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Co-evolutionary legacies on plant decomposition

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ABSTRACT

Co-evolution has driven speciation and evolutionary novelty in functional traits across the Tree of Life. Classic co-evolutionary syndromes such as plant-pollinator, plant-herbivore, and host-parasite have focused strongly on the fitness consequences during the lifetime of the interacting partners. Less is known about the consequences of co-evolved traits for ecosystem-level processes, in particular their “afterlife” legacies for litter decomposition, nutrient cycling and the functional ecology of decomposers. We review the mechanisms by which traits that result from co-evolution between plants and their consumers, microbial symbionts or humans, and between microbial decomposers and invertebrates, drive plant litter decomposition pathways and rates. This supports the idea that much of today’s global variation in the decomposition of plant material is a legacy of co-evolution.

Co-evolution: from fitness focus to decomposition driver

A key driver of speciation and trait development has been co-evolution, in which the evolutionary trajectories of two taxa depend on one another [1–4]. Co-evolution can be a feature of a highly specific interaction, as for instance the exclusive pollination of *Yucca whipplei* by the moth *Tegeticula maculata* [5]; or – more often – it is embedded in a complex, multi-species web of interactions [6]. Pollination is often seen as the most illustrative example of co-evolution. Other widely studied categories of co-evolution are plant-herbivore, seed-disperser, host-parasite, predator-prey, host-(endo)symbiont and competitive relationships [2].

In the current co-evolution literature, the focus has been on how co-evolved traits affect the respective partners’ fitness during their lifetime, whether positively in both partners (as in mutualisms) or negatively affected in one of them (as in host-parasite and plant-herbivore relationships). By comparison, secondary consequences of co-evolution for other processes have rarely been considered. One key secondary consequence is that many co-evolved plant traits continue

to be of ecological significance after the death of plant tissue. Their decomposition is thought of as an “afterlife” effect [7]. The relevant plant afterlife traits interact with different taxonomic and functional groups of decomposers: fungi, bacteria, and invertebrates. There is growing knowledge about how the trait evolution of plants [8–10], and that of decomposers [11], have contributed to the decomposition pathways and rates observed today. There is also growing knowledge about how evolutionary linkages between plants and other organisms they co-occur with, such as herbivores, pathogens, microbial symbionts or humans, impact decomposition rates. However, this knowledge is scattered through different fields of the decomposition-related literature. A comprehensive understanding of the co-evolution legacy on decomposition of dead plant matter, by different mechanisms, would greatly contribute to our ability to predict the effects of global change-induced alterations in vegetation composition on biogeochemical cycling. This is partly because biotic interaction networks important to ecosystem functions including decomposition [12], which are to a large extent the legacy of co-evolution, are fast being disrupted because of climate and land-use changes [13,14].

This paper aims to fill this research gap, by assembling different categories of co-evolutionary legacy on plant decomposition (Fig. 1), each with different pairs of biotic partners including: (1) plants with their consumers; (2) plants with mutualistic microbes; (3) plants with people; and (4) microbial litter decomposers with fauna. These four categories should bring complementary evidence for our hypothesis, i.e., that the variation in the decomposition of plant material in today’s world is, to a large extent, the legacy of the co-evolution between multiple pairs of evolutionarily distant organisms.

Legacy of plant-consumer co-evolution on decomposition

Co-evolution between plants and their consumers, including herbivorous and pathogenic vertebrates, insects, nematodes, viruses, fungi, protozoans and bacteria, is likely responsible for much of the Earth’s biological diversity [15]. Plant herbivores and pathogens have evolved myriad traits to break

