



Insects as drivers of ecosystem processes

Louie H Yang¹ and Claudio Gratton²

Insects and other small invertebrates are ubiquitous components of all terrestrial and freshwater food webs, but their cumulative biomass is small relative to plants and microbes. As a result, it is often assumed that these animals make relatively minor contributions to ecosystem processes. Despite their small sizes and cumulative biomass, we suggest that these animals may commonly have important effects on carbon and nutrient cycling by modulating the quality and quantity of resources that enter the detrital food web, with consequences at the ecosystem level. These effects can occur through multiple pathways, including direct inputs of insect biomass, the transformation of detrital biomass, and the indirect effects of predators on herbivores and detritivores. In virtually all cases, the ecosystem effects of these pathways are ultimately mediated through interactions with plants and soil microbes. Merging our understanding of insect, plant and microbial ecology will offer a valuable way to better integrate community-level interactions with ecosystem processes.

Addresses

¹ Department of Entomology and Nematology, University of California, Davis, CA, United States

² Department of Entomology, University of Wisconsin, Madison, WI, United States

Corresponding author: Yang, Louie H (lyang@ucdavis.edu)

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Introduction

Insects are among the most diverse groups of organisms on earth [1], but the cumulative biomass of insect bodies is a relatively small component of the total biomass in most ecosystems [2,3]. As a result, the direct contribution of insect biomass to global carbon and nutrient cycling is dwarfed by the vastly greater size of plant and microbial contributions [4,5,6*]. This raises the question of whether insects and other small invertebrates are important drivers of key ecosystem processes, or whether they are merely incidental players tracking larger biogeochemical patterns controlled by plants and microbes.

While it is clear that some species can have ecosystem effects that are disproportional to their abundance or biomass (i.e., keystone species), insects and other small invertebrates are generally assumed to play a minor role in ecosystem processes at the global scale ([6], but see also [30]). However, we suggest that these animals may play an important role in several key processes that influence ecosystem cycling of C and nutrients, although these effects often occur via indirect pathways (Figure 1).

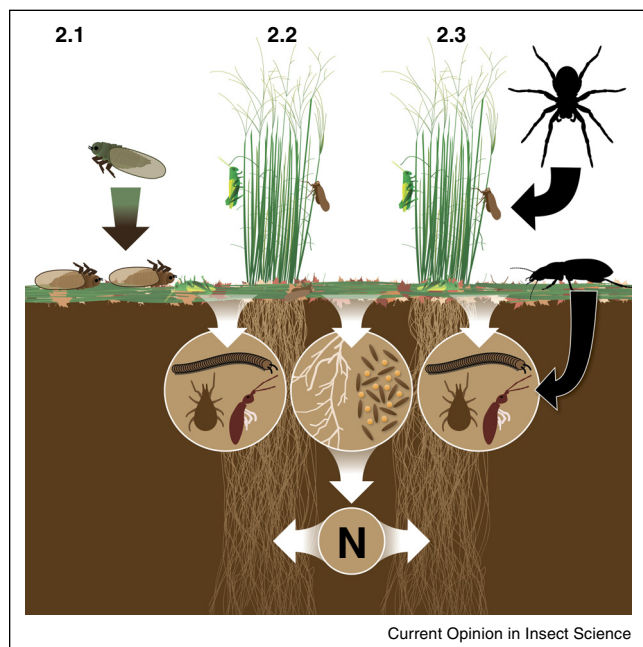
Insects and other small invertebrates as direct inputs to belowground systems

The cumulative biomass of insects is likely to represent a very small fraction of the total biomass in most systems. For example, Seastedt and Tate [2] estimated that the standing biomass of all live and dead arthropods represented only 1.0% and 5.2% of the biomass in the leaf litter layer of a temperate pine and hardwood forest, respectively. Similarly, Schowalter and Crossley [7] estimated that the cumulative biomass of forest canopy arthropods represented a very small contribution to the nutrient pools of standing litter biomass, even for calcium, potassium, and other elements that are present at higher concentrations in arthropod biomass compared to plant litter.

However, total insect biomass can represent an important direct contribution to ecosystem cycling in some systems. For example, the die-off of 13-year and 17-year periodical cicadas (*Magicicada* spp.) in North American forests can represent a significant input of insect biomass into the detrital pool of many North American forest ecosystems [8,9]. Cicada inputs can have significant direct and indirect effects on the belowground ecosystem, including increases in detritivore densities, soil bacteria and fungal abundances, nitrogen mineralization, plant uptake and growth, and subsequent herbivory on cicada-fertilized plants [9–11,12*].

