Functional Traits and Trait-Mediated Interactions: Connecting Community-Level Interactions with Ecosystem Functioning

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Abstract

Concerted effort in ecology is focused on developing synthetic frameworks that quantify general trends between diversity of organismal functional traits and ecosystem functioning. Yet much variation about the general trend routinely remains unexplained by trait diversity alone. We argue that this arises because these approaches fail to consider flexibility in trait expression as organisms adaptively respond to different environmental contexts (e.g., changes in resource quality or consumer pressure). We present here a framework for resolving how flexibility in functional trait expression is related to ecosystem functioning. We propose an approach that considers focal species, their resources and their consumers as a modular trophic unit. The approach then examines functional trait expressions of focal species when juxtaposed between different resource species (and associated traits) and consumer species (and associated traits). In such cases, focal species not only directly respond to different resource qualities and consumer pressure, but also mediate the indirect effects of consumer pressure on resource quality, causing feedbacks that ramify through ecosystems. Using case studies, we illustrate the utility of our modular approach for understanding how functional traits determine ecosystem

functioning in a variety of aboveground and belowground trophic modules within eco-systems. We offer some general principles for explaining how variation in interactions among species determines variation in ecosystem functioning through a lens of flexible functional traits expression.

1. INTRODUCTION

Ecologists' original conception of ecological systems considered the biotic and biophysical components of the environment and their functional interplay as an integrated whole (Leopold, 1939; Lindeman, 1942; Tansley, 1935). It follows then that biotic characteristics of ecological systems, represented broadly by species diversity, should instrumentally influence ecosystem processes, such as, for example, nutrient cycling (Cardinale et al., 2012; Chapin et al., 1997, 2000; Hooper et al., 2005). However, work to date that focuses on species diversity exclusively only gets us so far towards elucidating the mechanisms by which species determine ecosystem function (Díaz et al., 2006; McGill et al., 2006; Naeem and Wright, 2003; Schmitz, 2010). This is because much residual variation often remains unexplained when quantifying statistical trends between species diversity and ecosystem processes (Fig. 1A) (McGill et al., 2006; Schmitz, 2010).

A proposed alternative is to characterize species in terms of their 'functional traits'—defined as any organismal character or phenotype associated with a biotic interaction or ecosystem function of interest (Naeem and Wright, 2003)—and then determine how variation in functional traits between systems is associated with variation in levels of a function (de Bello et al., 2010; Eviner and Chapin, 2003; Lavorel and Garnier, 2002; McGill et al., 2006; Mlambo, 2014; Naeem and Wright, 2003; Petchey and Gaston, 2006). The rationale is that species' roles are not determined by their taxonomic identity but rather by their morphological, behavioural and physiological traits (McGill et al., 2006; Naeem and Wright, 2003), which can differ between species even within the same trophic level. Most approaches to linking functional traits and ecosystem functioning typically identify and catalogue suites of candidate functional traits, quantify their diversity within ecosystems and finally relate that diversity to ecosystem functioning (de Bello et al., 2010; Díaz et al., 2006; Eviner and Chapin, 2003; Lavorel et al., 2013; Naeem and Wright, 2003). These synthetic frameworks improve the resolution of species diversity approaches (Fig. 1B), by characterizing broad predictive relationships between
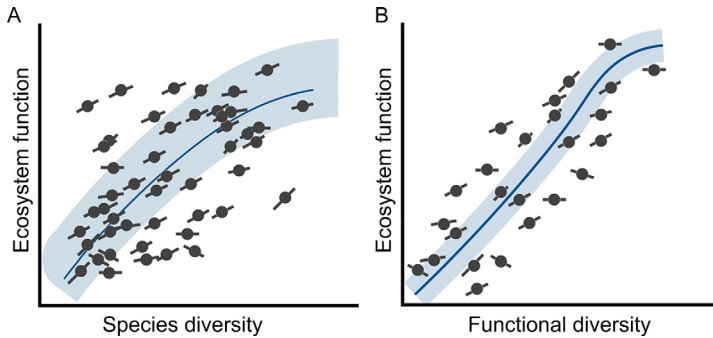
Figure 1 Hypothetical relationship between species diversity (A) or functional trait diversity (B) and level of ecosystem functioning based on syntheses of multiple studies. Points on each graph relate to the average values from individual studies used as part of the metadata in the synthesis. Lines through the points correspond to the directional trend (slope) between diversity and function within an individual study. The figures illustrate that much residual variation can arise (and often does arise) because the individual mean values deviate considerably from the overall average trend and relationships (slope) within a site may not correspond with the overall relationship between diversity and function. In this chapter, we argue that a modular functional traits approach can increase our power to explain the residual variation by explaining how flexibility in trait expression varies with biophysical context. *Adapted from Schmitz (2010).*

functional diversity and ecosystem processes (Eviner and Chapin, 2003; Lavorel et al., 2013). Nevertheless, much residual variation still often remains unexplained by the broad relationship (Fig. 1B).

We argue that much of this residual variation results from variation in the direction of relationships within sites or studies (Fig. 1B) due to flexibility or variation in functional trait expression in response to different biotic and abiotic contexts (e.g., thermal environment, resource quality and abundance, or predators). Moreover, ecological communities can be fundamentally depicted as species interconnected through trophic relationships. So, flexibility in trait expression often causes species to directly mediate trophic interactions between other species causing a host of indirect effects to propagate through the ecosystem (Burghardt and Schmitz, 2015; Hawlena and Schmitz, 2010b; Schmitz, 2008; Schmitz et al., 2008, 2010; Trussell and Schmitz, 2012). Thus, a fundamental challenge in relating functional traits to ecosystem functioning is to resolve how context–dependency in trait expression accounts for variation about any broadly divined trend (Schmitz, 2010). We elaborate here on an approach that shows how to explain context–dependency in ecosystem functioning based on flexibility in expression of functional traits.

