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REVIEWS

Opinion

On the Three Major Recycling Pathways in Terrestrial Ecosystems

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Plants are the largest biomass component of most terrestrial ecosystems, and litter decomposition is considered the dominant process by which nutrients return to plants. We show that in terrestrial ecosystems, there are three major pathways by which plant biomass is degraded into forms that release nutrients again available to plants: microbial decomposition; vertebrate herbivory; and wildfires. These processes act at different spatial and temporal scales, have different niches, and generates different ecological and evolutionary feedbacks. This holistic view in which microbes, herbivores, and wildfires play a joint role in the functioning of ecosystems contributes to a better understanding of the diversity of mechanisms regulating the biosphere.

Highlights

There are three major ways to recycle organic matter and nutrients in terrestrial ecosystems: microbial decomposition; vertebrate herbivory; and wildfires.

Each has different requirements, acts at different spatial scales, and occupies different (although overlapping) environmental niches.

The three recycling pathways generate different feedbacks and contribute to the ecology and evolution of plants, and to global biogeochemical cycles.

Plant Biomass

Plants dominate the Earth, at least in terms of biomass [1], and to keep this dominance plants continually absorb nutrients from the soil and CO_2 from the atmosphere. However, soils remain fertile and the atmosphere is not depleted of CO_2. This is because plant biomass is also continually degraded through the mineralisation of organic matter into inorganic compounds available again to plants (terrestrial carbon and nutrient cycling). Litter decomposition has been considered the dominant process generating this degradation [2]. Here, we argue that in terrestrial ecosystems, there are three major pathways by which the organic matter and nutrients in the plant biomass are made again available to plants: microbial decomposition; vertebrate herbivory; and wildfires (Figure 1). Each of these three processes has different requirements and acts at different spatial and temporal scales (Table 1). The three processes have been described independently elsewhere, and recent studies have linked fire with decomposition [3] or herbivory [4], with emphasis on leaf traits (flammability, decomposability, and palatability). Here, we aim to widen these views and suggest a unified framework that integrates the three major recycling pathways that drive the structure and biogeochemistry of terrestrial ecosystems (Figure 1), considering feedbacks and evolutionary implications.

Microbes, Herbivores, and Wildfires

Microbial decomposition (including decay fungi that may produce macroscopic structures) is a slow and efficient soil process that transforms organic matter into CO_2 and makes nutrients again available for plants. This process acts on dead above- and below-ground biomass (litter and roots), and most nutrients are returned to the soil near the original plant (local scale process). It is a well-known process, dominant in forest and moist environments, and has been reviewed elsewhere [2,5–7] including in major ecology textbooks. On an evolutionary timescale, microbial decomposition likely peaked in the Eocene, when the climate was warm and relatively wet, and forests were dominant (dinosaurs were already extinct and mammals were still small). Microbial decomposition is also promoted by termites, earthworms, and other invertebrates [8,9] without changing the spatial scale of the process and the type of biomass decomposed. Thus, the invertebrate contribution to decomposition is included as part of the microbial cycles.

