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# 1 **Why incorporate plant architecture into trait-based ecology?**

2

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11

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## 1        **Abstract**

2        Trait-based ecology has improved our understanding of the functioning of organisms,  
3 communities, ecosystems and beyond. However, its predictive ability remains limited as long as  
4 phenotypic integration and temporal dynamics are not considered. We highlight how the  
5 morphogenetic processes that shape the 3-dimensional development of a plant during its lifetime  
6 affect its performance. We show that the diversity of architectural traits allows us to go beyond  
7 organ-level traits in capturing the temporal and spatial dimensions of ecological niches and  
8 informing community assembly processes. Overall, we argue that consideration of multilevel  
9 topological, geometrical and ontogenetic features provides a dynamic view of whole-plant  
10 phenotype and a relevant framework for investigating phenotypic integration, plant adaptation and  
11 performance, and community structure and dynamics.

## 12       **Keywords**

13       Plant architecture; functional trait; ontogeny; phenotypic integration; community structure

## 14       **Consideration of phenotypic integration is urgently needed in trait-based ecology**

15       Trait-based ecology has gained momentum over the last decades through systematic comparison  
16 of genotypes and species across scales and organizational levels (organ, organism, population,  
17 community and beyond). This comparative approach has come with the rise of standardized  
18 protocols [1] for identifying and measuring organ-level traits that are expected to reflect whole-  
19 organism functioning [2]. The promise of deciphering mechanisms with this approach has  
20 contributed to its success. For instance, traits depicting the morphology and chemical composition  
21 of a leaf are tightly linked to leaf-level metabolism across species worldwide [3]. Nonetheless,  
22 functional traits remain poor predictors of local adaptation, plant performance, population

1 dynamics and community assembly in natural ecosystems [4-10]. This failure can be explained by  
2 the disintegration of the phenotype into elementary (often organ-level) features in trait-based  
3 ecology. Interestingly, botanists have long worked on comprehensive descriptions of **plant**  
4 **architecture** (see Glossary) [11] with explicit consideration of **phenotypic integration** across organs,  
5 time and space.

6         Plants are modular organisms built by three key processes: growth, branching and  
7 duplication of branching systems (i.e. **reiteration**). Stems and roots are **axes** growing in a given  
8 direction through successive phases of elongation and development of specific organs. For instance,  
9 stems are generally made of a series of annual shoots, which are themselves a series of internodes  
10 and nodes bearing acquisitive, reproductive and defensive organs such as leaves, flowers and spines  
11 respectively. Axes can have very different patterns of development, as well as specific functions  
12 across species and within the same individual. Most plant species thus have several types of stems  
13 and roots, called **axis categories**, each with distinct morphological attributes and functions (**Box 1**).  
14 Plant architecture describes the properties of these different types of axes, the way they are  
15 organised with each other (**topology**) and throughout the plant's development (**ontogeny**) [12].  
16 Plant architecture varies greatly between and within species [13-15] (**Box 1**). This variability can be  
17 characterized at different temporal and spatial resolutions using a set of dedicated tools and  
18 concepts initially developed for aboveground tree parts [16]. They were later extended to other  
19 growth forms (e.g., shrubs, herbs, mosses) [13, 14, 17, 18] and to belowground parts [19, 20]. The  
20 morphological specialization of axes [12], for example, can be used to characterize their functional  
21 differences both between and within species [13]. In this article we mostly address the aboveground  
22 architecture of woody plants for which we have more knowledge and references. We argue that  
23 bridging modern trait-based ecology and plant architecture approaches is a frontier research  
24 agenda that will enable us to tackle pivotal issues in plant ecology and evolutionary biology.

1           A comprehensive quantification of whole-plant functioning is a priority in trait-based ecology  
2 so as to further assess the phenotypic drivers of local adaptation and elucidate diversity-ecosystem  
3 relationships. Functional traits are most often recorded at the organ level, but they are assumed to  
4 capture whole-plant functioning [2]. Nonetheless, because architectures vary among and within  
5 species [21] and the distribution of organs within the plant varies in consequence [22], this basic  
6 assumption is poorly validated (**Figure 1A**). Phenotypic integration is partly captured by analyzing  
7 multiple trait-trait relationships [23, 24], but these can be blurred by interspecific differences in  
8 plant architecture, as exemplified in allometric and biomass allocation patterns (**Figure 1B-C**). A  
9 direct consequence of the failure to consider plant architecture is a poor estimation of whole-plant  
10 metabolism (**Figure 1D**) and reproductive effort (**Figure 1E**). Ultimately, these biases in quantifying  
11 whole-plant functioning and performance from plant functional traits alone have major implications  
12 for characterizing community dynamics. As a notable example, community assembly studies [25]  
13 have analyzed trait patterns to infer processes at the community level using a list of commonly used  
14 traits. Single traits and organ-level traits can, by nature, hardly capture all the processes involved in  
15 resource partitioning between competing plants (**Figure 1F**). Despite the potential of plant  
16 architecture to capture the multidimensional facets of plant phenotype and spatio-temporal  
17 variation in ecological strategies, it is still mostly seen as a static description of crown, stem or root  
18 dimensions [26, 27]. Plant architecture can capture the myriad events a plant endures over its  
19 lifetime, as well as the mechanisms involved in resource capture and use. Incorporating plant  
20 architecture in the theoretical corpus of trait-based approaches is thus of critical importance given  
21 the limited progress made over the past decade in explaining community-level mechanisms.

22           Comparative approaches seek generalities. They are based on trait screening programs  
23 covering large sets of organisms [28] to the detriment of precision and consideration of  
24 mechanisms. Conversely, plant architecture approaches offer a comprehensive understanding of

1 the plant phenotype but their context dependency and the massive amount of information they  
2 may require a priori seem incompatible with the philosophy of modern trait-based ecology. We  
3 argue that a bridge must be built between these two disciplines, and we aim to lay its foundations.

