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Insects as drivers of ecosystem processes

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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.

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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

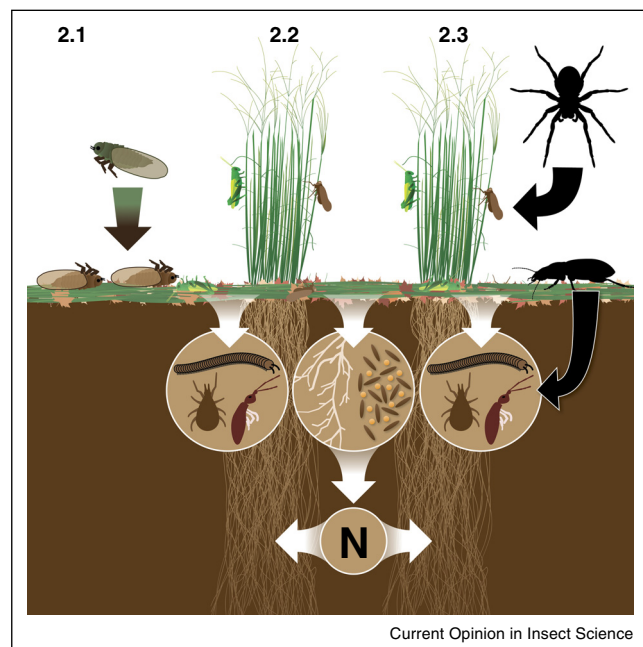
The cumulative biomass of insects is likely to represent a very small fraction of the total biomass in most systems. For example, Seastedt and Tate [2] estimated that the standing biomass of all live and dead arthropods represented only 1.0% and 5.2% of the biomass in the leaf litter layer of a temperate 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 kg N ha^{−1} year^{−1}, Dreyer *et al.*, submitted for publication) than atmospheric deposition and fertilizes terrestrial vegetation [23]. The effects

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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

native plant neighbors [41]. In many cases, plants are known to produce herbivore-induced secondary chemicals that also affect their interactions with microbes both aboveground and belowground [41–43]; the effects of these compounds for the decomposition of plant litter and ecosystem dynamics remains an important frontier for future study.

Insect herbivores can also change the quantity and quality of plant detrital inputs by transforming the composition of the plant community. Such herbivore-mediated changes in the composition of the plant community can profoundly alter ecosystem processes via fundamental changes in the nature of plant litter, and such fundamental herbivore-mediated impacts may be especially common in the context of biological invasions [12^{*}]. For example, the invasion by the hemlock wooly adelgid increases nutrient cycling rates in the short term by increasing the quality and quantity of hemlock litter, but causes much larger and more persistent changes in nutrient cycling by altering forest composition in favor of black birch, a species with relatively high litter N content [42,43].

While there are multiple pathways by which herbivores can transform plant inputs, there may be some general patterns emerging. For example, some of the same plant traits that provide resistance to herbivores may also commonly influence litter decomposition [44,45^{**}]. This suggests that even though the various mechanisms of transformation happen across a wide range of spatial and temporal scales, there may be some common key drivers that link plant–soil–herbivore interactions.

Detritivores can accelerate decomposition

The transformation of detritus by insect detritivores and other soil mesofauna includes an interaction of physical shredding, digestive processing in the animal gut, burial, and continued microbial processing in the ‘external rumen’ of the soil [31]. It is clear that soil animals have the potential to dramatically accelerate decomposition processes in some cases [10,46–48]. For example, dung beetles play a conspicuous role in the transformation and decomposition of animal wastes, with large and well-described consequences at the ecosystem level [49,50]. However, other studies suggest that the importance of soil mesofauna for ecosystem function may be constrained by abiotic factors on a global scale [47,51]. For example, Wall *et al.* [47] conducted a global study of soil animal impacts on the decomposition of standard plant litterbags using naphthalene as a generalized suppressor of soil animals. This study found that the suppression of soil animals reduced litter decomposition rates in temperate and wet tropical regions, but not in cold or arid regions [52], suggesting that abiotic conditions may fundamentally constrain the role of the soil fauna on decomposition processes. Consistent with the idea of abiotic constraints,

van Geffen *et al.* [53] suggested that climate change might allow the range expansion of soil mesofauna into subarctic ecosystems where they were not present before, accelerating litter decomposition and CO₂ efflux rates. However, significant experimental challenges associated with excluding or experimentally depressing arthropods may confound the interpretation of mesofauna exclusion experiments (e.g., [54]), and few studies have performed the appropriate controls to definitively evaluate the direct effects of arthropod decomposers on decomposition in the field.