through the plants' defences [16] (Fig. 2). For instance, many mandibulate insects that feed on latex-producing plants cut leaf veins to prevent latex flowing towards their feeding site [17]. In turn, diverse plant species evolved defences against their natural enemies, including thorns or urticating hairs, latex exudation, physically reinforced cell walls and wide-ranging toxic molecules (e.g. flavonoids, polyphenols). The latter chemical compounds may also yield other protective functions (e.g. against solar radiation, frost, mechanical damage) or attraction of natural enemies of herbivores [18]. Nonetheless, the evolution of different resistance strategies, for instance to insect herbivory, is at least partly responsible for the increased complexity of secondary plant metabolites, which in turn led to a wide diversification of herbivores [19]. The consequence of such co-evolution has mostly been to slow down litter decomposition, although this is likely dependent on the specific plant adaptation (Fig. 2). Indeed, structural/mechanical [20] or chemical defences [21] that decrease the palatability of living plant organs are often still found in shed plant organs. Structural defences *per se* against animals likely do not affect decomposability upon senescence, while chemical defences should continue to affect litter decomposability across species (Fig. 2) [20,22]. The persistence of the defences driving this negative relationship between plant palatability and decomposability ranges from long-lasting to ephemeral after senescence. Polymers such as lignin are particularly long-lasting and slow decomposition both directly and indirectly: recalcitrant lignin molecules are often interwoven with cellulose and hemicellulose, rendering the latter inaccessible to the extra-cellular enzymes of potential decomposers [23].

At the ephemeral end of the range, compounds, such as (nitrogen (N)-based) cyanogenic glycosides, are water-soluble toxins that are broken down rapidly by microbes both in herbivore guts and in the litter layer, allowing for their fast decomposition. Resistance compounds of intermediate lifespan in the decomposition environment include terpenes (including "essential oils") and polyphenols such as tannins [24]. These compounds, with a likely anti-herbivory or anti-microbial function in the living plant, may partly explain the very slow decomposition of leaf litter and deadwood of many gymnosperms and eucalypts [25]. However, these compounds are probably generally less recalcitrant

to decomposition than lignin. Additionally, gymnosperms are known to have particularly recalcitrant forms of lignin [26]. Some of the extensive physical and chemical defences of extant gymnosperms are likely a co-evolutionary legacy from the Mesozoic, when large herbivorous dinosaurs (e.g. sauropods) are thought to have fought an evolutionary arms race with gymnosperm taxa such as araucarias (Araucariales), cycads (Cycadales) and conifers (Pinales) [27,28]. An example is *Araucaria araucana* (monkey-puzzle tree), which has large, physically very tough green scales with sharp tips filled with secondary compounds that function as its leaves and similar scales protruding from the bark of the trunk. Based on visual observations of deadwood of this species (J.H.C. Cornelissen), these scales probably have low decomposability. This case also raises an interesting more general question, i.e. to what extent does co-evolution of plants with herbivores or pathogens occur in more than one plant organ simultaneously; and what might be the legacy of this co-evolution on decomposition? For instance, defensive resins are commonly produced in leaves, bark and seed cones of many gymnosperm taxa and are thought to inhibit fungal decomposition of their own litter [29]. Specific defensive compounds have also been reported from both foliage and bark in some angiosperm taxa including *Alnus* (alder) [30] and *Populus* (poplar) [31], but these defenses may be too transient to strongly affect litter decomposition. Resource-conservative plant life strategies favoring high plant tissue density, which are linked to increased organ mechanical defence and lifespan, appear coordinated at the global scale between leaves and roots [32], possibly owing to both whole-plant ecophysiological and allometric constraints and phenotypic integration [33]. Such a trend translates into coordinated variation in leaf and root decomposability globally [34].

The above discussion about different types of consumer-plant co-evolution and their legacy on litter decomposition has focused solely on litter decomposability, i.e. on anti-consumer trait afterlife effects on the decomposition of litter derived from the defended plant tissues themselves. However, there is ample evidence that the anti-consumer legacy extends beyond the litter itself and affects the decomposition, carbon and nutrient dynamics of soil organic matter much more broadly, including

organic matter derived from other plant species. For instance, polyphenols such as condensed and hydrolysable tannins are known to affect – often inhibit – the decomposition and nutrient mineralization of soil organic matter by affecting saprotrophic fungi, mycorrhizal fungi and soil invertebrates [24, 35]. An interesting example was shown for the boreal ericoid dwarf shrub *Empetrum hermaphroditum* (crowberry), which has high concentrations of the stable polyphenol batatasin-III in its leaves and leaf litter. Litter of various plant species was experimentally shown to decompose significantly more slowly when placed in humus collected from below *E. hermaphroditum* as compared to humus collected from below *Vaccinium myrtillus* (bilberry) and this inhibition of decomposition was explained as an allelopathic effect of batatasin-III [36]. How co-evolution of plants and consumers affects the decomposition of litter and soil organic matter beyond the decomposition of defended tissues themselves is a relatively poorly studied but promising research field, given its likely important implications for soil carbon and nutrient dynamics globally.

