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Review

Coevolutionary legacies for plant decomposition

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Coevolution has driven speciation and evolutionary novelty in functional traits across the Tree of Life. Classic coevolutionary 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 coevolved 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 resulting from coevolution 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 current global variation in the decomposition of plant material is a legacy of coevolution.

Highlights

Plant litter decomposition adds a different process and ecological context to the coevolution literature, which has thus far focused on the ecology of symbionts during their lifetimes.

This context integrates the literature on how arms races between plants and their consumers (herbivores, pathogens) or mutualists (nitrogen-fixing bacteria, mycorrhizal fungi) drive the quality of plant tissue, with an important legacy for litter decomposability.

We know little about recent coevolutionary decomposition legacies involving plant domestication by humans via farming, plant breeding, and modified landscapes with feedback to evolution of human brain, digestion, and dentition.

How myriad coevolutionary links between invertebrates and microbial decomposers affect global carbon cycling needs further investigation.

Overall, plant decomposition rates are largely the legacy of wide-ranging coevolutionary relationships.

Coevolution: from fitness focus to decomposition driver

A key driver of speciation and trait development has been coevolution, in which the evolutionary trajectories of two taxa depend on one another [1–4]. Coevolution can be a feature of a highly specific interaction, for example, 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 coevolution. Other widely studied categories of coevolution are plant–herbivore, seed–disperser, host–parasite, predator–prey, host–(endo)symbiont, and competitive relationships [2].

In the current coevolution literature, the focus has been on how coevolved traits affect the fitness of the respective partners during their lifetime, either positively in both partners (as in mutualisms) or negatively in one partner (as in host–parasite and plant–herbivore relationships). By comparison, secondary consequences of coevolution for other processes have rarely been considered. One key secondary consequence is that many coevolved 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 decomposers [11] has 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, and humans, impact on decomposition rates. However, this knowledge is scattered through different fields of the decomposition-related literature. A comprehensive understanding of the coevolution legacy for 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 that are important for ecosystem functions including decomposition [12], and which are to a large extent the legacy of coevolution, are rapidly being disrupted because of climate and land-use changes [13,14].

This paper aims to fill this research gap by assembling different categories of coevolutionary legacy for plant decomposition (Figure 1), each with different pairs of biotic partners including

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https://doi.org/10.1016/j.tree.2022.07.008

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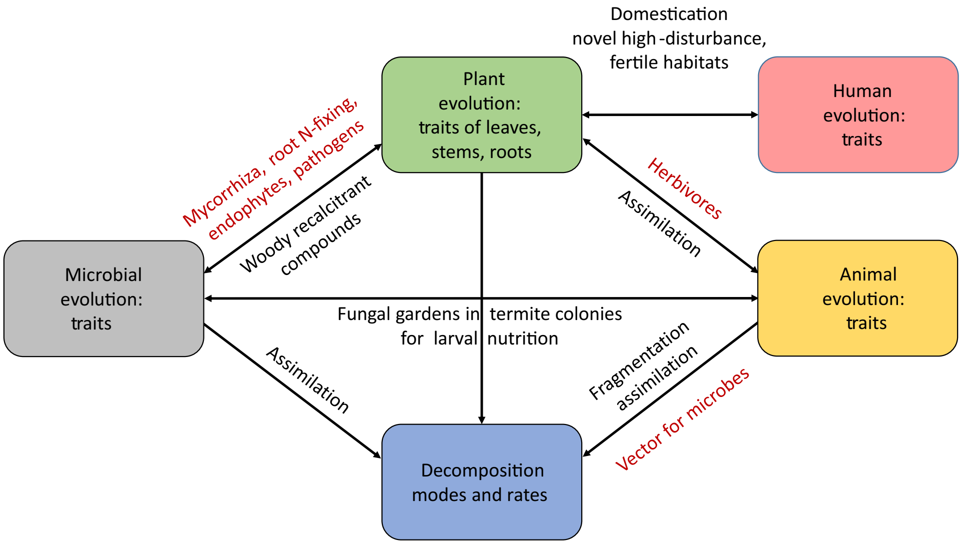

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Figure 1. Conceptual framework showing the types of coevolution in terms of partner–partner and their legacy for plant decomposition. These include coevolution between microbes (gray), plants (green), animals (yellow), and humans (red) with cascading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

(i) plants with their consumers, (ii) plants with mutualistic microbes, (ii) plants with people, and (iv) microbial litter decomposers with fauna. These four categories should bring complementary evidence for our hypothesis – that the variation in the decomposition of plant material in today's world is, to a large extent, the legacy of the coevolution between multiple pairs of evolutionarily distant organisms.

