



PHOTOSYNTHETIC ADAPTATIONS AND NICHING OF PLANTS IN THE TROPICS: A QUARTER-CENTURY OF FIELDWORK AT A VARIETY OF PHYSIOGNOMIES OF THE CERRADOS AND ATLANTIC FOREST OF BRAZIL

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Abstract: For about 25 years the photosynthetic performance of plants has been measured at a variety of different types of vegetation physiognomies of the cerrados and Atlantic forests of Brazil. The results of all these 28 publications, at the great majority of which Eduardo Arcoverde de Mattos has actively and most inspiringly participated, are overviewed here. A plea is made for an approach of physiological synecology with comparisons between different habitats, between species within given habitats and between given species across different habitats. This is exemplified for habitats within the geographical coordinates of 15°44' and 23°08'S and 47°53' and 41°15' W. The sites, their environmental characteristics and typical vegetation physiognomy, are described. The observations and results of the ecophysiological field work with respect to performance of photosynthetic gas exchange and other traits, including morphotypic adaptations, viz. plant morphotypes, and water relations, are summarized. The, both facilitating and competing, performances of plants with C₃-photosynthesis, and different levels of expression of crassulacean acid metabolism (CAM) are evaluated. Diversity and plasticity of niches and species is considered. The consequences for a “post-modern-synthesis” of evolution theory are assessed.

Key words: Biodiversity; evolution; habitat diversity; niche dynamics; tropical vegetation mosaics

INTRODUCTION

For about 25 years we have performed plant ecophysiological research in the field in Central- to South-Eastern Brazil, which is revisited in this overview dedicated to the memory of Eduardo Arcoverde de Mattos, who participated in the majority of these 28 publications. The various sites chosen for the work are listed in Table 1 together with their geographic coordinates. These

are within 15°44' and 23°08'S and 47°53' and 41°15' W, as indicted by the black rectangle in Figure 1 covering a significant part of Brazilian vegetation.

Our aim was not only to assess autecological ecophysiological performance of individual species and lineages but also to understand synecological ecophysiology (Lüttge 2005, Lüttge and Scarano 2004, 2007, Scarano *et al.* 2005a) of plants in sites, habitats and ecosystems with its consequences for niching and evolution. We were mostly interested



Figure 1. Area harboring the study sites in Central to South-Eastern Brazil: 15°44' to 23°08'S and 47°53' to 41°15' W.

on how ecophysiology could help us understand and eventually describe processes ranging from biogeographic to community level patterns. This was enabled by the richness of the habitat biodiversity in this part of Brazil, including various types of open habitats and forests and complex vegetation mosaics. The major approach for documenting the performance of plants was assessment of light reactions and gas exchange of photosynthesis. These photosynthetic features are the basis of productivity characteristic of fitness beyond pure generation of propagules as advocated in detail earlier (Lüttge 2020). Whenever possible, key primary metabolites (as essential for growth, development and reproduction) and stomatal conductance (for its central role in regulating transpirational water loss and CO₂ uptake) were also assessed. We seek to integrate the habitat and the plant responses, because both dynamically affect each other. Niches provide support for plant species. The performance and activity of plant species modifies niches. Our main goal is to elicit reflections on niching and post-modern-synthesis theory of evolution by addressing cases of comprehensive physiological synecology for the ruling of plasticity and diversity in ecophysiological settings.

From a biogeographic perspective, we were then interested in the relationships between forests and non-forest, open habitats. For that purpose, the Brazilian Cerrado and Atlantic Forest were obvious choices for two reasons: 1) these are biomes that combine open and forest habitats within their domains; and 2) they have a transition ecosystem between them, known as rupestrian fields, mostly open, which allowed us to explore linkages in specific plant groups present in these various physiognomies. From a community level perspective, we were interested in to which extent ecophysiological behavior could or could not explain occurrence and dominance patterns of given species and plant groups. We were also interested in ecophysiological processes at plant and leaf level.

FIELD TECHNIQUES USED FOR OUR ASSESSMENTS

We reviewed all 28 papers published out of the collaboration of the teams led by the three of us, Eduardo Mattos, and eventually the teams of other partners. This spanned 25 years. Details about the

publications are summarized in Table 1. The wide range of field work performed in Central- to South-Eastern Brazil (Figure 1) had become possible by the availability of miniaturized equipment for leaf-level measurements of chlorophyll fluorescence and infrared gas analysis (IRGA) (Figure 2). Chlorophyll fluorescence allowed measurements of photosynthetic capacity based on quantum yield and electron transport rate as well as of photochemical and non-photochemical quenching. IRGA provided information on photosynthetic CO₂-uptake of leaves and assessment of water use efficiency (WUE), the amount of CO₂ taken up per unit water transpired. Samples were collected for analyzing metabolite contents, namely C- and N-compounds, pigments (chlorophylls and carotenoids) and the stable isotope ratios $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Among C₃ plants the latter allowed conclusions about WUE. $\delta^{13}\text{C}$ also provided distinction of performance of C₃-photosynthesis and crassulacean acid metabolism (CAM), respectively. In some cases, structural leaf traits were also determined. The use of these various methods at the different sites is listed in Table 1 and more details are available in the various publications reviewed here.

CAM is an adaptation to limited availability of water and can be characterized by four metabolic phases that are interdependent and coincide with changes in stomatal opening during a 24-h cycle. In CAM plants, the stomata are opened during nighttime, phase I. The air humidity tends to be higher while temperature tends to be lower at night, saving transpiratory loss of water during dark fixation of CO₂ via phosphoenol-pyruvate carboxylase, which has a low ¹³C discrimination, resulting in storage of the fixed carbon as malic acid. Stomata are closed during the light period, and CO₂ is remobilized from malate and assimilated, phase III. There is a transition phase II in the morning and the possibility to open stomata in the afternoon in a phase III for direct CO₂ fixation from the atmosphere if water availability permits (Osmond 1978).

INDIVIDUAL HABITATS AND PLANT SPECIES

Next, we describe sites, plants and topics we addressed in each case. Both the Atlantic forest and the Cerrados have forest and open physiognomies. Inselbergs, rocky outcrops (as those measured here

Table 1. Overview of the 25 years of ecophysiological field work at a variety of different types of vegetation sites and habitats in cerrados and forests of Brazil with 28 reports emerging from it. Geographical coordinates (given only at first mention of the site) and brief annotations characterizing the sites are given together with the species studied and their modes of photosynthesis, methods used and key words highlighting the major conclusions. PS = photosynthesis; GAS = gas exchange; STO = stomatal conductance; FLU = chlorophyll fluorescence; LEAF = leaf traits; ACID = organic acid levels; SUC = succulence. Most sites in Rio de Janeiro state, unless otherwise stated at first mention are: MG = Minas Gerais state; DF = Federal District; SP = São Paulo; ES = Espírito Santo. All sites in RJ, ES and SP are physiognomies of the Atlantic forest biome. The rupestrian fields in MG are a transition between the Atlantic Forest and the Cerrado. Sites in MG and DF are physiognomies of the Cerrado biome.