Legacy of co-evolution between plants and microbial symbionts on decomposition

Plants participate in a huge diversity of ecological interactions with microorganisms living on all plant surfaces, both below-ground (rhizosphere), in aerially exposed tissues (phyllosphere), and within the plant (endosphere). These interactions vary widely in their fitness outcome for plants (positive, neutral, negative) and their degree of partner specificity [37]. Effects of co-evolution of plants and associated microbial symbionts on decomposition can be expected to arise via three main mechanisms, namely changes in: 1) chemical and physical (anatomical or morphological) composition of plant tissue; 2) plant biomass allocation to different organs, tissue types, and/or spatial compartments; and 3) ecological strategies of the microbiota associated with the plant, and with adjacent soil and litter layer habitats.

From both ecological and evolutionary perspectives, one of the most striking plant-symbiont interactions is the nutritional mutualisms involving mycorrhizal fungi (here considered as microbes for

convenience in spite of often extensive hyphal networks) and root-inhabiting N-fixing bacteria, in which plant roots exchange photosynthate for nutrients, with consequences for the development of terrestrial biogeochemical cycles [38,39]. The decomposability of dead leaves, roots and stems (including wood) is usually well correlated with both their secondary chemistry and their tissue nutrient content [7,24,40–42]. Mutualistic interactions with microbes, by enhancing uptake of nutrients in different chemical forms, have greatly expanded the potential range of plant nutrient-use strategies [43,44]. This is reflected in the higher values of leaf and root N in N-fixing plants [45,46] and the association between mycorrhizal association type and the N and P content of plant tissues [47,48]. These symbioses have ancient evolutionary origins, from 65 million years ago for N-fixing [49] to at least the Silurian colonization of land by plants more than 400 million years ago for mycorrhiza [43,50]. By influencing the range of concentrations of plant nutrients and phenolic defence compounds, this plant-symbiont co-evolution has driven litter decomposability.

Another important aspect of plant–fungi co-evolution is the capacity of ericoid mycorrhizal (ErM) and ectomycorrhizal (EcM) fungi in infertile ecosystems (e.g. tundra, heathland, forest on acidic soils) to exude powerful enzymes to digest complex phenolic compounds and pass on their residues in simpler organic forms (e.g. amino acids) to the plant partner. The latter is thereby largely independent of nutrient mineralisation, as such minerals tend to be very limited in these ecosystems [38]. By producing tissues protected with large-chain phenolic compounds for longer lifespan, EcM and ErM plant partners generally produce recalcitrant, slow-decomposing leaf and root litter [47,51,52], thereby giving both the fungus (with its special enzymes) and itself a competitive advantage [47] (Fig. 3). However, given the importance of mycorrhizal fungi for litter decomposition processes and soil formation, we know surprisingly little about their role in degrading and recycling plant root tissue to which they are associated and their interactions with other saprotrophs [53,54].

In contrast, the generally higher N concentrations of N-fixing plants compared to non-fixers do not seem to have a strong afterlife legacy, as decomposability does not differ consistently between these

two groups [40]. However, the nutritious litter may promote the growth of other, nitrogen-demanding species such as grasses [55] which may then reduce the relative abundance of the N-fixers in the community (Fig. 3). Mycorrhizal and N-fixing co-evolution have strong phylogenetic structure for both the microbial and plant partner; this is seen most strongly in rhizobial N-fixing mutualism as well as EcM, ErM and orchid mycorrhizae. Arbuscular mycorrhizae are more broadly spread phylogenetically [43]. Besides mycorrhizal and N-fixing mutualisms, many other interactions of plants with symbionts living in and on all their tissues are due to co-evolution of ecological traits of both partners [56], with potential knock-on influence on decomposition dynamics.

Besides contributing to variation in litter chemical composition, co-evolved plant-symbiont interactions can influence decomposition dynamics by determining the relative amounts, and spatial distribution, of litter inputs above- and below-ground. Plant associations with mycorrhizal fungi can shape plant biomass allocation between roots and shoots [57]. Root-associated microbes can also alter the relative proportion of fine vs coarse roots, and their depth distribution [58,59]. Decomposition rates [34] and carbon stabilization pathways [60] differ between leaf, shoot, fine root and coarse root litter, and vary with soil depth [61]. Co-evolved plant-microbe interactions that influence root architecture and biomass allocation should therefore affect decomposition, soil organic matter formation, and nutrient cycling.