Legacy of plant–consumer coevolution for decomposition

Coevolution 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 plant defenses [16] (Figure 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 have evolved defenses against their natural enemies, including thorns and 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 attract 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 has led to a wide diversification of herbivores [19]. The consequence of such coevolution has mostly been to slow down litter decomposition, although this is likely dependent on the specific plant adaptation (Figure 2). Indeed, structural/mechanical [20] or chemical defenses [21] that decrease the palatability of living plant organs are often still found in shed plant organs. Structural defenses *per se* against animals likely do not affect decomposability upon senescence, whereas chemical defenses should continue to affect litter decomposability across species (Figure 2) [20,22]. The persistence of the defenses 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

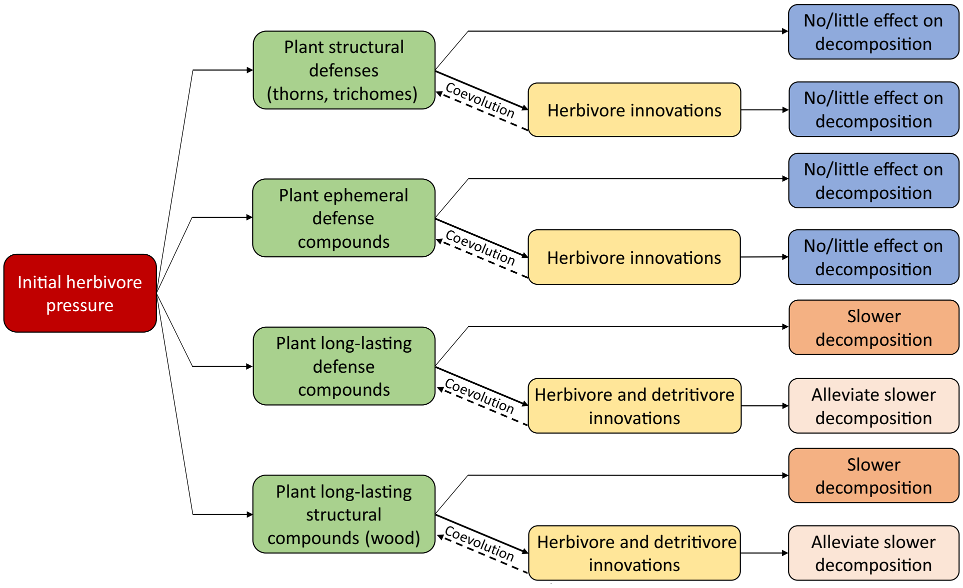

Figure 2. Potential legacy of plant–consumer coevolution for decomposition. The rise of herbivores (red box) has resulted in myriad plant defenses (green boxes), with potential effects on litter decomposition. Evolution of different resistance strategies in plants has led to a wide diversification of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

lead to slow decomposition both directly and indirectly: recalcitrant lignin molecules are often interwoven with cellulose and hemicellulose, rendering the latter inaccessible to the extracellular 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 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, that probably have anti-herbivory or antimicrobial functions 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. In addition, gymnosperms are known to have particularly recalcitrant forms of lignin [26]. Some of the extensive physical and chemical defenses of extant gymnosperms are likely a coevolutionary 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, unpublished), these scales probably have low decomposability. This case also raises an interesting more general question – to what extent does coevolution of plants with herbivores or pathogens occur in more than one plant organ simultaneously, and what might be the legacy of this coevolution for 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 defense and lifespan, appear to be coordinated at the global scale between leaves and roots [32], possibly owing to both whole-plant ecophysiological/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 coevolution and their legacy for litter decomposition has focused solely on litter decomposability, namely, 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 hydrolyzable tannins are known to affect – and 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. The 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 coevolution 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 coevolution between plants and microbial symbionts for decomposition

Plants participate in a huge diversity of ecological interactions with microorganisms living on all plant surfaces, including belowground (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 coevolution of plants with associated microbial symbionts on decomposition can be expected to arise via three main mechanisms, namely, changes in (i) the chemical and physical (anatomical or morphological) composition of plant tissue; (ii) plant biomass allocation to different organs, tissue types, and/or spatial compartments; and (iii) ecological strategies of the microbiota associated with the plant, as well as with adjacent soil and litter layer habitats.