#	Sites, coordinates	Site description	Species studied	Mode of PS	Methods of studies	Conclusions	Refs
1	Carapebus restinga (22°14'S, 41°34'W)	Coastal sandy plains	<i>Clusia hilariana</i>	CAM	GAS, FLU	Well adapted, danger of photoinhibition exposed plants	Franco et al. (1996)
2	Sugar loaf, Rio (22°57'S, 43°59'W) Cabiúnas (22°14'S, 41°34'W)	Rock outcrops; sand dunes	<i>Clusia parviflora</i> , <i>Stillingia dichotoma</i> , <i>Vriesea geniculata</i> , <i>Protium icicariba</i> , <i>Andira legalis</i>	C ₃ , CAM	STO, FLU, δ ¹³ C, LEAF	Both C ₃ and CAM species well adapted to exposure stress	De Mattos et al. (1997)
3	Serra do Cipó, MG (19°12'S, 43°28'W)	Rupestrian fields	Holoparasitism, <i>Pilosyles ingae</i> on <i>Mimosa naguirei</i>	C ₃	FLU, δ ¹³ C	Performance of infected and non-infected host plants similar, well balanced host/parasite relations	Fernandes et al. (1998)
4	Serra do Cipó (800 – 1200 m a.s.l.); Brasília, DF (15°44' – 46°S, 7°52' – 56°W)	Rupestrian fields, cerrado, gallery forest	Wide species diversity of host tree/ mistletoe pairs	C ₃	FLU, δ ¹³ C	PS activity similar in host and mistletoe pairs, except in highly exposed rupestrian fields host better	Lüttge et al. (1998)
5	Carapebus restinga	Coastal sandy plains	<i>Clusia hilariana</i>	CAM	FLU, GAS, ACID	Adjustment of photosynthetic machinery in the CAM phases at high exposure to irradiance	Franco et al. (1999)
6	Brasília 1050 (m a.s.l.)	Gallery forest – ecotone to cerrado	<i>Clusia criuva</i>	C ₃ and weak CAM	FLU, GAS, ACID	Expression of a very plastic potential of photosynthetic options in the genus <i>Clusia</i>	Herzog et al. (1999a)
7	Carapebus restinga	Coastal sandy plains	<i>Clusia parviflora</i> , <i>Clusia hilariana</i>	C ₃ /CAM, CAM	FLU, GAS, ACID, δ ¹³ C	Photoinhibition CAM not superior to C ₃ /CAM at exposed sites, PS-plasticity: wide range of habitats	Herzog et al. (1999b)

Table 1. continues on next page...

Table 1. ... continued

#	Sites, coordinates	Site description	Species studied	Mode of PS	Methods of studies	Conclusions	Refs
8	Poço das Antas (22° 30'S, 42° 15'W)	Swamp forest	<i>Nidularium innocentii</i> , <i>Nidularium procerum</i>	C ₃ , CAM	FLU, g _{H2O} , titratable acidity	Bromeliads, both shaded photoinhibited, habitat segregation: C ₃ shaded, CAM semi-exposed	Scarano et al. (1999)
9	Restinga de Jurubatiba (22°00' - 23'S, 41°15' - 45'W (a) Búzios (22°49'S, 41°59'W) (b) Arraial do Cabo (22°56'S, 42°13'W) (c) Jacarepiá (22°47' - 57'S, 42°20' - 43'W) (d) Itatiaia (20°25'S, 44°50'W, 2400 m a.s.l.)	Bush-shrub mosaic on white sandy ground (a) Semi-deciduous dry forest (b) dry restinga, soil water deficit (c) wet restinga, dry dune forest (d) rocky hills, boulders	<i>Clusia hilariana</i> , floristic analysis of vegetation islands: 87 species	CAM, C ₃	FLU, ACID, SUC	Differences between male and female <i>C. hilariana</i> minimal, no effects on niching	Liebig et al. (2001)
10			32 species, site and habitat distribution	CAM, C ₃	FLU, δ ¹³ C, δ ¹⁵ N, C and N contents	Functional groups are distributed throughout all habitats, photoinhibition even in CAM plants, high ecophysiological diversity, wealth of strategies for responses to stress and environmental dynamics	Scarano et al. (2001)
11	Brasilia (15°56'S, 47° 53'W, 1100 m a.s.l.)	Cerrado	5 different C ₃ tree species	C ₃	FLU, GAS	Control and differences in photosynthetic capacity and midday depression, high photorespiratory costs	Franco and Lüttge (2002)
12	(a) Brasilia (b) Arraial do Cabo (c) Macaé	(a) Cerrado (b) dry restinga (c) coastal sandy plains	Different species of mistletoes, Loranthaceae and Viscaceae, all over the world, including 15 from Brazil	C ₃	Carotenoid composition, phylogenetic analysis	Occurrence of the lutein- epoxide-cycle in parallel to violaxanthin cycle for photoprotection	Matsubara et al. (2003)
13	Restinga de Jurubatiba	Bush-shrub mosaic on white sandy ground	<i>Clusia hilariana</i>	CAM	FLU, ACID, SUC, sugars in 4 developmental stages	CAM expression more pronounced in leaves of young plants having less ground water access	Berg et al. (2004)