#### 4 **Plant growth and persistence through the lens of architecture**

5 As sessile organisms, plants spread vertically and laterally depending on local environmental  
6 heterogeneity in resource and space availability. Current trait-based approaches largely focus on  
7 organ-level functions and usually overlook the distribution and number of acquisitive and  
8 reproductive organs across space and time [29-31]. Ecological studies often reduce plant  
9 architecture to its geometrical aspects [27, 32, 33], describing stature or allometric traits and  
10 forgetting the nature and organization of the axes. In root architecture studies, these two  
11 components are more often considered, but the focus is more on anchorage and acquisitive  
12 functions than spatio-temporal occupancy [34]. Thus despite its relevance for exploring the various  
13 constraints that drive plant form across ecological scales [35, 36], this allometric view of plant  
14 architecture does not fully capture the differences among species and individuals in their ability to  
15 explore and colonize belowground and aboveground space in the course of their **ontogeny**, nor the  
16 many other functions performed by plant architecture [37]. Plant ontogeny can be divided into  
17 several stages, from germination to senescence, each being characterized by a specific branching  
18 pattern and specific morphological trait values [38]. The **architecture-based approach (Figure 2)** is  
19 a framework that explicitly acknowledges different patterns of plant development in space and time  
20 to better understand the linkages between plant structure, function and performance [12, 39].  
21 Below, we introduce the key **morphogenetic processes** involved in plant growth and persistence  
22 that should be considered in future ecological studies.

23

1 *Growth strategies arise from the structural and functional differentiation of axes*

2 Hallé and Oldeman [16] distinguished 23 **architectural models** to represent basic plant growth  
3 strategies for exploring space, competing for light and reaching and occupying the canopy.  
4 Architectural models capture developmental constraints on plant organization but their links with  
5 ecological performance have not been extensively explored. Analysis of their components has  
6 revealed types of stems and roots, known as axis categories, based on morphological traits [12].  
7 Interestingly, morphological differentiation strongly mirrors functional differentiation, with each  
8 axis category contributing to one or several functions (**Box 1**), including space exploration [40],  
9 resource acquisition [22, 37], vegetative or sexual reproduction [41], resource storage [42],  
10 response to disturbance [43], defence against herbivores [44], and mechanical [45] and hydraulic  
11 properties [46]. For example, trunks and branches with long internodes are responsible for most  
12 vertical and lateral exploration, respectively, while a large number of twigs and short shoots  
13 augments leaf area and contributes to flower and fruit production [22, 47]. The relative proportions  
14 of the axis categories change as ontogeny progresses through the juvenile, adult, mature and  
15 senescent stages. The nature, distribution and proportion of axis categories as well as their relative  
16 biomass at a given stage are critical components of plant functional strategies for resource capture  
17 and space occupancy [20]. As well as differentiating axes, we need to analyze, integrate and scale  
18 up growth and branching dynamics from shoot to whole-plant level. This is essential for  
19 disentangling and understanding the many sources of variability in crown properties (such as crown  
20 size and shape or foliage arrangement) [48, 49] and whole-plant performances. Incorporating these  
21 features in trait-based studies should help improve our understanding of growth and ecological  
22 strategies.

23

24

1 *The pivotal role of reiteration in persistence strategies*

2 A key aspect of plant architecture is the reiteration process, which can greatly extend the plant's  
3 lifespan [50]. Reiteration can occur as part of the developmental sequence of the species (sequential  
4 reiteration), or in response to a change in resource availability (adaptive reiteration) or a  
5 disturbance (traumatic reiteration). Traumatic reiteration or resprouting is part of the recovery  
6 process following mechanical damage or in response to biotic or abiotic stress [51]. Traumatic  
7 reiteration usually begins when **epicormic shoots** become active after disturbance. It helps to  
8 increase species performance in disturbance-prone ecosystems [52]. While identifying reiteration  
9 patterns is doable in practice at species level [12], large-scale screening programs have yet to be  
10 conducted to determine which mechanisms promote reiteration abilities, how reiteration abilities  
11 trade-off with other key traits (e.g. reproduction) and how reiteration promotes species  
12 performance along environmental gradients. Vegetative propagation and clonal multiplication  
13 mainly result from total reiteration. They are frequently associated with a specialized organ, namely  
14 a horizontal stem (a stolon or a rhizome) that provides a means to escape from competition and to  
15 forage for nutrients far from the mother plant [53]. Vegetative reproduction is expressed differently  
16 across and within species, notably in relation to changing environmental conditions. For example,  
17 vegetative reproduction by resprouting is closely related to carbohydrate storage in belowground  
18 or aboveground organs [54]. Klimesova et al. [55] provide a valuable handbook of overlooked plant  
19 **modularity** traits, but their approach does not address their temporal and ontogenetic variation.  
20 Consideration of architecture provides a common framework for characterizing the diversity of  
21 processes and structures involved in growth and persistence throughout the plant life cycle.

22

23

24

1            *Architecture sheds light on growth dynamics*

2    Empirical studies in plant architecture over the last four decades have provided valuable knowledge  
3    about the link between architecture, growth, survival, and the environment [56]. Plant morphology  
4    captures individual responses to environmental factors, similarly to the way tree rings record  
5    secondary growth variations. The analysis of plant structure at a given time conveys key information  
6    not only on the past developmental trajectory but also on future potential growth and survival [57].  
7    Conducting a retrospective analysis based on morphological descriptors is a powerful and accessible  
8    way to assess and analyze individual performance in trait-based or demographic approaches [10,  
9    58]. Similarly, by characterizing morpho-anatomical markers [59, 60] such as scars left by buds,  
10    branches, flowers and inflorescences we can retrospectively analyze the dynamics of the axis  
11    elongation, branching and flowering that determine individual growth, survival and reproduction  
12    [61].

13    Plant architecture can be characterized at different levels of organization and in varying degrees of  
14    detail by a set of generic **architectural traits** (e.g. number of branching orders, axis categories,  
15    reiteration patterns) (**Box 1**). As with any functional trait [62, 63], the choice of which architectural  
16    traits to measure must depend on the ecological context of the study (notably the biotic and abiotic  
17    filters concerned), and on the research question. Interesting work has been done on savannah  
18    vegetation in this regard [64]but has yet to be carried out on other ecosystems. We emphasize that  
19    considering plant architecture does not only involve measuring architectural traits related to space  
20    occupancy, resource foraging and persistence strategies. The architecture-based approach (**Figure**  
21    **2**) can also be used for identifying and selecting individual plants according to their ontogenetic  
22    stage or for standardizing functional trait measurements per axis category (**Box 1**). If functional traits  
23    are measured on several axes types, patterns of intra-individual trait variation can be analyzed and  
24    compared across species or individuals in different contexts. Lastly, given their plasticity and

1 integrative nature, some architectural traits allow easy assessment of individual whole-plant  
2 performance.

