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Insect herbivory: An inordinate fondness for plant cell wall degrading enzymes

Noah K. Whiteman
Department of Integrative Biology, Department of Molecular and Cell Biology, University of California, Berkeley, CA 94618, USA
Correspondence: whiteman@berkeley.edu

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Tens of thousands of species of leaf beetles rely on plant cell wall degrading enzymes in order to make the most of nutritionally depauperate plant tissues. Many of the genes encoding these enzymes were acquired from microbial donors, either through horizontal gene transfer or by hosting microbial endosymbionts. A new study explores how these insects have leveraged this metabolic potential to diversify and expand into new niches.

In 1973, Sir Richard Southwood illuminated a paradox: although the vast majority of standing carbohydrate within terrestrial biomes is contained in the tissues of seed plants (Spermatophyta), only one-third of extant insect orders include species that feed exclusively on the living tissues of plants — herbivores[1]. The most common feeding strategy among the insect orders is feeding on dead or decaying tissue, and coming in second place is predation. When one considers that roughly 50% of living insect species are herbivorous, the paradox is even more vexing[2]. Most of the major living insect lineages do not include herbivorous species, but those that do tend to be more speciose than other major lineages. Resolving this paradox is a major problem in evolution considering the sheer biodiversity of herbivorous insects — the most diverse guild of macroscopic life on the planet — and their ecological importance. In this issue of *Current Biology*, a new study by Kirsch *et al.*[3] on the leaf beetles (Chrysomelidae — one of the most diverse animal families on the planet with >40,000 species) brings us a step closer to resolution.

Herbivory may be a catalyst for diversification at least in some of the major lineages, based on both sister-group[4] and phylogenetic approaches[5]. Still, the question is fraught because isolating causal variables underlying net diversification patterns across such vast expanses of evolutionary time is, at least in my mind, simply not epistemologically possible because we cannot rerun the tape of life[6]. Nonetheless, patterns of convergent evolution can provide a useful proxy. This is because of the simple truth that evolution follows the same course, at least phenotypically, again and again, given the optimization challenge posed by the physical laws acting around us and the salience of deep homology. Whether and to what extent the same genetic changes underlie similar adaptations is an important question to answer[7]. We can begin to address it now, because phenotype and genotype can be causally linked in different environmental contexts, at least in part. Ideally, we would also attempt to pair these findings with their macroevolutionary implications, but doing so has proven challenging. Kirsch *et al.*[3] bring this challenge into focus by studying the diversification of the most species-rich herbivorous beetle lineage known and clarify that it is rooted in the evolution of a particular metabolic adaptation: the capacity to degrade plant cell wall components like cellulose and pectin.

Southwood[1] proposed that the transition to herbivory was the most difficult of all insect feeding strategies owing to four 'hurdles' or barriers to colonization: nutritional, attachment or 'holding-on', desiccation, and host finding, including the synchronization of life cycles. When he drilled down on the subject of nutritional hurdles, Southwood discussed how many tissues of seed plants are depauperate in protein and sterols necessary for insect nutrition, as well as having skewed profiles of certain amino acids. Most impressive though was his quantitative analysis of the conversion efficiencies of herbivorous versus predaceous insects. The caloric value of plant tissue is lower than that of insect tissue and so the efficiency of converting the food ingested to growth is lower for herbivorous insects than predaceous insects. One strategy that some herbivorous insects have taken to compensate for this disparity is to leverage enzymes that efficiently degrade the cell walls of host plants, so called ‘plant cell wall degrading enzymes’ or PCWDEs for short.