Furthermore, the microbial community in living leaves and wood will affect plant performance and *vice versa* [62–65]. The presence of seed-mediated transmission of microbes across plant generations suggests long-term co-evolution between plants and their microbiota [66]. Leaf and wood endophyte communities can persist after tissues senesce [67] with potential legacies on decay. These microbial residents likely have privileged access to dead plant material, potentially shaping decay directly through their own decay enzyme expression and indirectly as they alter succession of later microbial communities, thereby also driving the Home Field Advantage effect in decomposition [68].

A very interesting type of symbiotic relationship is that between plants and endophytic fungi, where the latter contain alkaloids that can serve as anti-herbivore defence for the plant. The legacy of this symbiosis on litter decomposition rates and nutrient mineralization is complicated and still incompletely understood [69]. This is partly because these alkaloids have been reported to have (or lack) inhibitory effects on microbial decomposers while in some cases the fungal symbionts may turn saprophytic after the senescence of plant tissues, which could accelerate their litter decomposition. Moreover, the endophytic fungi may interact with decomposing microbes either directly or by altering the chemistry of the plant tissues, which may also accelerate or decelerate litter decomposition [69]. How plants outsource their chemical defenses to endophytic microbes, and what the net consequences are for litter decomposition via these different mechanisms, make for a promising field of study on co-evolutionary legacies on decomposition.

Legacy of plant-human co-evolution on decomposition

Early domestication by humans may have started with people accidentally dropping gathered plant seeds near human settlements [70] and continued into the present with increasingly sophisticated selection of favorable crop traits. In turn, the development of crop domestication has fundamentally changed human diets leading to the evolution of multiple human traits, such as changes in dental morphology and increases in brain size [71]. This very special case of co-evolution between plants and people has had many consequences for crop traits and their afterlife effects on decomposition (Fig. 4).

Food crop species have been subjected to ‘natural’ selection caused by human modification of crop growing conditions, such as improved soil structure, enhanced nutrient and water supply, protection from herbivory and weed competition and regular soil disturbance (e.g. ploughing) and harvesting [33]. The efficiency of human food production resulting from this crop domestication helped to develop human capacity (e.g. improved cognition abilities, and modified societal organization) to

come up with increasingly sophisticated tools (e.g. the use of biological and chemical solutions to fight herbivores and pathogens) to further modify crop growing conditions. In addition, crop evolution has been influenced by directed artificial selection or engineering of crop genotypes for favorable traits for human use, such as increased crop yield and palatability. These two types of selection, in combination, have led to the emergence of a crop domestication syndrome for annual plants of fast growth with resource acquisitive strategies [33,72], based on plant traits promoting fast after-life decomposition. Aboveground, domestication reduces living plant resource investment in anti-herbivore defence [73,74] and increases leaf N and P concentrations [75]. Such differences in leaf traits have also been observed on the litter of domesticated plants, with lower lignin concentrations, lignin:P ratios and N:P ratios leading to an average increase of 36% in litter mass loss rate across 24 crop species as compared to those of their wild relatives [76]. Belowground, however, no clear influence of domestication on root traits across species has been demonstrated yet [77].

Legacy of fauna-microbial decomposer co-evolution on plant decomposition

Some microbial decomposers are tightly linked to detritivorous arthropods. Many litter-feeding detritivores rely on their hindgut microbes to digest dead plant tissue, especially those that lack the enzymes to breakdown the ingested recalcitrant polymers [78]. Certain arthropod groups form obligatory internal mutualistic relationships with microbes. For instance, higher termites (Termitidae) harbor exclusively prokaryotic communities in their dilated hindguts [79]. On the other hand, their actual community composition is largely determined by their diet and microhabitat [79], suggesting low taxonomic affiliation between prokaryote and host.