On a global level, control of decomposition rates has often been placed into a ‘black box’ determined by microbial activity, with temperature and moisture as the principal governing factors [55]. Recently, Schmitz and others have challenged this notion [6^{*},56], suggesting that soil animals may make underappreciated contributions to global ecosystem cycling through their ecological interactions, despite their relatively limited biomass. Understanding the indirect pathways by which insects and other small invertebrates can affect ecosystem processes — and the abiotic factors that constrain their role — remains a key frontier for future studies.

Social insects as biomass transformers

Social insects, such as termites and ants, can have especially large effects on ecosystem processes through biomass transformation. For example, several species of ants are well-known to create heterogeneity in soil nutrients by their aggregation of detrital wastes (e.g., [57,58]). Through their methanogenic digestion of cellulose, termites also contribute directly to the decomposition of recalcitrant plant biomass and the global emission of greenhouse gases [59,60].

Predators have indirect effects on ecosystem function

Trophic cascades

Recent studies that experimentally manipulate the predators of detritivores suggest that trophic cascades may have important effects on decomposition processes. Analogous to ‘green world’ trophic cascades, similar ‘brown world’ trophic cascades are hypothesized to occur when predation on decomposers results in decreased decomposition rates [61]. For example, Wu *et al.* [62^{**}] showed that the addition of predatory beetles to decomposing dung in arid grasslands significantly decreased disappearance rates of dung primarily because of predation on coprophagous beetles, the primary dung decomposers in this system. Decreased decomposition rates were further correlated to lower nutrient availability and plant growth around the dung. A recent meta-analysis found that although there are not enough studies to establish any definitive generalities, the indirect effects of predators on decomposition rates are just as likely as those on primary production [63]. What these studies and others [64] show

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is that predaceous invertebrates can have large and measurable effects on key ecosystem rates such as C cycling and nutrient mineralization through indirect pathways mediated by the consumption of decomposers.

Alteration of litter quality inputs to soil

Predaceous insects can alter the quality of litter inputs via multiple mechanisms. For example, the excreta and waste from one species of predaceous and honeydew-consuming, canopy-nesting tropical ant represents significant nutrient inputs that are enriched in N, P and K relative to leaf litter, which increased rates of litter decomposition on the forest floor under nests [58]. The effects of carnivores on litter and decomposition can also occur through nonconsumptive (or 'trait-mediated') indirect effects [65,66] that cascade through herbivores to affect belowground interactions and ecosystem function. For example, the mere presence of spider predators can create an environment of risk and stress for grasshoppers [67], increasing their metabolic rates. These grasshoppers showed a remarkable degree of adaptive plasticity in their metabolic physiology and foraging: increased metabolic rates required greater carbohydrate consumption, increasing the C:N ratio of their bodies, their frass and the surrounding forb community [68,69]. Risk of predation forces grasshoppers to feed on suboptimal forbs (higher C:N) instead of the normally preferred high quality grasses. This shift in feeding results in plant communities with greater evenness, and a concomitant change in the dominant litter that enters the soil, which ultimately increases N mineralization rates [70]. Working in the same system, Strickland *et al.* [71^{••}] found that the presence of predators changes C turnover and allocation within plants, and even though total plant biomass does not change, plants become C sinks because of greater allocation to belowground structures. Moreover, feeding on plants of lower quality results in grasshoppers with higher C:N ratios. After their death, deposition to the soil, and decomposition, the rate of plant litter decomposition in the same places decreased, likely due to a change in the soil microbial communities [72^{••}]. This extended example illustrates a common thread: indirect predator effects on herbivore behavior had pervasive effects on ecosystem functions through the alteration of the quality (as indexed by C:N) of organic matter input into the soil [73].

Discussion

Explaining context dependence of insect-mediated effects on ecosystem function

The literature describing insect mediated effects on ecosystem processes is rich with evidence of context dependence. While biotic interactions may explain a considerable amount of the observed variation in decomposition rates around the world [6,47], the complexity and variability of these biotic interactions is daunting. Identifying and understanding the factors that

cause this variation in ecosystem responses to biomass inputs is likely to be a continuing challenge for ecology.

