

## Bioconnectivity: a blueprint for biodiversity?\*

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*Abstract:* Human wellbeing tomorrow will require expertise in biodiversity on all levels of organization, including metabolism, morphology and biogeography. In angiosperms, quantification and correlation of these levels through our holistic approach, reveals, as the fundamental mechanism of evolutionary ecology, intervention of opposing features or forces such as: (i) metabolic complementations/substitutions, positive/negative biosynthetic feedbacks and reduction/oxidation potentials (for the integration of metabolism and morphology); (ii) forest/cerrado (savanna) metabolic profiles (for the integration of metabolism and biogeography); (iii) species/genetic diversities, northern/southern networks and biodiversity/bioinvasion trends (for the integration of morphology and biogeography). While case (i) can be rationalized by lignin rigidity/flexibility transitions, cases (ii) and (iii) are coherent with the existence of multi-component floral networks based on symbiotic mycorrhizal links. Thus, knowledge of the mechanism of bioconnectivity would allow, through modeling, to foresee deleterious consequences or to design beneficial situations. Such a holistic concept of a powerful global chemo-biological control would amplify the research potential of natural products chemistry, from its present rather restricted role in prospecting for potential drugs, into a challenge for the next century.

### INTRODUCTION

For the poorest population on Earth it is impossible to grasp that they should be living in the richest environment. Indeed, little convincing evidence demonstrates how far the Amazonian splendor can be sustainably capitalized in currency of human welfare. Present methods of evaluating social cost/benefit ratios continue subject to many conceptual and empirical problems. There can be no doubt that their solution features among the most anxiously awaited scientific breakthroughs. The economics of the Earth would grind to a halt without the services of ecological life support systems, such as provided by the forest in Amazonia. Only observation and measurement-oriented modeling of biomechanisms will avoid the error of constructing projects whose social costs outweigh their benefits [1]. Now clearly, such modeling requires preliminarily experimental data or at least empirical concepts concerning diversification of life.

### BACKGROUND

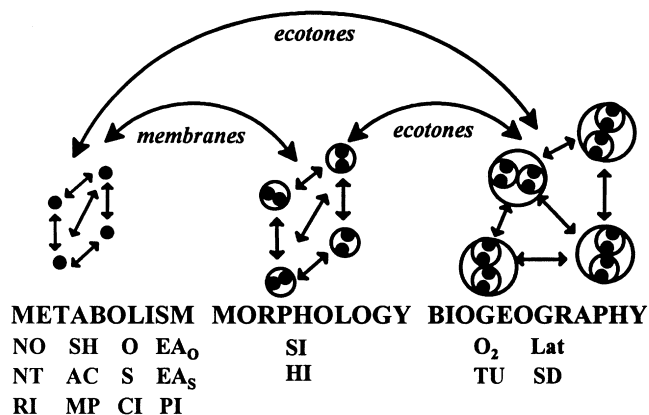
The manifestation of life comprises three levels of organization: metabolism, morphology and biogeography. Evidence for correlations among these levels would be of fundamental importance, revealing rules concerning the functioning of living organisms. In order to explore their connectivity with this purpose, two prerequisites must be fulfilled. First, and most importantly, each level must be amenable to quantitative measurement by suitable parameters, and second, the mechanisms responsible for the integration should be recognizable (Fig. 1).

Our arguments are based on codification of data derived from flowering plants. But why flowering plants? Angiosperms dominate most land areas of the present world in an astonishing variety of form and

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**Fig. 1** Connectivity between organizational levels. Quantitative parameters: NO number of occurrences (number of compounds of a biosynthetic category registered for each species of a taxon); NT number of structural types of compounds; RI relative importance index ( $RI = NT \times NO$ ); SH and AC resp. percentage of shikimate and acetate derivatives with relation to total number of compounds; MP metabolic profiles for a selected micromolecular category *per area*; O and S resp. oxidation and skeleton specialization states of a compound; CI evolutionary precedence-oriented chemical index; EA<sub>O</sub> and EA<sub>S</sub> resp. evolutionary advancement according to oxidation and skeleton specialization states; PI protection index (substituted vs. free phenolic hydroxyls); SI Sporne index (morphological advancement in angiosperm families); HI herbaceousness index (decreasing lignin content); O<sub>2</sub> atmospheric oxygen level; TU taxonomic uniqueness; Lat latitude; SD species dominance [14,17,18].

