Clarifying Terrestrial Recycling Pathways

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Pausas and Bond [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 has three principles. First, that each pathway recycles nutrients into plant-available forms. Second, that each pathway is broadly equivalent in that they consume 'biomass'. Third, that the dominance of each pathway varies under different environmental conditions. We welcome the reframing of terrestrial recycling pathways in this way, but have identified three areas where the 'Three Pathways Framework' could be built upon:

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 plant biomass is recycled. However, we suggest that decomposition and herbivory should be treated as different stages of a single biotic degradation pathway (Figure 1), rather than separate processes. 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 material (i.e., excreta and carrion, with the exception of urine) to be available again for plant uptake, it requires a further step: decomposition (Figure 1) [2, 3.]. It is well-recognised that the flow of resources from animals back to plants must first pass through the brown food-web [4]. 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, this modification promotes the investigation of how rates of nutrient recycling are mediated by passage through the green and brown food-webs.

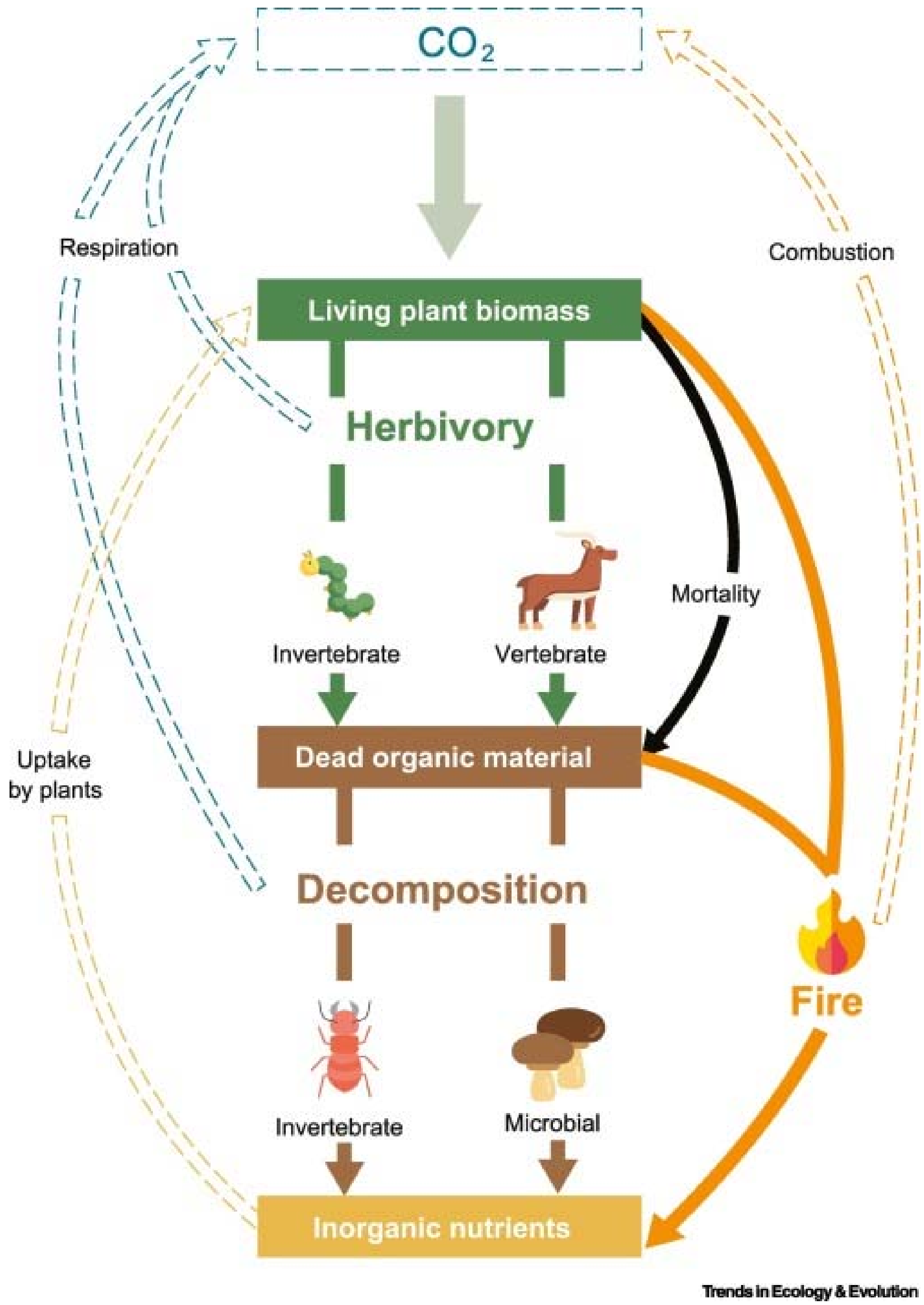

Figure 1. A Conceptual Diagram of the Major Pathways through Which Plant Material Is Degraded and Recycled through Terrestrial Ecosystems.

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. 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 typically operate at larger spatial and faster temporal scales than microbial decomposers [7, 8.]. Further, invertebrate herbivores 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 carbon and nitrogen cycling across forests globally. [11.] Acknowledging the importance of invertebrates strengthens the core ideas presented by Pausas and Bond: that the degradation agents and pathways operate over different spatiotemporal scales and occupy different 'niches' [1]. 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 (Figure 1). This modification allows the different scales [7, 8] and niches (e.g., ectothermy vs. endothermy) of invertebrates, vertebrates, and microbes to be captured. Using this updated framework, we propose that future research should focus on interrogating the spatiotemporal scales under which different degradation agents operate and the resultant consequences for plant performance and community processes.

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 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 above-ground herbivores [12]. We agree that abiotic gradients are important determinants of 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 biogeography of differing recycling pathways. We suggest that applying these ideas to more accurate and representative recycling conceptual models that are built upon the large body of literature exploring these themes (e.g., Figure 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 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.

References

1. Pausas, J.G. and Bond, W.J. (2020) On the three major recycling pathways in terrestrial ecosystems. Trends Ecol. Evol. 35, 767–775

2. Barton, P.S. et al. (2019) Towards quantifying carrion biomass in ecosystems. Trends Ecol. Evol. 34, 950–961
3. van Klink, R. et al. (2020) Rewilding with large herbivores: positive direct and delayed effects of carrion on plant and arthropod communities. PLoS One 22, 1–17
4. Swift, M.J. et al. (1979) Decomposition in Terrestrial Ecosystems, University of California Press
5. Bar-On, Y.M. et al. (2018) The biomass distribution on Earth. Proc. Natl. Acad. Sci. U. S. A. 115, 6506–6511
6. Crowther, T.W. et al. (2019) The global soil community and its influence on biogeochemistry. Science 365, 1–10
7. Griffiths, H.M. et al. (2019) Termites can decompose more than half of deadwood in tropical rainforest. Curr. Biol. 29, 118–119
8. Veldhuis, M.P. et al. (2017) Termites promote resistance of decomposition to spatiotemporal variability in rainfall. Ecology 98, 467–477
9. Davies, A.B. et al. (2016) Seasonal variation in the relative dominance of herbivore guilds in an African savanna. Ecology 97, 1618–1624
10. Metcalfe, D.B. et al. (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. Ecol. Lett. 17, 324–332
11. Kristensen, J. et al. (2019) Below-ground responses to insect herbivory in ecosystems with woody plant canopies: a meta-analysis. J. Ecol. 108, 917–930
12. Veldhuis, M.P. et al. (2018) Ecological autocatalysis: a central principle in ecosystem organization? Ecol. Monogr. 88, 304–319