One approach to explaining this variability would be to focus on characterizing changes in the quantity, quality, and timing of detrital inputs as a key transition point between the aboveground-components and belowground-components of ecosystems. This approach may require examining some of the poorly known dimensions of detrital inputs, such as the effects of secondary plant chemistry, the mechanisms of microbial priming and the seasonal phenology of detritus inputs. Another approach would be to focus on large perturbations (such as insect outbreaks, e.g., [9]) or simple systems (such as those in early stages of soil formation, e.g., [45^{••}]), where key pathways can more easily be identified. Such studies may suggest potential mechanisms by which insects and other invertebrates could have ecosystem-level effects more generally.

The microbial frontier

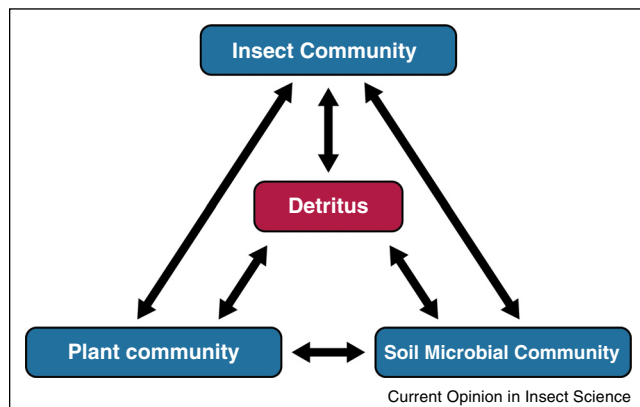
We believe that there is an important and expanding frontier at the intersection of insect ecology and soil microbial ecology. It is already clear that soil microbes are key drivers of ecosystem function, with a large role in mediating terrestrial and aquatic productivity [5]. It is also evident that insects and other small invertebrates can play an important role in the interactions between plants and the soil by accelerating the transition from living biomass to detrital biomass, influencing plant communities [30]. However, we are only beginning to explore the ways in which insects and other invertebrates can shift soil microbial communities, and the impacts of these interactions for ecosystem processes.

Ultimately, many of the ecosystem impacts of insects and their allies are likely to be mediated by direct or indirect changes in the quality, quantity or timing of detrital inputs, with consequences for microbial communities and their effects on decomposition and plant nutrient uptake. Yet, the factors that constrain or influence the role of insects in ecosystem dynamics through their effects on detrital quality and quantity remain uncertain [74,75]. Moreover, the effects of insects may also affect interactions among microbial functional groups (e.g., [76]) with further consequences for important ecosystem processes. Understanding the interactions between insects, plants and the soil will require the combined efforts of ecologists with different areas of expertise applying microbial, arthropod, and ecosystem perspectives to processes occurring at the plant–soil interface [77].

Conclusions

The call for unifying community-level interactions with ecosystem processes has a long and storied history in ecology [31,78]. Insects are the most diverse group of

Figure 2



A conceptual framework showing the combined and reciprocal interactions among insects, plants, soil microbes and a common detrital pool. Insects have both direct and indirect effects that influence the quality and quantity of detritus (litter) with the potential for feedbacks to plants and ultimately back to the detrital pool. The C:N:P ratios and the specific chemical composition of the litter inputs can be influenced by insects with indirect effects on microbial communities and ecosystem rates.