Our approach requires a methodological shift from conventional approaches that develop *a priori* synthetic classification schemes that map functional trait diversity onto levels of ecosystem function. We argue for a more modular experimental approach that identifies a focal ecosystem function first and then observes key functional traits in action among different ecosystem contexts to quantify their effect on ecosystem functioning. For example, conventional classification schemes that identify important functional traits focus on the plant level and typically ignore the fact that plant traits may have evolved in response to pressures from consumers in higher trophic levels (e.g., herbivore-induced changes in growth form and chemical elemental content, anti-herbivore defence composition, etc.; Burghardt and Schmitz, 2015; Schmitz, 2010). Such traits that significantly affect a plant species' functional role may remain latent until the plant confronts its consumers.

Consider as a case in point the goldenrod *Solidago rugosa*, which is a competitively dominant plant in New England old-field ecosystems. Analyses of biodiversity–ecosystem function relationships that exclusively focus on the old-field plant community would quickly conclude that this species pre-empts resources and light and thus dictates ecosystem function—particularly production and elemental cycling—because it dominates the community. This interpretation is consistent with the mass-ratio hypothesis (Grime, 1998; Mulder et al., 2013). But, in this case, the mass-ratio hypothesis alone fails to predict context-dependence in ecosystem functioning, as top-down trophic control by grasshopper herbivores determine whether or not this plant species comes to dominate in the first place (Schmitz, 2010). This prediction is impossible before making the experimental observation that the traits that make it strongly competitive—its erect, leafy structure that allow it to attenuate light to the lower canopy and secure space (Schmitz, 2003)—also makes it highly desirable as a predation refuge for grasshopper herbivores. It is the fact that *S. rugosa* serves as a refuge for grasshoppers from predation that *ultimately* determines the ecosystem functioning within this context; its competitive ability due to its mass effect is a secondary determinant (Schmitz, 2003).

Resolving how functional traits vary according to ecological context begins with the starting premise that organisms ultimately try to maximize individual fitness measured in terms of either or all of survival, growth and reproduction (Holt, 1995). The drive to maximize fitness then determines the strategies used by organisms when they interact with other organisms (either predators or resources) or in different environmental contexts (Grime and Pierce, 2012; Schmitz, 2010). Clearly, not all strategies have an adaptive basis and so exceptions do occur (Miner et al., 2005).

Nevertheless, potentially explaining variation in the nature and strength of species interactions using principles from evolutionary ecology is a useful starting point that can help to identify generalities (Agrawal, 2001; Berg and Ellers, 2010; Miner et al., 2005; Schmitz et al., 2008). Through examination of how and why the same organisms express their traits in different ways in different environmental contexts, we hope to show that the nature of organismal responses to their biotic and abiotic environment through adaptive changes in traits can lead to a complementary predictive understanding of the structure and functioning of ecosystems called for in a functional traits research programme. It also responds to the larger call to link evolutionary ecology to ecosystem functioning (Grime and Pierce, 2012; Holt, 1995; Loehle and Pechmann, 1988; Schmitz, 2010; Schmitz et al., 2008).

2. TOWARD A PROCEDURAL FRAMEWORK

We propose that in order to move towards a predictive functional traits framework it is necessary to step back and consider not just the direct effects of these traits, but also how genetic variation within and between species and adaptive plasticity in functional traits can result in indirect feedbacks between community-level trophic interactions and ecosystem processes. This approach hinges on the fact that functional traits can play important roles in communities and ecosystems through two different pathways: adaptive and functional processes. These different pathways have received unequal consideration between community and ecosystem ecology (Fig. 2). Historically, community ecologists, particularly animal ecologists, have considered functional traits to be fitness-related traits and have spent most of their effort in elucidating adaptive trait dynamics as they scale from the individual to the community (Ohgushi et al., 2012).

In contrast, ecosystem ecologists have focused on connecting easily measured, aka 'soft', species traits (e.g., leaf area; *sensu* Hodgson et al., 1999) to ecosystem processes in an attempt to predict how environmental change will alter ecosystem functioning (Lavorel and Garnier, 2002). Both approaches have separately provided useful insight. We argue that these approaches can be combined into a common conceptual framework that can then be applied to any focal organism to highlight potential feedbacks between community and ecosystem processes. This reconciled conceptual framework reveals that traits that are acted on by adaptive processes may also indirectly alter ecosystem processes via their changes to community interactions (Fig. 2). Similarly, changes in ecosystem processes due to 'effect traits' (*sensu* Lavorel and Garnier, 2002; Lavorel et al., 1997) may indirectly alter
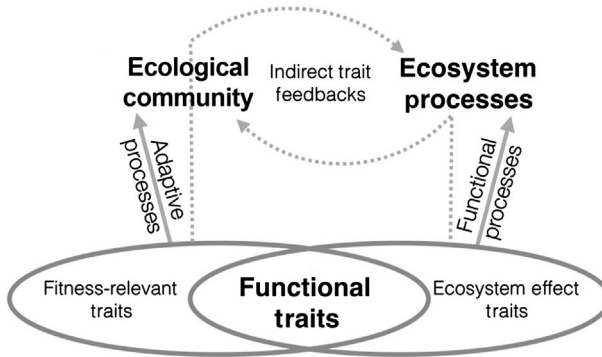
Figure 2 Illustration of the multiple pathways through which functional traits can affect species interactions and ecosystem properties. A suite of behavioural, morphological and physiological traits defines the life history characteristics of an organism. Adaptive processes affect a subset of those traits (fitness-relevant traits), while another subset have direct effects on ecosystem processes (ecosystem effect traits; *sensu* Lavorel and Garnier, 2002). However, effect traits may also have indirect effects on community interactions by altering ecosystem processes. In addition, an organism's fitness-relevant traits may indirectly affect ecosystem processes through the alteration of community composition and interactions. Thus, both categories of traits are potentially connected through indirect feedbacks (dashed lines). The functional traits expressed here may be altered through phenotypic plasticity (or genetic variation) (illustrated in Fig. 3), which makes the expression of traits dependent on the context the organism experiences. Therefore, the same organism placed within a different environmental context may have differing effects on community and ecosystem processes.