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Table 1. ... continued

#	Sites, coordinates	Site description	Species studied	Mode of PS	Methods of studies	Conclusions	Refs
14	Various	Various	Various	C ₃ , CAM	Various	Review on ecophysiology with examples from this table, e.g., #8, #10, #17	Lüttge and Scarano (2004)
15	(a) Restinga de Jurubatiba (b) Arraial do Cabo (c) Itatiaia (2740 m a.s.l.) (d) Sugar Loaf (e) Búzios	(a) Beech ridges, swamp (b) dry restinga, beech ridges, dune system, swamp (c) high altitude forest (d) inselberg, dry forest (e) semi-deciduous dry forest	<i>Calophyllum brasiliense</i> , <i>Croton compressus</i> , <i>Myrsine parviflora</i> , <i>Myrsine gardneriana</i> , <i>Rheedia brasiliensis</i> , <i>Stillingia dichotoma</i>	C ₃	C-, N-contents, N- compounds, sugars, FLU $\delta^{13}\text{C}$, $\delta^{15}\text{N}$,	Ecophysiological responses related to individual species not to habitat due to high plasticity and biodiversity, variation explained by light and water, generalists and specialists do not differ in ecophysiological behaviour, generalists are very versatile	Duarte et al. (2005)
16	Itatiaia (2000 m a.s.l.)	High altitude <i>Araucaria</i> forest	<i>Araucaria angustifolia</i>	C ₃	C-, N-contents, NH_4^+ , NO_3^- , amino-compounds, sugars, FLU, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, phloem exudate, xylem sap	<i>Araucaria angustifolia</i> restricted to moist sites at the higher altitudes	Franco et al. (2005)
17	Periphery of Atlantic rain forest of SE-Brazil	Forests and open habitats	3 spp of <i>Clusia</i> trees, 4 of legume trees	C ₃ , CAM	Review of papers #18, #19, #20	Spatio-temporal variations of ecophysiological performance at intraspecific level; ecophysiological performance related to species dominance; ecophysiological performance not related to geographic distribution patterns	Scarano et al. (2005a)
18	(a) Sugar loaf, Rio (b) Jacarepiá (c) Arraial do Cabo (d) Búzios (e) Restinga de Jurubatiba	(a) Rock outcrops (b) dune forest, wet restinga (c) dry restinga (d) semideciduous forest, (e) intermediate restinga	<i>Clusia hilariana</i> , <i>Clusia fluminensis</i> , <i>Clusia parviflora</i>	CAM, C ₃	C-, N-contents, N- compounds, carbohydrates, FLU, $\delta^{13}\text{C}$	<i>C₃ C. parviflora</i> overall weaker performance, restinga dominant <i>CAM C. hilariana</i> better than <i>CAM C. fluminensis</i> , site gradients important for the two CAM species	Scarano et al. (2005b)

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Table 1. ... continued

#	Sites, coordinates	Site description	Species studied	Mode of PS	Methods of studies	Conclusions	Refs
19	Arraial do Cabo Restinga de Jurubatiba Jacarepiá	Moisture gradient: dry, intermediate, wet restinga, and dune forest	<i>Andira legalis</i>	C ₃	C-, N-contents, N-compounds, carbohydrates, FLU, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, phloem exudates, xylem sap	Large phenotypical plasticity, essential for performance root access to ground water table, important factor shading in the dune forest	Gessler et al. (2005a)
20	Búzios	Semideciduous forest	<i>Caesalpinia echinata</i> , <i>Caesalpinia ferrea</i> , <i>Machaerium</i> <i>obovatum</i>	C ₃	C-, N-contents, NH_4^+ , NO_3^- , N- compounds, carbohydrates, FLU, $\delta^{13}\text{C}$	<i>C. ferrea</i> highest photosynthetic capacity. Other two species more prone to photoinhibition. Differences unrelated to local abundance, niche separation and temporal dynamic	Gessler et al. (2005b)
21	Periphery Atlantic Forest, SE Brazil	Gradient of wet to dry ecosystems and habitats	Various species, ecophysio- logical fingerprinting	C ₃ , CAM	FLU, intrinsic photosynthetic capacity	Review including from this table #10, #15, #17, #18, #19, #20; panels of generalists and specialists	Lüttge et Scarano (2007)
22	Serra do Cipó (19°17'S, 43°33'W), 1170m a.s.l.	Rupestrian fields; xerophytic vegetation	Five sympatric species of Velloziaceae of different tallness	C ₃	FLU	Unknown constraints of photosynthetic capacity built up during the day	Lüttge et al. (2007)
23	Restinga de Jurubatiba	Intermediate restinga	<i>Clusia hilariana</i> , <i>Andira legalis</i> , <i>Allagoptera arenaria</i>	CAM, C ₃	C-, N-contents, N- compounds, carbohydrates, FLU, GAS, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Physiotypic characteristics CAM in <i>C. hilariana</i> , nodulation in <i>A.</i> <i>legalis</i> , tap roots in <i>A. arenaria</i> . important for space occupation and niche acquisition	Gessler et al. (2008)
24	Pedra Grande, SP (23°08'S, 46°35'W), 1300 m a.s.l.	Inselberg	<i>Campylopus</i> <i>savannarum</i> , <i>Racocarpus</i> <i>fontinaloides</i> , <i>Ptychomitrium</i> <i>vaginatum</i>	C ₃	FLU, pigment levels, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$	Desiccation tolerant mosses in a zonation around soil vegetation islands on the rocks, similar rehydration kinetics	Lüttge et al. (2008)

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Table 1. ... continued

#	Sites, coordinates	Site description	Species studied	Mode of PS	Methods of studies	Conclusions	Refs
25	Serra do Cipó (19°12' S, 43°29' W), 1400 m a.s.l.	Rupestrian fields	<i>Clusia arrudae</i> with Cecidomyiidae galls	CAM- cycling	FLU	Photosynthetic performance of galled and healthy leaf tissue is similar	Fernandez et al. (2010)
26	Santa Teresa, Santa Lucia Station, ES 19°57' -58' S, 40°31' - 32' W, 600-750 m a.s.l.	Montane and sub- montane Atlantic rain forest. Mosaic of habitats: riverine and hill forest, rock outcrops	<i>Clusia intermedia</i> , <i>Clusia spiritu- sanciensis</i> , <i>Clusia aemygdioi</i> , <i>Clusia marizii</i> , <i>Kielmeyera occhioniana</i> , <i>Tibouchina heteromalla</i>	CAM, C ₃ , C ₃ /CAM interme- diacy	FLU, GAS, δ ¹³ C, δ ¹⁵ N, titratable acidity, LEAF	Ecophysiological performance not sufficient for explaining habitat distribution patterns of species among physiognomic subsites. CAM in <i>C. spiritu- sanciensis</i> not related to habitat occupation. C ₃ /CAM intermediacy profitable in mesic habitats obligate CAM in exposed habitats	Lüttge et al. (2015)
27	(a) Serra do Cipó 19°14' S, 43°30' W, 1300 m a.s.l. (b) Tiradentes, Serra do São José, MG (21°08' S, 44°17' W), 1010 – 1030 m a.s.l.	(a) Rock outcrop in rupestrian savanna (b) mosaic of rupestrian rocky savanna	<i>Eremanthus glomerulatus</i> , <i>Clusia arrudae</i>	C ₃ , CAM- cycling	FLU, GAS, ACID, leaf angles	C ₃ midday depression, CAM- cycling for survival under drought, C ₃ for productivity in favorable seasons	Scarano et al. (2016)
28	Tiradentes, Serra do São José	Vegetation mosaic, micro-habitats of rupestrian grasslands, cerrados, riverine and gallery forests	<i>Clusia criuva</i> , <i>Clusia arrudea</i> , <i>Kielmeyera coriacea</i> , <i>Calophyllum brasiliense</i>	C ₃ , C ₃ /CAM interme- diacy, CAM- cycling	FLU, GAS,, δ ¹³ C, LEAF, leaf angles	C ₃ -photosynthesis suitable option at a variety of environmental conditions, CAM-cycling an escape under severe stress. At microsite level overlapping functional diversity of species and diversity of habitats determines the complexity of the vegetation.	De Mattos et al. (2019)