Various termites, stick insects and beetles evolved endogenous digestive enzymes targeting less complex carbon polymers [80–82], while others (e.g. *Termitomyces* termites and certain ants) cultivate fungal gardens outside their guts to decompose complex polymers [83,84]. In all cases, a given piece of litter is decomposed in a more stable and favorable environment than if it lay on the

soil surface. The evolution of digestive mutualisms, which dates back to at least the Cretaceous [85], is believed to be derived from the coprophagic behavior of certain arthropod groups, where concentrated microbial consortia in feces may have facilitated the evolution of host-microbe interdependence [86].

The most striking co-evolutionary examples are microbe-host relationships involved in the breakdown of woody debris from trees. The emergence of highly lignified wood ~400 mya [87] led to a major shift in global terrestrial carbon cycle. Currently, decomposition across all carbon polymers in wood is only possible by select groups of bacteria and fungi that have the enzymatic capacity to degrade lignin [88]. These groups also form symbioses, both internal and external, with a few insect lineages, to allow the insect partner to consume wood, which is then degraded, internally or externally to the insect gut, by the microbial symbiont. Of special note are ambrosia beetles, belonging to Scolytinae and Platypodinae [89], and termites belonging to Macrotermitinae, with their advanced fungal agriculture system [83,90], in which inoculating litter with fungi in a stable and relatively mesic environment promotes litter decomposition. Co-evolution has resulted in arthropods (e.g. termites, ants, wasps, beetles) acting as vectors for the fungal decomposers from which they benefit by accessing more digested litter, or being farmers of fungi in so-called fungal gardens [91,92]. Ambrosia beetles, for instance, form an obligate mutualism with various ascomycete and basidiomycete fungi [90,93–95]. These symbiotic fungi depend on their host for colonization and inoculation of new trees. Spores are rubbed off when the beetle excavates tunnels in woody plants and forms a fungal garden of mycelia on which the beetle and their larvae feed. Ambrosia beetles live predominantly in stressed, dying or dead woody plants and do not feed on wood directly. They excavate stems to form galleries, creating a species-specific architecture of tunnels in which the fungi establish kick starting wood decomposition. Some xylophagous beetles, clearwing moths (Sesiidae) and termites invade living trees, consuming heartwood and senesced branches. Some of these (e.g., *Coptotermes*, drywood termites) even live within their live plant hosts and there is evidence that such compromised trees

have reduced growth and increased mortality [95], leading to selective advantages for those trees that avoid such invasions, which may carry into the plant afterlife.

The diversity and efficiency of the modern wood decomposers' pathways lagged behind evolution of wood itself [96]. Four wood decay innovations are thought to have emerged much after the evolution of wood, in order of emergence: (1) the enzymatic pathway key to white rot fungi which breaks down lignin [11], (2) the less metabolically expensive chelator-mediated Fenton pathway in which free radicals modify lignin, allowing brown rot fungi to access other carbon polymers [97–99], (3) the modification of the invertebrate gut symbiosis [100], and (4) the origin of fungus-farming insects [91]. There is little direct evidence about the effect of these innovations on the global carbon cycle. It is thought that this lag may have led to the buildup of lignin-rich litter in the Carboniferous; although, others argue that wood decay was slowed due to differences in climatic conditions of these early environments [11,96]. The evolutionary innovations associated with gut symbiosis of xylophagous invertebrates and fungal-farming insects may both have had strong effects on the carbon cycle of tropical forests. Currently termites consume more than 50% of the wood in some tropical forests [101,102] and thereby contribute significantly to decomposition.

Concluding remarks

In this synthesis we make a case for the importance of multiple aspects of plant co-evolution with herbivores, parasites, pathogens, (microbial) mutualists and humans, but also between microbial decomposers and fauna, for litter decomposition. Without being exhaustive (see Outstanding Questions), we believe that the evidence presented here supports the hypothesis that co-evolution can play an important role beyond the well-studied aspects of organism fitness, i.e. in driving ecosystem processes.