community dynamics by changing the environmental context of an organism and thus community interactions (Fig. 2).

To illustrate the point, an adaptive trait of an herbivore such as a shift in foraging behaviour in response to predators can impact plant community dominance structure, which in turn results in changes in ecosystem productivity (Schmitz, 2003). Alternatively, it is also possible for a non–adaptive plant trait such as leaf tissue nitrogen content, to change ecosystem properties altering community dynamics and thus the adaptive landscape (Wardle et al., 2004). This in turn changes selection on other traits indirectly. Within the case studies below we emphasize phenotypic plasticity as the mode of adaptation that creates environmental context–dependence in the role of functional traits and associated feedbacks. This is simply due to our particular focus on plasticity in our research over the years. Nevertheless, this framework can also apply to adaptation to environmental context through genetic trait variation between populations within a species or between species characterized by different functional traits.

Feedbacks can arise because indirect effects propagate through top-down effects within communities to influence ecosystem processes, which in turn exert bottom–up effects on communities. These indirect effects occur because organisms must continually reconcile the competing demands of consuming resources to meet requirements (bottom–up forcing of resource abundance and quality) and avoiding becoming resources for other consumers (top–down forcing from consumers). The ecosystem impacts of these interactions may drastically change as organisms reconcile the trade-offs between bottom–up and top–down factors in different environmental contexts. It follows that these changes can be best predicted by understanding the trade-off made by the middle trophic level. This leads to a universal, and disarmingly simple, modular rule. Namely, individuals are continually balancing trade-offs between resource consumption and avoiding being consumed in order to maximize individual fitness (Schmitz, 2010). As environmental context changes, species should flexibly adjust their trait expressions to re-balance fitness gains from foraging with fitness losses from their consumers. Such adaptive responses to community-level interactions can and do precipitate changes to whole-ecosystem functioning (Fig. 2; Schmitz, 2010).

2.1 Conceptualizing an ecological system

As stated above, our conception of a modular approach does not start with a specific set of traits. Instead, it develops a simple abstraction of ecosystem structure and processes in terms of their most fundamentally important components (Schmitz, 2010). This can be done by organizing the biotic and abiotic components of ecosystems into linear chains in which consumers of resources are themselves resources for other consumers and energy and materials flow along the consumption chains (Fig. 3). Greater biological realism can be infused by recognizing that two basic kinds of chains exist in ecosystems: those whose basal resources are live plant biomass (plant-based, 'green' chains) and those whose basal resources are non-living organic matter (detritus-based, 'brown' chains). Plant-based chains are composed of plants, herbivores and carnivores (Fig. 3). Detritus-based chains are slightly branched being composed of detritus, detritivores and carnivores or microbes, microbivores and carnivores (Fig. 3). These chains are not independent; they are coupled at their base because most plant production enters the non-living detrital pool (Cebrian, 1999; Hairston and Hairston, 1993; Moore et al., 2004). They could also be coupled at the apex should carnivores that feed on herbivores also feed
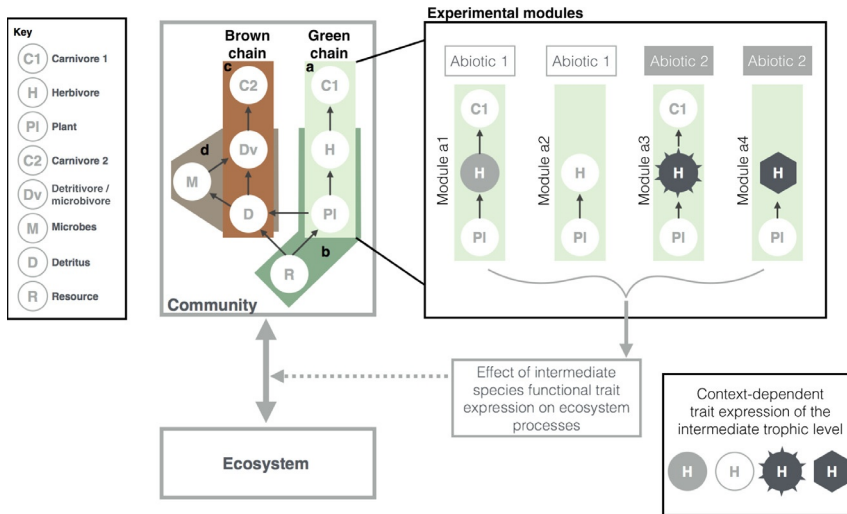
Figure 3 The central goal of functional traits is to clarify the feedbacks between communities and ecosystems (double arrow). Typically, research is focused on a particular ecosystem process such as nutrient cycling. These feedbacks can change due to differences in community or environment. Our approach picks dominant, focal species within trophic modules in this complex community and considers the main forces that control their ecology and evolution: abiotic factors, resources and predators. Functional traits are those traits that control a species response to these forces in different contexts. They determine how the group of species as a whole influences the ecosystem processes (solid arrow from experimental modules). As a result, the impact of these particular species on the ecosystem process is an approximation of the impact of the entire community on the ecosystem process (dotted arrow). The approximation becomes successively better as we consider more species and their interactions. However, this approximation differs from traditional synthetic approaches that divine a single broad-scale trend. Traditional approaches produce a coarse approximation because they assume species or functional traits act the same everywhere. We are proposing a means of getting a finer approximation by being sensitive to context.