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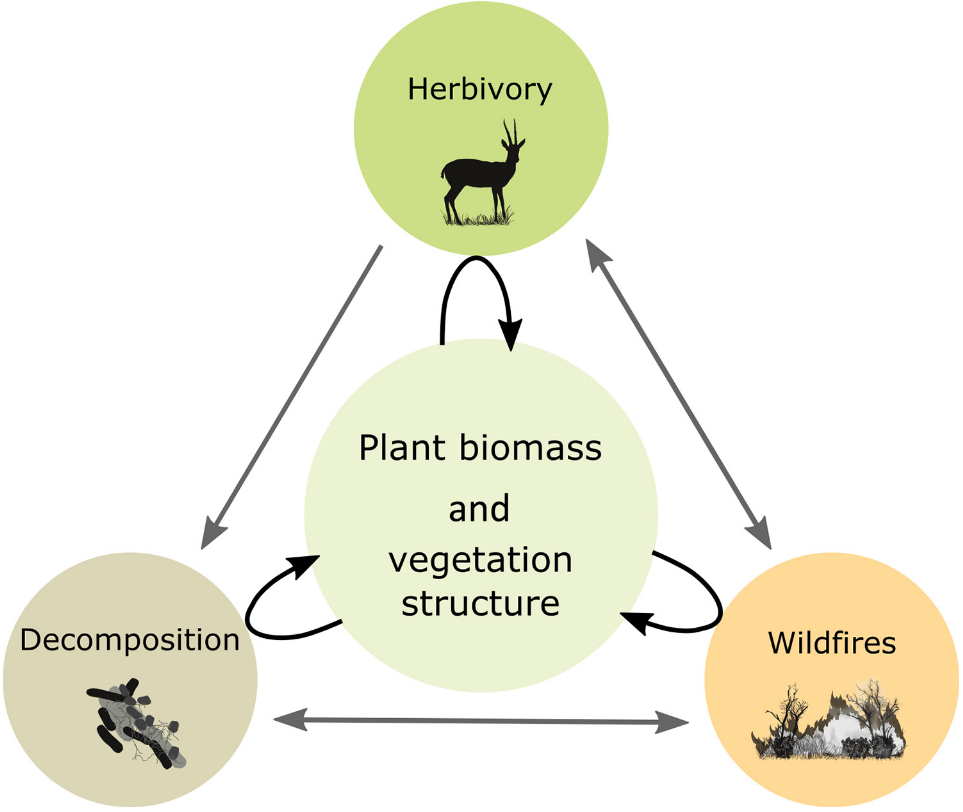

Figure 1. Plant Biomass and Vegetation Structure in Terrestrial Ecosystems is Determined by Three Feedback Processes: Vertebrate Herbivory, Microbial Decomposition, and Wildfires. These three processes also interact with each other (thin straight lines). All these interactions are negative (competition for biomass), but positive interactions also exist. Illustration by Dharmaberen Studio (www.dharmaberen.com).

Herbivory by vertebrates also makes a major contribution to regulating plant biomass and carbon and nutrient cycling [10,11]. Unlike soil microbial decomposition, vertebrate herbivory acts primarily on aboveground green biomass, and the C emission is often in the form of methane, especially by ruminants. Vertebrate herbivores are highly mobile plant consumers, and by harbouring microbes in their guts (i.e., rumen-associated Archaea), they spatially distribute organic matter and nutrients across the landscape [12,13]. In the case of migratory herbivores, the spatial scale of the redistribution can be large (10^2–10^4 m). Herbivory is an old ecological process [14,15] and there have been significant numbers of large herbivores at least since the Middle Jurassic (180 Ma) and the Cretaceous (145–66 Ma; when the largest ever terrestrial herbivores, the sauropods, roamed the planet [16]).

The third process is wildfire [17–19]. Fires can consume any aboveground plant biomass (green and dead), and transform it into forms available to plants. This pyromineralisation is directly produced by ash inputs or through heat (thermal mineralisation [18]). Some of these breakdown products remain at the site or nearby (ashes), including very recalcitrant (poorly decomposable) forms that act as soil C sink (pyrogenic C [20]), while other forms move far from the site during the fire (via smoke), or afterwards with rain (runoff). Consequently, wildfires can redistribute nutrients on very large spatial scales (Table 1), making a great contribution to global biogeochemical cycles. For instance, African savannas supply nutrients to adjacent forests [21,22] but they can

Table 1. Main Characteristics of Three Major Routes for Breaking-Down of Organic Matter into Simple Inorganic Compounds and Nutrients. These characteristics define the niche of each process.