### 3 **Integrating functional traits into a whole-plant developmental context**

#### 4 *Architecture as a framework for assessing phenotypic integration*

5 Studying plant architecture highlights the intraspecific trait variation and phenotypic integration  
6 that are critical to species' adaptation and distribution along environmental gradients [65-67].  
7 Functional traits influence individual performance through their separate and joint effects on  
8 different functions [2, 68], and these effects depend on the ontogenetic stage and the  
9 environmental context [69]. By describing topological and geometrical relationships across  
10 elementary units, plant architecture offers a hierarchical and modular framework for progressing  
11 toward a cause-effect analysis of trait covariations. By considering traits related to axis and  
12 branching patterns, we can assess the impact of organ-level traits on whole-plant traits, which in  
13 turn influence individual performance [49, 70]. Corner's rules [11], encompassing a wide range of  
14 organ-level and architectural traits, enable us to build key hypotheses about the linkages between  
15 plant architecture and functioning [71, 72]. Architectural traits are assumed to be pivotal in  
16 phenotypic networks because of the many competing functions they fulfil and constraints they  
17 impose [64, 65].

#### 18 *Ontogenetic and phenological variation in functional traits and strategies: towards an eco-devo* 19 *perspective*

20 Variations in plant traits during ontogeny and their ecological implications are increasingly  
21 documented [73]. By addressing the ontogenetic trajectories of individual plants in their  
22 environmental context, architecture analysis provides an opportunity to integrate the role of

1 developmental variation into the ecological context (“eco-devo”, [74]) and thereby gain insights into  
2 functional differentiation during lifetime.

3 Throughout its ontogeny, a plant experiences a range of environmental conditions and is subject to  
4 distinct abiotic and biotic conditions which can drive ontogenetic changes in functional traits [75,  
5 76]. On a seasonal time scale, plants also adjust their functioning through the **phenology** of growth  
6 and branching processes, so this is also a source of variation in functional traits [77]. Plant  
7 architecture provides markers of ontogenetic stages that enable us to track the adjustments made  
8 by the plant at various time scales and levels of organization.

9 Developmental plasticity is also a key aspect of a plant’s response to its environment. The  
10 ontogenetic sequence of organ growth and production can be adjusted in terms of the nature and  
11 duration of its stages [56, 78]. The ontogenetic trajectory of an individual thus depends both on its  
12 genotype and on its plastic response to environmental conditions (**Figure 3**). For instance, low  
13 resource availability generally slows the individual’s progress throughout the developmental  
14 sequence, and this can delay the expression of the first branches or reproductive structures. It is  
15 crucial to consider this ontogenetic plasticity (*sensu* [79]) for interpreting trait variations and  
16 understanding their underlying evolutionary and ecological mechanisms [62].

### 17 **How can plant architecture inform community structure and dynamics?**

18 To elucidate the drivers of the structure and dynamics of a population or community one must  
19 aggregate information collected at the individual level [4, 80]. However, most past and current  
20 approaches in population ecology have ignored such information for lack of knowledge about the  
21 linkage between organismal physiology and demographic parameters [4]. In community ecology,  
22 the widespread use of organ-level traits is an obstacle to fully capturing processes associated with  
23 whole-organism resource capture and acquisition, notably resource competition. Below, we

1 highlight the need to integrate plant architecture into the theoretical corpus of population and  
2 community ecology, given its capacity to provide ecophysiological information at the whole-plant  
3 level and throughout the plant's lifespan (**Figure 4**).

4

#### 5 *Architecture-dependent population dynamics*

6 One way to address population dynamics is to incorporate the influence of functional traits on vital  
7 rates, i.e. on the probabilities of survival, growth, mortality and reproduction in populations. Taking  
8 this Integral Projection Model (IPM) approach, Merow et al. [81] acknowledge how an individual's  
9 state affects its vital rates, and make population projections based on these rates. IPMs are usually  
10 built by predicting vital rates from state variables related to size or age and from environmental  
11 drivers. Since architecture reflects the way individual plants develop, forage for resources and  
12 reproduce in space and time, architectural traits can directly and functionally determine vital rates  
13 in IPMs (**Figure 4A**). For instance, Charles-Dominique et al. [82] showed that whole-plant  
14 architectural traits (e.g. spatial density of branches, plant module sizes) and the rate of ontogenetic  
15 variation in morphological traits had a significant effect on population cover in five shrub species.  
16 Using morphological traits rather than age to delimit ontogenetic stages stems from earlier  
17 population dynamics studies [83].

#### 18 *Architecture mediates plant interactions and assembly*

19 In a community ecology perspective, species niche differences shape the outcome of biotic  
20 interactions among individuals and thereby contribute to species coexistence [84]. Plant-plant  
21 interactions occur between neighboring individuals and involve competition for aboveground and  
22 belowground resources (light, water, nutrients) and attacks by shared herbivores and pathogens  
23 [85]. There is a link between individual vital rates and the density and functional composition of

1 their forest neighborhood (using the Neighborhood Crowding Index - NCI - [86]). Because the  
2 variation in architectural traits should reflect variation in competitive ability across individuals and  
3 throughout their lifetime [87], NCI should also capture architectural differences and  
4 complementarity among neighboring plants (**Figure 4B**) [88]. This agenda should help us better  
5 understand the assembly and coexistence of individuals with different architectural strategies.