eukaryotes on the planet [1], plants are essential links between the aboveground-components and belowground-components of the biosphere [31,79**], and microbes are the 'unseen majority' in biomass and ecosystem impacts [4,5]. Through their combined and reciprocal interactions, these three groups mediate key ecosystem functions (Figure 2). We believe that there are new frontiers at the intersection of insect ecology, microbial ecology and ecosystem ecology that will focus on understanding the mechanisms and pathways by which insect, microbes and plants affect the flow of carbon and nutrients through ecosystems.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Gaston KJ: **The magnitude of global insect species richness.** *Conserv Biol* 1991, **5**:283-296.
2. Seastedt TR, Tate CM: **Decomposition rates and nutrient contents of arthropod remains in forest litter.** *Ecology* 1981, **62**:13-19.
3. Seastedt TR, Crossley DA: **The influence of arthropods on ecosystems.** *Bioscience* 1984, **34**:157-161.
4. Whitman WB, Coleman DC, Wiebe WJ: **Prokaryotes: the unseen majority.** *Proc Natl Acad Sci U S A* 1998, **95**:6578-6583.
5. Van Der Heijden MGA, Bardgett RD, Van Straalen NM: **The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems.** *Ecol Lett* 2008, **11**:296-310.
6. Schmitz OJ, Raymond PA, Estes JA, Kurz WA, Holtgrieve GW, Ritchie ME, Schindler DE, Spivak AC, Wilson RW, Bradford MA et al.: **Animating the carbon cycle.** *Ecosystems* 2014, **17**:344-359.
- This paper suggests that animals may play a more important role in biogeochemical processes at the global scale than has been previously recognized, and suggests some mechanisms for animal mediated effects on global carbon cycling.
7. Schowalter TD, Crossley DA: **Forest canopy arthropods as sodium, potassium, magnesium and calcium pools in forests.** *Forest Ecol Manage* 1983, **7**:143-148.
8. Whiles MR, Callahan MA, Meyer CK, Brock BL, Charlton RE: **Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian forest: densities, biomass and nitrogen flux.** *Am Midl Nat* 2001, **145**:176-187.
9. Yang LH: **Periodical cicadas as resource pulses in North American forests.** *Science* 2004, **306**:1565-1567.
10. Yang LH: **Interactions between a detrital resource pulse and a detritivore community.** *Oecologia* 2006, **147**:522-532.
11. Yang LH: **Pulses of dead periodical cicadas increase herbivory of American bellflowers.** *Ecology* 2008, **89**:1497-1502.
12. Yang L: **The ecological consequences of insect outbreaks.** In *Insect Outbreaks Revisited*. Edited by Barbosa P, Letourneau D, Agrawal A. West Sussex, UK: Wiley-Blackwell; 2012.
- The ecological consequences of insect outbreaks are examined, including the effects of insects on ecosystem processes, habitat heterogeneity and succession. The impacts of outbreaks are found to be highly variable, even in the same system. This variability emerges from multiple interacting mechanism that occur over different spatial and temporal scales.
13. Sabo JL, Power ME: **River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey.** *Ecology* 2002, **83**:1860-1869.
14. Gratton C, Donaldson J, Vander Zanden MJ: **Ecosystem linkages between lakes and the surrounding terrestrial landscape in northeast Iceland.** *Ecosystems* 2008, **11**:764-774.
15. Epanchin PN, Knapp RA, Lawler SP: **Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies.** *Ecology* 2009, **91**:2406-2415.
16. Hoekman D, Dreyer J, Jackson R, Townsend P, Gratton C: **Lake to land subsidies: experimental addition of aquatic insects increases terrestrial arthropod densities.** *Ecology* 2011, **92**:2063-2072.
17. Dreyer J, Hoekman D, Gratton C: **Lake-derived midges increase abundance of shoreline terrestrial arthropods via multiple trophic pathways.** *Oikos* 2012, **121**:252-258.
18. Murakami M, Nakano S: **Indirect effect of aquatic insect emergence on a terrestrial insect population through by birds predation.** *Ecol Lett* 2002, **5**:333-337.