	Vertebrate herbivory	Microbial decomposition	Wildfires
Conditions			
Climate optima	Dry, temperate	Moist	With a dry season
Soil preferences	Nutrient rich	Moist	Nutrient poor
Vegetation types	Open	Closed	Open
Requirements			
Type of biomass	Aboveground plant	Above and belowground plant; animal	Aboveground plant
Plant biomass consumed	Green and fleshy	Dead (litter, roots)	Dead and green
Relevant plant attributes	Leaf quality (palatability)	Litter quality	Biomass structure, flammability
Biomass C/N, Lignin/N	Low	Low	High
Biomass continuity	Temporal continuity	Contact with soil	Spatial continuity
Additional requirement	Water	Defaunation	Ignitions
C and nutrient cycling			
CO_2 emission	Low	High	High
Methane emission	High	Low (e.g., termites)	Low (e.g., peat fires)
Recycling rate	Intermediate/fast	Slow	Fast, episodic
Spatial scale (m)	10^2–10^4	$<10^2$	$>10^4$
Seasonality (nutrient turnover)	Low	Low	High
Consequences			
Vegetation feedback	Yes, palatability (grasses)	Yes, plant–soil	Yes, flammability
For the ecosystem	Maintain open habitats	Maintain local fertility	Generate and maintain open habitats
Plant response traits (adaptations)	Plant structural and chemical defences, trample resistance (grasses)	Decomposability	Flammability, lignotubers, seed dormancy, thick bark, etc.
Interactions			
Regulated by	Predators, pathogens	Moisture, temperature, soil	Topographic barriers, ignitions, humans
Regime factors	Density, size, gut type, sociability	Climate	Intensity, frequency, size, season
Sensitivity to climate change	Low	Intermediate	High
History			
Evolutionary origin (Ma)	300 Ma (Synapsids)	400 Ma (arbuscular mycorrhiza fungi)	400 Ma
Peaks	Mesozoic (dinosaurs), Pleistocene (mammals)	Eocene (warm, moist, forests)	Carboniferous, Permian, Cretaceous
Sources of variability	Ruminant, nonruminant; grazers, browsers	Ectomycorrhiza, arbuscular mycorrhiza, root diameter	Grass-, litter-, woody-fuelled

also supply up to a half of the P deposited annually in the Amazon basin [23]. The specific biogeochemical effect of a fire varies greatly with climate, vegetation type, postfire weather, and especially with fire characteristics (mainly intensity), but at the local scale, fires tend to increase soil cations and decrease N [19,24]. In addition, wildfires also contribute to rock weathering [25] and thus influence the input of nutrients into ecosystems. In contrast to microbial decomposition and herbivory, wildfires consume biomass quickly and episodically. During the fire-free interval, biomass in fire-prone ecosystems builds up, as decomposition and herbivory is unable to cope with productivity. Most wildfires do not produce as much methane as herbivory [26]. Peat fires are an exception and may produce large amounts of methane and other organic compounds [27]. Wildfires are an ancient process (from ~420 Ma), older than vertebrate herbivory, appearing soon after plants colonised the land in the Silurian, and gaining importance with the increase in plant complexity and vegetation density and, especially, during the high atmospheric O_2 peaks [28]. Wildfires have also been suggested as a key factor stabilising oxygen levels during the past 370 million years [29].

Niche Partitioning

All three processes can occur in a given ecosystem (competing for the same resource, biomass), but the relative importance of each varies with the micro- and macro-environmental conditions (Figures 2 and 3, Table 1). For instance, wildfires are prevalent at intermediate levels of productivity [30] where climates are seasonal (with a period of high productivity that builds up fuels, followed by a dry period that makes those fuels flammable), and especially in poor soils [31]. They require regular ignitions and spatial continuity of vegetation [31]. Vertebrate herbivory is important in climates with low rainfall seasonality and fertile soils (to maintain animal populations, although animal migration may, to some extent, buffer some of these requirement [32]). Herbivore activity is naturally modulated by predators and parasites, and currently by human activities. Microbial decomposition is dominant where wildfires are limited (e.g., too moist), or in areas with few herbivores (e.g., because of the Pleistocene defaunation); decomposition requires some moisture (which also reduces flammability), and thus this pathway dominates in many temperate forests [33]. In savannas and dry environments, where such conditions are scarce, microbial decomposition of the aboveground biomass may be helped by photodegradation, and especially by termites and (fungal farming) ants which digest organic matter in their guts [8].

