Tons of leaves fall from trees every year. Meet the organisms responsible for recycling everything.

Where Do All the Leaves Go?

(Photo by Michael Jeffords)

Story and Illustrations
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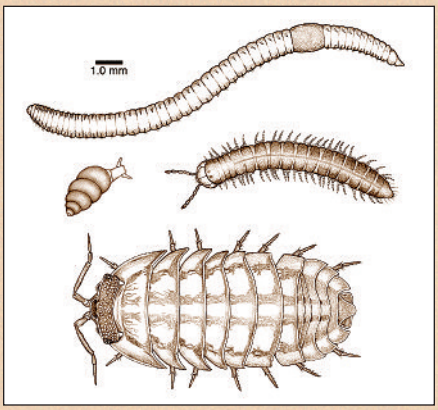
A bright yellow slime mold spreads across the surface of a decaying oak leaf. Innumerable beetles and their larvae (inset) graze on these leaf surfaces.

By the time the last leaves have fallen to the earth each November, about one and a half tons of leaves have settled on each acre of forest floor. Recycling of this immense pile of leaves is accomplished through the efforts of a multitude of organisms. Even before autumn leaves settle on the forest floor, some bacteria and fungi have already colonized their surfaces and begun recycling the nutrients and energy that each leaf contains.

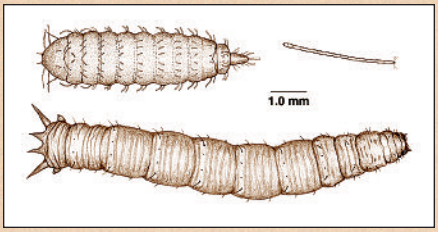
As partners in recycling, invertebrates such as earthworms, potworms, snails and slugs chew off pieces of leaf tissue. Small arthropods such as mites, springtails and larger arthropods such as millipedes, woodlice and insect larvae bite off more chunks. In addition to chewing on decaying leaves, potworms and woodlice also recycle the droppings of their fellow invertebrates. All this chewing helps create pits and holes, rips and tears that expose additional surface area on remnants of fallen leaves for colonization by bacterial and fungal recyclers.

Fungi and bacteria pour out enzymes that digest and recycle those compounds in fallen leaves that were built with energy from the sun and with nutrients from the soil. Microbes absorb the energy and nutrients that they obtain from the digested molecules of decaying leaves, eventually passing on their inheritance to future generations of plants and animals of the forest.



A potworm (top), a tiny snail (middle left), an immature millipede (middle right) and a woodlouse (bottom) help shred fallen leaves and facilitate colonization and recycling of leaves by bacteria and fungi.

The proteins, nucleic acids, sugars, starches and lipids of fallen leaves are among the first components to be digested and recycled since practically all organisms have the ability to digest these molecules. However, it's the tough fibers of a leaf's cell walls (made



Fly larvae help recycle the forest. Larvae of soldier fly (upper left), midge (upper right) and crane fly (bottom) are shown. "Little Wheel" mushrooms (*Marasmius rotula*), represent a fungal species involved in recycling leaves and wood.

up of cellulose [chains of glucose sugars] and hemicellulose [chains of glucose as well as other sugars] fibrils cross linked by lignin) that are the most challenging and time-consuming to digest.

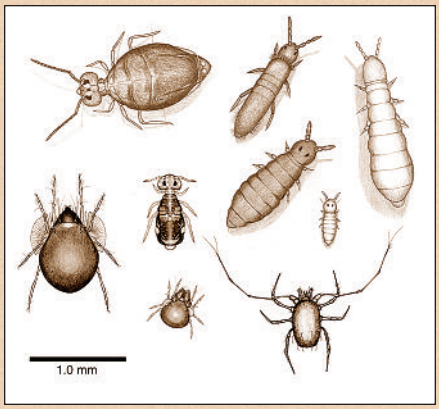
Cellulose makes up about half the dry mass of each fallen leaf, with hemicellulose contributing anywhere from 10-30 percent and lignin from 5-30 percent. Microbes that digest the leaf's cell walls clearly have the most raw materials to recycle.

