Clarifying terrestrial recycling pathways

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~~In their recent paper, ~~Pausas and Bond (2020) [1] argue that there are three major pathways by which the carbon and nutrients assimilated by plants are recycled through ecosystems: microbial decomposition, vertebrate herbivory, and wildfires. This framework ~~is governed by~~has three principles. First, that each pathway recycles nutrients into~~degrades nutrients and biomass from plant-unavailable to~~ plant-available forms. Second, that each pathway is broadly equivalent in that they consume “biomass”~~, but that herbivory and decomposition focus on green and dead matter, respectively~~. Third, that the dominance of each pathway varies under different ~~sets of micro- and macro-~~environmental conditions~~, largely related to water availability and soil fertility~~. We welcome the reframing of terrestrial recycling pathways in this way, but have identified three ~~key ~~areas where the “Three Pathways Framework” could be built upon:

1. Herbivory and decomposition are part of the same biotic degradation pathway

A strength of Pausas and Bond’s framework is to highlight the importance of herbivory and fire, as well as litter decomposition~~, as processes by which the carbon and nutrients in plant biomass are recycled to again be made available to plants~~. We agree: litter decomposition is not ~~necessarily ~~the dominant recycling pathway in all habitats. However, we suggest that ~~rather than considering ~~decomposition and herbivory ~~as separate components in this model, they ~~should be treated as different stages of ~~one ~~a single biotic degradation pathway ~~through which biomass can be recycled in terrestrial ecosystems ~~(Fig. 1). This is because herbivory is only a part of the recycling process and, along with mortality, results in dead organic material that is not yet accessible by plants. ~~In order for herbivore-derived carbon and nutrients to be made available for plant uptake in an inorganic form, animal waste~~This material (i.e. excreta and carrion, with the exception of urine) requires a further step: decomposition (Fig. 1) [2,3]. It is well-recognised that the flow of resources from herbivores back to plants must first pass through the brown food-web [4]. ~~Therefore, w~~We propose that merging the herbivory and decomposition pathways will allow the framework to more accurately describe the principle mechanisms that regulate the biosphere. Furthermore, ~~using ~~this modificationed~~ framework, we~~ promotes the investigation of how rates of nutrient recycling are mediated by passage through the green and brown food-webs.

2. Inclusion of invertebrates facilitates the distinction of ecological scales and niches

Globally, terrestrial invertebrate biomass outweighs wild vertebrate biomass 44 times [5], yet Pausas and Bond do not consider invertebrates as important mediators of recycling within their framework. This is a fundamental oversight. ~~Evidence as to the ecological importance of invertebrates is mounting. For example, ~~In tropical systems, where the majority of the Earth’s plant biomass is concentrated [6], invertebrates can decompose at least half of dead plant material [7], and~~. Invertebrates also~~ typically operate at larger spatial and faster temporal scales than microbial decomposers [7,8]. Further, invertebrate herbivores ~~are major consumers of live plant matter. Insects~~ can consume comparable quantities of living biomass to vertebrates in savanna systems [9]; remove up to 19% of foliar production in tropical rainforest [10]; and have far reaching effects on C and N cycling across forests globally [11]. The importance of invertebrates strengthens the core, novel ideas presented by Pausas and Bond: that the degradation agents and pathways operate over different spatiotemporal scales and occupy different "niches" [1]. ~~However, w~~We suggest that the components of the biotic degradation pathways should each be split into two discrete branches: vertebrate and invertebrate mediated herbivory, and microbial and invertebrate decomposition (Fig. 1). This modification allows the different scales [7,8] and ~~abiotic~~ niches (e.g. ectothermy vs endothermy) of invertebrates, vertebrates and microbes to be captured~~ by the recycling framework. This facilitates a more precise understanding of the flow of carbon and nutrients through ecosystems.~~ Using this updated framework, we propose that future research should focus on illuminating the different temporal and spatial scales under which different degradation agents operate and the consequences that this has for plant performance and community processes.

3. Using temperature and water availability to define the niche

Pausas and Bond suggest soil fertility as an environmental factor that determines the relative dominance of ~~herbivory and other~~ recycling pathways in their framework. However, in this context, soil fertility is circular. It is dependent not only on underlying geology, but on feedbacks between soil biotic communities, vegetation composition and aboveground herbivores [12]. ~~Attempting to describe the relative importance of herbivory and decomposition for nutrient cycling in contrasting biomes based on an attribute (soil fertility) that is itself mediated by herbivory and decomposition is circular.~~ We agree ~~with Pausas and Bond~~ that abiotic gradients are important determinants of ~~the biogeography of life on Earth~~biogeographic patterns. However, we suggest temperature as an alternative to soil fertility because it is not dependent on herbivory and decomposition rates and has direct impacts on the distribution, activity, and metabolic rate of organisms. Consequently, the niches of the degradation agents and ecosystem-level patterns in recycling pathways, will be better captured by temperature than soil fertility.

Research directions

While we have criticised aspects of Pausas and Bond's proposed framework, we recognise the value of their holistic approach toward characterising the~~ global~~ biogeography of differing ~~pathways of nutrient~~ recycling pathways. We suggest that applying these ideas to more accurate and representative recycling flow diagrams that are built upon the large existing body of literature exploring these themes (e.g. Fig. 1) [2,4,10,12] is a productive way forward. Further, to be truly holistic, no ecological framework can omit invertebrates. Finally, rather than contrasting wildfire, herbivory, and decomposition, it would be more useful to focus on the relative dominance of the different agents of recycling that are acting on the same type of material. For example, in a given ecosystem, how much live plant matter ~~, in kg ha^{-1} yr^{-1},~~ is consumed separately by vertebrate and invertebrate herbivores? How much dead plant material is decomposed separately by invertebrate and microbial decomposers? Only with these data can we understand the changing dominance of different mediators of carbon and nutrient recycling across biogeography. Experimental approaches both within and across biomes will be needed to determine these numbers (e.g. [7,9]), together with the abandonment of the traditional taxonomic and geographic silos in which many researchers operate. This ecosystem-level, experimental macroecological approach will allow us to map the changing dominance of different recycling agents across space and time. ~~Only then will we be able to assess the full ecological and evolutionary consequences of these complex recycling networks.~~

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Figure 1. *A conceptual diagram of the major pathways through which plant material is degraded and recycled through terrestrial ecosystems. Live plant biomass can be degraded into inorganic nutrients through the herbivory-decomposition pathway (green and brown arrows) or through the fire pathway (orange arrows). This framework builds upon Pausas and Bond's original figure 1 by (1) highlighting that herbivory and decomposition are not separate, but different stages in one biotic recycling pathway; (2) including invertebrate herbivores and decomposers as agents of recycling; and (3) explicitly differentiating between live and dead biomass. We propose that in order to determine the ecological and evolutionary consequences of these recycling networks, research efforts should focus on quantifying the relative contribution that each agent of recycling makes to a pathway (thick downward arrows) within a given ecosystem. For context, we include the flows of inorganic matter back into plant biomass and atmospheric pools (dashed upward arrows).*