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Title: Evolution of plant metabolism: A (bio)synthesis

Studying the evolution of metabolism is technically challenging. A novel study combining in silico metabolic maps and phylogenomics allows reconstructing the diversification of plant metabolism across one billion years of evolution.

Text:

Following the initial primary endosymbiotic event leading to the evolution of the chloroplast approximately a billion years ago, plants (Viridiplantae or Chloroplastida) have evolved into a tremendous diversity of organisms such as green algae, mosses or ferns [1]. Each of these lineages has evolved prominent developmental and physiological innovations linked to the colonization of new ecological niches. Although roots and flowers will come to everyone's mind when asked for plant innovations, one can hardly argue against specific metabolites, say caffeine, as iconic lineage-specific novelties. Besides such recent evolution, metabolic novelties that evolved at deep nodes in the plant phylogeny may have played essential roles in the evolution of extremely diverse and successful plant lineages such as the land plants. However, while scoring for the presence or absence of a given macroscopic trait – such as roots or flowers – is relatively straightforward, determining the distribution of metabolites requires the use of sophisticated and time-consuming approaches, hindering the description of the plant metabolism in an evolutionary perspective.

In their work published in this issue of *Current Biology* Cannell *et al.* [2] overcome these limitations and propose a comprehensive view of the plant metabolism evolution. To do so, the authors first computed metabolic maps on eight focal taxa belonging to the major plant lineages. Rather than reflecting the presence or absence of a given enzymatic property, reconstructing biosynthesis pathways allow inferring whether the “modules” are present and thus the metabolic end-product. Mapping these predictions on the plant phylogeny, the authors were able to propose gains and losses of specific metabolic pathways in an untargeted manner. The initial set of eight species, although covering a large diversity of lineages, made the approach very sensitive to misannotation or assemblies. To strengthen their conclusions the authors included a total of 72 diverse plant genomes in an OrthoFinder run, identifying orthologs across all the species, and later added 305 transcriptomes. With these orthogroups, the authors were able to predict the evolution of the plant metabolism. Some of these predictions reflected the known evolutionary pattern of well-described metabolic pathways, such as the gain of thalianol biosynthesis in the *Arabidopsis thaliana* lineage [3] others turned out to be much more surprising.

Revisiting the evolution of plant hormones

Gibberellins (GAs) are plant hormones regulating multiple developmental processes. Their biosynthesis is well described in angiosperms. Initial phylogenetic studies conducted on the biosynthetic enzymes on the model moss *Physcomitrella patens*, and metabolomics survey, suggested that active GAs (derivative of GA12) were not produced in mosses, suggesting that their evolution was specific to the vascular plants [4]. Here the authors discovered in liverworts and hornworts, the other two bryophyte clades, the entire suit of enzymes

necessary to produce bioactive GA implying a much earlier evolution of this class of compounds. According to the author's reconstruction, both liverworts and hornworts should be able to produce GA4. Comparing the metabolome of wild-type and mutants in the responsible enzyme (kaurenoic acid oxidase - KAO) in, for instance, the liverworts *Marchantia polymorpha* should allow determining whether GA4 is indeed produced in these species and whether it actually depends on the same pathway than in angiosperms. Alternatively, it could reveal the involvement of KAO in the biosynthesis of other compounds.