function. Their conservation and successful exploitation closely affected the fortunes and future of humanity [2]. With more than 250 000 species (55 000 in Brazil), angiosperms easily exceed the numbers of all other groups of plants taken together. Furthermore, being by far the largest group of living organisms in which it is still necessary to specify on each occasion the particular phylogenetic arrangement to be followed [3], the study of angiosperm phylogeny and taxonomy requires novel multidisciplinary approaches [4]. Last but not least, they contain an extraordinarily large number of natural products. Therefore, flowering plants should constitute significant model systems for the investigation of bioconnectivity as an universal concept. In the present work, while chemical data refer to angiosperm families irrespective of their distribution, biogeographical data are limited to neotropical dicotyledons.

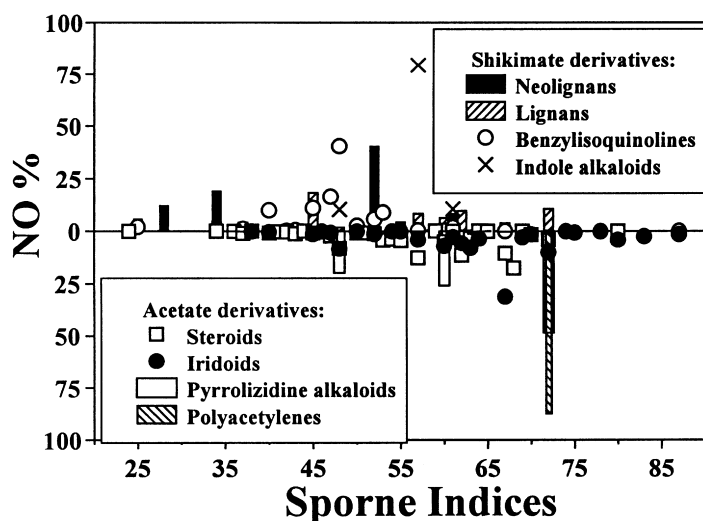
## ARE METABOLISM AND MORPHOLOGY CONNECTED?

### Phylogeny

In dicotyledon families, metabolic evolution is characterized in outline by replacement of shikimate by acetate derivatives. In detail, data on the diversity of micromolecular categories lead to two major findings (Fig. 2):

- 1 The evolutionary sequences of the categories. First neolignans are replaced by benzylisoquinolines, second benzylisoquinolines are replaced by anthranilate derived alkaloids (not indicated on Fig. 2) and indole alkaloids, and third indole alkaloids are replaced by steroids, iridoids, polyacetylenes and pyrrolizidine alkaloids.
- 2 The identical kinetics of all these replacements. Slowly increasing numbers of compounds occur gradually from less to more highly evolved families, as gauged by Sporne indices [5]. This induction of occurrence is followed by a maximum prior to fast decrease and substitution of one category by another one, but not by clearcut exclusions.

Thus in angiosperms, micromolecular metabolism can be envisaged in space by ecological complementations and in time by evolutionary substitutions. From the spacial standpoint, any evolutionary status (indicated by Sporne indices) is characterized by the simultaneous presence of at least two micromolecular categories. Coexistence of different metabolic categories in a family (e.g.

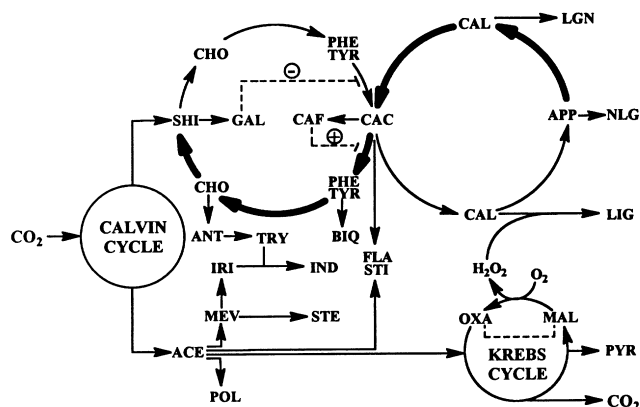


**Fig. 2** Numbers of occurrences, in percentage values, of the indicated shikimate derived (top) and acetate derived (bottom) micromolecular categories (each normalized to 100) per morphological advancement indices (SI) of chemically better known dicotyledon families. For database see [14,27].

