## Linking Population Processes and Ecosystem Processes Through Changes in Plant Chemistry

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It's refreshing to watch the ongoing synthesis between population-level processes and ecosystem-level processes that is taking place in the ecological literature. After decades during which the two fields developed without adequate interaction, population ecology and ecosystem ecology are coming back together. And we shouldn't be surprised; ecosystem ecology emerged in large part from studies of successional processes (Gleason 1926, Clements 1936), and Tansley (1935) was explicit in pointing out that ecosystems exist as interactions between organisms and the abiotic environment.

Our ability to use these two bodies of theory to inform each other will only be as good as our mechanistic understanding of the links between them. One among many ecological links between populations and ecosystems occurs through the chemical structure of plant material. Plant chemistry responds to population level processes, such as trophic interactions, and mediates ecosystem processes, such as nutrient cycling. Plant chemistry is therefore a fundamental nexus that links trophic interactions with ecosystem processes.

Although many authors have contributed to our understanding of this nexus, there is one "paper trail" of published work that has substantially influenced my own thinking. It concerns specifically how chemical defense induction in plants influences the rate at which nutrients cycle in terrestrial systems.

The paper trail starts with the recognition that plants are not passive recipients of herbivore damage, but rather respond to herbivore and pathogen attack by inducing chemical defenses (Green and Ryan 1972). Defense induction often includes increases in classes of recalcitrant organic molecules (Schultz and Baldwin 1982) that can reduce herbivore fitness (Rossiter et al. 1988). Critically, these same recalcitrant molecules, such as tannins and lignin, were already known by ecosystem ecologists to resist decomposition by soil microbes (Meentemeyer 1978). In other words, herbivore attack could induce changes in foliar chemistry that could slow the rate of litter decomposition (Findlay et al. 1996).

It turns out that the chemical traits that make plants less palatable to herbivores are often the same chemical traits that reduce rates of litter decomposition (Cornelissen et al. 1999). Because we now recognize the fundamental role that litter chemistry plays in decomposition and nutrient dynamics across diverse biomes (Cornwell et al. 2008), we have grown to appreciate the importance of "afterlife" effects of induced chemical defenses on ecosystem processes (Chapman et al. 2006).

This paper trail illustrates how a population-level process (herbivory on individual plants) can mediate an ecosystem process (decomposition and nutrient cycling in soil). Given that herbivore

populations are influenced in part by interactions with their natural enemies (Ripple et al. 2014), it should be no surprise to find fundamental links between the population ecology of predators and the dynamics of ecosystems (Strickland et al. 2013). Of course, variation in nutrient dynamics in ecosystems can then "cascade back up" to influence the ecology of herbivores and their enemies. But that's a paper trail for another day.

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