on detritivores or microbivores (Schmitz, 2010). The chains are further linked belowground because fungal and bacterial decomposers mineralize nitrogen and carbon and contribute to the release of other materials. To properly understand these intricate interplays, we propose to focus attention on variation in trait expression of a dominant focal species to its consumers, resources and abiotic environment (Fig. 3).

2.2 Illustration of the modular approach

As a practical starting point, we will focus on species in the middle trophic levels of four illustrative chains (Fig. 3a–d, corresponding to text

Sections 2.2.1–2.2.4, respectively) because they are important mediators of indirect effects through adaptive trait expression (e.g., 'trait-mediated indirect effects') (Werner and Peacor, 2003). Our proposed modular approach then focuses on the functional traits of a species in the middle of that tri-trophic chain—the mediating species—and quantifies how they are influenced by abiotic conditions and the functional traits of species in the next higher and lower trophic levels. Finally, using these case studies, we discuss how to implement this modular approach by linking functional traits, community-level interactions and ecosystem functioning through experimental methods that address context-dependency.

2.2.1 Carnivore—herbivore—plant module

A dominant herbivore in old-field ecosystem functioning (Schmitz, 2010) is the grasshopper *Melanoplus femurrubrum*, a generalist feeder (a functional trait) that consumes a mixture of grasses and herbs. In the absence of predation, the grasshopper prefers grass because of its comparative high nitrogen content needed to meet metabolic demands for maintenance and production (Fig. 4). But, grass is a risky place to feed because its simple structure does not allow the grasshopper to hide from predators. The grasshopper also faces several species of hunting spider predators that differ in their hunting mode ranging from active pursuit to sit–and–wait ambush (Miller et al., 2014).

Sit–and–wait spiders hunt from fixed locations in the upper canopy of the field providing a persistent threat. Grasshoppers respond to these predators via adaptive plasticity in two ways. They change their foraging behaviour (a functional trait) by trading-off the risk of consuming grass to hiding and foraging in structurally more complex herbs like the competitively
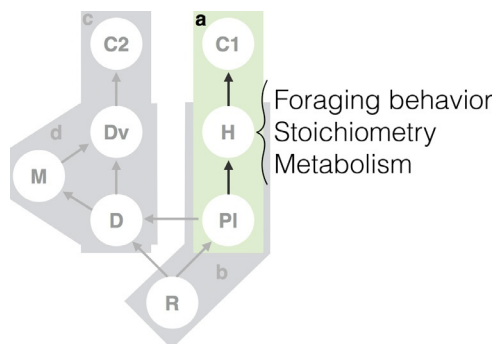
Figure 4 The carnivore—herbivore—plant module highlighting context-dependence of herbivore foraging behaviour, stoichiometry and metabolism.

dominant goldenrod (*S. rugosa*) that serves as a refuge from predation (Schmitz, 2010). Perceived predation risk also induces chronic physiological stress responses in the herbivores (a functional trait) that elevate their metabolic rate (Hawlena and Schmitz, 2010a). Such stress responses keep the grasshoppers in a heightened state of alertness to increase the chance they can escape their predators in the face of persistent risk (Hawlena and Schmitz, 2010b). But, elevated metabolism (respiration) shifts demand to energy containing soluble carbohydrates to meet heightened maintenance demands at the expense of consuming nitrogen for production. Soluble carbohydrate is readily supplied by the same goldenrod species that provides refuge. This adaptive foraging shift leads to higher plant species diversity because the grasshopper suppresses this competitively dominant plant (Schmitz, 2003). It also changes the C:N content of the plant community, and hence the C:N content of plant biomass entering the detrital pool to be decomposed (Hawlena and Schmitz, 2010a). Moreover, the change in physiological demand for nutrients causes the herbivore to excrete more N, to avoid toxicity and respire more C to the atmosphere relative to conditions where the predator is absent (Hawlena and Schmitz, 2010a). The herbivore adaptive foraging shift also impacts plant physiology because it causes plants to alter photosynthesis and respiration rates and aboveground–belowground C allocation in plant tissue (Strickland et al., 2013). Finally, the difference in grasshopper body C:N content between predation and predation-free conditions causes differences in priming of soil microbes such that there is up to a sixfold difference (e.g., a multiplier effect; Schmitz et al., 2014) in microbial carbon mineralization rate of subsequent plant detrital inputs (Hawlena et al., 2012). Collectively, the large multiplier effect of the sit-and-wait spider on elemental cycling, mediated by trait changes in the herbivore prey, came about because significant changes occurred to the C:N balance of organic matter of the largest trophic compartments (plants and detritus) and the ability of another large trophic compartment (microbes) to decompose that organic matter for recycling.