Lauraceae [6]), may lead to alternate predominances in species accompanying changes in local ecological environments.

### Biosynthesis

The precedent phylogenetic analysis suggests the biosynthetic sequences of metabolic categories to initiate with neolignans, metabolites characteristic of primitive Magnoliidae (Fig. 3). With the considerable diversification of neolignans [7], evolutionary canalization leads to the second stage back to benzyloquinolines in Magnoliidae and Ranunculidae. Continuation of positive feedback leads to the third stage with the accumulation of gallates in the Hamamelidae-Dilleniidae-Rosidae complex. Activator of the enzyme phenylalanine ammonialyase (PAL), gallic acid at the same time diminishes the



**Fig. 3** Biosynthetic (thin arrows) and evolutionary (thick arrows) processes (i.e. activation/inhibition) regulated by negative (-) and positive (+) feedbacks leading to selected categories of secondary metabolites in angiosperms. SHI, shikimic acid; CHO, chorismic acid; PHE, phenylalanine; TYR, tyrosine; CAC, cinnamic acids; CAL, cinnamyl alcohols; APP, allyl- and propenylphenols; GAL, gallic acid; CAF, caffeic acid; ANT, anthranilic acid; TRY, tryptophane; IND, indole alkaloids; BIQ, benzyloquinoline alkaloids; FLA, flavonoids; STI, stilbenoids; LIG, lignins; NLG, neolignans; LGN, lignans; ACE, acetic acid; MEV, mevalonic acid; STE, steroids; IRI, iridoids; POL, polyacetylenes; OXA, oxalic acid; MAL, malic acid; PYR, pyrrolizidine alkaloids.

rate of benzyloisoquinoline-synthesis and enhances the rate of cinnamic acid synthesis, opposing, *via* negative feedback, the trend of evolutionary canalization. Thus gallic acid plays a decisive regulatory role in this history. Restricted to families of lower evolutionary status (SI), it inhibits the major trend of angiosperm evolution from woody forms to herbaceous forms. In the fourth stage, caffeic acid, an inhibitor of PAL, supplies positive feedback in Asteridae, i.e. revigorates the pathway in its original evolutionary direction by further debilitation of the shikimate route to the chorismic acid/anthranilic acid system. Concomitant strengthening of the acetate route leads to polyacetylenes, steroids, iridoids and pyrrolizidine alkaloids [8]. These facts indicate dicotyledon metabolism to form a dynamic network comprising shikimate and acetate derived processes involving activation/inhibition (antagonistic oscillations) of the biosynthetic reactions [9].

## Redox potential

In angiosperms, diversification within each metabolic category involves a gradually changing oxidation value of the corresponding metabolites. These chemical lineages accompany morphological sequences, recognized *via* evolutionary indices (HI, SI) [10,11]. Thus oxidation/reduction cascades may constitute an additional example of antagonistic oscillations of natural products.

## Mechanism

The current problem faced by plant life upon colonization of the terrestrial habitat, transport of water to all organs, was resolved by the dichotomy into more flexible lineages (e.g. bryophytes) too soft to oppose gravity and escape swampy ground, and more rigid tracheophytes. The resulting strengthened cell systems or tracheids are able to resist negative and positive pressures, generated, respectively, by sucking of water and water soluble inorganic ions from roots to leaves, and by pumping sucrose solutions from leaves to roots. All these rigidity/flexibility dichotomies can be explained by adequate combinations of lignin quantity and quality.

In the 100 million years separating the early Phanerozoic from the middle Carboniferous, increasing atmospheric oxygen pressure resulted in very considerable lignification [12]. Besides, the feeble aromatic oxygenation of the monolignol precursors (p-coumaryl alcohol, coniferyl alcohol) favoured the formation of crosslinks in the polymer. Hence the massive primitive lignins must have been rather rigid, as was required to sustain the huge trees of the Carboniferous. With diminishing lignification, due to attenuation of oxygen pressure, rigidity ceased to be an advantage. Indeed flexibility would have helped trees to resist winds and snow-loads. Flexibility is heightened by increasing intervention of a precursor monolignol endowed with stronger aromatic oxygenation (sinapyl alcohol) and hence less prone to establish crosslinks in the polymer (Fig. 4).