6 Ecology

19. Jonsson M, Wardle DA: **The influence of freshwater-lake subsidies on invertebrates occupying terrestrial vegetation.** *Acta Oecol* 2009, **35**:698-704.
 20. Davis JM, Rosemond AD, Small GE: **Increasing donor ecosystem productivity decreases terrestrial consumer reliance on a stream resource subsidy.** *Oecologia* 2011, **167**:821-834.
 21. Bartrons M, Gratton C, Spiesman BJ, Vander Zanden MJ: **Taking the trophic bypass: aquatic-terrestrial linkage reduces methylmercury in a terrestrial food web.** *Ecology* 2014. (in press).
 22. Hoekman D, Bartrons M, Gratton C: **Ecosystem linkages revealed by experimental lake-derived isotope signal in heathland food webs.** *Oecologia* 2012, **170**:735-743.
 23. Bultman H, Hoekman D, Dreyer J, Gratton C: **Terrestrial deposition of aquatic insects increases plant quality for insect herbivores and herbivore density.** *Ecol Entomol* 2014 <http://dx.doi.org/10.1111/een.12118>.
 24. Gratton C, Vander Zanden MJ: **Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems.** *Ecology* 2009, **90**:2689-2699.
 25. Bartrons M, Papeş M, Diebel MW, Gratton C, Vander Zanden M: **Regional-level inputs of emergent aquatic insects from water to land.** *Ecosystems* 2013, **16**:1353-1363.
- This modeling study used empirical data, GIS and predictive models to estimate aquatic insect production at a regional scale in Wisconsin, USA. This work predicts that aquatic insects emerging from lakes and streams can create hotspots of C and N deposition to land adjacent to water with potential effects of food web and ecosystem functions. Aquatic insect inputs to terrestrial system were substantial in the area around lakes and streams, and exceeded terrestrial production in many areas near large waterbodies.
26. Carlton RG, Goldman CR: **Effects of a massive swarm of ants on ammonium concentrations in a subalpine lake.** *Hydrobiologia* 1984, **111**:113-117.
 27. Yang LH, Edwards K, Byrnes JE, Bastow JL, Wright AN, Spence KO: **A meta-analysis of resource pulse-consumer interactions.** *Ecol Monogr* 2010, **80**:125-151.
 28. Mattson WJ, Addy ND: **Phytophagous insects as regulators of forest primary production.** *Science* 1975, **190**:515-522.
 29. Belovsky GE, Slade JB: **Insect herbivory accelerates nutrient cycling and increases plant production.** *Proc Natl Acad Sci U S A* 2000, **97**:14412-14417.
 30. Hunter MD: **Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics.** *Agric Forest Entomol* 2001, **3**:77-84.
 31. Wardle DA: *Communities and Ecosystems: Linking the Aboveground and Belowground Components.* Princeton, NJ: Princeton University Press; 2002, .
 32. Lovett GM, Ruesink AE: **Carbon and nitrogen mineralization from decomposing gypsy-moth frass.** *Oecologia* 1995, **104**:133-138.
 33. Metcalfe DB, Asner GP, Martin RE, Silva Espejo JE, Huaraca Huasco W, Farfan Amezcua FF, Carranza-Jimenez L, Galiano Cabrera DF, Durand Baca L, Sinca F *et al.*: **Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests.** *Ecol Lett* 2014, **17**:324-332.
- Working across an elevation gradient in the tropics, this study found a relatively small effect of insect herbivores on carbon fluxes, but herbivory contributes significant quantities of highly labile N and P to the soil through deposits of excreta, bodies, cast exuviae, and unconsumed leaf fragments.
34. Fonte SJ, Schowalter TD: **The influence of a neotropical herbivore (*Lamponius portoricensis*) on nutrient cycling and soil processes.** *Oecologia* 2005, **146**:423-431.
 35. Schowalter TD, Fonte SJ, Geaghan J, Wang J: **Effects of manipulated herbivore inputs on nutrient flux and decomposition in a tropical rainforest in Puerto Rico.** *Oecologia* 2011, **167**:1141-1149.