The importance of fire and herbivory as key ecological factors has been traditionally underestimated [34]; however, the fact that in many environments they can maintain open ecosystems in places that can potentially support forests [35,36] suggests that in those conditions, fire or herbivores routinely cause greater loss of plant biomass than decomposition. For instance,

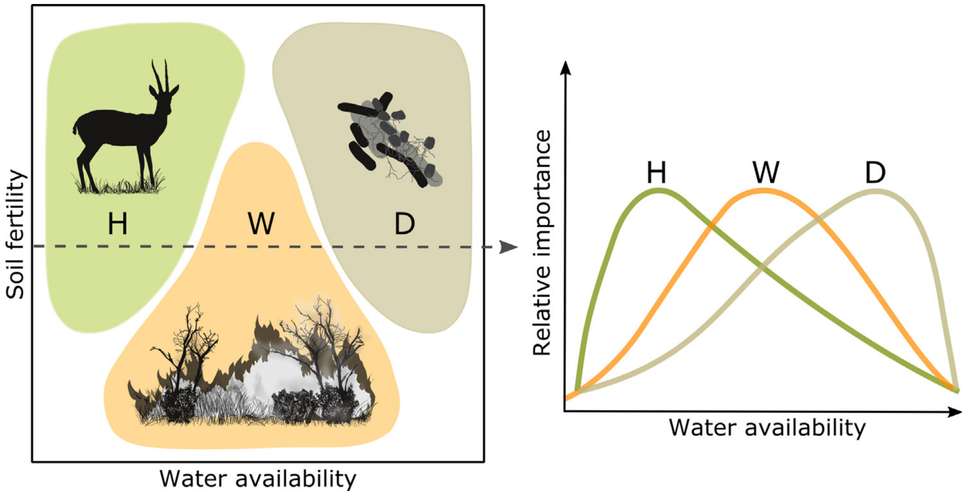

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Figure 2. Relative Importance of Each of the Three Ecosystem Pathways (H: Vertebrate Herbivory; W: Wildfires; D: Microbial Decomposition) in the Environmental Space (Niche) Defined by the Water Availability and Soil Fertility. Note that at the intermediate levels of water availability, rainfall is typically seasonal, Illustration by Dharmaberen Studio (www.dharmaberen.com).

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Figure 3. Examples of Microbe-driven (Top), Fire-driven (Middle), and Herbivory-driven (Bottom) Ecosystem in Tropical (Left) and Extratropical (Right) Environments. Understory of a rainforest (A; Peruvian Amazon) and beech forest (B; NE Spain), with high humidity and no grasses, where litter is easily decomposed. View of a South American savanna (C; Central Brazil) dominated by flammable grasses and thick-barked trees. Frequently burned pine woodland (D, *Pinus palustris*, North Carolina) that has a flammable grassy and litter understorey showing fire-resistant pine saplings. Warthog (*Phacochoerus africanus*) grazing an African short-grass savanna (E, Kruger National Park, South Africa), and vicunas (*Vicugna vicugna*) grazing in arid grasslands (F, Atacama, Chile). Photos by J.G. Pausas (A, C), J. Garcia-Pausas (B, F), and W. Bond (D, E).

in tropical Australia, average annual burnt area is about 25% of the net primary productivity, with regions where this proportion approach 100% [37]. If fires are excluded, decomposition does not make such consumption, but biomass builds up and generates a new vegetation state [35]. Only when this new state becomes fire or herbivory proof (closed forests) is when decomposition become dominant.

Given the different requirements and conditions among the three pathways, we can classify the world's ecosystems following the dominant process of aboveground biomass degradation: herbivore-driven, microbe-driven, and fire-driven ecosystems. These types are linked to the brown, green, and black worlds (respectively) proposed for describing the drivers of vegetation structure [38]. We focus on these three main processes as they should account for most of the variability in structuring communities and in biogeochemical cycles (Table 1); however, we recognise some variability within each process with some biogeochemical consequences. For instance, in herbivory-driven ecosystems, ruminants emit more methane than nonruminants do [32]; in fire-driven ecosystems, different fire regimes (e.g., surface vs. crown-fire regimes) generate contrasted patterns of biomass turnover (and CO_2 emission) [20,31]; and in microbe-driven ecosystems, different microbe types (e.g., ectomycorrhizae, arbuscular mycorrhizae, and N_2-fixing bacteria) have different niches [33].