Thus rigidity/flexibility properties of lignins are able to explain the evolution of the previously noted phenomena: replacement of shikimate by acetate derivatives and redox potentials. In other words, the lignification processes rationalize the connection of metabolism and morphology in plants.

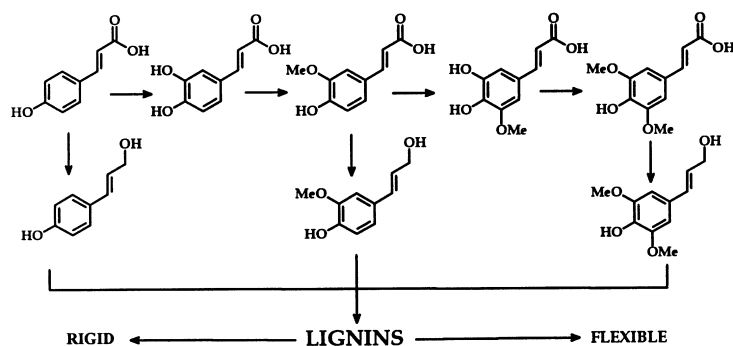
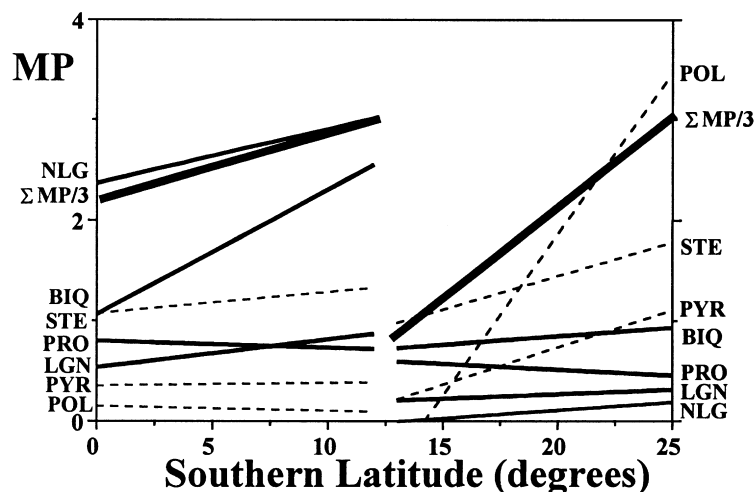


Fig. 4 Biosynthetic derivation of monolignol precursors of more rigid vs. flexible lignins.

## ARE METABOLISM AND BIOGEOGRAPHY CONNECTED?

Metabolism-oriented phytochemical data corresponding to the Brazilian territory revealed three patterns (Fig. 5) [13–16]:

- 1 Shikimic acid derived natural products, such as lignans, neolignans and benzyloisoquinoline alkaloids are produced in great frequencies by species in forests, while acetic acid derived natural products, such as steroids, polyacetylenes and pyrrolizidine alkaloids, occur in great frequencies in cerrado species.
- 2 Chemistry of forests is characterized by stronger variations of shikimate derivatives, while chemistry of cerrados is characterized by stronger variations of acetate derivatives. Furthermore, forests are distinguished from cerrados by strikingly more feeble variations of total metabolic profiles.
- 3 The two types of vegetation are separated by ecological boundaries. Such ecotones, possessing creative potential, interrupt abruptly all chemical gradients.