Bacteria tend to be specialists at digesting plant molecules; individual bacteria usually secrete an enzyme that breaks down only one component of the multi-component plant cell walls. Different groups of bacteria usually work together in dividing the labor of digesting the tough cell walls.

Fungi are multi-talented at recycling these complex molecules. Each fungal cell can simultaneously secrete a battery of enzymes that digests the entire plant cell wall with its complex of cellulose, hemicellulose and lignin.

Two main groups of fungi are recognized for their abilities to digest cell walls. White rot fungi can eventually digest all the fibers of leaves by first transforming them to bleached fibers and finally completely degrading fallen leaves to carbon dioxide, water and minerals. Brown rot fungi leave a brown, but soil-enriching, residue of lignin that still persists even after all their enzymes have been deployed.

The leaf litter of a forest is infiltrated with miles of fungal filaments or hyphae. These hyphae take on a diversity of forms (morphs), demonstrating that metamorphosis (*meta* = change; *morph* = form; *-sis* = process of) is not just for insects, frogs and some other animals.



Fungi can be very specific in their recycling duties. *Marasmius delectans* mushrooms appear only on fallen leaves. Six-legged springtails (top) and three mites, each with eight legs (bottom) are by far the most abundant arthropod recyclers of leaf litter.

Many species of fungi recycle leaves and wood, including the wood-decomposer (left) known as *Hericium coralloides*. Some species of fungi produce special filaments (above) to trap and digest nitrogen-rich nematodes of the leaf litter.

Many filaments form mushrooms for sexual reproduction (teleomorphs; *teleo* = complete; *morph* = form) when the environmental conditions are right, but some do not leave their home under the cover of fallen leaves. Instead the individual filaments adopt a vast array of beautiful forms called conidiophores (*conidia* = "little dust" or spores; *phore* = to carry) that reproduce spores (conidiospores) without sex (anamorphs; *ana* = without; *morph* = form). Other fungal filaments aggregate to form bundles of many parallel filaments called rhizomorphs (*rhizo* = root; *morph* = form). These rhizomorphs form striking patterns as they radiate and intertwine over decaying leaves, twigs and logs.

Fungi are constantly assuming these three different forms and expressing their different talents. Even fungi that recycle fallen leaves by feeding on cellulose and lignin sometimes need the extra nitrogen (protein) that a meatier diet provides and will transform not only their diets but also their shapes. In their anamorph forms, filaments can secrete enzymes that digest leaf tissue, or they can be modified into nooses or adhesive nets or knobs that trap the nematodes that are so abundant in leaf litter.

Not all mushrooms of the forest floor assume forms that are involved in recycling of leaves. Their nutrition derives from an entirely different source than dead leaves. These other fungi join forces with the roots of trees and smaller plants of the forest to form mycorrhizae partnerships (*myco* = fungus; *rhizae* = roots) where the fungal partner passes mineral nutrients on to plant roots in exchange for sugars manufactured by the plants. Many of these fungi form the colorful mushrooms of late summer and autumn woods.

Although the miles of crisscrossing filaments that these fungi extend through the forest soil and around the many fine roots of trees extract minerals for the nourishment of their host trees, they are completely incapable of recycling the lignin and cellulose of fallen leaves and extracting nutrition from dead leaves. When not associated with tree roots, these fungi and their mushrooms do not survive for long in forest soils.

By the time the decaying leaf has been digested by enzymes released by bacteria and fungi and passed through the jaws and digestive tracts of numerous invertebrates, what remains is the hard-to-digest remnants of the leaf such as resins, waxes and lignins. Along with remnants of fungi and bacteria that have passed through the digestive tracts of the invertebrates and end up in their droppings, these items enrich the forest soil by contributing to the formation of humus.

Humus is the matter in soil that holds nutrient elements and water where they are accessible to plant roots and where they can nourish many future crops of leaves. Humus persists in the soil for many years, guaranteeing a slow and steady release of nutrients in the forest soil.

Thanks to the tireless services of the innumerable recyclers, the soil of the forest is now all the richer for the decay of its fallen leaves.

Saprophytic fungi such as these *Psathyrella* mushrooms recycle the remains of organic material including leaves, sticks and logs.

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