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# *Reticulate evolution, lateral gene transfer, and innovation in plants*

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## **i. Introduction**

The evolutionary diversification of organisms is commonly pictured as following a bifurcating tree of life. As time passes, species divide and follow their own evolutionary path along separate branches. In this strict bifurcating tree scenario, any evolutionary novelty or innovation is restricted to the lineage in which it arose. However, it is well known that branches of the tree of life can be porous, with episodic or even frequent genetic exchanges between species. Hybridisation is especially frequent in some groups of plants and allows various amounts of gene flow between closely related taxa (Goulet et al. 2017). During hybridization, genes are passed from the two parents to the offspring via sexual reproduction, but recent evidence furthermore indicates that genetic material is occasionally transferred between distantly related plant species by means other than sexual reproduction, a process known as lateral gene transfer (LGT). The cases of LGT reported to date involve various groups of plants and donors from different parts of the plant phylogeny or different phyla (reviewed by Richardson and Palmer 2007; Gao et al. 2014; Wickell and Li In press), and genes received from bacteria have even been linked to the emergence of land plants (Cheng et al. 2019). In this short essay, we discuss the potential impacts of these genetic transfers for our understanding of plant evolution. We focus on LGT, as these provide very tractable systems to assess the effect of reticulations on plant functional diversification, but also discuss the broader impacts of hybridization and introgression.

## **25 ii. LGT represent novel mutations of major functional effect**

The remarkable adaptations that have allowed plants to colonize most environments around the globe did not arise over night. In some cases, protracted evolutionary periods were required to incrementally modify genes either inherited from their ancestors or originating *de novo* in the genome (Bianconi et al. In press). Reticulation events have the potential to speed up this process  
30 and even provide access to new traits that would otherwise have been out of reach of natural selection.

For the recipient genome, LGT represents the insertion of foreign DNA, effectively generating major structural variants that natural selection can act upon. The fate of each LGT depends on its selective value in the recipient, and the frequency we observe will be significantly  
35 lower than the actual rate in nature as most transfers will be either deleterious or selectively neutral. However, given a high enough frequency, random transfers of DNA will occasionally increase the fitness of the recipients. Such beneficial LGT include those transferring functional genes that have undergone substantial modification through prolonged periods of positive selection in the donor genomes before being transferred (Christin et al. 2012). A gene that is selected for may also be  
40 accompanied by hitch-hikers on the same fragment of foreign DNA, which can act as standing-genetic variation for secondary selection (Olofsson et al. 2019). LGT therefore provides a mechanism by which plants can effectively 'steal' the genetic blueprints for molecular adaptation, thereby recycling the product of natural selection and altering the evolutionary trajectory of a species.

45 LGT has spread functional metabolic, disease resistance and abiotic stress tolerance genes among plants (Dunning et al. 2019). These transfers can have an adaptive effect and bypass the necessary time required for the repeated action of natural selection to adapt the orthologous gene in the recipient species. For example, PEPC (phosphoenolpyruvate carboxylase) is a key enzyme in the C<sub>4</sub> photosynthetic pathway that has repeatedly undergone convergent positive selection in  
50 independent C<sub>4</sub> origins to boost the enzymes efficiency (Christin et al. 2012). The grass *Alloteropsis*

*semialata* represents a recent C<sub>4</sub> origin, and its native PEPC lacks the adaptive amino acid substitutions typically observed in older C<sub>4</sub> groups (Christin et al. 2012; Dunning et al. 2017). Given enough time, it is likely the native gene from *A. semialata* will undergo similar convergent changes as witnessed in other species. However, certain populations of this species acquired via  
55 LGT a PEPC that had been adapted for the C<sub>4</sub> function by the older C<sub>4</sub> lineage of grasses that gave the gene (Christin et al. 2012; Dunning et al. 2017). In this example LGT acts as an evolutionary shortcut to a novel phenotype.

LGT may also allow an organism to evolve beyond its innate capability. The adaptive potential of an organism is limited by its evolutionary history, and the necessary material for  
60 specific innovations may be missing from some lineages if certain genes have been lost or never evolved (Blount et al. 2012). LGT can bypass this problem, allowing organisms to reach previously inaccessible areas of the adaptive landscape. For example, the chimeric neochrome photoreceptor for growing in low-light conditions was unique to the hornwort lineage, a small group of bryophytes that diverged early during land plant evolution (Li et al. 2014). A gene encoding the  
65 bryophyte-restricted neochrome was laterally acquired by ferns over 170 million years ago and is cited as a key innovation underpinning the Cretaceous diversification of this group under the emerging angiosperm canopy (Li et al. 2014). It is possible that ferns may never have been able to exploit this new niche had they not laterally acquired the hornwort gene.