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FIGURES

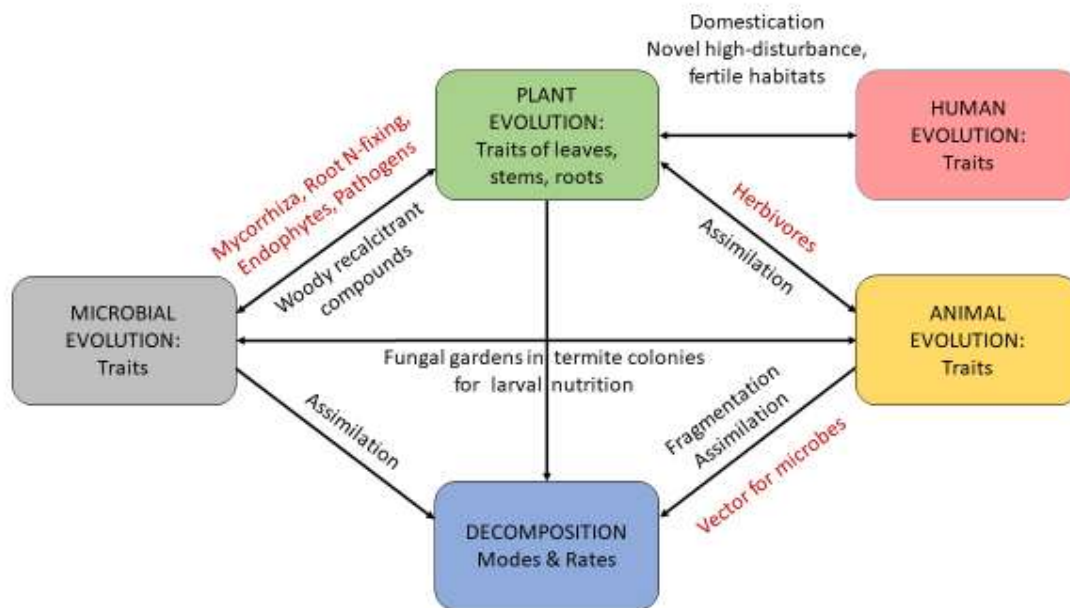


Figure 1: Conceptual framework showing the types of co-evolution in terms of partner-partner and their legacy on plant decomposition. These include co-evolution between microbes (grey), plants (green), animals (yellow) and humans (red) with cascading impacts on decomposition (blue). Processes and chemistry linking the boxes are in black text and examples of the biotic interactions are in red text.