PCWDEs are hypothesized to have been a critical factor enabling the diversification of the most diverse beetle clade, the Phytophaga, which includes long-horned beetles (Cerambycidae), leaf beetles (Chrysomelidae), and weevils (Curculionidae). In beetles, these enzymes are derived from three sources: they are encoded in the genome by ancient ‘glycoside hydrolase family 9’ enzymes shared by metazoans, others are encoded by genes borrowed from microbes through horizontal gene transfer, and finally, the genomes of microbial symbionts living within the beetles’ bodies. For the first time, Kirsch and colleagues[3] provide a comprehensive picture of the relative roles of each of these sources across 180 million years of beetle evolution and apportion the roles of endogenous, horizontally transferred, and symbiont-derived metabolic capacity in degrading plant cell wall components. What they find is a dynamism in the gain and loss of genes obtained via horizontal gene transfer, coupled with the gain and loss of microbial symbionts with PCWDE capabilities. They also focus on similarities and differences in how the symbionts are housed in the insect body, including across different life stages of the same species. The scale of this study is truly from cells to clades. The authors also explore how key host-plant-switching events in leaf beetle evolution interface with loss and gain of symbionts encoding PCWDEs, such as the transition of some leaf beetles to pectin-poor grasses. Although the focus of their work is PCWDEs, the authors helpfully point to the importance of other nutrients that symbionts can provide, which also subtends switching between host plants or expansion of host breadth in leaf beetles.

In key ways, their analysis takes a bird’s eye view, but perhaps a more precise analogy is an eagle-eye view, since diurnal raptors have two fovea, allowing a simultaneously focused view of two points, one nearer and one more distant. Here, we have a clearer picture of how dynamic evolution through horizontal gene transfer, subsequent gene duplication (and neo- and sub-functionalization), and gain and loss of nutritional symbionts shaped the diversification of one of the most speciose beetle lineages onto nutritionally depauperate host plants.

Kirsch *et al.*[3] show how horizontal gene transfer and symbiosis can be viewed as two sides of the same coin, although endosymbionts clearly carry more costs and potential benefits given that they are cells and not simply one or a handful of genes. Endosymbionts can be thought of as ‘primary’ when they are required for normal growth and development, or ‘secondary’ when they are not required for normal growth and development but facilitate adaptation to stressors. A ‘musical chairs’ parallel can be found in certain well-studied, sap-feeding insects that have both primary (e.g., *Buchnera aphidicola*) and secondary (e.g., *Hamiltonella defensa*) symbionts. *H. defensa* provides protection to aphid hosts from parasitoid wasp attack, but only when the *H. defensa* itself is infected with a phage or prophage carrying a toxin cassette[8]. This phage toxin cassette can encode diverse eukaryotic toxins, including cytolethal distending toxin subunit B (CdtB), a DNase I homolog found in many Proteobacteria, such as *E. coli*, that causes apoptosis of eukaryotic cells through the cytolethal distending toxin holotoxin. Remarkably, some aphids, like *Myzus* spp., actually encode a copy of *cdtB* in their genomes and are not known to have secondary endosymbionts[9]. These insect homologs of *cdtB* are most closely related to those in *H. defensa* and other insect endosymbionts. Similarly, *cdtB* is found in the genomes of four different drosophilid fly clades (each an independent horizontal-gene-transfer event), and in one species, *D. ananassae*, three copies are necessary for full resistance to parasitoid wasps[10]. What this points to is that the biochemical capacities of microbes have been leveraged by insects through both horizontal gene transfer and endosymbiosis to cope with nutritional hurdles (bottom-up ecological forces) and natural enemies (top-down ecological forces). The macroevolutionary impacts of these horizontal-gene-transfer and symbiosis events are just beginning to emerge but the lateral gain of function through either means is far from trivial from the perspective of adaptation.

Using a comparative framework that leverages patterns of convergence across levels of organization is increasingly being paired with functional genetics and the tools of molecular and cell biology to test how genetic changes that occurred in the distant past might have changed ancestral phenotypes[11,12]. In that vein, the field of macroevolution seems to be moving beyond ancestral-character-state reconstruction across the nodes of phylogenies or inferring the process of biological diversification from the shapes of phylogenies. The bar is now higher, fortunately, as more tools allow a sharper focus of evolution to emerge through the mists of deep time. We are in a golden era for addressing the most fundamental questions in evolution and Kirsch *et al.*[3] provide a good example of how to make the most of it.

What can be drawn in general from this study? J.B.S. Haldane is said to have quipped that “God must have an inordinate fondness for beetles” given their diversity. Another way of looking at the problem in light of the findings from Kirsch *et al.* is that phytophagan beetles, the most diverse lineage in the order, have evolved an inordinate fondness for PCWDEs, whether encoded by genes inherited vertically, horizontally, or in endosymbionts.

DECLARATION OF INTERESTS

The author declares no competing interests.

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