From both ecological and evolutionary perspectives, one of the most striking plant–symbiont interactions is nutritional mutualism involving mycorrhizal fungi (here considered to be microbes for convenience although they often have 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 the 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 phosphorus (P) content of plant tissues [47,48]. These symbioses have ancient evolutionary origins, from 65 million years ago (Mya) for N-fixing [49] to at least the Silurian colonization of land by plants >400 Mya for mycorrhiza [43,50]. By influencing the range of concentrations of plant nutrients and phenolic defense compounds, this plant–symbiont coevolution has driven litter decomposability.

Another important aspect of plant–fungi coevolution 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 mineralization because 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 themselves a competitive advantage [47] (Figure 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 with which they are associated and their interactions with other saprotrophs [53,54].

By contrast, the generally higher N concentrations of N-fixing plants compared to non-fixers do not seem to have a strong afterlife legacy because decomposability does not differ consistently between these two groups [40]. However, the nutritious litter may promote the growth of other N-demanding species such as grasses [55] which may then reduce the relative abundance of the N-fixers in the community (Figure 3). Mycorrhizal and N-fixing coevolution have a 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]. In addition to mycorrhizal and N-fixing mutualisms, many other interactions between plants and symbionts living in and on all their tissues are due to coevolution of the ecological traits of both partners [56], with a potential knock-on influence on decomposition dynamics.

In addition to contributing to variation in litter chemical composition, coevolved plant–symbiont interactions can influence decomposition dynamics by determining the relative amounts, and spatial distribution, of litter inputs above- and belowground. 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 versus 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]. Coevolved 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 coevolution between plants and their microbiota [66]. Leaf and wood endophyte communities can persist after tissues senesce [67], with potential legacies for 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 the succession of later microbial communities, thereby also driving the 'home field advantage' effect in decomposition [68].