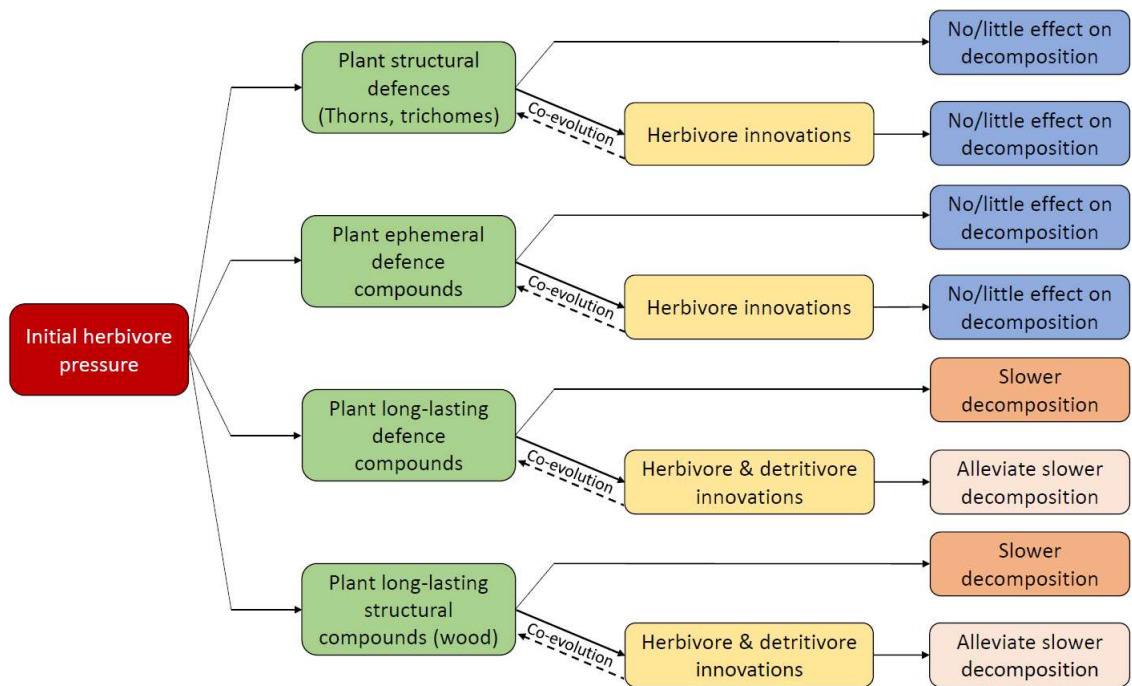
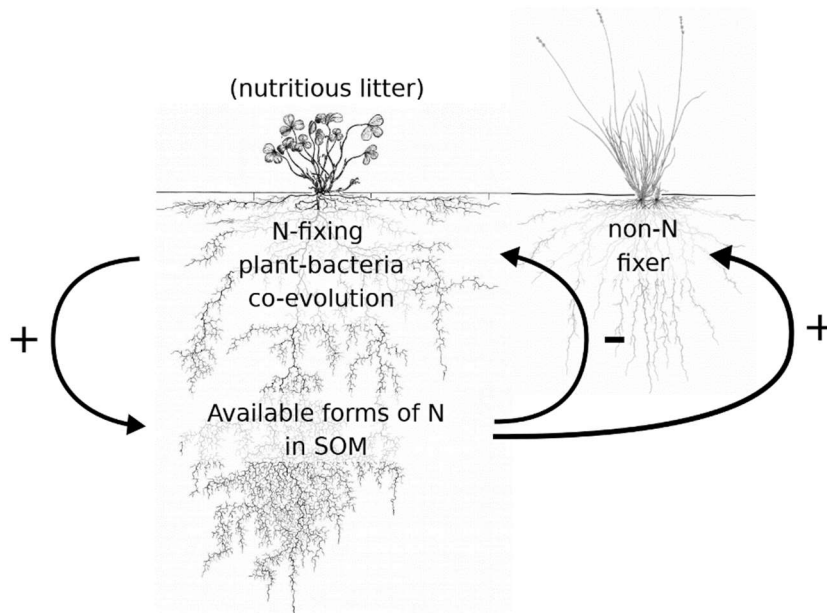
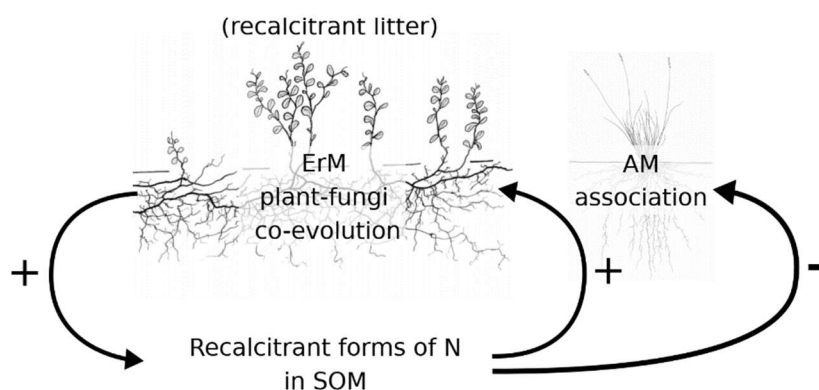


Figure 2: Potential legacy of plant-consumer co-evolution on decomposition. The rise of herbivores (red box) has resulted in myriad plant defences (green boxes), with potential effects on litter decomposition. Evolution of different resistance strategies in plants has led to a wide diversification of herbivore innovations (yellow boxes), resulting in an evolutionary arms race with plants. Especially the formation of long-lasting defence and structural compounds as a result of plant-herbivore co-evolution are thought to have resulted in slow decomposition (orange boxes). Detritivore (microbes and animals) innovations to afterlife effect of these recalcitrant substrates in litter weakens the negative effects of long-lasting compounds on decomposition (light beige boxes). Whether or how defensive thorns, trichomes, or urticating hairs, and ephemeral (e.g. soluble) defence compounds, affect leaf decomposition is not known, but any impact is unlikely to be strong (blue boxes).

a. Negative feedback on N-fixing association



b. Positive feedback on ErM association



538

539 **Figure 3:** Examples of the consequences of plant-microbe co-evolution for community and ecosystem-
 540 level processes. N-fixing symbiosis impacts on soil organic matter, decomposition and nitrogen
 541 availability in soil eventually lead to a lower reliance of the plant host on N-fixing bacteria (a.) The
 542 reverse is true for of ericoid mycorrhizal (ErM) symbiosis, where the impacts of the plant litter
 543 recalcitrance on soil organic matter decomposition reinforces the plant host reliance on ErM fungi
 544 with efficient capacity to extract nutrients from soil organic matter (b.). Drawings are from references
 545 [103–105]. SOM, soil organic matter; AM, arbuscular mycorrhiza.

