently higher *R*-values for the strongly bioconnected ecotones in comparison with ecosystems (Table 3). This seminal finding, is a clue to the function of ecotones in the development of affinity links in networks.

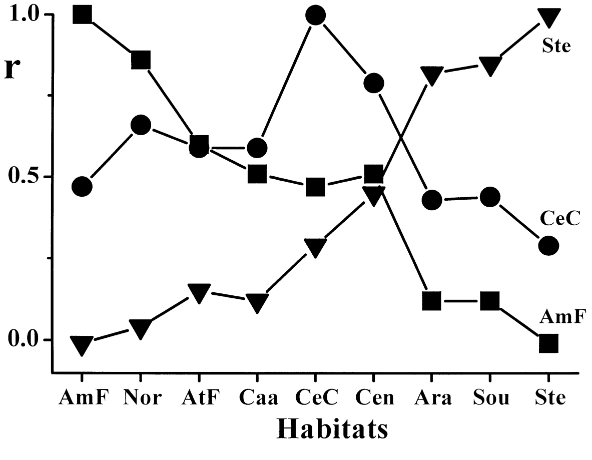

Fig. 2. Comparison of compositional affinities, indicated by correlation coefficients (r), between the three major biome complexes, northern (squares), central (circles) and southern (down triangles). The correlation coefficients were obtained by the pairwise correlation of SD_h values of 162 neotropical dicotyledon families (Table 2). For all correlations $P < 0.01$, except for AmF with Ara, Sou and Ste; as well as for Nor, AtF and Caa with Ste.

In all three ecotone/ecosystem pairs exemplified above, the differences between their respective correlation