Figure 2. Ecophysiological measurements. Main photograph: Eduardo A. de Mattos (standing) and one of the authors (FRS) measuring chlorophyll fluorescence on a shrub of *Clusia* on the inselberg Pão de Açúcar, state of Rio de Janeiro (27th October 1995). Insert left: Eduardo measuring gas exchange in Tiradentes (9th October 2002). Insert right: Eduardo measuring chlorophyll fluorescence on desiccation tolerant *Selaginella sellowii* on the inselberg Itacoatiara, Rio de Janeiro (24th October 1995).

in the Atlantic forest domain) and rupesrian fields (transition between Atlantic forest and cerrado) are open vegetation. Cerrados are predominantly open here, but the Cerradão and the gallery forest physiognomies are forested. Restingas, dunes and high altitude fields (rocky or not) are open physiognomies of the Atlantic rainforest. For reference to the many plant species studied we use the names common at the times when the various studies cited in Table 1 were published, so that the reader can follow contexts in the table, the present text and the references. Meanwhile some of the species have been renamed. A special case is *Clusia parviflora* which is not considered a separate species anymore but a subspecies of *Clusia criuva* (Nascimento & Alencar 2023). However, for the reason given, we also keep it as *C. parviflora*. New names of other plants remaining separate species can be retrieved from Flora e Funga do Brasil (<https://floradobrasil.jbrj.gov.br/reflora/listaBrasil/>).

Open habitats

Cerrado

It is often generalized that cerrados are the Brazilian savannas. However, this is a strong oversimplification. Cerrados in a broad sense cover 20 % of the whole country of Brazil and 40 % of the non-Amazonian part (Eiten 1972). There are various subtypes of cerrado (Table 2) that are characterized by a variable tree cover on a relatively continuous herbaceous layer that shifts over time in response to localized variation in disturbance brought by fires and across topographical gradients that mostly reflect changes in soil depth or in groundwater level. The cerrado with these complex gradients of tree canopy cover and the high diversity of woody and herbaceous species in them, is an outstanding example of habitat-biodiversity.

There is a large structural and functional diversity of cerrado woody species. In a habitat near Brasilia which comes close to the cerrado *sensu stricto* (Table

2) we studied five of them (#11 in Table 1, Franco & Lüttge 2002), where *Didymopanax macrocarpum* (Araliaceae) is an evergreen tree, *Qualea grandiflora* (Vochysiaceae) is a deciduous tree remaining leafless for a few weeks by the end of the dry season, *Miconia fallax* (Melastomataceae), *Roupala montana* (Proteaceae) and *Ouratea hexasperma* (Ochnaceae) are evergreen shrubs in the field site, but they can reach tree size. *Ouratea hexasperma* produces new leaves and loses the old leaves simultaneously by the end of the dry season, whereas leaves in *M. fallax* and *R. montana* last over a year.

High irradiance loads and high evaporative demands of the atmosphere on sunny days are the major stressors for the woody species in the open cerrado habitats. With their diurnal patterns of plastic responses, the five species made different use of the available array of reactions of photochemical and non-photochemical dissipation of solar excitation energy, such as photosynthesis, photorespiration, photoinhibition that changed in concert with stomatal regulation of CO₂ and H₂O fluxes and for four species resulted in midday depression of CO₂ uptake from the atmosphere. Within the variations among species using functions for the control of damage due to the stress, the shrub *M. fallax* was somewhat unique in that it kept stomata open all day and showed no midday-depression and no photoinhibition. The other species made use of the functional diversity in different ways, suggesting subtle modifications of niche-occupation dynamics. Similarly, De Mattos (1998) found chronic photoinhibition in some but not all of eight cerrado species studied at a similar close-by site.

Rupestrian fields

Rupestrian fields are montane, fire-prone vegetation mosaics with scattered rock outcrops and a high diversity of different types of micro-sites (#27 and #28 in Table 1) that are associated to changes in edaphic properties, rugged relief and microclimatic variation. They are typically a transition between Cerrado and the Atlantic forest. Therefore, they are also covered in other sections. We observed various forms of plant parasitism (#3, #4, #25 in Table 1).

In the rupestrian fields of Serra do Cipó the Velloziaceae is one of the families that stands out with 57 species and 5 genera. *Vellozias* to our knowledge are not much studied ecophysiologicaly. They have a unique gestalt with leaf rosettes on the top of much branched pseudo-stems built up of retained leaf bases and dead leaves. The plants are desiccation tolerant (Lüttge 2008). In a gradient of 800 – 1700 m a. s. l. in the Serra they are not evenly distributed, which indicates preference of particular micro-sites. We found spatially limited but dense stands of *Vellozia* species both on rock-outcrops (Scarano *et al.* 2016) and in the vicinity of a small river (#22 in Table 1, Lüttge *et al.* 2007). At the latter site there were 15 species in a plot of 2 500 m². We measured photosynthesis in five of them (Lüttge *et al.* 2007). There was the new so far unexplained phenomenon of a substantial drop of intrinsic photosynthetic capacity in the afternoon without any evidence of photoinhibition during earlier times of the day.

Table 2. The Cerrado-concept of Brazil after Eiten (1972, 1986) and Lüttge (2008)

Species habit	Description	Terminology
No woody species taller than the herbaceous substratum	Grassland	Campo limpo
	Shrubs and trees isolated or in small groups < 2 % of total surface	Campo sujo
Low woody species (< 8 m)	Shrubs and trees 2 – 15 % of total surface	Campo cerrado
	Trees >15 % of total surface	Cerrado (<i>sensu stricto</i>)
Tall trees (> 8 m)	Trees >30 % of total surface	Cerradão
Tall trees in small groups	Park like	Campo coberto

Rock outcrops

Rock outcrops can be found in cerrados, rupestrian fields, or as large solitary inselbergs emerging from other vegetation, such as in the Atlantic forest. Two major stress factors are high solar irradiation and the supply of water, due to exposure and run-off, respectively.