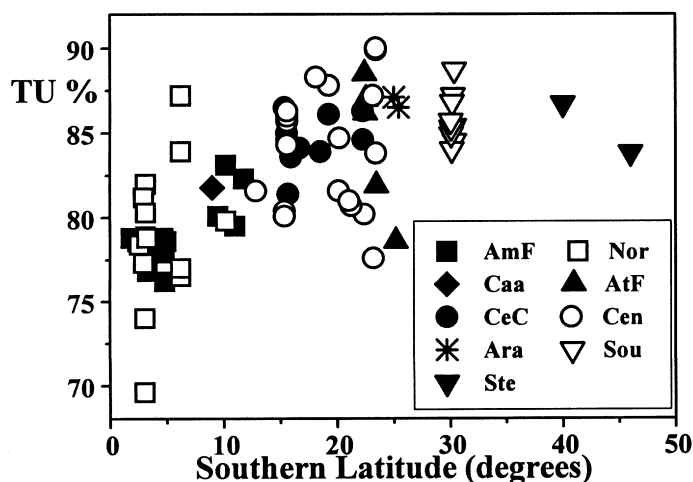
**Fig. 5** Correlations of metabolic profiles and southern latitudes for 13 floristic inventories of rain forest (0–10°) and 8 of cerrado (15–23°). Linear regression lines for three shikimate profiles (NLG, BIQ, LGN) and proanthocyanidins (PRO), of mixed biosynthesis, are represented by thin lines; three acetate profiles (POL, STE, PYR) are represented by dashed lines and the total of metabolic profiles ( $\Sigma$  MP) are represented by thick lines. For other abbreviations see legend to Fig. 3.

## ARE MORPHOLOGY AND BIOGEOGRAPHY CONNECTED?

Biodiversity is usually expressed by the number of species in a given area or region. This will provide data on productivity, but not on the relative importance of the area for conservation purposes or as natural 'genetic bank'. Creative (i.e. diversificatory) power, can be evaluated by the degree of independent evolutionary history, i.e. taxonomic uniqueness (TU). This parameter measures classificatory distances between species of organisms in an area or region [8,12–14,17]. The hierarchical concept embodied in this process suggests its applicability to a major problem: the appraisal of global biodiversity in an area.

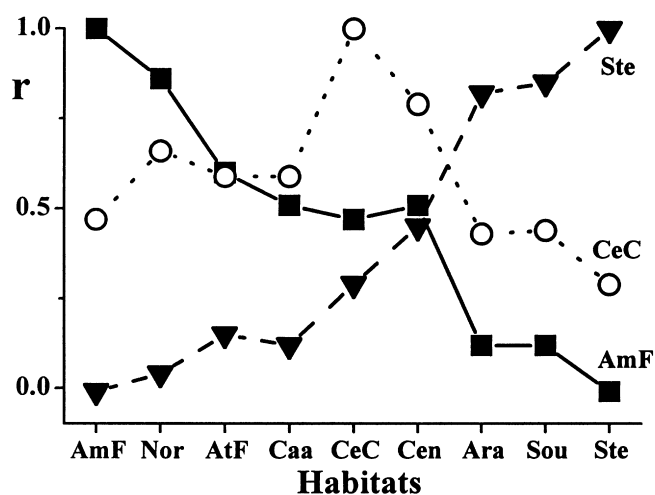
The measurement of TU for 76 South American areas constitutes independent evidence for the relatively stronger expression, or wider adaptive plasticity, of the ecotones of northern, central and southern Brazil over the adjoining respective ecosystems: Amazonian terra firme forest, cerrado *plus* cerradão, Araucaria and steppes (Fig. 6). Indeed, taxonomic uniqueness, rather than diminishing gradually from equator to poles, suggests flowering plant diversity to be higher in central Brazil than in more peripheral regions.

Characterized by maximal TU-values, central Brazil can be envisaged an ecotone between two ecosystems, northern and southern Brazil, due to convergent population pressures. This integrative dicotyledon radiation suggests the existence of a multicomponent neotropical network driven by central



**Fig. 6** Taxonomic uniqueness [in percentage values (TU%)] of 76 neotropical floristic inventories [18] distributed according to their geographical localizations. Ecosystems: Amazonian terra firme forest (AmF), Atlantic forest (AtF), caatinga (Caa), cerrado *plus* cerrado (CeC), Araucaria (Ara) and steppes (Ste). Ecotones bordering these ecosystems: geographically related to the northern (Nor), central (Cen) and southern (Sou) neotropics.