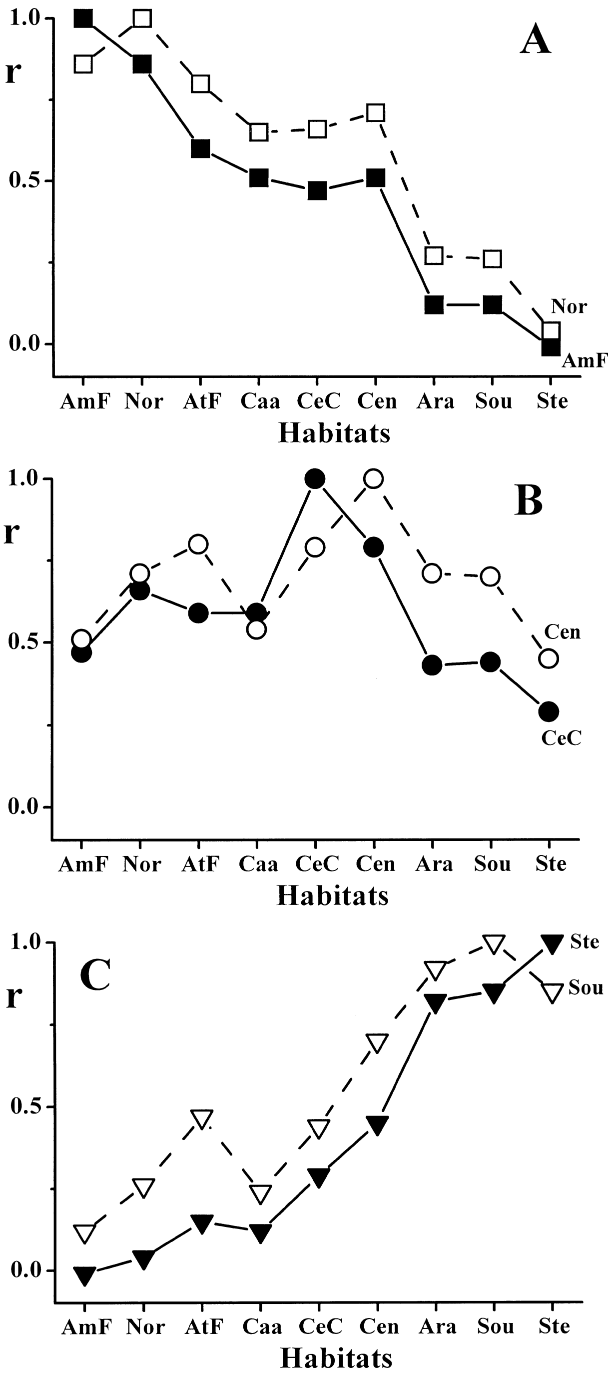

Fig. 3. Comparison of compositional affinities, indicated by correlation coefficients (r), between three pairs of ecotones (open symbols and dashed lines) and their ecogeographically close ecosystems (solid symbols and lines): **A** Nor/AmF, **B** Cen/CeC and **C** Sou/Ste.

coefficients (*r*) are positive, indicating the highest values for ecotones; and very similar, indicating the nearly identical floral composition (Fig. 3). Closeness of affinities can be used for the identification of integrated regions, e.g. the correct ecotone partner for the Atlantic forest is For and not Gal or Rup of central Brazil (Fig. 4). This procedure is a powerful tool for the identification of appropriate habitats to serve as ecotones ("natural corridors") for each ecosystem, revealing the adaptive flexibility of taxa and hence the creative potential of ecotones.

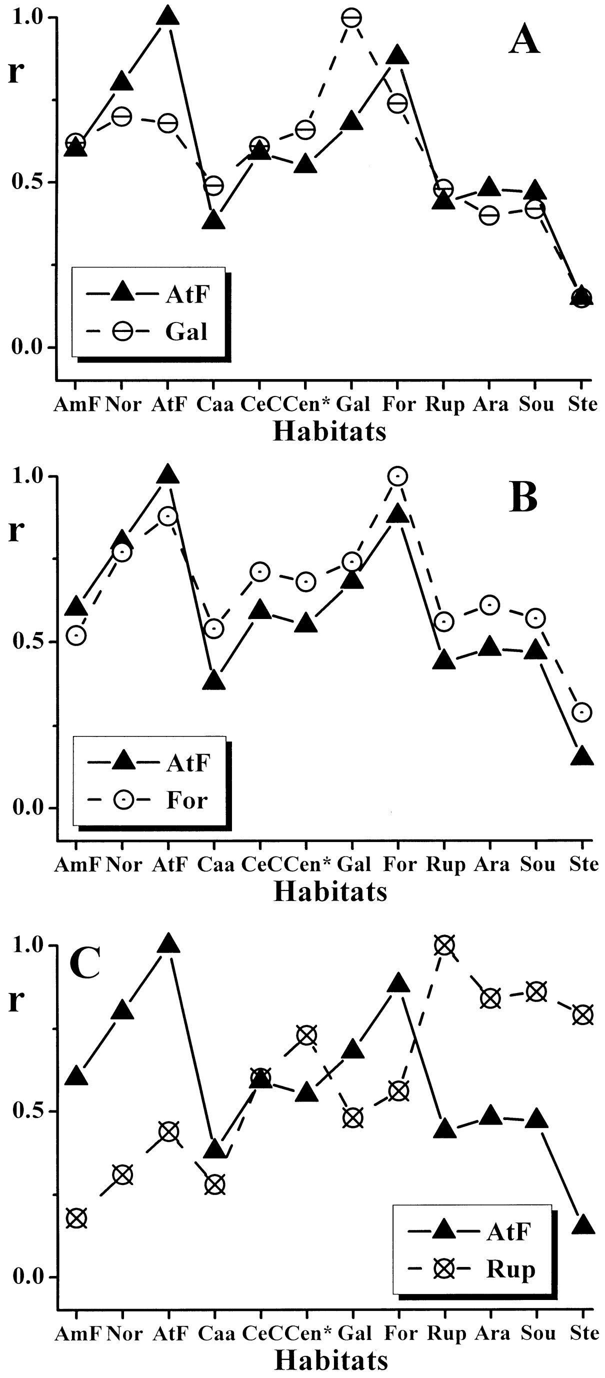

Fig. 4. Comparison of compositional affinities, indicated by correlation coefficients (*r*), between Atlantic forest (AtF) and three different ecotones: (A) Gallery forest (Gal), (B) Montane forest (For) and (C) Campo rupestre (Rup).