On an inselberg, the Pedra Grande in the State of São Paulo – Atlantic forest domain – niche acquisition was studied for some bryophytes, namely three species of desiccation tolerant mosses (#24 in Table 1, Lüttge *et al.* 2008). Two of them form a zonation around soil vegetation islands with an inner and outer belt, respectively. The third one grows as isolated moss cushions on bare rock. The photosynthetic capacity and associated drying and wetting dynamics were quite similar. Differences in periodic water supply and diffusion limitation of CO₂-acquisition with the correlated growth forms of belts and cushions must be decisive for niche-occupation of these mosses.

Measurements on several angiosperms were made on the Sugar Loaf (Pão de Açúcar), Rio de Janeiro, also within the Atlantic forest domain. The C₃-plants *Stillingia dichotoma* and *Croton compressus* are sympatric species there. The former one is a coastal-inselberg specialist, while the latter one also occurs in coastal dry forests (see *Semideciduous Dry Forests*). Both species show similar photosynthetic capacity and patterns of photoinhibition. Surprisingly *C. compressus* is less drought stressed on the inselberg than in the dry forest (#15 in Table 1, Duarte *et al.* 2005). In spite of the run-off of precipitation on the inselberg, the availability of water must be still lower in the very dry forest at Búzios.

Autecological behavior of *Clusia parviflora*, *S. dichotoma* and *Vriesea geniculata* with the diurnal patterns of photosynthesis showed best performance of *S. dichotoma* among the three species (#2 in Table 1, De Mattos *et al.* 1997). *Clusia parviflora* also co-occurs with *C. hilariana* in the restingas, where it is more abundant in shaded places (#18 in Table 1, Scarano *et al.* 2005 a, b, see also *Restinga*, next). In a rupestrian field, very much in the transition Cerrado-Atlantic forest at Tiradentes, State of Minas Gerais, autecological characterization suggested that *C. arrudae* performs CAM-cycling. It is sympatric there with

the C₃-species *Eremanthus glomerulatus*. (#27 in Table 1, Scarano *et al.* 2016).

Restinga

Restingas are mosaics of plant communities that occupy the sandy plains formed by marine deposits in the late Quaternary. They stand between the sea and the Atlantic forest mountain chain. Most sandy coastal plains in the State of Rio de Janeiro, where our studies were concentrated, consist of two beach ridges dating from the Holocene (5,000 to 3,000 yr BP). The oldest sandy plains in the state date from the Pleistocene (120,000 yr BP; see Martin *et al.* 1993). Araujo (2000) classifies the restingas of the state of Rio de Janeiro in ten zones according to their flora, which is related to local variation in climate and geological history. Our sites ranged from the Environmental Protection Area of Massambaba in the municipalities of Saquarema and Arraial do Cabo, to the Restinga de Jurubatiba National Park, ca. 100 km further north from this region. Climate here is drier due to the cold oceanic upwelling of the Cabo Frio region (Araujo 1997). For a detailed description of these sites and their biogeographic history, see Scarano (2002, 2009), and Scarano *et al.* (2001, 2005a,b).

Clusia hilariana, present at the Restinga de Jurubatiba National Park, was our most studied species. This peculiar tree can be as tall as 8 m (Dias *et al.* 2006) and displays a number of interesting features, such as (1) dioecy (Faria *et al.* 2006), (2) seedling occurrence predominantly inside the tanks of terrestrial bromeliads (Correia *et al.* 2010), and (3) CAM metabolism (Lüttge 2006). Moreover, it has been shown that through facilitation processes this species in the restinga is largely responsible for diversity in land (Dias and Scarano 2007), soil (Kreuzer *et al.* 2007) and possibly even in adjacent water bodies (Pimentel *et al.* 2007). In addition to these positive effects on community diversity, *C. hilariana* plays a marked functional role: its aboveground biomass stock and understorey litter is comparable to the entire woody component of many neotropical savannas (Dias *et al.* 2006). Scarano and Garbin (2013) described it as a “stem species”, *i.e.*, a “stem cell”, a regenerant of Gaia. It has enough ecological, physiological and morphological plasticity to, in time, colonize novel habitats and subsequently facilitate the onset of a diverse

community underneath it by acting as a perch for seed dispersers and changing microclimate and soil conditions. This species is generally at the centre of hemispherical vegetation clumps, where a variety of other species occur.

We also studied other *Clusia* species, both CAM (*C. fluminensis*) and C_3 (*C. parviflora*), legume trees (*Andira legalis*), bromeliads (*Neoregelia cruenta*), aroids (*Philodendron corcovadense*), hemiparasites (*Psittacanthus dichrois*). Despite encompassing just a sample of the many other trees, shrubs and herbs present in these ecosystems, they are demonstrative of the tremendous wealth and diversity of ecophysiological repertoire to deal with the often harsh conditions of high temperatures, water and nutrient shortage of the restingas.

Forests

Semideciduous dry forests

The semideciduous coastal dry forest at Búzios was included in an ecophysiological study of 32 species distributed in four habitats bordering the Atlantic rain forest that differed in altitude and water availability (#10 in Table 1, Scarano *et al.* 2001). It houses Pau-brasil (*Caesalpinia echinata*), the tree that gave the country of Brazil its name. Búzios is in the driest region of the State of Rio de Janeiro, and the dry forest there is strongly arid and markedly seasonal. Comparative measurements addressed five shrub and tree species, which were habitat generalists and specialists, respectively.

The C_3 -species *Croton compressus* is a generalist occurring also on coastal inselbergs (see *Rock outcrops*). It is more drought stressed in the dry forest than on the inselbergs, where it has a lower water use efficiency (WUE) and a higher photosynthetic capacity. Between the sites it exhibits intraspecific ecophysiological differences with plasticity regarding WUE and a higher accumulation of proline as an intracellular osmo-protectant (Duarte *et al.* 2005).

Similarly, the CAM-species *Clusia fluminensis* is a generalist occurring in the dry forest and in open restingas. Like *C. hilariana* it is a nurse plant. However, it is not so habitat-determining in the dry forest as *C. hilariana* is in the restingas. Búzios is the northern limit of its distribution. Its plasticity includes growth form. In the dry forest it grows as trees of up to 8 m height and as a hemi-

epiphytic strangler and in the open restinga as shrubs of 2 m height. Photosynthetic capacity of *C. fluminensis* is lower in the dry forest than in the open restingas (Scarano *et al.* 2005 b).

The specialists in the dry forest selected for our studies were three legume trees (Fabaceae) with C_3 -photosynthesis, *i.e.*, *Caesalpinia echinata* and *Caesalpinia ferrea* growing up to 10 – 20 m in height and *Machaerium obovatum*, 2 – 4 m tall. There is some contrasting behavior of the otherwise compatriot species. The highest photosynthetic capacity is seen in *C. ferrea*. The other two species were to some degree photoinhibited at high irradiances which was not fully reversed overnight, *i.e.*, they showed some persistent loss in energy conversion efficiency and in photosynthetic capacity. Like *C. compressus*, *C. echinata* pronouncedly performs protective proline enrichment. Despite the interspecific differences the three species showed similar abundance, *i.e.*, the ecophysiological differentiation was not related to local abundance in the dry forest. Niche-separation between them is dynamic and temporal (Gessler 2005b).