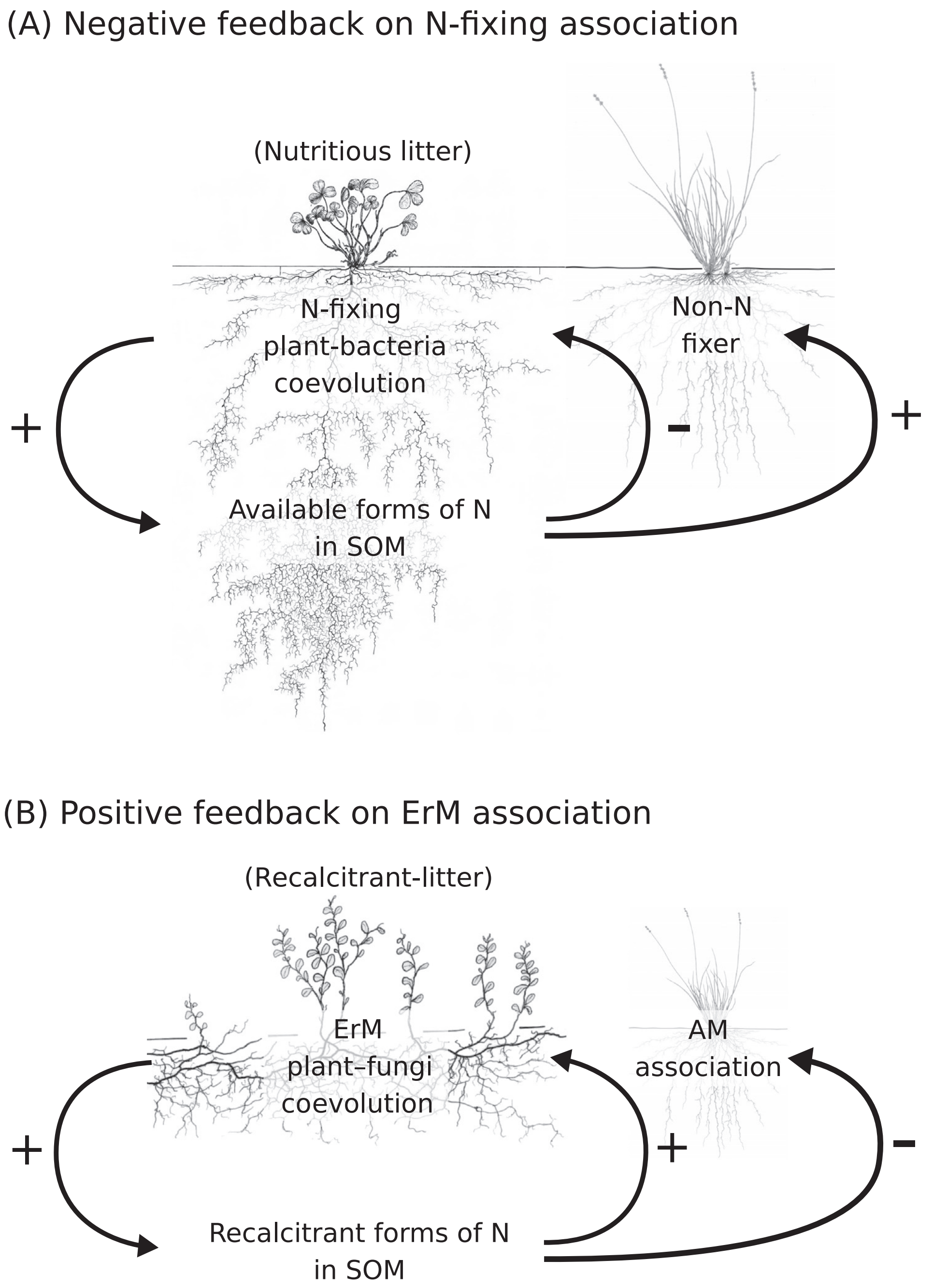

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Figure 3. Examples of the consequences of plant–microbe coevolution for community and ecosystem-level processes. (A) Nitrogen (N)-fixing symbiosis impacts on soil organic matter (SOM), decomposition, and N availability eventually lead to a lower reliance of the plant host on N-fixing bacteria. (B) The reverse is true for of ericoid mycorrhizal (ErM) symbiosis, where the impacts of the plant litter recalcitrance on SOM decomposition reinforce plant host reliance on ErM fungi that are able to efficiently extract nutrients from SOM. Drawings are from references [103–105]. Abbreviation: AM, arbuscular mycorrhiza.

A very interesting type of symbiotic relationship is between plants and endophytic fungi where the latter contain alkaloids that can serve as anti-herbivore defense for the plant. The legacy of this symbiosis for litter decomposition rates and nutrient mineralization is complex 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, are a promising field of study in understanding the coevolutionary legacies for decomposition.

Legacy of plant–human coevolution for 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 coevolution between plants and people has had many consequences for crop traits and their afterlife effects on decomposition (Figure 4).