Despite these differences among the three processes (Table 1), they also overlap in the environmental space (Figure 2). This is because the three processes partially target different biomass components (e.g., belowground biomass is mostly degraded by decomposition in any environment; Table 1), but also because there are some positive interactions. For instance, wildfires generate open spaces and, in savannas and steppes, maintain a fresh grass layer for herbivores, while postfire conditions (high pH, light, and temperature) temporarily increase microbial activity and mineralisation rates [39]; browsers can kill trees, fuelling microbial decomposition, but they can also maintain flammable fuel beds for fires to spread; and herbivores can promote microbial decomposition from faeces, and stimulate root exudation of carbon and microbial activity [40]. However, further work is needed to fully understand and quantify interactions between these three processes at a global scale.

Feedbacks and Evolutionary Implications

Wildfires and herbivory are two powerful biomass consumers [32,34,36,41]; they generate feedback processes that maintain vegetation at states of lower biomass than would be expected from the physical environmental conditions (alternative vegetation states [35]). This lower biomass vegetation is more flammable or more palatable and thus feeds back into maintaining the consumer. Wildfires and herbivory not only generate these ecological feedbacks that maintain open ecosystems, but also select for light-loving species with a set of adaptive traits to persist under these consumers [36]. That is, plant consumers have a clear evolutionary role in fire-prone and grassy environments. Thus, there are plant traits strongly associated with fire (e.g., thick bark, serotiny, epicormic resprouting, lignotubers, postfire flowering, and flammability [31,42–44]), and others strongly associated with herbivory (e.g., spines, toxicity, and low palatability in woody plants; basal resprouting and trample resistance in grasses; [15,45]), reflecting their contrasted niche. That is, both herbivory and fire can influence the mix and attributes of plant species, while the mix and attributes of plants also influence the fire and grazing regimes. This feedback makes fire and herbivory distinct from other physical disturbances such as cyclones, landslides, avalanches, volcanoes, or floods, where plants may respond – but the disturbance will not change in response to these plant responses. Although less studied, there are also animal traits associated with fire and herbivory [46,47].

Decomposability traits are different from flammability traits, including at the leaf level [3,48,49] which is where decomposition could mostly interact with fire (e.g., contrasted N and lignin concentration; Table 1); decompositions also acts in roots. In contrast, leaf decomposability and palatability share some similarities, as highly palatable plants are more attractive to both herbivores and microbes [50]; however, the former acts on green biomass and the latter on dead biomass, and their dominance is in different environments (open vs. closed vegetation types; Table 1, Figures 2 and 3). Decomposability traits have been well studied and determine the rate of the plant–soil feedback loop

[3,5,51,52]; that is, plant species composition determines litter quality and decomposition rates (at least for the first stages of litter degradation) which feedback to nutrient availability and plant growth and vegetation composition. Thus, there is growing evidence of microbial-mediated coexistence in plants [53]. However, the evolutionary role of changing decomposition has been little explored [54,55], and is sometimes related to the evolution of novel root traits [56].

All three pathways have also been invoked to generate feedbacks that contribute to explain Darwin's 'abominable mystery', that is, the origin and expansion of angiosperms in the Cretaceous (from gymnosperm-dominated landscapes). Bakker [57] suggested that a swift and extensive change in feeding behaviour of herbivorous dinosaurs was one key event that opened opportunities for the rapid initial diversification of angiosperms. Bond and Scott [58] suggested that the high levels of O_2 and high climate seasonality in the Cretaceous, along with novel fast-growing plants, generated novel fire regimes and open conditions promoting the spread of angiosperms. Berendse and Scheffer [59] suggested that the higher growth rate of angiosperms promoted litter that more easily decomposes and so generates a positive feedback favouring angiosperms. Our framework suggests that all these processes are not mutually exclusive as they could have been occurring in the Cretaceous under different environments (Figure 2).