Gallery forests

Gallery forests at the margin of rivers are part of the vegetation mosaics discussed below (*Microsites in an Atlantic forest* and *Microsites in a Rupestrian Field*). In a gallery forest to cerrado transect at the ecological reserve of the Instituto Brasileiro de Geografia e Estatística (IBGE) we measured *Clusia criuva* checking the expression of the very plastic potential of photosynthetic options in the genus *Clusia* (#6 in Table 1; Herzog *et al.* 1999a). The species has a minor capacity for CAM but rarely makes use of it. Instead, the measurements show that its photosynthetic apparatus can well adjust for effective performance of C_3 photosynthesis in different adjacent habitats of the transect from deep shade inside the gallery forest to the semi-shaded ecotone towards the cerrado and in the fully exposed cerrado close to the ecotone. This species does not progress more deeply into the cerrado, though. Since elsewhere it does in fact grow at rather dry sites, it is unlikely that this is due to water relations. The habitat segregation in this case could be due to frequent fires occurring in the cerrado.

Swamp forests

In the restingas we can find lakes and swamp forests adjacent to the dry sandy dune sites, such as in the Restinga of Jurubatiba National Park (#15 in Table 1). This allowed us to study gradients from swamp to wetter and drier restingas. The observations underline the role of intraspecific plasticity for site occupation, *e.g.*, for the C₃-species *Rheedia brasiliensis* occurring as a generalist across the gradient. It had a lower water use efficiency and lower levels of soluble carbohydrate in the phloem as well as a reduced sun-plant nature in the swamp forests than in the drier restinga sites (Duarte *et al.* 2005).

In a swamp forest at Poço das Antas (#8 in Table 1), Borges *et al.* (2022) compared the acclimation to flooding of three tree species, the pioneer species *Vernonanthura discolor* (Asteraceae), the early secondary species *Guarea guidonia* (Melicaceae) and the late secondary species *Andira anthelmia* (Fabaceae). The stress of permanent flooding is predominantly reduced aeration, and hence low O₂-availability, and nutritional scarcity. In all cases, acclimation was based on plasticity. However, in their morphoanatomical and physiological investigations the authors showed that responses to flooding vary according to species. One response under flooding was increased leaf lamina thickness. Species specific differences were that in one case, *i.e.*, *A. anthelmia*, this was due to spongy parenchyma, facilitating gas exchange and aeration, and in the other two cases to palisade parenchyma, supporting photosynthesis with increased numbers of chloroplasts in the space available. Flooding did not influence photochemical performance of *G. guidonia* and *V. discolor* but led to a reduced efficiency in *A. anthelmia*. Overall, the three species appeared well acclimated to the flooding. However, the differences observed underline the general conclusion from all the work presented in this essay, that with species-diversity associated plasticity-diversity is a prominent aspect of the performance of plants in their habitats.

In particular habitats one can find C₃- and CAM-species side by side. An interesting example of plastic and competitive occupation of microsites by plants with either mode of photosynthesis is seen by two species of *Nidularium* (Bromeliaceae) covering the ground in the understory of the swamp forest at Poço das Antas Biological Reserve (Scarano *et al.* 1997,

1999; #8 in Table 1). Both species are shade adapted and intolerant of full insolation. Nevertheless, they segregate in different patches in the swamp forest. *Nidularium innocentii* is a C₃-species, with a slight indication of some CAM-capacity though, which grows in deep shade of a periodically flooded part of the swamp. *Nidularium procerum* is a CAM-species covering semi-exposed parts under a more open canopy with permanent flooding. The capacity of CAM-performance may explain the clear habitat segregation allowing *N. procerum* but not *N. innocentii* the occupation of semi-exposed parts and, with the plasticity of CAM also ingression into the more shaded space. There it is outcompeted, however, by *N. innocentii* with its C₃-photosynthesis being more productive for growth in the deep shade.

High-altitude forests

A very special habitat where we made measurements is the Araucaria-forest at the high altitude of 2,000 m a.s.l. in the Itatiaia mountains (#16 in Table 1; Franco *et al.* 2005). It is the northern most occurrence of *A. angustifolia* on the South-American continent. The general distribution of *A. angustifolia* shows an inverse relationship between latitude and altitude. It prefers moist sites, and at the lower latitudes in Brazil it occurs above the limit of the Atlantic rain forest from 1,300 to 2,000 m a.s.l. Because of the high quality of its wood, it is an anthropogenically highly endangered species, and in native forest stands it shows low regeneration potential. However, our broad study including photosynthesis and metabolism of C- and N-compounds shows, that the species has good ecophysiological performance and healthy regeneration in the vegetation relict of Itatiaia. Unfortunately, comparable studies at other sites are not available. However, studies on *Araucaria* forest/grassland mosaics in southern Brazil have provided evidence that this species can be a nucleating species, by providing perch for seed dispersers, attenuating microclimate variations and increasing soil nutrient availability (Korndörfer *et al.* 2015).

This *Araucaria*-site was also included in a comparative study of six shrub species in different plant communities. At Itatiaia mountains we performed measurements on *Myrsine gardnerina* which occurs at 2,000 m a. s. l. and also grows up to high altitude grasslands and rocky outcrops (#15 in Table 1). It has the plasticity of developing both shade-plant and sun-plant characteristics.

Its performance at the high altitude was similar to that of shrubs with similar growth gestalt in the lowland sites (Duarte *et al.* 2005).

Habitat occupation by parasites

When a parasite intrudes into a host, this is obviously a habitat for it. This niche-acquisition, *i.e.*, functioning within the host, with mutual interaction also affects the host. Thus, parasitism - although at a very low scaling level - is an example of an albeit rather special habitat occupation, which was at times included in the course of our studies.