6 Taking a process-based perspective, we can make interaction coefficients in community dynamics  
7 models (derived, for example, from the Lotka-Volterra (LV) equations) depend on architectural trait  
8 variations among individuals in the community [25]. Recently, Chalmandrier et al. [89] proposed an  
9 LV-based model of community dynamics in which the parameters depend on functional trait values.  
10 We suggest exploring the influence of architectural traits that drive competitive ability (e.g.  
11 reiteration pattern, growth direction) on LV parameters. Recent advances in 3D modelling and  
12 simulation also offer new perspectives for designing virtual experiments of multispecies growth  
13 dynamics and identifying the influence of architectural diversity on the relative abundance and  
14 biomass of coexisting species.

#### 15 *Variations in the functional structure of plant communities along environmental gradients*

16 Variations in composition, in terms of architectural traits, along environmental gradients reflect the  
17 way different architectural trait values best fit different environmental conditions (**Figure 4C**). Using  
18 community assembly modelling approaches, e.g., based on null models, we can test how  
19 architectural trait composition responds to environmental filtering [90]. For instance, in a field  
20 experiment, Churski et al. [90] showed that the long-term survival of temperate tree species is  
21 influenced by their capacity to branch in response to herbivore predation. Variations in light  
22 conditions, especially during ecological succession, change architectural trait composition in a forest  
23 [91].

1 At a broad spatial scale, functional biogeography aims to characterize the macroecological patterns  
2 and processes underlying the variation of functional composition across assemblages [92]. These  
3 recent advances have focused on characterizing functional variation in terms of organ-level  
4 morphological and ecophysiological traits. But plant life forms also vary across biomes depending  
5 on the abiotic environment [13], and plant architecture research should integrate broad-scale  
6 variations in organ-level properties with variations in plant structure. Understanding the way  
7 communities respond to environmental variation lays the foundation for predicting their response  
8 to future conditions. This is a paramount objective for assessing the impacts of pervasive global  
9 change. Functional diversity, especially the presence of functionally original strategies [93], can  
10 ensure a community's resilience to changing environmental conditions. Whether and how the  
11 hypervolume (n-dimensional geometrical shape) representing the functional composition of  
12 communities along key dimensions varies under climate change reflects whether and how those  
13 communities can adapt over time (**Figure 4D**). Because architectural traits contribute to the  
14 communities' responses to key resource gradients and disturbances, we expect them to contribute  
15 to their responses to expected changes in climatic conditions and anthropogenic disturbance.

## 16 **Concluding remarks**

17 Plant structure and development are important but overlooked drivers of individual performance  
18 and community assembly along environmental gradients. The architecture-based approach can  
19 significantly contribute to a better understanding of the variation between and within species,  
20 regardless of their growth form. This is a promising avenue for tackling major challenges in trait-  
21 based ecology such as the roles of time and space in species interactions [73, 94]. It is now standard  
22 practice to revisit community ecology using a trait-based approach [95]. But such approaches are  
23 mostly based on organ-level functional traits, neglecting key aspects of plant architecture. By

1 characterizing below- and above-ground plant architecture, we can take into account individual-  
2 level functional variations that better capture fundamental niche differences between neighboring  
3 individuals. A second challenge is to gain insight into the drivers and ecological implications of  
4 intraspecific trait variation [96]. The three-dimensional structure of a plant at a given time yields  
5 markers of different sources of inter- and intra-individual trait variation (e.g. ontogeny, biotic or  
6 abiotic environmental conditions). This makes it a powerful tool for disentangling cause and effect.  
7 A third and pivotal challenge concerns the shift to an integrated view of plant phenotype.  
8 Architectural traits can integrate multiple trait dimensions into a multilevel phenotypic network in  
9 a biologically coherent way. This requires further understanding of the functional space defined by  
10 architectural and organ-level traits, and of whole-plant metabolic or allometric rules (see  
11 **Outstanding questions**). We therefore encourage future research to identify the relevant  
12 architectural traits to measure, depending on ecological context, plant growth form and research  
13 question. We believe that lidar technology can make a significant contribution to this goal by  
14 providing metrics on the topological and geometrical properties of plant parts [35, 97, 98]. Finally,  
15 we argue that the dynamic, integrative view of plants proposed in the present work creates a much-  
16 needed bridge between trait-based, ontogenetic and demographic approaches.

17

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1

## 2 **Glossary**

3 **Architectural model:** inherent growth strategy defined by a combination of four morphological  
4 characteristics observed on trunk and branches: growth pattern, branching pattern, morphological  
5 differentiation of axes and presence or absence of sexual organs. These models were first defined  
6 on tropical trees and then applied to temperate trees and to other growth forms (lianas, shrubs and  
7 herbs).

8 **Architectural traits:** traits describing plant structure at different organizational levels.

9 **Architectural unit:** refers to the elementary structural organization of a given species described by  
10 the number, characteristics and spatial arrangement of axis categories. This concept can be used  
11 for both shoot and root branching systems.

12 **Architecture-based approach:** refers to different ways of taking the plant structure into account  
13 depending on the research question. It includes consideration of intra- and inter-individual trait  
14 variations and screening for new phenotypic traits that cover overlooked dimensions of plant  
15 strategies.

16 **Axis:** stem or root growing in a given direction and whose development can be expressed in  
17 different ways.

18 **Axis category:** a type of root or stem characterized by its morpho-anatomical and functional  
19 properties within the tree architecture (e.g. a short shoot whose function is resource acquisition  
20 and reproduction). To identify an axis category, one must observe traits like growth direction,  
21 branching pattern, phyllotaxis and the presence or absence of sexual organs. There is a limited  
22 number of axis categories for a given species.

23 **Epicormic shoot:** a shoot growing from a long dormant meristem or bud.

1 **Modularity:** the repetition of morphological elements (node/internode, annual shoot, axis,  
2 architectural unit) through growth, branching and reiteration.

3 **Morphogenetic process:** a biological process by which a cell, tissue or organism develops its  
4 organization and shape. The different components of the plant (phytomer, growth unit, annual  
5 shoot, axis and architectural unit for shoots; axis and architectural unit for roots) are generated by  
6 three main morphogenetic processes : growth, branching and reiteration.

7 **Ontogeny:** the sequence of developmental phases characterizing a species' life cycle, independently  
8 of the individual's chronological age.