### 70 **iii. LGT spread traits across the tree of life**

Understanding when, where and why a trait evolves are the major goals of evolutionary biology. Most methods used to address these questions rely on phylogenetic trees, but gene flow between taxa can disconnect the history of the underlying trait from the species tree (Pardo-Diaz et al. 2012; Meier et al. 2017). Genes encoding one of the C<sub>4</sub> enzymes (phosphoenolpyruvate carboxykinase -  
75 PCK) have been passed among a number of grass lineages (Dunning et al. 2019), which therefore

share the encoded enzyme yet have not evolved it independently. A detailed analysis of the C<sub>4</sub> phenotype of the grass *A. semialata* showed that its C<sub>4</sub> photosynthetic machinery is composed of both native genes and LGT (Fig. 1; Dunning et al. 2017). The number of origins therefore differs among the constitutive elements of a single ecological innovation (Fig. 1; Dunning et al. 2017).

80 Relying on species trees to assess the timing and drivers of adaptive evolution of these genes would mislead the analyses, including assessment of the levels of convergent evolution of the genes.

The importance of LGT for plant evolution is currently difficult to quantify. Most cases of LGT have been incidentally identified, and few systematic scans have been performed. In the case of parasitic plants, *Striga* has 34 LGT identified out of a total of 34,577 nuclear genes (Yoshida et al. 2019), and 108 are expressed in the *Cuscuta* transcriptome (Yang et al. 2019). Similarly, in the grass *Alloteropsis semialata*, 59 of its 22,043 nuclear genes were identified as LGTs (Dunning et al. 2019). Because of detection difficulties and extreme caution in these studies, these numbers might underestimate the true amounts of LGT. Yet, it is clear that LGT represent a small fraction of all plant genes. The transfer of genes among close relatives via hybridization would however similarly  
90 disconnect the species and gene trees. Hybridization is known to be frequent in some groups (Goulet et al. 2017), but the taxonomic scales concerned are very different. Yet, all types of reticulate evolution create conflicts among gene trees, which can be problematic even when studying functional divergence on deep evolutionary scales (Koenen et al. In press). There is therefore a need for the field of plant macroevolution to consider the effects of reticulations in the  
95 tree of life on the sorting of functional traits among lineages.

#### **iv. LGT generates intraspecific variation in important genes**

Over the past decade, it has been increasingly recognized that individuals from the same species do not always share the same genes. In bacteria, this well-known phenomenon lead to the “pan-genome” concept where a single species contains both a core set of genes present in all individuals  
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and a dispensable set of genes with a discrete distribution (Tettelin et al. 2005). Similar pan-genomes have been reported in several model plant species, with many thousands of genes absent from the original reference genome (reviewed in Tao et al. 2019). We suggest that LGT and hybridization might be important, yet underappreciated, contributors to the functional diversity in  
105 plant pan-genomes. Transfers of genes into an established species will result in a patchy distribution, where, initially at least, only some populations possess the new genes (**Fig. 2**; Dunning et al. 2019). Local adaptation might moreover lead to variation in LGT content among members of the same populations (Prentice et al. 2009). The first methodological consequence is that the full extent of LGT cannot be estimated with a single reference genome per species. More importantly,  
110 in the case of functional genes of adaptive significance, it means that individuals from the same species can differ while those belonging to distinct species can share the same key genetic elements (**Fig. 1**). This phenomenon could have important consequences on the sorting of morphological and functional traits within and among species of plants, especially in groups where genetic exchanges are frequent. While hybridization effects are widely studied, the consequences of LGT for  
115 intraspecific diversity need to be assessed, as it can impact conservation, crop improvement programs, but also our understanding of functionally relevant taxonomic units.

#### **v. Conclusion:**

The transfer of functional genes among distantly related groups of plants can mislead our  
120 reconstruction of plant evolution by disconnecting the history of relevant genes from species trees. The impact of genetic exchange at the intra- and inter-specific levels should thus be considered in comparative botany, as both LGT and introgression are known to occur and move genes of functional importance among plants. Work on plant LGT is however still embryonic, and there is a need to evaluate the prevalence of the phenomenon in different groups. As more genomes become  
125 available, comparative analyses will be able to answer this question, potentially moving plant LGT

from an obscure oddity to be appreciated as an important contributor of adaptive diversification in plants and beyond.

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**Figure 1: Lateral gene transfer disconnects the origins of parts of the C<sub>4</sub> photosynthetic trait from the species tree.** This cartoon illustrates the situation of the grass *Alloteropsis semialata* (native genes in red), where some populations acquired a key C<sub>4</sub> gene from Andropogoneae (in blue; Dunning et al. 2017). After the gene transfers, the C<sub>4</sub> cycles can be composed of genes from different origins, as indicated with different colours in the schematics of the cycle.

**Figure 2: Lateral gene transfers create intraspecific variation in gene content.** For six genes laterally acquired by the grass *Alloteropsis semialata*, their presence (in colour) or absence (in white) are indicated for 20 populations spread around the world (Dunning et al. 2019); 1 – Burkina Faso, 2 – Cameroon, 3 – Democratic Republic of Congo, 4 – Tanzania, 5 – Mozambique, 6 - Kenya, 7 – Zimbabwe, 8 and 9 – South Africa, 10 – Madagascar, 11 – Sri Lanka, 12 – Thailand, 13 – China, 14 – Taiwan, 15 – The Philippines, 16 – Aru Island, Indonesia, 17 – Daru Island, Papua New Guinea, 18 – Darwin, Australia, 19 – Cairns, Australia, 20 – Brisbane, Australia.