These effects are not observed when this species is in a different context, such as when it co–occurs with widely roaming active hunting spiders. Actively hunting spiders impose low predation risk because they have an ephemeral presence in any one location. Consequently, grasshopper prey would waste considerable energy and nutrient intake, and thereby unnecessarily compromise fitness, if they remained chronically stressed (Schmitz, 2010). Instead, grasshoppers only respond to the imminent threat that arises during the rare encounters with the predator. This results in altogether

different plant species diversity, plant elemental content and levels of eco-system functioning than when grasshoppers face sit–and–wait predators (Schmitz, 2008). Certainly, spider predator body size is important because it determines whether or not they can capture and consume the grasshopper prey to begin with (Schmitz and Suttle, 2001). But predator hunting mode, not body size, is what explains context–dependency in the nature and strength of the community– and ecosystem-level effects. Prey responses to predator hunting mode enables prediction of how changes in herbivore trait expression (Fig. 2) mediate predator effects to impact both community and ecosystem dynamics (reviewed in Miller and Rudolf, 2011).

The way indirect effects of carnivores on communities and ecosystems are mediated by herbivores also depends on an important herbivore func-tional trait, feeding mode, which may also determine the nature of herbivore species responses to different environmental contexts (Schmitz, 2010; Singer et al., 2014). Herbivores can be highly specialized on one or a few plants or be broad generalists; and they can engage in leaf chewing (grazing and browsing), sap-feeding or leaf mining feeding behaviour (Schmitz, 2010; Singer et al., 2014). Dietary specialization, especially, appears to be an evolved response to generalist predators because specialist herbivores can more effectively enlist characteristics of their host plants for defence or ref-uge than generalist herbivores (Singer et al., 2014). For example, specialist herbivorous insects often are able to sequester plant toxins that make them unpalatable or toxic to their predators, or they can mimic structural traits or coloration of their host plants to become cryptic, something that would be difficult for a generalist species to do given the variety of different plant types they rely on. Moreover, many specialist species are leaf miners and sap feeders that tend to be sedentary. Thus, the nature and strength of predator indirect effects become predictably contingent on the hunting mode of the predator in relation to the feeding mode and movement behaviour of the prey (Schmitz, 2010). Predator indirect effects on plants are likely to be much weaker when specialist species dominate the herbivore community than when generalist species predominate (Schmitz, 2010; Singer et al., 2014). Furthermore, the sign of the indirect effect on plants may differ between specialist and generalist herbivores even if they have similar func-tional body mass (Schmitz and Price, 2011).

Specialist herbivores also can incur elevated metabolic rates in response to stress from predation risk (Thaler et al., 2012). But, specialists have no recourse to shift their plant selection and thus compensate not by decreasing foraging effort but by altering the passage rate of food, resulting in altered

N assimilation efficiency (Thaler et al., 2012). This in turn alters the chemical elemental composition of their body tissues in opposite ways to generalist herbivores.

2.2.2 Herbivore—plant—soil elements module

Much of the work linking plant traits to ecosystem functioning is on the direct pathway between plant biomass and detritus-based food chains through litter inputs. Herbivores are not often considered within terrestrial plant functional trait research because they consume a relatively small fraction of plant biomass (Cebrian and Lartigue, 2004). However, the modular approach emphasizes that herbivores may also indirectly influence ecosystem processes through the lingering presence of induced plant defensive traits within uneaten leaf tissue (Choudhury, 1988). Here, we use plant-induced defensive strategies as a case study for a focal functional trait that may provide predictive ability for understanding the effect of herbivory on nutrient cycling (Fig. 5).

Plants engage in a wide variety of anti-herbivore defence strategies. The way plants express those traits depends on the interplay between soil nutrient (element) availability and herbivory (Power, 1992). Across nutrient environments the cost-benefit trade-off of defending tissue with N- and C-rich defensive compounds changes, creating situations where the best-performing allocation strategy in one environment may be maladaptive in another (Coley et al., 1985). Phenotypic plasticity in plant allocation to defence across nutrient environments alleviates this problem by allowing flexibility in allocation patterns to the presence of another trophic level (e.g., herbivory; Agrawal, 2001). These defensive traits are often organized into plant defensive syndromes, suites of co-occurring structural,
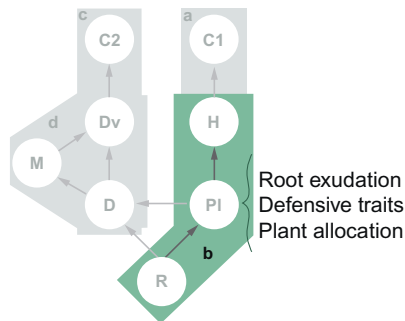

Figure 5 The herbivore—plant—soil elements module highlighting context-dependence in plant root exudation, defensive traits and allocation.

physiological and allocational patterns within the plant (Agrawal and Fishbein, 2006). Similar to Grime's C-S-R strategies (Grime and Pierce, 2012), selection and allocation trade-offs within the plant limit the combinations of traits that are likely to co-occur.

One syndrome is an induced resistance strategy which is associated with plant traits that are known to decrease decomposition rates in ecosystems (e.g., increased leaf toughness, chemical defences, C:N ratio), while the alternative syndrome is induced tolerance associated with changes in plant traits that are known to increase nutrient cycling in the presence of herbivores (Belovsky and Slade, 2000; Ritchie et al., 1998; Schweitzer et al., 2005). Herbivore feeding may also alter ecosystem processes by changing plant inputs belowground (e.g., litter, root exudates) or through alteration in dominance and interactions across the landscape (Fig. 3). Most current plant functional trait frameworks cannot account for this contingency because they focus exclusively on direct effects of plant litter traits on ecosystem impacts rather than considering how environmental context through alterations in community dynamics or species interactions determine the level of trait expression in the first place.