2.4. Biodiversity via taxonomic uniqueness

Creative, i.e. diversificatory power, can be evaluated by the degree of independent evolutionary history, i.e. taxonomic uniqueness (TU). The hierarchical concept embodied in this process suggests its applicability to a major problem: the estimation of global biodiversity in an area.

In the present work angiosperm species, listed in each one of the 76 floristic inventories (Table 1), were compared pairwise in order to find the highest classificatory rank at which each pair diverges, according to quantitative methodology described in previous papers (Gottlieb and Borin, 1994, 1998).

3. Discussion

3.1. Multicomponent networks

Geography oriented gradual modifications of correlation coefficients at the same time support and refine the network concept. The impact of biomes on the network can be simulated omitting the respective *SD* values in multiple correlation analysis (Table 3). Omission of a single biome per operation causes modifications of *R*-values corresponding to geographically associated habitats. Strikingly, omission of ecotones is perceived by ecosystems more intensely, than omission of ecosystems is perceived by ecotones. E.g. excluding the *SD*-Nor values, three different effects can be observed: large effects for vicinal regions [ΔR AmF = 0.17 (0.89–0.72)], intermediate ones for more distant regions (ΔR Caa = 0.10 and AtF = 0.05) and no effects for regions situated still farther to the south (ΔR CeC, Cen, Ara, Sou and Ste = 0.00) (Table 3). On the other hand, the exclusion of AmF produces relatively feeble effects on its vicinal ecotone (ΔR Nor = 0.05). Hence, the information flux from ecotone toward ecosystem exceeds the flux in the opposite direction. Decreasing bioconnectivity, indicated by diminishing *R*-values, demonstrates the integration and polarization of ecotones. This procedure is a powerful tool for the qualification of asymmetry, the general property of any network (Legris et al., 1981; Margalev, 1991).

The measurement of *TU* for 76 South American areas constitutes independent evidence for a wider adaptive flexibility in the ecotones than in the adjoining respective ecosystems (Fig. 5). *TU*-values are surprisingly high, between 80 and 90%, for central and south Brazilian habitats.

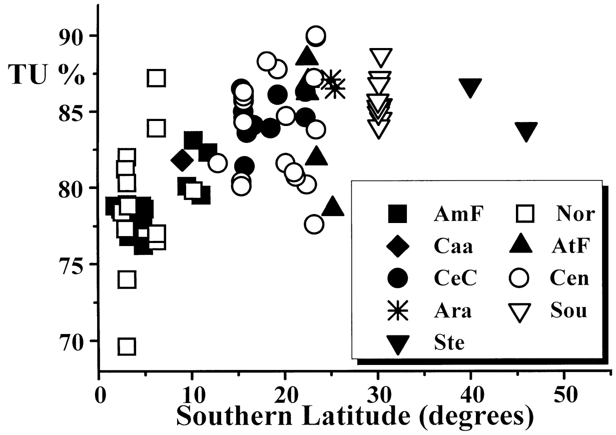

Fig. 5. Taxonomic uniqueness [in percentage values (*TU*%)] of 76 neotropical floristic inventories distributed according their geographical localizations.

3.2. Mechanistic considerations

Besides energetic induction of populational affinity of ecosystems, and horizontal or lateral gene transfers, symbiotic mycorrhizal links (Simard et al., 1997) may be required for plant connectivity in networks. Although this latter mechanistic proposal would need further investigation, its holistic nature is supported by three direct evidences. First, the ancestral status of symbiosis, enabled the colonization of land by vascular plants (Simon et al., 1993), evidenced by the present worldwide distribution of such associations. Indeed the symbioses between arbuscular mycorrhizal fungi (class Zygomycetes, order Glomales) and plants attain ca. 80% of all terrestrial plant species (Smith and Read, 1997). Second, mycorrhizal fungi affect the plant community structure, including the diversity of plant species, their spatial distribution, and their relative abundance, in decisive manners (van der Heijden et al., 1998a,b). Finally, small spores of ectomycorrhizal fungi are transported by wind and animals permitting their dispersal over great distances (Smith and Read, 1997).