Beside the presence of a near-complete GA biosynthesis pathway in bryophytes, the absence of multiple enzymes required in angiosperms for the biosynthesis of another plant hormone, the brassinosteroids (BRs), came as another surprise. Indeed, these compounds have been detected in most plant lineages including bryophytes and algae. Such discrepancy between the inferred biosynthetic abilities and the actual presence of metabolites may result from either of two evolutionary processes: convergence, where BRs would have evolved independently in all the investigated lineages, or diversification. Given the distribution of BRs, the most parsimonious hypothesis would be that BR biosynthesis evolved once and then diversified independently in multiple lineages. Here, a parallel can be drawn with observations made on the diversification of gene regulatory networks. Selection acts on the output of these networks, which is the activation of target genes in response to a given environmental or developmental clue, and not on the topology of the network itself that may vary over time via intermediate, redundant, stages [5,6]. Similarly, while BRs production seems conserved across plants (the output) the structure of the biosynthetic pathway can be predicted to be under lower selective constraint, resulting in different enzymes contributing to the biosynthesis. In the future, it would be of interest to determine whether evolutionary mechanisms contributing to the diversification of gene regulatory networks may be transposed to the diversification of metabolic pathways across large evolutionary timescale. The predictions reported by Cannell *et al.* provide the framework for such future studies. Beyond diversification, a number of rules for the evolution of metabolic pathways in the plants can be proposed based on these predictions.

Evolutionary principles of plant metabolism evolution

Exaptation, the process by which an existing character is recruited for a novel function it was not initially selected for, is becoming a common theme in plant evolution [7,8]. For instance, the perception of the plant hormone abscisic acid (ABA), which is playing multiple roles in the biology of land plants including the responses to biotic and abiotic stresses, evolved by exaptation. In land plants, the perception of ABA is mediated by receptors of the PYL protein family. Homologs are present in Zygnematophyceae [9,10] where they are, however, activated in absence of ABA, indicating that ABA-binding evolved in land plants by exaptation of this ancient protein family [9]. In their study, Cannell *et al.* identified a number of examples of metabolic exaptation. The authors found that all the plant – both algal and land plant – genomes and transcriptomes investigated harboured the pathway for the biosynthesis of precursors of biopolymers such as cutin and suberin while lacking a number of enzymes for their subsequent modification and polymerization. Another example of metabolic exaptation is the biosynthesis of flavanol in seed plants, which branches out of the phenylpropanoid metabolism that the authors found present in all investigated land plants, via the gain of three enzymes. Although without biochemical analyses it cannot be ruled out that Zygnematophyceae or other streptophyte algae produce cutin, or that non-seed plants produce flavanol, the data suggest that both chemicals evolved by exaptation of ancestral

pathways. This is in line with previous report focusing on specialized metabolism, such as caffeine [11], and demonstrates that, as for signalling pathways, exaptation is a major player in defining the diversity of the plant metabolism even at deep evolutionary nodes.

The role played by the loss of traits in shaping biodiversity is becoming more and more prominent, with the loss of genes often found as causal for these losses. This is for instance the case for the diversification of leaf shapes [12]. Whether trait loss is adaptive (the more-is-less hypothesis) or the result of relaxed selection depends on the lineage and the trait being investigated [13]. In their study, Cannell *et al.* found at least three clear examples of metabolic losses. Among them the biosynthesis of diacylglycerol-N,N,N trimethylhomoserine and GAs seem to have been lost in seed plants and in mosses respectively. Interestingly, both losses perfectly illustrate cases of trait loss due to relaxed selection. Indeed, diacylglycerol-N,N,N trimethylhomoserine and GA have been functionally substituted in seed plants and in mosses by phosphatidylcholine and ent-3 β -hydroxy-kaurenoic acid respectively. Due to functional redundancy the selection acting on the ancestral metabolites would have been relaxed, leading to their loss. Interestingly, metabolic redundancy with the metabolism of their hosts is often the cause of gene and pathway losses in obligate parasites or symbionts. As compare to the loss of multiple other traits that may be adaptive [13] the loss of metabolic pathway seems to be predominantly the result of relaxed selection. Functional studies on pathway found by Carnell *et al.* to be lost, for instance the biosynthesis of L-selenocysteine in land plants, should allow testing this hypothesis further.

By proposing a kingdom-wide evolution of the plant metabolism, this study perfectly illustrates the power of combining approaches at different scales (metabolic maps with orthogroups) to address complex questions, and provide the framework for further experimental approaches to understand the evolutionary processes building (metabolic) diversity.

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