9 **Phenology:** the study of the timing of recurrent biological events, its causes with regard to biotic  
10 and abiotic forces, and the relations between phases in the same or different species.

11 **Phenotypic plasticity:** the ability of an organism to change its morphology, physiology and behavior  
12 in response to environmental change.

13 **Phenotypic integration:** refers to the patterns of functional, developmental and/or genetic  
14 correlations among different traits in a given organism.

15 **Plant architecture:** describes the nature and relative arrangement of the different parts of a plant  
16 in space and time.

17 **Reiteration:** a morphogenetic process generating the partial or total duplication of an architectural  
18 unit. This process may be part of the normal development sequence of the plant or may occur in  
19 response to stressful conditions. Reiteration can be expressed in the root system as well as the shoot  
20 system. The ability to reiterate has been well described in trees but is also expressed in herbs, lianas  
21 and shrubs.

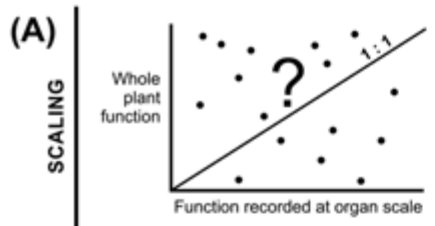
22 **Topology:** the relative arrangement of morphological elements at different spatial scales.

23

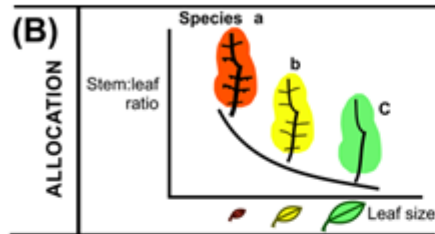
1 **Figure 1. Biased estimation of whole-plant functioning and performance when plant architecture**  
2 **is overlooked.**

3 All research fronts in trait-based ecology (right column) would benefit from plant architecture  
4 analysis. This is theoretically illustrated here by the following: a weak correlation between organ-  
5 level and whole plant functions (A); the architecture-dependence of allocation (B), allometry  
6 patterns (C), the ontogenic trajectory of whole-plant metabolism (e.g., photosynthesis) (D), and  
7 reproductive effort (E). As a consequence, the way species' ecological differences are assessed can  
8 strongly influence quantification of the mechanisms underlying species coexistence (e.g. the niche  
9 overlap of species may vary with or without consideration of architecture) (F). Simplified trait values  
10 of hypothetical species are shown. Letters a, b, c and d represent different species.

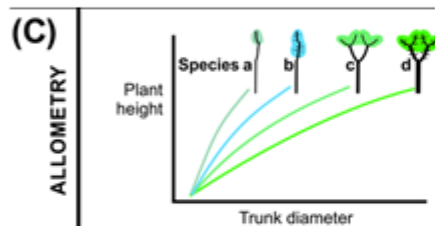
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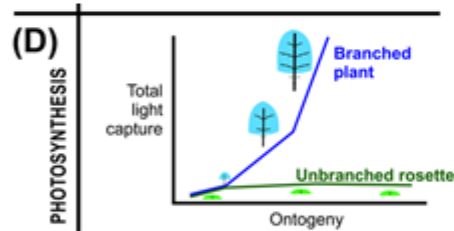
Phenotypic integration



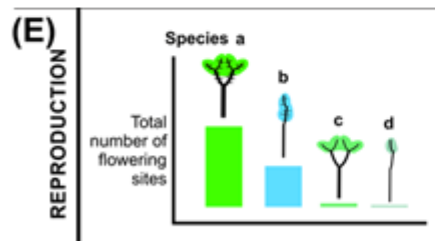
Determinants of allometric and allocational scaling



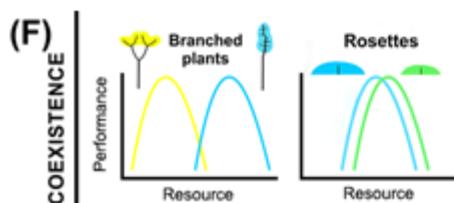
Ontogenetic variation of traits



Understanding and prediction of plant performance



Biotic and abiotic interactions across time



## 1 **Box 1 – How to describe the variability in plant architecture?**

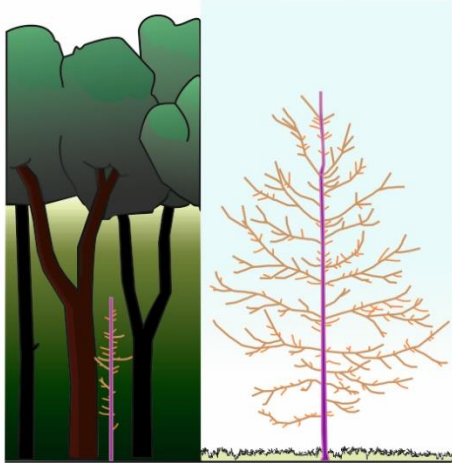
2 The intra- and interspecific variability of plant architecture has three main causes (Figure I-A-C) [13-  
3 15]. It can be described by morphological characteristics related to the key processes of growth,  
4 branching and reiteration (Figure I-D) at different levels of organization, depending on the question  
5 and the scale of the processes being studied. By combining different architectural traits, we can  
6 perform various types of categorizations: across species, different architectural types can be  
7 identified and used to classify the architectural diversity observed within a community or a clade  
8 [13, 21]. For a given species, the variability of axis traits is used to define axis categories (Figure I-E).  
9 Their number indicates the degree of functional specialization of the axes. Figure I-F shows the  
10 importance of considering the axis categories and intra-individual gradients expressed during  
11 ontogeny when designing strategies for sampling functional traits. Considerable work remains to be  
12 done to better understand how axis differentiation influences intra- and interspecific variations in  
13 functional traits and whole-plant performance [70, 99].