Thus, contingency as to whether herbivores increase or decrease nutrient cycling in ecosystems may be explained by differential defence induction across nutrient gradients (Burghardt and Schmitz, 2015; O'Donnell et al., 2013). A shift in nutrient availability can change the opportunity costs of induced defences and potentially the outcome of plant–herbivore or plant competitive interactions (Cipollini et al., 2003). Thus, the efficacy of and selection for the plant defensive traits outlined above are influenced by the environmental context in which they are expressed (Belovsky and Schmitz, 1994). This means that negative or positive feedbacks are possible between nutrient environments and selection for the expression of particular plant defensive strategies (Burghardt and Schmitz, 2015). A functional plant traits framework can only become predictive once the flexible interplay between nutrient availability, plant defence syndrome and the nature of herbivory are explored through systematic experimentation.

2.2.3 Carnivore—detritivore/microbivore—detritus module

Detritivores and microbivores are a highly diverse group of species that influence elemental cycling through their effects on (1) the physical structure of detritus (Bastow, 2011; Salmon, 2004; Seastedt, 1984), (2) microbial community structure and biomass (Crowther et al., 2011a, 2012) and (3) soil C and N availability (Bouché et al., 1997; Carrillo et al., 2011; De

Ruiter et al., 1993; Holtkamp et al., 2008; Seastedt, 1984; Teuben and Verhoef, 1992) (Fig. 6).

Research on species interactions within detrital chains is not widely given to consideration of trait-mediated effects (Moore et al., 2004). Yet, it is altogether conceivable that animal species within detrital chains are subject to the same foraging-predation avoidance trade-offs faced by species within plant-based chains, even though, unlike plants, detritus is non-living and therefore, will not have countervailing adaptive responses to consumption (Moore et al., 2004). Still, synthesis that applies a trait-mediated perspective to understand mechanisms of interactions along detritus-based chains (Schmitz, 2010) reveals considerable parallels. Like herbivores, detritivore species selectively feed on resources in order to maximize fitness (Hättenschwiler et al., 2005; Scheu and Folger, 2004). They also alter their foraging behaviour in response to predation risk through changes in the time spent foraging or through shifts in habitat use (Grear and Schmitz, 2005; Schmitz, 2010; Sitvarin and Rypstra, 2014).

Some trade-offs can involve detritivores moving from surface to subsurface soil layers to avoid predation. This can change the distribution of organic matter in the soil with cascading effects on the degree to which microbes can access organic matter and decompose it into elemental form (Coleman et al., 1983; Moore et al., 2004; Seastedt, 1984). Moreover, the nature of the detritivore-mediated indirect effect of predators on microbes may depend on the elemental content of soil. For example, Lenoir et al. (2007) found that the nature of cascading effects of predators
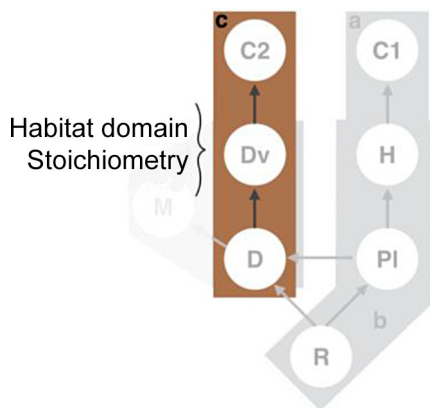

Figure 6 The carnivore—detritivore/microbivore—detritus module highlighting changes in detritivores, habitation domain and stoichiometry according to context.

on fungal biomass, mediated by fungivores (collembolans and orabatid mites) depended on the nitrogen content of the humus. In high nitrogen humus, predators had no effect on fungal biomass, while in low nitrogen they decreased it. Lenoir et al. (2007) suggest that the differences may have arisen because fungi can exhibit compensatory growth under high nutrient conditions (a potentially adaptive trait response) but not in low nutrient conditions.

The potential for adaptive trait responses is revealed in a second example, involving effects of predaceous and microbivorous nematodes on nutrient cycling (Mikola and Setälä, 1998). Microbivorous nematodes can be strongly limited by the presence of their predator, which can counteract their enhancing effects on nitrogen cycling. These effects were not mediated by a strong impact of the microbivore on microbial abundance in this particular case (Mikola and Setälä, 1998), while other experiments have found that microbial abundance is strongly dependent on microbivores (Allen-Morley and Coleman, 1989). Clearly, the importance of interactions between microbivores and their prey is context-dependent.

There are other traits of detritivores and microbivores that could mediate interactions along trophic chains. Temperature and moisture tolerance is particularly important because detritivores subsist in environments where both variables change across small spatial extents (Brady and Weil, 2009). The level of tolerance to changing temperature and moisture regimes determines detritivore movement behaviour and hence the ability to evade predators or redistribute detritus within the soil layers with cascading effects on litter heterogeneity and the distribution of microbes (e.g., Fujii and Takeda, 2012). Also, detritivore body morphology can influence how they move through soil and litter environments, what litter types they degrade (fine root litter or leaf litter) and whether they are specialist or generalist consumers (Fujii and Takeda, 2012). Hence, body morphology can determine how detritivores mediate indirect effects of predators.

Like herbivores, detritivores and microbivores must meet homeostatic elemental balances determined by physiological processes that govern their element uptake and excretion (Martinson et al., 2008; Reiners, 1986; Sterner and Elser, 2002). This suggests that detritivores and microbivores could exhibit the same predation-induced physiological stress responses as herbivores, given that the physiological and hormonal machinery that drives such adaptive responses is highly evolutionarily conserved among animal taxa (Hawlena et al., 2012).