Brazilian gearings. Quantitative comparison of the floristic composition, according to frequency of species occurrence for each family (species dominance, SD) [17,18], allows the determination of degrees of similarity of these different neotropical biomes, *via* correlation coefficients ( $r$ ) [17]. Such comparisons confirm affinity of northern biomes with all other biomes to diminish in the southern direction, and affinity of southern biomes with all other biomes to diminish in the northern direction, while indeed, central biomes show significant affinities with northern (AmF and Nor), eastern (Caa and AtF) and southern biomes (Sou and Ste) (Fig. 7).



**Fig. 7** Correlation coefficients, based on Species Dominance of 162 neotropical dicotyledon families, between the three major ecosystems, AmF (solid squares, connected by solid lines), CeC (open circles, connected by dotted lines) and Ste (solid triangles, connected by dashed lines), and all other biomes. For all correlations,  $P < 0.01$ , except for AmF with Ara, Sou and Ste; as well as for Ste with Nor, AtF and Caa (for abbreviations see legend to Fig. 6).

At present and at an ever-increasing rate, specially in South America, the Earth's natural communities are being disrupted by exotic species, organisms that took up residence in ecosystems where they did not evolve. Bioinvasion, the spread of exotics, is fast becoming one of the greatest threats to the Earth's biological diversity [19].

## Mechanism

Besides energetic induction of populational affinity of ecosystems, horizontal or lateral gene transfers and symbiotic mycorrhizal links [20] may constitute mechanisms responsible for plant connectivity in networks. In analogy with the 'butterfly effect' [21], local alterations of such a maze may affect climate, crops, cattle, wildlife, and even human health [22], elsewhere. These effects would be expected to be more intense, if the alterations took place at key locations (i.e. ecotones), in direct contact with several far reaching networks. Thus, knowledge of holistic mechanisms of bioconnectivity would allow, through modeling, to foresee deleterious consequences or to design beneficial situations.

## ANTAGONISMS: A UNIFYING CONCEPT OF EVOLUTIONARY ECOLOGY?

Rigidity/flexibility transitions, metabolic complementations/substitutions, positive/negative biosynthetic feedbacks, reduction/oxidation potentials, forest/cerrado metabolic profiles, species/genetic diversities, northern/southern networks and biodiversity/bioinvasion trends are all pairs of opposing features or forces [8]. Clearly, biodiversity on Earth arises by modulation of qualitatively alternate strategies to solve current ecological problems. This suggests a striking corollary concerning the obligatory functional analogies of the level's cellular, organismic and biogeographic boundaries (Fig. 1). Like in organelles *via* membranes, the integrity and connectivity within networks of ecosystems is sustained *via* ecotones. Indeed membranes support proteins for the biosynthesis and the transport of products between cells, while ecotones affect the exchange or redistribution of materials, energy and organisms between landscape elements. Besides, and very importantly, membranes and ecotones are highly structured and polarized. This asymmetry, a general property of any network [23], permits in membranes selectivity among compounds *via* chirality-control and in ecotones selectivity among organisms *via* ecological conditions.

## CONCLUSION

Should these leitmotifs of our present endeavour need further, popular appeal, please listen to Orlando Villas Bôas, the great Brazilian indigenist: 'During the next millennium, countries comprising more primitive cultures and primordial forests will benefit from scientific research and food products' [24]. Expressing this feeling in precise terms, Beardsley reports after the United Nations Conference on Environment and Development held in Rio de Janeiro in 1992: 'Economists may be getting greener, but they will not anytime soon be able to lead the way to a sustainable future. When it comes down to hard numbers, sustainability remains an imprecise idea' [25]. The present demonstration of a holistic, multidisciplinary approach to the study of nature hoped to call attention to the fact that only quantitative biomodeling can support and guide the long-term interests of rural populations.

## FUTURE PROSPECTS

The present efforts in biomechanistic modeling revealed the realistic possibility to project biodiversity science from local to global status, opening some novel perspectives for studies. First, rationalization of phytochemical data will require consideration of symbiotic mycorrhizae. Second, predictability of bioinvasion will be needed to control the yet seemingly erratic movements of exotic organisms, chiefly into significantly degraded ecosystems. Third, understanding the general principles underlying contemporary processes of evolutionary ecology will provide increasingly satisfying models for the origins of life. 'What more awesome problem could invite our attention?' [26].

## ACKNOWLEDGEMENTS

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