14

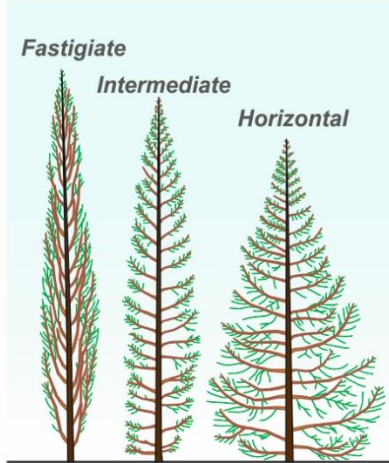
15 **Figure I- Variability in tree architecture.** *Sources of variability (A-C):* (A) Phenotypic plasticity: two  
16 walnut trees (*Juglans regia*) of the same age and the same population have very different  
17 architectures owing to differences in local plant density (adapted from Sabatier Sylvie, PhD thesis,  
18 University of Montpellier, 1999). (B) Intraspecific genotypic diversity: these forms of Cypress  
19 (fastigate, intermediate and horizontal) correspond to different genotypes, making them heritable  
20 (adapted from [100]). (C) Interspecific diversity: a profile of a forest in French Guiana shows the  
21 wide diversity of architectures across the forest's vertical strata (adapted from Oldeman R.A.A, PhD  
22 thesis, University of Paris, 1978).

1 *Methodological approach (D-F):* (D) Examples of architectural traits selected for describing and  
2 classifying the great architectural diversity of trees, shrubs and herbs in the genus *Euphorbia*; (figure  
3 modified from [87]); (E) Axis categories are defined according to distinguishing morphological  
4 criteria in the shoot and root systems of a theoretical species. Each axis category contributes to one  
5 or several functions; (F) Distribution of axis categories within the plant. The histograms show the  
6 proportion of leaf area borne by each axis category for each vertical layer. Leaves of the upper layer  
7 (the most often sampled in trait-based studies) are attached to axes of three different categories  
8 and should express differences in leaf trait values. Note that axis categories do not correspond to  
9 branching order. The discriminating criteria chosen to characterize axis categories are not  
10 exhaustive and could vary between species.

(A) Phenotypic plasticity



(B) Genotypic intraspecific variability



(C) Interspecific variability



(D) Examples of architectural traits

**At the axis scale** **At the whole-plant scale**

(1) Phyllotaxy

spiral    opposite

(2) Branching pattern

rhythmic    continuous    diffuse    absent

(5) Short shoots

absent    present

(6) Number of axis categories

1    2    3    4

(3) Growth direction

vertical    horizontal

(4) Flowering

lateral    terminal    absent

(7) Reiteration location

no reiteration    distal    basal    sub-apical

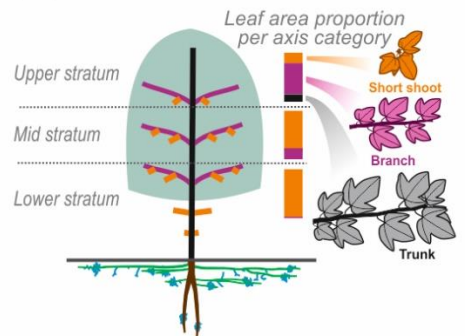
(8) Reiteration type

sequential    delayed

(E) Axis categories

	Trunk	Branch	Short shoot	Taproot	Horizontal root	Rootlet
Growth direction	Vertical	Horizontal	None	Vertical	Horizontal	None
Growth unit length	Long	Medium	Short	NA	NA	NA
Branching pattern	Rhythmic	Continuous	None	Rhythmic	Diffuse	Continuous
Lifespan	Perennial	Long	Short	Perennial	Long	Short
Flowering	No	No	Yes	NA	NA	NA
Functions	Exploration Support Storage	Expansion Defense	Acquisition Reproduction	Storage Anchoring	Anchoring Exploration	Acquisition

(F) Whole-plant architecture



1

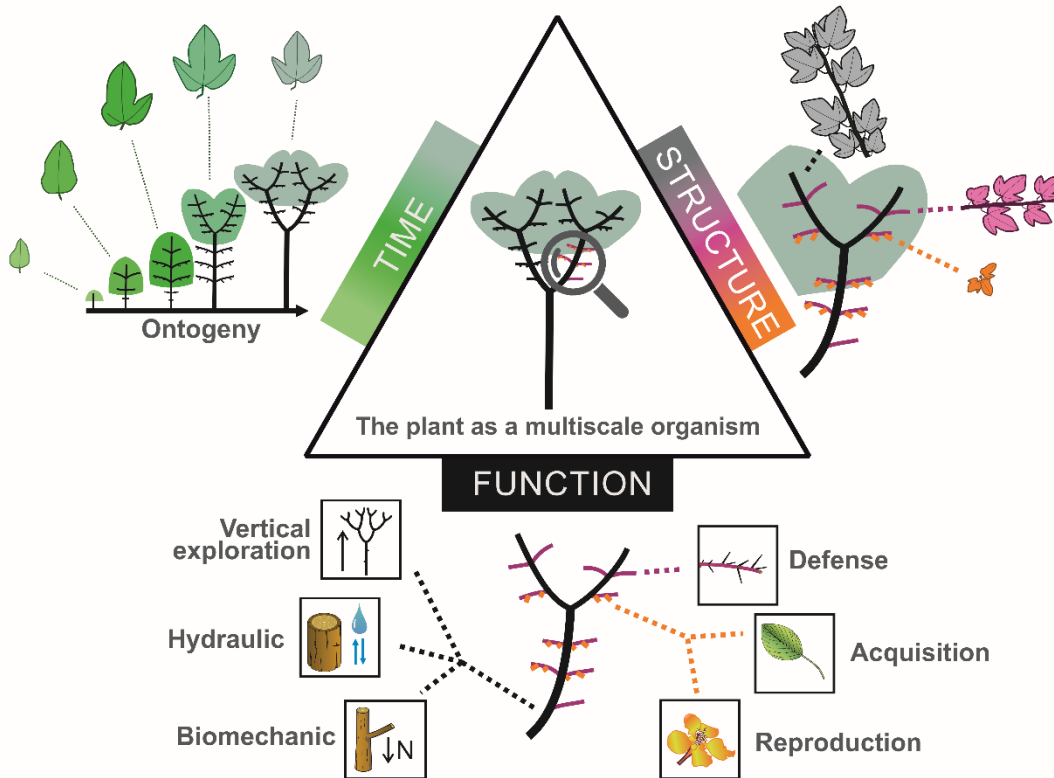
2

3

1 **Figure 2- The many dimensions of the architecture-based approach.**

2 The three sides of the triangle below represent the three main axes of integration of the  
3 architecture-based approach in trait-based ecology. The architecture-based approach considers a  
4 plant as a multilevel organism and explicitly includes the temporal dimension through ontogenetic  
5 and phenological processes. It makes it possible to account for inter and intra-individual trait  
6 variations, such as those in leaf size and shape, between ontogenetic stages (left side of triangle) or  
7 between axis categories (right side of triangle). Three axis categories are represented and colored  
8 in black, pink and orange on the right side of the triangle. The architecture-based approach also  
9 enables one to document phenotypic traits related to overlooked functions in functional strategies.  
10 The diversity of functions performed by plant structures is displayed below the triangle.