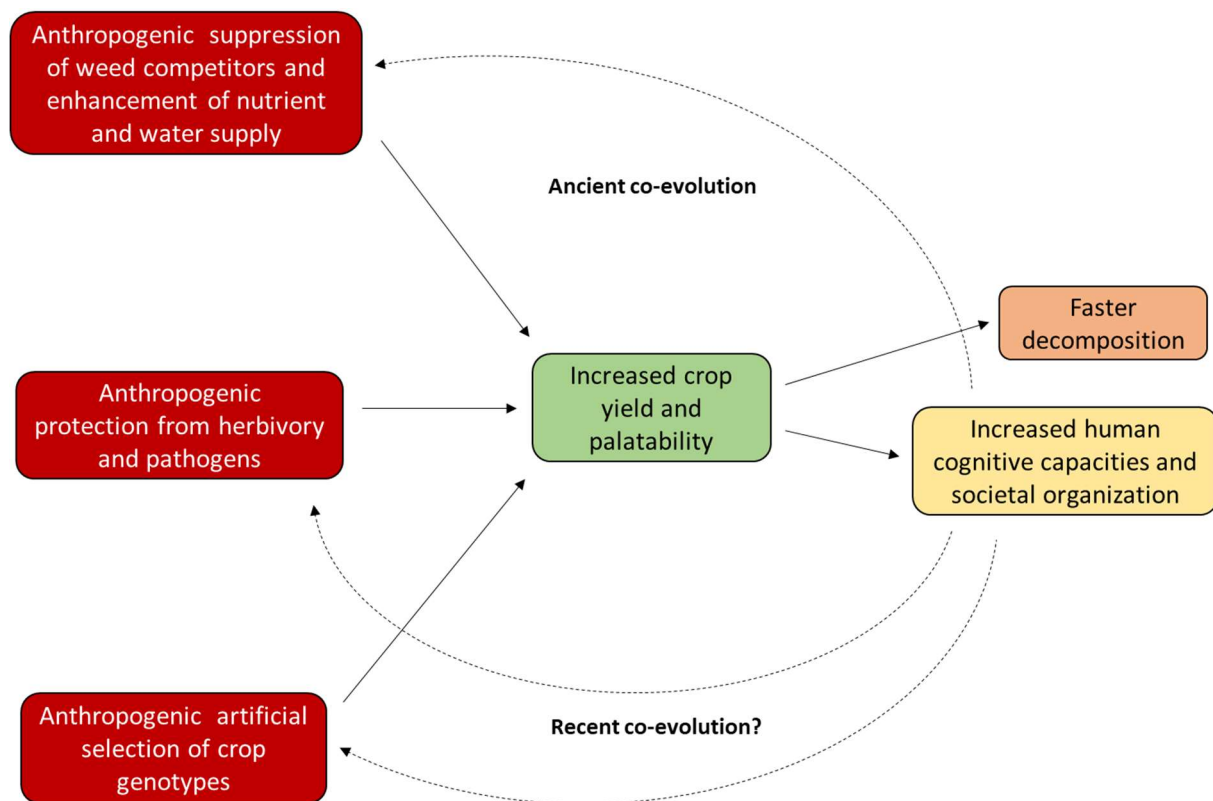


Figure 4: Potential legacy of plant-human co-evolution on decomposition. Food crop species have been subjected to ‘natural’ selection influenced by human modification of crop growing conditions. The efficiency of human food production resulting from this crop domestication has helped to develop humans’ capacity for increasingly sophisticated tools which further modify crop growing conditions. In addition, crop evolution has been increasingly influenced by directed artificial selection or engineering of crop genotypes that favor yield and palatability. These two types of selection, in combination, have led to the emergence of a crop domestication syndrome for annual plants of fast growth with resource acquisitive strategies, based on plant traits promoting fast afterlife decomposition.