Alternative vegetation states [35] can be viewed as shifts between different dominant pathways. For instance, in forest–savanna mosaics [41,60,61] the biogeochemical cycles of forest (microbe-driven) are very different from those in savanna which can be dominated by fire-driven or herbivore-driven processes [32]. The increasing understanding of the abrupt loss of megaherbivores in the late Quaternary [62] suggests not only landscape and biodiversity shifts [63], but also a shift from herbivore-driven to microbe-driven ecosystems in many temperate landscapes [64], as well as to fire-driven ecosystems in seasonally dry landscapes such as Australia [65]. The biogeochemical consequences of these shifts have been little explored. For instance, the recent reduction in the number of hippopotamuses that feed in grasslands in the watershed of the African Great Lakes has caused changes in nutrient cycling, with strong shifts of planktonic communities of the lakes [13]. Even stronger consequences may have occurred during past massive defaunation events. In fact, it has been suggested that before the Miocene expansion of C_4 grasses, silica was in short supply; afterwards, grazers accelerated the delivery of silica to water bodies, greatly facilitating diatom success [66]. The Miocene expansion of grasslands over forests enhanced both herbivory and wildfire activity, with huge biogeochemical consequences; but the change in the dominant life form (grasses over trees) implied a strong reduction of the chemical weathering by plants (and of the carbonate deposition on the seafloor) that contributed to stabilize atmospheric CO_2 levels [67].

Another abrupt shift in the biogeochemical cycles is likely to have occurred in the Carboniferous. The evolution by plants of the ability to synthesise tough lignin increased litter accumulation, leading to an increase in the atmospheric oxygen concentrations [66,68]. Oxygen concentration could have dropped later thanks to a peak of wildfires in an oxygen-rich environment [28,29], and to the evolution of enzymes to break down the lignin in decomposers [69].

Concluding Remarks

The three pathways occur in terrestrial ecosystems; however, the implications are not limited to those ecosystems as they affect watershed nutrient cycling by recirculating nutrients through water bodies [70] and to the ocean (losses from the land system). That is, the three pathways have and had implications for the whole Earth system [29,71,72]. Overall, we propose that the three processes provide important ecological feedbacks for understanding the ecology and evolution of our biosphere.

Outstanding Questions

What is the relative contribution of microbes, herbivores, and wildfires to global biogeochemical cycles (e.g., carbon cycle)?

Can we map the relative role of each pathway across the globe?

How has the importance of each pathway changed through evolutionary time and with what consequences? For example: how were biogeochemical cycles modified after the Cretaceous and the Pleistocene extinctions? Or after the Cenozoic rise of large mammals? Or after the evolution of lignin in the early Carboniferous (before the evolution of enzymes to break it down)? Or after the Miocene expansion of C_4 grasses and grazers? What are the indicators (proxies) to track those changes?

Could soil fertility differences among continents be partially explained by the different history of the three pathways (e.g., differential fire history or herbivore extinction rates)?

What is the relative contribution of insect outbreaks to the biogeochemical cycle of ecosystems? How do they modify those cycles?

What are the implications of anthropogenic shifts in the dominant pathway (e.g., due to fire and grazing regime changes) in broad scales (e.g., landscapes, watersheds)?

How will climate change alter the geography and relative contribution of the three pathways and their feedback processes? and with what ecological consequences?

Our framework opens up a global research agenda to quantify and map the relative role of each process in biochemical cycles across the world and through evolutionary history (see Outstanding Questions). It should also help focus on key processes when modelling the dynamics of our biosphere. The dominant paradigm of soil decomposition as the key degradative factor of biomass may be due to the fact that it acts at small scale (the scale of most traditional research), but also, because mainstream ecology emerged in temperate environments [34] where high water availability, relatively fertile soils, and Pleistocene defaunation, makes this process the most prominent (Figure 2). However, in recent years, new technologies (such as advances in geospatial information, phylogenetic techniques, and palaeoecology) enable us to better understand herbivory and wildfires at large spatial and temporal scales, and thus ascertain their key role in maintaining the structure, dynamics, and nutrient cycling of many extant and extinct ecosystems worldwide [13,34–36,60,61,73].

By setting microbial activity, herbivory, and wildfires in a unified framework, we hope to promote bringing together ecosystem ecology and disturbance ecology. We propose that plant consumers (herbivory and fire) play (and have played) a fundamental role in the Earth's system. By reducing biomass, they not only delay competition and allow the growth of a diversity of organisms [74], but they also play a major role in biogeochemical cycles. How these cycles have changed over evolutionary time, and how are currently changing in a globally changing world, requires the integration of all the different recycling pathways at large spatial and temporal scales (see Outstanding Questions). By embracing a more holistic view in which microbes, herbivores, and fires play a joint role in the functioning of the Earth system, ecology is contributing to a better understanding of the niche construction of life.

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