 36. Kaukonen M, Ruotsalainen AL, Wali PR, Mannisto MK, Setälä H, Saravesi K, Huusko K, Markkola A: **Moth herbivory enhances resource turnover in subarctic mountain birch forests?** *Ecology* 2013, **94**:267-272.
 37. Hollinger DY: **Herbivory and the cycling of nitrogen and phosphorus in isolated California oak trees.** *Oecologia* 1986, **70**:291-297.
 38. Lovett GM, Christenson LM, Groffman PM, Jones CG, Hart JE, Mitchell MJ: **Insect defoliation and nitrogen cycling in forests.** *Bioscience* 2002, **52**:335-341.
 39. Chapman S, Hart S, Cobb N, Whitham T, Koch G: **Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis.** *Ecology* 2003, **84**:2867-2876.
 40. Bardgett RD, Wardle DA, Yeates GW: **Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms.** *Soil Biol Biochem* 1998, **30**:1867-1878.
 41. Callaway RM, DeLuca TH, Belliveau WM: **Biological-control herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*.** *Ecology* 1999, **80**:1196-1201.
 42. Jenkins JC, Aber JD, Canham CD: **Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests.** *Can J Forest Res* 1999, **29**:630-645.
 43. Cobb R: **Species shift drives decomposition rates following invasion by hemlock woolly adelgid.** *Oikos* 2010, **119**:1291-1298.
 44. Classen AT, Chapman SK, Whitham TG, Hart SC, Koch GW: **Genetic-based plant resistance and susceptibility traits to herbivory influence needle and root litter nutrient dynamics.** *J Ecol* 2007, **95**:1181-1194.
 45. Classen AT, Chapman SK, Whitham TG, Hart SC, Koch GW: **Long-term insect herbivory slows soil development in an arid ecosystem.** *Ecosphere* 2013, **4**.
- This study uses a long-term herbivore removal experiment to study how herbivores affect early soil formation under individual trees on a widely spaced landscape with cinder soils. The authors find that herbivory increased N fluxes to the soil, but actually decreased C and N accumulation in the soil, due to the long-term effects of herbivores on tree growth.
46. Carter D, Yellowlees D, Tibbett M: **Cadaver decomposition in terrestrial ecosystems.** *Naturwissenschaften* 2007, **94**:12-24.
 47. Wall DH, Bradford MA, St John MG, Trofymow JA, Behan-Pelletier V, Bignell DE, Dangerfield JM, Parton WJ, Rusek J, Voigt W *et al.*: **Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent.** *Global Change Biol* 2008, **14**:2661-2677.
 48. Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal O, Dhillon S: **Soil function in a changing world: the role of invertebrate ecosystem engineers.** *Eur J Soil Biol* 1997, **33**:159-193.
 49. Hughes RD: **Introduced dung beetles and Australian pasture ecosystems.** *Papers Presented at a Symposium During Meeting of Australia-and-New-Zealand-Association-for-Advancement-of-Science at Canberra in January 1975.* *J Appl Ecol* 1975, **12**:819.
 50. Nichols E, Spector S, Louzada J, Larsen T, Amezcua FF, Favila ME: **Ecological functions and ecosystem services provided by Scarabaeinae dung beetles.** *Biol Conserv* 2008, **141**:1461-1474.
 51. Araujo PI, Yahdjian L, Austin AT: **Do soil organisms affect aboveground litter decomposition in the semiarid Patagonian steppe, Argentina?** *Oecologia* 2012, **168**:221-230.
 52. Austin AT, Vivanco L: **Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation.** *Nature* 2006, **442**:555-558.
 53. Van Geffen KG, Berg MP, Aerts R: **Potential macro-detrivore range expansion into the subarctic stimulates litter decomposition: a new positive feedback mechanism to climate change?** *Oecologia* 2011, **167**:1163-1175.