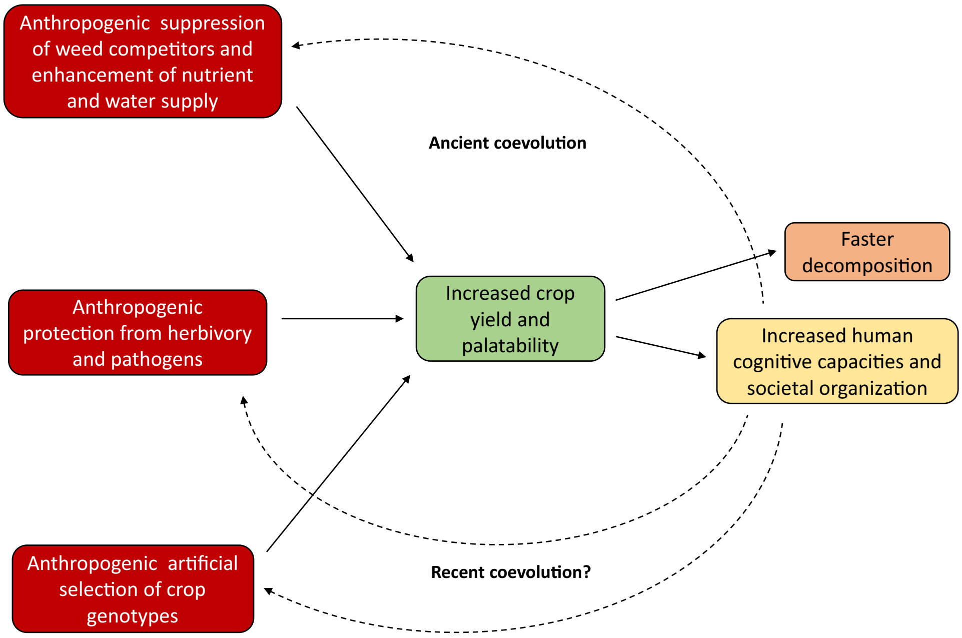

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Figure 4. Potential legacy of plant–human coevolution for decomposition. Food crop species have been subjected to 'natural' selection influenced by human modification of crop growing conditions. The efficiency of human food production resulting from this crop domestication has helped to develop human 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 and resource acquisition strategies based on plant traits that promote fast afterlife decomposition.

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 devise increasingly sophisticated tools (e.g., the use of biological and chemical methods to fight herbivores and pathogens) and 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 acquisition strategies [33,72] based on plant traits that promote fast afterlife decomposition. Aboveground, domestication reduces living plant resource investment in anti-herbivore defense [73,74] and increases leaf N and P concentrations [75]. Such differences in leaf traits have also been observed in the litter of domesticated plants, where lower lignin concentrations, lignin:P ratios, and N:P ratios lead to an average increase of 36% in litter mass loss rate across 24 crop species compared to 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 coevolution for 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 break down the ingested recalcitrant polymers [78]. Some arthropod groups form obligatory internal mutualistic relationships with microbes. For instance, higher termites (Termitidae) harbor exclusively prokaryotic communities in their dilated hindguts [79]. By contrast, 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 have evolved endogenous digestive enzymes that target less-complex carbon polymers [80–82], whereas 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 was lying 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 particular arthropod groups where concentrated microbial consortia in feces may have facilitated the evolution of host–microbe interdependence [86].

The most striking coevolutionary 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 of 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 that 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, that have advanced fungal agriculture systems [83,90] in which litter is inoculated with fungi in a stable and relatively mesic environment to promote litter decomposition. Coevolution 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 the 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 can establish, thus kick-starting wood decomposition. Some xylophagous beetles, clearwing moths (Sesiidae), and termites invade living trees where they consume 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, and which may carry over into the plant afterlife.

The diversity and efficiency of the modern wood-decomposer 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: (i) the enzymatic pathway key to white rot fungi which breaks down lignin [11]; (ii) 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]; (iii) the modification of invertebrate gut symbiosis [100]; and (iv) 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 because of differences in the 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 >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 coevolution with herbivores, parasites, pathogens, (microbial) mutualists, and humans, as well as 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 coevolution can play an important role, beyond the well-studied aspects of organism fitness, in driving ecosystem processes.

Declaration of interests

No interests are declared.

Outstanding questions

How do we assess the multiple coevolutionary interactions? In a single plant, several coevolutionary interactions take place simultaneously, with complex effects on ecosystem function. For example, many plants form a tight association with mycorrhizal fungi, and this can have both positive (e.g., increase in tissue N or P content) and negative (e.g., increase in recalcitrant fungal chitin) effects on decomposition rates. At the same time, plants must also cope with attack by leaf or root herbivores (e.g., by having high polyphenol content).

Is there evidence for the coevolution of animal detritivores and their gut microflora? Macrodetritivores such as isopods, millipedes, termites, and many beetle and fly larvae largely completely rely on the diversity and activity of their associated gut microflora for the digestion of recalcitrant plant litter, which has important ecosystem-level consequences. Some of the mutualistic microbes are only found within their host, but actual coevolution remains to be demonstrated.

Is agricultural crop selection, together with crop management, currently changing the afterlife effect of crop residues on soil and ecosystem processes? What is the effect on global soils of a recent widespread geographic expansion of cultivation of a small set of crop species – and of a recent increased focus on crop selection for traits conferring resistance to biotic or abiotic threats – both on the rate of carbon cycling and soil organisms, including microbes and animals?

What is the importance of possible coevolutionary legacies for ecosystem functions other than decomposition – for example, on aspects of soil organic matter formation, bedrock weathering (e.g., by lichens, mycorrhizal fungi, the rhizosphere), cycling of elements other than plant carbon and nitrogen, and soil hydrology (including vegetation drought resistance through mycorrhizal networks)?

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