Similarly, aquatic insect subsidies to land can affect terrestrial predators and scavengers [13–20] and alter food chain length [21]. For example, the extremely high productivity of chironomid midges at Lake Mývatn in northern Iceland, creates an aquatic-to-terrestrial subsidy of insect biomass that represents a subsidy of carbon, nitrogen and phosphorus into the surrounding terrestrial community with clear effects on terrestrial productivity [14,22]. Here, biomass input to the surrounding terrestrial ecosystem results in nitrogen deposition that is as much as threefold to fivefold greater ($11 \text{ kg N ha}^{-1} \text{ year}^{-1}$, Dreyer *et al.*, submitted for publication) than atmospheric deposition and fertilizes terrestrial vegetation [23]. The effects

Figure 1



Insects and small invertebrate arthropods can have various direct and indirect effects on ecosystem functioning through their modification of detrital pools in belowground systems. Direct inputs (section 2.1) of insects to the detrital (dead biomass) pool can introduce copious amounts of high quality (low C:N) biomass into belowground systems. Insects and arthropods can transform live and dead (section 2.2) biomass with both positive and negative effects on ecosystem rates such as C and N cycling. Arthropod predation of decomposers (section 2.3) can create trophic cascades that alter the size of the detrital pool and decomposition rates. In addition, risk of arthropod predation can alter the foraging behavior of insect herbivores such that plant communities and litter inputs to the soil are altered. This, in turn, can affect ecosystem rates such as C and N cycling. Ultimately, the size and quality of the detrital resource pool, both in terms of the stoichiometry of key elements (C:N:P) and secondary chemistry, are key determinants of microbial communities and activity in the soil. The ability of aboveground and soil-dwelling insects and arthropod activities to alter the composition of the detrital pool therefore has the capacity to modulate ecosystem processes through the effects on microbes.

of these subsidies may be more widespread than previously appreciated. Models suggest insect emergences are expected to be especially large and concentrated near large freshwater bodies (e.g., lakes and rivers, [24]), where aquatic insect inputs to land can be exceed terrestrial secondary production [25].

In both of these cases, the significant ecological effects of these insect biomass pulses likely reflect the magnitude of the input, the high quality and labile nature of insect biomass (i.e., low C:N ratio), and the timing of this input during a period of rapid plant growth and high nutrient demand. More generally, the rapid population growth and turnover rates of insect biomass suggest that their standing biomass may underestimate the importance of their

direct contributions to detrital pools. Although mass insect outbreaks have the potential to create local hot-spots of nutrient deposition through direct biomass inputs [9,16,26], a broader survey suggests that the ecosystem effects of insect outbreaks are likely to be highly context-dependent, with multiple interacting processes operating on different timescales [12,27]. Understanding the factors driving this context-dependence remains a key challenge for building a more general understanding of the direct effects of insect biomass deposition on ecosystem processes.

Herbivores, detritivores and social insects as biomass transformers

Herbivores transform plant inputs

Insect herbivores could potentially have large effects on ecosystem cycling by changing the quality, quantity, and timing of plant detrital inputs [28,29]. Herbivores have long been recognized as important drivers of ecosystem processes because of their direct transformation of living plant biomass into frass, greenfall, and throughfall [30,31]. The magnitude of these inputs can be substantial. Under outbreak conditions, these inputs may be comparable to the direct nutrient inputs of senesced plant litter [32]. Even under nonoutbreak conditions, insect herbivory may drive a significant fraction of aboveground to belowground N and P fluxes across entire ecosystems [33]. Insect herbivores often transform plant biomass in ways that increase the lability and mobility of nutrients [33,34–36]. However, herbivore-mediated inputs can also reduce soil nutrient availability in other systems, because of increased microbial immobilization [32] or the net export of mobile nutrients from the system, stemming from increased leaching or runoff [37,38].

Plant responses to insect herbivores may also indirectly change the quality or quantity of plant inputs to the soil [31]. In some systems, plant responses to insect herbivory increase the quality of plant litter, increasing plant litter decomposition and nutrient cycling relative to litter in the absence of herbivory (the ‘acceleration’ hypothesis, e.g., [39]), while herbivory has also been shown to reduce litter quality and slow decomposition in some cases (the ‘deceleration’ hypothesis, e.g., [39]). Insect herbivores can also change the quality or quantity of root exudates [30,40], with potentially complex indirect effects on community dynamics (e.g., [41]). These changes in the quality or quantity of root exudates belowground are analogous to changes in the quality or quantity of aboveground plant litter inputs, in the sense that the herbivore is transforming the nature of plant inputs to the ecosystem. For example, the introduction of biocontrol herbivores to suppress the invasive spotted knapweed (*Centaurea maculosa*) may actually increase the competitive ability of knapweed by inducing the increased production allelopathic root exudates which have a negative effect on

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