In the cerrados the trees are often abundantly housing mistletoes. The intrusion of host trees by mistletoes is often heavy, particularly in the rupestrian fields influencing different trophic levels, the structuring of the plant-associated communities and their dynamics and ecosystem processes (Guerra *et al.* 2018; Belchior *et al.* 2022). A large number of mistletoe/host-pairs were studied with a gradient being given from very exposed rupestrian fields to semi-exposed cerrado and highly shaded gallery forest (#4 in Table 1; Lüttge *et al.* 1998). Mistletoes are hemiparasites with green photosynthetically active leaves and feeding on the xylem of the host trees for transpiratory water and dissolved minerals and in addition also parasitizing on carbon compounds. There are some differences in the performance between host leaves and mistletoe leaves, because the latter must keep stomata more open to maintain a higher stomatal conductance for dragging the transpiration stream of the host towards themselves. Therefore, they have a lower water use efficiency and operate at higher internal partial pressure of CO₂. However, it turned out that along the gradient of sites photosynthetic capacity of the leaves of both partners was similar except at the very exposed site, where the hosts even performed better. This was due to particularly pronounced expression of sun plant characteristics also controlling photoinhibition. Mistletoes have several mechanisms of safe dissipation of potentially harmful excess light energy to alleviate the danger of photodamage. In plants xanthophyll cycles are operating for non-photochemical dissipation of surplus excitation energy of irradiance and thereby controlling photoinhibition. Mostly it is the violaxanthin cycle. In some plants, in addition a luteïne-epoxide cycle is participating. This has been demonstrated in several genera of mistletoes of the Loranthaceae and

Viscaceae sampled in the Brazilian cerrados (#12 in Table 1; Matsubara *et al.* 2003). With respect to photosynthetic capacity there are no indications of mistletoe load affecting habitat segregation of trees.

A rarer example of parasitism, albeit quite abundant in certain places at the open campo rupestre of Serra do Cipó, is the host/parasite-pair of *Mimosa nagueirei* (Mimosaceae)/*Pilostyles ingae* (Rafflesiaceae) (#3 in Table 1). *Pilostyles ingae* is an endophytic holo-parasite with cellular threads growing vigorously within the host's bark. Infection can be intensive with the host being densely covered by small flowers protruding from the bark. However, surprisingly leaves of parasitized and healthy host plants show identical performance of photosynthesis (Fernandes *et al.* 1998) indicating a well-balanced relation between host and parasite.

In addition to plant-plant parasitism, plant-insect parasitism is also frequent especially by gall-forming insects, which induce tumor-like structures of plant tissues. In the rupestrian fields of the Serra do Cipó we found *Clusia arrudae* and in the Atlantic Forest at Santa Teresa *Clusia aemygdioi* parasitized by gall wasps of the Cecidomyiide (#25 in Table 1, Lüttge 2007). A chlorophyll fluorescence imaging system showed that in a ring around the galls efficiency of photosystem II was increased and in the gall tissue itself it was low (Lüttge 2007). However, apart from subtle differences photosynthetic performance in healthy parts of infected leaves was rather similar to that of non-galled leaves (Fernandes *et al.* 2010).

There are reports in the literature showing that parasitism hampers host photosynthesis. However, in the examples we encountered during our ecophysiological studies in Brazil we found no evidence for an impact of parasites on host photosynthesis.

MOSAICS AND GRADIENTS

Scaling levels

While assessing the impact of photosynthetic performance on habitat occupation it turns out that we must distinguish scaling levels (Lüttge 2020) as follows. The global dominance of C₃-photosynthesis is a basic feature of (1) macrohabitats of our

planet's vegetation. Specific macrohabitats, where C_4 -photosynthesis is dominant are cerrados, savannas, steppes and prairies with C_4 -grasses and -sedges. Conversely, plants with the water saving Crassulacean Acid Metabolism (CAM) are not shaping habitats of global dimensions but clearly can determine the physiognomy of (2) plant communities, where CAM plants are prominent but not exclusively dominant, *e.g.*, in semi-deserts of SW-USA and Mexico, cactus forests in Venezuela and the thorn-bush vegetation of Madagascar (Lüttge 2020). One of such communities as encountered during the present studies in Brazil are the restingas, where the CAM-tree *Clusia hilariana* prominently determines the vegetation (see Restinga). However, typical correlations between the modes of photosynthesis (C_3 , C_4 , CAM) in relation to habitat occupation dissipate at lower scaling levels and a completely different picture emerges when we turn our attention to (3) microhabitats of gradients and vegetation mosaics.

Bridging the gap between community levels and smaller scale mosaics, the Atlantic-forest of SE-Brazil itself is an example for scaling down. We distinguish different habitats at its periphery with sympatric C_3 and CAM species (#15, #17 and #21 in Table 1), namely: coastal sand dune vegetation of moist, dry and intermediate restingas; dry sand dune forests; swamp forests; semi-deciduous dry forests; inselbergs; high altitude vegetation (Lüttge 2020, Lüttge *et al.* 2015). Within the Atlantic-forest in the Estação Biológica Santa Lucia at Santa Teresa (#26 in Table 1, Figure 3) we found microsities of forest on sharp hills, forest on flat lands mostly by the river Timbuí, and granitic-gneissic rock outcrops. An example of chess-board like mosaics are the rupestrian fields of Serra de São José at Tiradentes (#28 in Table 1, De Mattos *et al.* 2019, Figure 4) with rupestrian grassland (rocky savanna), cerrado/savanna, small rock outcrops, and gallery forest alongside a small river.

The fundamental question raised by the comparisons at scaling levels is why they provide different pictures. This is possibly due to spatiotemporal events, the evolution of, *e.g.*, large grasslands and sizeable communities having lasted much longer than that of microsities in small scale mosaics. We return to this below, when we consider the opening, the diversity

and the evolution of niches after looking at the microsities more closely supporting the conclusion that particular ecophysiological traits and modes of photosynthesis do not explain distinct distribution of plant species.

Microsities in an Atlantic rainforest

When closely studying comparatively the occupation of five subsites in the Atlantic rainforest at the Estação Biológica Santa Lucia, Santa Teresa, State of Espírito Santo, as listed in Scaling Levels (#26 in Table 1), by four shrub-species of the genus *Clusia* and in addition shrubs of *Tibouchina heteromalla* and *Kielmeyera occhioniana*, it emerged clearly that the success of the species indifferent habitats is not due to generic adaptation but to ecophysiological plasticity (Lüttge *et al.* 2015). This is given notwithstanding the fact that the two highly different modes of photosynthesis, C_3 and CAM, were expressed among the plants studied. These were *Clusia aemygdioi* (potentially C_3 /CAM-intermediate), *Clusia intermedia* (C_3), *Clusia marizii* (C_3), *Clusia spiritu-sanctensis* (obligate CAM), *Tibouchina heteromalla* (C_3), and *Kielmeyera occhiniana* (C_3).