In fact, the recent investigations suggest that the functions of the symbioses go far beyond the simple capture of mineral nutrients by individual plants and of organic carbon by the associated fungi. The albeit few experiments in tropical ecosystems provide additional evidence for involving the mycorrhizae in ecosystem/ecotone connectivity. Thus, in riverine Amazonian forests on white sand many species are ectomycorrhizal (ECM) and almost all species are associated with fungi. In contrast, in Amazonian forests on common heavy-clay oxisol many species are associated with vesicular-arbuscular fungi (VAM), and some species lack mycorrhizae altogether (St. John, 1985). Hence, ECM exceed VAM in association specificity, suggesting special adaptive forces to exist in white sand ecotones. The higher degree of selectivity makes ECM associations more vulnerable to disturbance, emphasizing the consideration of ecotones as preferential targets for conservation. Nevertheless, a coherent picture is still lacking, although colonization of a restricted number of plant taxa by a number of endophytes has now been described (Rodrigues and Petrini, 1997).

Furthermore, it is now clear that the basic metabolism of a host plant can be radically modified by interaction with fungal invaders, whether they are pathogen or not (Mayer, 1989). A recent example suggests that carbon transfer between *Betula papyrifera* and *Pseudotsuga menziesii* is primarily through the direct hyphal pathway and influenced by shading of receiver plants (Simard et al., 1997). Indeed, angiosperms being rich in diverse, bioactive secondary metabolites, their interconnected chemical networks would either protect or inhibit the dispersion of newly introduced lineages. Pursuit of these studies at the cellular, whole-plant and community levels (Smith and Read, 1997) will enrich our understanding of the mycorrhizal regulation of plant metabolic composition in extant ecosystems.

4. Conclusion

The neotropical dicotyledon flora forms a multicomponent network. This is an important conclusion. Indeed, “modelling nature as networks” has been recognized a relevant approach toward the theoretical study of ecosystems (Higashi and Burns, 1991). In the special case of the South American flora, Amazonian, Patagonian and Atlantic components converge toward a central Brazilian region. Indeed, taxonomic uniqueness of species per habitat, rather than diminishing gradually from equator to poles, suggests flowering plant diversity to be higher in central Brazil than in more peripheral regions.

Local alterations of such a maze may affect climate, crops, cattle, wildlife, and even human health (Rapport et al., 1998), elsewhere. These effects would be more direct, if the alterations took place at the convergent key locations (ecotones). Thus, knowledge of holistic mechanisms of bioconnectivity would allow, through modelling, to foresee deleterious consequences or to design beneficial situations.

The corresponding spatial radiation of dicotyledons among ecosystems is significantly favoured by the intermediacy of ecotones. Asymmetric fluxes emanating from such transition zones, rather than from the vicinal ecosystems, lead to demographical affinities with the remaining habitats. The intensities of these fluxes diminish gradually with increasing geographical distances.

Ecotones play a decisive role in the exchange or redistribution of information, energy and organisms (Gosz, 1991) among the ecosystems of the neotropics, and thus conceivably of all biogeographic regions on Earth. Forming dynamic boundaries, ecotones generate and relay evolutionary novelty (Gottlieb and Borin, 1996), and integrate all neotropical ecosystems into a single vegetation net. From the practical standpoint, this demonstrates the need to preserve the dynamics of these transitional zones in order that biodiversity can be sustained and replenished (Enserink, 1997; Smith et al., 1997). From the theoretical standpoint, the mechanistic rationalization requires knowledge of the ecological behaviour of plants and their biotic and abiotic environment, particularly fungi in mycorrhizal associations. Hence development in the understanding of the taxonomic position and specificity of microbial (and other) symbionts (Harley, 1989) will entail a dramatic task: the re-evaluation of the massive phytochemical work of the past century within the framework of the integrated terrestrial plant web.

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