11

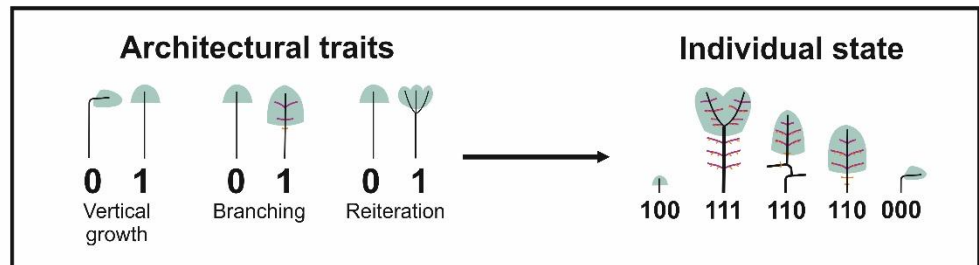
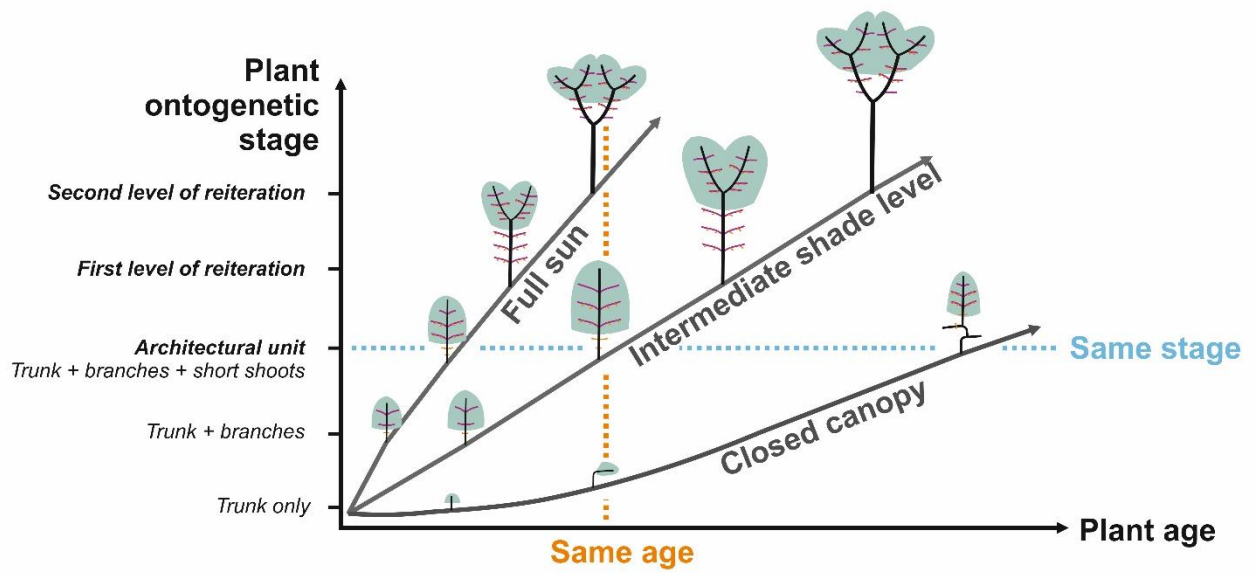


12

13

1 **Figure 3 – Disentangling age, ontogenetic stage and size across environments.**

2 The ontogenetic trajectories of a theoretical tree as a function of its environment, here represented  
3 by different light conditions. The trajectory is represented in a two-dimensional space with the age  
4 of the tree on the x-axis and its ontogenetic stage on the y-axis. Ontogenetic stage can be defined  
5 according to the degree of complexity of the plant structure in terms of branching, reiteration and  
6 flowering. The individual's architecture, age and dimensions constitute three complementary  
7 features. In full sun conditions, as with an isolated tree, the ontogenetic stages progress rapidly and  
8 the tree will reach maturity relatively quickly and remain relatively small. In intermediate shade, the  
9 ontogenetic stages progress more slowly, adulthood will be reached later and the adult tree will be  
10 larger. Under limiting conditions (closed canopy) the transition from one stage to another is slower  
11 and the full sequence is not necessarily achieved. Different trees of equivalent age may display  
12 widely different ontogenetic stages and growth dynamics. These different individual states can be  
13 characterized by a sequence of coded architectural traits, allowing the diversity of trajectories to be  
14 modelled at population or community level.