Despite the potential for widespread trade-offs between foraging and predation risk avoidance (Schmitz, 2010; Sitvarin and Rypstra, 2014), it remains uncertain whether this trade-off can be a dominant driver of cascading effects within the detrital chain. Only further experimentation (perhaps using a modular approach) will reveal whether or not these changes will have strong effects detritus-based systems.

2.2.4 Detrivore/microbivore—soil microbe—detritus module

Soil microbial communities are diverse and interconnected in a complex web of trophic interactions (Clarholm, 1994; Neutel et al., 2002), so that identifying all of the individual species in these food webs is currently impractical. Such diversity begs for beginning with a more modular approach that aggregates species into trophic compartments (Moore et al., 2004; Schmitz, 2010) in which microbes are middle trophic levels that interact with detrital resources and predators. A useful starting point is either to focus on dominant microbial species or taxa (e.g., Clarholm, 1985; Crowther et al., 2011a) or examine whole microbial community function using changes in biomass or exoenzyme activity (Ritz et al., 1994). Both of these methods have been used to explore how microbes participate in trophic interactions that include detritus and detritivores (Crowther et al., 2011a,c; Lenoir et al., 2007; Mikola and Setälä, 1998) (Fig. 7).

Soil microbial communities are influenced by bottom–up factors like the quality and structural properties of their detrital resources (Allison, 2006). They are particularly limited by the quality and the, often heterogeneous, spatial distribution of their detrital resources (Allison, 2006). The distribution of microbial species is also spatially heterogeneous, because individuals
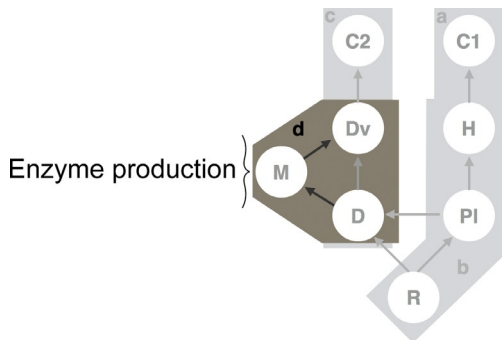

Figure 7 Detritivore/microbivore—soil microbe—detritus module with a focus on context-dependent enzyme production among microbes.

are filtered at local sites based on relatively low nutrient availability, harsh environmental conditions or competition (Goberna et al., 2014; Moore et al., 2004). The diversity of microbial communities, which results from these local selective pressures, creates very different functional capacities across soil conditions. For example, Keiser et al. (2014) argued that some communities have a strong home field advantage, wherein they degrade litter from their environment better than foreign litter. Thus, microbial communities likely have a large capacity to exhibit context-dependent changes in their functional traits based on the quality of their resources.

Microbe functioning also may be determined by the capacity to shift foraging strategies and take up organic nutrients in the rhizosphere when plants release root exudates (Drake et al., 2013; Hamilton and Frank, 2001). In fact, the biomass and exoenzyme production of the microbial community generally changes when nutrients are added to the soil (Bardgett and McAlister, 1999; Carreiro et al., 2000; Sinsabaugh et al., 2002, 2005). There is clearly strong context-dependency in responses of microbial communities to their resource base that may interact with top-down effects to determine how soil microbial communities function in different contexts.

Grazers (detritivores/microbivores) also exert top-down effects on microbes. High grazing pressure by large or abundant soil fauna can reduce microbial biomass (Crowther et al., 2011b; Lenoir et al., 2007), with microbes compensating by increasing their growth rates to maintain the same or higher biomass when nutrients are not limiting (Coûteaux and Bottner, 1994; Mikola and Setälä, 1998; Vedder et al., 1996). Hence, the magnitude of the compensatory growth response depends on interplay between the strength of the grazing impact and nutrient availability. Microbial biomass (Lenoir et al., 2007) and function (Coûteaux and Bottner, 1994; Coûteaux et al., 1991) may remain high under grazing pressure in nutrient-rich environments but are more likely to be depressed in nutrient poor environments. Given that microbial biomass is related to exoenzyme production, microbes thus can mediate the cascading effects of predators on organic matter decomposition rate (Crowther et al., 2011a,c).

Despite the variability in microbial communities within soils and their response to environmental contexts, some generalities are beginning to emerge when examining processes through the lens of a modular approach. First, the response of the microbial community to grazing pressure is highly dependent on the resource environment, with high resource environments leading to compensatory growth and low resource environments leading to net biomass loss. Second, the effect of grazing pressure likely has a greater

influence on microbial community composition and function than on biomass per se. However, microbial communities are rarely studied using this modular perspective (Schmitz, 2010). More empirical examples of how the resource environment and grazers impact microbial community interactions are required to build the predictive framework we are proposing.

3. MOVING FORWARD

Historically, the study of organisms within different trophic groups has been concentrated in disparate, isolated areas of our framework (Fig. 2). Detritivores and microbes are generally viewed as primarily impacting functional processes (often to the exclusion of plasticity and adaptive processes; but see Crowther et al., 2011a), while herbivores and predators are examined primarily through the lens of community rather than ecosystem impacts. Plant ecologists have focused most equitably between these pathways, but rarely account for the indirect connections between them, and generally ignore the interacting effects of higher trophic levels. Some pioneering work on plants is beginning to fill this gap (Baxendale et al., 2014; Bezemer et al., 2013; Schweitzer et al., 2008). We believe particularly ripe places for future progress lie within those areas of the framework not previously explored that link community and ecosystem feedbacks. We have elucidated some of these mechanisms in our old-field ecosystem. For example, goldenrod dominance exerts strong bottom–up control and slows elemental cycling, yet, the presence of sit-and-wait predators cause grasshopper herbivores to consume more goldenrod. This consumption changes the plant community and elemental cycling, which has a new degree of bottom–up control on these communities. However, we argue that further empirical examples that include other ecosystems or other components of the ecosystem (e.g., detritivores) are necessary to develop a predictive framework.