The only obligate CAM-species was *C. spiritu-sanctensis*. *Clusia aemygdioi* indicated having some intrinsic capacity of CAM but a C_3 /CAM intermediacy needs to be confirmed. During the present measurements it performed C_3 -photosynthesis. According to the distribution patterns at microhabitats within the rainforest *C. aemygdioi* and *C. intermedia* are locally widespread, and *C. marizii* and *C. spiritu-sanctensis* are locally restricted, although *C. spiritu-sanctensis* in large scale geographical terms has the most widespread distribution patterns of the four *Clusia* species as it also occurs in drier restingas. However, generalists and specialists were not notably different in occupying the rainforest subsites. Observations sticking out with respect to the relations of performance and microhabitat occupation are coming from *C. intermedia* and *C. spiritu-sanctensis*. The obligate C_3 -plant *C. intermedia* showed consistently inferior performance among the plants studied, regarding photosynthetic capacity, low water use efficiency and suffering photoinhibition. Yet, it was the only one of the species occurring at three of the five sites, namely



Figure 3. Atlantic rainforest (top) of Estação Biológica Santa Lucia at Santa Teresa with the Timbuí river and riverine forest (lower left) and vegetation with *Clusia spiritu sanctensis* on top of an orographic rock outcrop (lower right).

the gallery and hill forests and the dry orographic rock outcrops. *Clusia spiritu-sanctensis* occurred not only on the dry rock-outcrops as expected from the water saving functions of CAM but also in the wet riverine forest. Its performance resulted from the plastic use of the diurnal phases of CAM, where in the highly shaded hill forest site in addition to nocturnal CO₂ uptake also phase IV of

CAM (transition from the light to the dark period) played a role with CO₂ uptake in the afternoon. Plastic flexibility of the *Clusias* across microsites is evident by the C₃-species showing sun-plant nature at all sites with the clear exception of the shaded hill forest site, where they displayed shade-plant characteristics.



Figure 4. Vegetation mosaic in the rupestrian fields of Serra de São José at Tiradentes.

Microsites in a rupestrian field

In the rupestrian fields of Serra de São José at Tiradentes like in the Atlantic rainforest we encounter microsites, which in the latter case are visibly well differentiated (Figure 4, #28 in Table 1, De Mattos *et al.* 2019). We studied four shrubby species in closely neighboring habitats (Table 3). They performed different modes of photosynthesis, namely *Kielmeyera coriacea* and *Calophyllum brasiliense* were obligate C_3 -plants, while the two *Clusia* species had intrinsic capabilities of CAM. There was C_3 /CAM intermediacy in *C. criuwa* and CAM-cycling in *C. arrudea*, where the latter means nocturnal recycling of CO_2 without gas exchange with the surrounding atmosphere for retrieving the carbon released by respiration. This functional diversity opens different ways of ecophysiological plasticity in niche occupation. However, *C. criuwa* did not make use of the CAM-option and performed C_3 -photosynthesis even in the dry season with a C_3 -typical midday depression. In *C. arrudea* CAM-cycling appeared as an escape under severe stress. With the overlapping functional diversity

of species with different modes of photosynthesis side by side and the diversity of closely established habitats the microhabitat diversity remains an issue of complexity.

Niche dynamics occurring in the microsites

The central message of our widely spaced observations of the mosaics is that the microsites have provided and are still providing niches to be occupied. This causes spatiotemporal patterns of selection, since in mutual feedback species shape the environment and the environment shapes species. Niche separation and development are dynamic and temporal (Laland *et al.* 2017; #20 in Table 1). As seen in studies of 32 species in four habitats marginal to the Atlantic rain forest (Scarano *et al.* 2001), we find the functional groups of plants in all habitats and the different modes of photosynthesis, C_3 and CAM, respectively, side by side (#10 in Table 1), which demonstrates that ecophysiological performance per se, such as photosynthesis, is insufficient for explaining small scale microsite occupation (Lüttge 2020). In these ways niche diversity

Table 3. Microsites of rupestrian grasslands at Serra de São José, Tiradentes (MG), with the plants studied (De Mattos et al. 2019)

Species	Microhabitats	Mode of photosynthesis
<i>Clusia criuva</i>	Semi-exposed close to denser forest vegetation	C ₃ /CAM intermediate
<i>Clusia arrudea</i>	Rock outcrops at gallery forest exposed and shaded, rupestrian grassland, cerrado	C ₃ and CAM-cycling
<i>Kielmeyera coriacea</i>	Cerrado	C ₃
<i>Calophyllum brasiliense</i>	Riverine forest, flooded and non-flooded	C ₃

emerges from species diversity. According to the biodiversity-related niches differentiation theory by enhanced diversity more niches are shaped (Gatti 2011). Modifying their local environment, species alter the grounds for natural selection, but niche development is an evolutionary process on its own (Laland & Sterelny 2006). Species and niche diversity together determine evolution as envisaged beyond the gene centered concept of the modern synthesis (Matyssek *et al.* 2023).

CONCLUSIONS

Our comprehensive overview of the biodiversity of habitats in an area covering from Central to South-Eastern Brazil (Figure 1, Table 1) and of the ecophysiological performance of many conspicuous plant lineages in them considering microhabitats, allows stimulated views on processes of niche dynamics and evolution. Comparisons of species being habitat generalists and specialists, respectively, and performing different modes of photosynthesis, *i.e.*, C₃ or CAM, display plant-group performance with sharing space and niche occupation. Only in one case, however, this showed well delineated habitat dominance, namely by *Clusia hilariana* in the restingas. Its feature of performing CAM at the high exposure to solar irradiance and restricted availability of water obviously is the decisive specific adaptation allowing it to perform as a pioneer species and nurse plant, starting vegetation islands for growth of other species.

A closely related species, *C. fluminensis*, seems also to play the same role in the restingas. The restingas are rather large extended ecosystems, and it agrees with the observation of varying functional plant dominance at different scaling levels (see section above) that the restinga vegetation is shaped so much by the CAM-performing *C. hilariana*.

Conversely in the microhabitats along gradients and transects and especially in vegetation mosaics flexibility and plasticity is the rule rather than the exception. CAM with variable expression of its diurnal phases appears to be just one among other means of adding to photosynthetic plasticity. There is plasticity of both the niches and the plants. Such niche-plant interactions take theory of evolution beyond the gene-centered modern synthesis.

From critical evaluations of anthropogenic impact and climate-change, the prominent role of biodiversity of niches and species in maintaining our living environment on the planet, is increasingly emerging. For understanding the ruling of plasticity and diversity in ecophysiological settings, it is essential that reductionist autecological description of the performance of individual species is overlaid by comparative synecological assessments (Lüttge 2005, Lüttge & Scarano 2004, 2007). Such comparisons must be made (1) between different habitats, considering habitat diversity, (2) between species within given habitats, considering species diversity, and (3) between given species across

different habitats, comprehending the links between habitat and species dynamics. This essay presents many examples for this approach addressing habitat and plant-species dynamics in tropical Brazil.

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