1

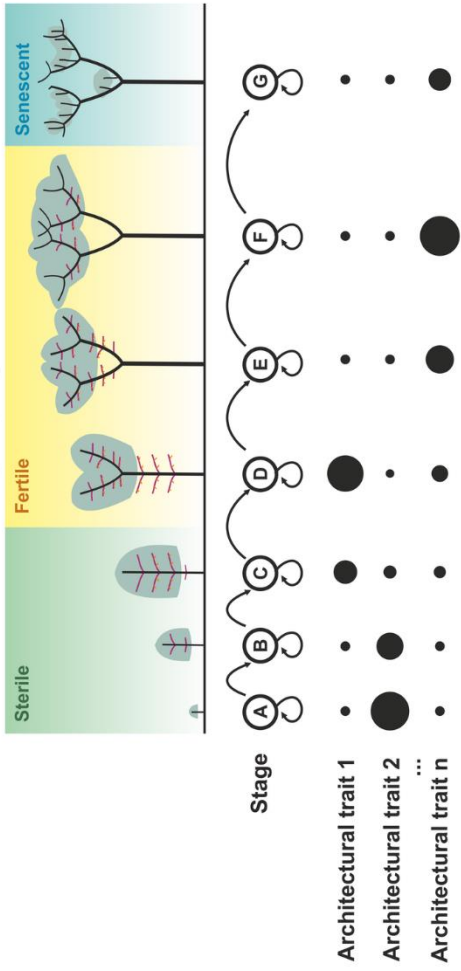
2

1 **Figure 4 - How do architectural traits contribute to population and community structure and**  
2 **dynamics?**

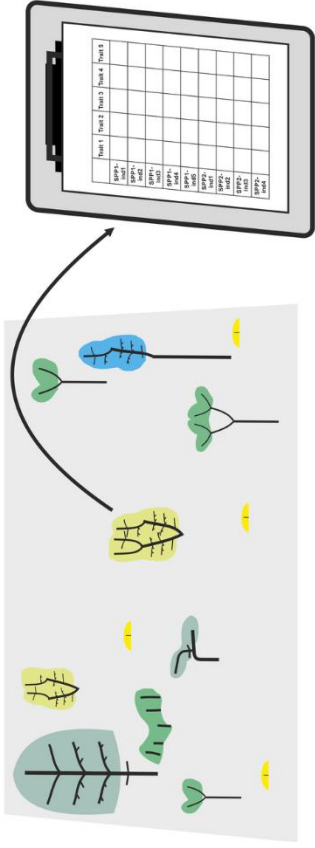
3 Depending on the scale and level of organization, different ecological processes and architectural  
4 traits are at play. (A) Population dynamics. Architectural traits may be related to reiteration  
5 (presence/absence; partial or total; number of total reiterated complexes), branching  
6 (presence/absence; maximum order), epicormics (presence/absence; orientation) or crown  
7 mortality (%). They can be combined to inform population dynamics, using Integral Projection  
8 Models (IPMs) that consider changes in individual trait values in a stage-structured population. Dot  
9 sizes are proportional to the number of individuals in the population. (B) Local plant-plant  
10 interactions and species coexistence and (C) functional structure of communities along  
11 environmental gradients. The architectural traits to be measured at these scales partially depend  
12 on the ecological context, biotic and abiotic filters particularly. For example, in the savannah  
13 ecosystem with its regular fire events and herbivore pressure, resprouting ability, index of cage  
14 architecture and height of fifth fork are key functional traits. (D) Community responses to climate  
15 change: the response of community functional composition to climate change is represented by the  
16 shift in trait hypervolumes (from yellow to blue) within a three-dimensional trait space involving  
17 architectural traits related, for example, to persistence strategies (types of reiteration in shoot and  
18 root systems, nature of axis categories) or resource foraging.

19

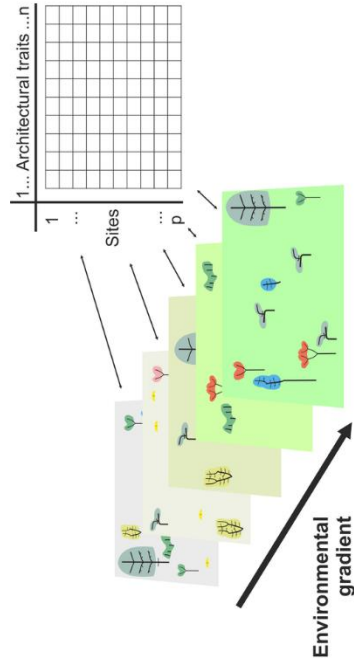
### A Demography



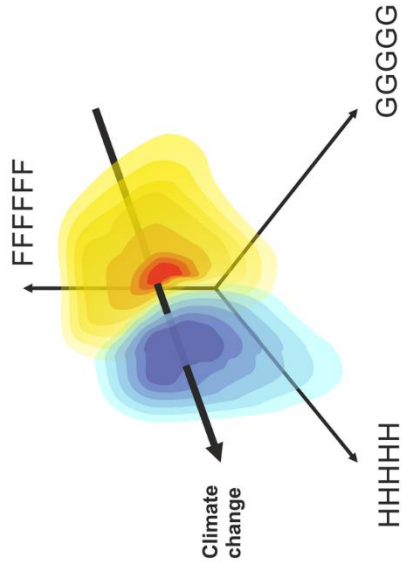
### B Community structure



### C Environmental filtering



### D Predicting community changes



## 1 **Highlights**

- 2 • Plant functional traits are considered indicators of whole-plant functioning but are often  
3 measured only at the organ level and at a single developmental stage.
- 4 • The way plants build shoot and root axes determines their ability to explore and acquire  
5 resources in space and time in interaction with environmental conditions.
- 6 • The three-dimensional architecture of an individual plant at a given time reflects its  
7 ontogenetic stage and its environmental conditions, thus providing a powerful tool to  
8 disentangle the different sources of intraspecific trait variation.
- 9 • Plant architecture offers a hierarchical and modular framework for characterizing integrated  
10 plant phenotype and structuring plant trait networks.
- 11 • Plant architectural traits reflect key functional responses to abiotic and biotic conditions and  
12 should be considered when studying community assembly processes.

13

## 1 **Outstanding questions**

2

3 ● What are the critical above- and belowground architectural traits that drive whole-plant  
4 performance across growth forms and ecological contexts?

5 ● How do above- and belowground architectural traits coordinate with each other and with  
6 the major functional dimensions described so far?

7 ● How does inter- and intraspecific variation in functional and architectural traits during  
8 ontogeny contribute to niche-based dynamics and community assembly?

9 ● How does the distribution of architectural traits vary across environmental gradients?

10 ● How does architectural diversity influence the spatial and temporal dynamics of multi-  
11 trophic interactions (including plant-herbivore and plant-microbe interactions)?

12 ● How does the diversity of architectures in plant communities affect ecosystem functioning?

13

14

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