We focus here on elemental cycling because of its fundamental importance to ecosystem function (DeAngelis, 1992; Loreau, 2010). The principles discussed nonetheless can assist in understanding other kinds of ecosystem processes and properties (e.g., trophic transfer efficiency, number of trophic levels; Trussell and Schmitz, 2012). Once a basic set of interacting species are identified through the proposed modular approach, additional detail and complexity can be added to our conceptual model (Fig. 8). Drawing from the examples used in this text, one can begin to predict essential aspects of elemental cycling (DeAngelis, 1992; Loreau, 2010; Moore

et al., 2004). Here, we depict elemental uptake by plants from the abiotic environment (i.e., carbon uptake from the atmosphere and nitrogen uptake from soils) and elemental transfer and loss to and from all compartments through trophic interactions, respiration, excretion, egestion and leaching out of the ecosystem (Fig. 8). The flow of elements up plant–based and detritus–based chains results from trophic (consumptive) interactions between a consumer and a resource trophic level. The strength of this
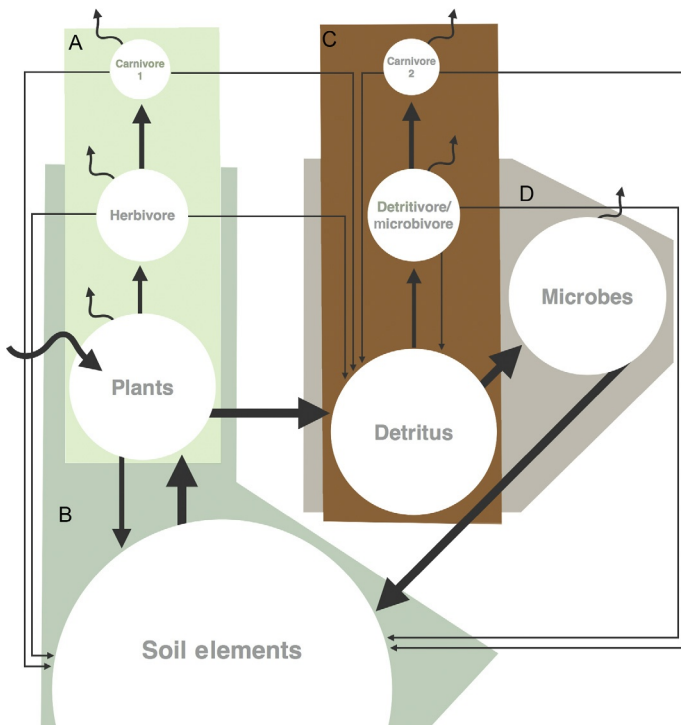

Figure 8 Conceptualization of ecosystem structure needed to combine the functional traits approach to understand whole-ecosystem functioning. This conceptualization reveals key trophic compartments that can control functioning. It depicts different processes related to elemental cycling, including atmospheric CO_2 uptake into the plant compartment, respiratory CO_2 release from all living trophic compartments to the atmosphere, nutrient (elemental) uptake by one compartment from an adjacent lower compartment, inorganic inputs from trophic compartments to the soil elemental pool, organic inputs from living trophic compartments to the detrital pool and conversion of organic matter into elements via foundational cycling of matter through plant, detrital, microbial and soil elemental compartments and pools. The modular approach examines trait responses of species within a trophic compartment when explicitly juxtaposed between at least two other trophic compartments.

consumptive interaction determines the flux rate of elements between trophic compartments. In essence, we propose that using experimentation within trophic modules facilitates incorporating biological detail about organismal functional traits that can help to determine the magnitude of the flux and thus connect consumptive interactions to ecosystem functioning.

The approach we describe here acknowledges that ecosystems are dominated by plant, detrital and microbial biomass and that biomass of animals in higher trophic levels are typically orders of magnitude less (Fig. 8). It also recognizes that the majority of plant biomass in ecosystems does not flow up plant-based chains but enters the soil as detritus where it is decomposed by microbes into constituent minerals that are released to the soil and then recycled back to plants (Cebrian, 1999; Hairston and Hairston, 1993; Moore et al., 2004). Nevertheless, it also shows that biomass representation may not always adequately quantify the contribution of a species to ecosystem functioning when considering mediation of species effects by flexible expression of functional traits.

For example, smaller biomass pools, including animals, may have disproportionately strong effects on ecosystems because, as consumers, they induce flexible, adaptive trait responses in their resource species (Schmitz et al., 2008; Trussell and Schmitz, 2012). Adaptive trait responses can in turn precipitate a sequence of responses between species in adjacent trophic compartments that can cause a host of indirect effects that propagate through ecosystems.

By quantifying these trait-mediated indirect effects, the framework we propose advances the predictive ability of traditional community and ecosystem ecology, which both struggle to explain context-dependency. By focusing on how differences in trait expression of a middle trophic level changes in response to predators, resources or abiotic context, this approach provides the needed mechanistic basis to predict context-dependent outcomes in ecosystem processes. Therefore, when one understands the important players within an ecosystem and their respective fitness trade-offs across environments, then the patterns of context-dependency in the link between functional traits, community-level interactions and ecosystem functioning become clear. Given that the evolutionary ecological principles we apply here are foundational to all taxa (Agrawal, 2001; Grime and Pierce, 2012; Miner et al., 2005; Schmitz, 2010), our modular approach is broadly applicable to a wide variety of species and food-web modules.

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