54. Kampichler C, Bruckner A: **The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies.** *Biol Rev* 2009, **84**:375-389.
55. Swift MJ, Heal OW, Anderson JM: *Decomposition in Terrestrial Ecosystems*. Berkeley, CA: University of California Press; 1979, .
56. Schmitz OJ, Hawlena D, Trussell GC: **Predator control of ecosystem nutrient dynamics.** *Ecol Lett* 2010, **13**:1199-1209.
57. Boulton AM, Jaffee BA, Scow KM: **Effects of a common harvester ant (*Messor andrei*) on richness and abundance of soil biota.** *Appl Soil Ecol* 2003, **23**:257-265.
58. Clay NA, Lucas J, Kaspari M, Kay AD: **Manna from heaven: refuse from an arboreal ant links aboveground and belowground processes in a lowland tropical forest.** *Ecosphere* 2013, **4** art141.
59. Zimmerman PR, Greenberg JP, Wandiga SO, Crutzen PJ: **Termites: a potentially large source of atmospheric methane, carbon dioxide, and molecular hydrogen.** *Science* 1982, **218**:563-565.
60. Sanderson MG: **Biomass of termites and their emissions of methane and carbon dioxide: a global database.** *Global Biogeochem Cycles* 1996, **10**:543-557.
61. Lensing JR, Wise DH: **Predicted climate change alters the indirect effect of predators on an ecosystem process.** *Proc Natl Acad Sci U S A* 2006, **103**:15502-15505.
62. Wu X, Duffy JE, Reich PB, Sun S: **A brown-world cascade in the dung decomposer food web of an alpine meadow: effects of predator interactions and warming.** *Ecol Monogr* 2010, **81**:313-328.
- This experimental study found that decomposition of dung by coprophagous scarabs decreased in presence in predatory beetles, with subsequent decreased plant growth in the vicinity of the dung pats.
63. Schmitz OJ: *Resolving Ecosystem Complexity*. Princeton, NJ: Princeton University Press; 2010, .
64. Atwood TB, Hammill E, Greig HS, Kratina P, Shurin JB, Srivastava DS, Richardson JS: **Predator-induced reduction of freshwater carbon dioxide emissions.** *Nat Geosci* 2013, **6**:191-194.
65. Schmitz OJ: **Herbivory from individuals to ecosystems.** *Annu Rev Ecol Syst* 2008, **39**:133-152.
66. Peckarsky BL, Abrams PA, Bolnick DI, Dill LM, Grabowski JH, Luttbegg B, Orrock JL, Peacor SD, Preisser EL, Schmitz OJ *et al.*: **Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions.** *Ecology* 2008, **89**:2416-2425.
67. Hawlena D, Schmitz OJ: **Physiological stress as a fundamental mechanism linking predation to ecosystem functioning.** *Am Nat* 2010, **176**:537-556.
68. Schmitz OJ: **Top predator control of plant biodiversity and productivity in an old-field ecosystem.** *Ecol Lett* 2003, **6**:156-163.
69. Hawlena D, Schmitz OJ: **Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics.** *Proc Natl Acad Sci U S A* 2010, **107**:15503-15507.
70. Schmitz OJ: **Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass.** *Ecology* 2006, **87**:1432-1437.
71. Strickland MS, Hawlena D, Reese A, Bradford MA, Schmitz OJ: **Trophic cascade alters ecosystem carbon exchange.** *Proc Natl Acad Sci U S A* 2013, **110**:11035-11038 <http://dx.doi.org/10.1073/pnas.1305191110>.
- Sit and wait predators (spiders) increased carbon uptake and increased root biomass allocation in grasses relative to control treatments with no spiders. Spiders increased C uptake and allocation to root biomass in grasses, even though the total amount of plant biomass and the abundance of the herbivores was not significantly different between treatments. These predator effects were largely trait-mediated. The trophic cascade was not strong in goldenrod, but was strong in grasses.
72. Hawlena D, Strickland MS, Bradford MA, Schmitz OJ: **Fear of predation slows plant-litter decomposition.** *Science* 2012, **336**:1434-1438.
- Spiders had trait-mediated indirect effects that ultimately slowed plant litter decomposition, apparently mediated by small increases in the C:N ratio of grasshopper bodies. The mere presence of predators (spiders) alters the body composition of herbivores (grasshoppers) such that their C:N increases due to lower protein content. Although the bodies of dead grasshoppers that had been stressed by predators had the same decomposition rates in the soil as control grasshoppers, the subsequent decomposition of plant material in the same soil was slower, presumably due to changes in the microbial community.
73. Leroux SJ, Hawlena D, Schmitz OJ: **Predation risk, stoichiometric plasticity and ecosystem elemental cycling.** *Proc R Soc B: Biol Sci* 2012, **279**:4183-4191.
74. Hättenschwiler S, Tiunov AV, Scheu S: **Biodiversity and litter decomposition in terrestrial ecosystems.** *Annu Rev Ecol Syst* 2005, **36**:191-218.
75. Mulder C, Boit A, Bonkowski M, De Ruiter PC, Mancinelli G, Van der Heijden MGA, Van Wijnen HJ, Vonk JA, Rutgers M: **A belowground perspective on dutch agroecosystems: how soil organisms interact to support ecosystem services [Internet].** In *Advances in Ecological Research*. Edited by Woodward G. Amsterdam, Netherlands: Elsevier; 2011: 277-357.
76. Averill C, Turner BL, Finzi AC: **Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage.** *Nature* 2014, **505**:543-545.
77. Balser TC, McMahon KD, Bart D, Bronson D, Coyle DR, Craig N, Flores-Mangual ML, Forshay K, Jones SE, Kent AE *et al.*: **Bridging the gap between micro- and macro-scale perspectives on the role of microbial communities in global change ecology.** *Plant Soil* 2006, **289**:59-70.
78. Jones C, Lawton JH: *Linking Species and Ecosystems*. New York, NY: Springer; 1995, .
79. Wurst S: **Plant-mediated links between detritivores and aboveground herbivores.** *Front Plant Sci* 2013, **4**:380.
- This review is focused on the indirect effects of detritivores on plants. Soil detritivores can induce secondary compounds in plants and change microbial communities among many other impacts.