Out of the dark: Using energy flux to connect above- and belowground communities and ecosystem functioning

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Abstract
Soil ecosystems are both particularly important to humans and vulnerable to human-made global change. Here, we identify some key aspects of soil community and ecosystem research that need to be more widely studied to understand soil responses to global change and enable us to efficiently protect them. This perspective integrates multiple taxa and trophic levels, combines structural community variables with ecosystem processes, and considers multiple energy channels rather than focusing on only bacterial, fungal, or plant-derived resources. Moreover, it enables implementing the claim that terrestrial ecosystem research should more widely adopt an integrative view of above–belowground processes. Having identified these key areas requiring higher attention, we suggest a wider application of the food-web energetics approach to calculating energy flux as a suitable and very powerful tool to simultaneously integrate these aspects. The approach combines food-web and metabolic theory to quantify energy flux through trophic networks as a universal currency of multitrophic ecosystem functioning. In addition to whole-community metrics, it allows for quantifying various important processes by summing up the flux out of autotrophs, detritus, or animals to their respective consumers. This includes the assessment of processes that are otherwise hard to quantify, such as belowground herbivory or predation. The calculation requires data on the focal community and its metabolic demand, trophic interactions, feeding preferences and assimilation efficiency, some of which can be measured, whereas other components can be inferred from readily available literature resources. We outline how novel, high-throughput methods, such as metabarcoding, can be combined with the energy-flux approach to improve our understanding of soil ecosystem structure and functioning. We hope that our article motivates fellow soil researchers to adopt energy-flux approaches for their community data and support the further development of this promising approach for soil community and ecosystem science.
1 | CONTEXT: SOIL ECOSYSTEMS ARE CHANGING—DRIVERS AND CONSEQUENCES

Earth’s soil ecosystems are subject to multiple stressors threatening their physical, chemical and biological integrity (Díaz et al., 2019; Rillig et al., 2019). Climate change, land-use intensification, pollution and biological invasions are key global-change drivers (Díaz et al., 2019) with severe impacts on the structure and functioning of soil ecosystems (FAO et al., 2020). Soil systems are of particular interest for three main reasons: First, they are particularly impacted by and vulnerable to these global-change drivers (Díaz et al., 2019). Second, soil ecosystems are central to some of the most important human needs, such as food provisioning and water purification, and to the integrity of Earth’s terrestrial and freshwater systems, above and below the ground (Bardgett & van der Putten, 2014; Wall, Nielsen, & Six, 2015). Third, soil ecosystems are still under-represented in biodiversity and global-change research (Geisen et al., 2019; Guerra et al., 2021). Unfortunately, our knowledge on belowground biodiversity and ecosystem functioning is nowhere near that of their aboveground counterparts (Cameron et al., 2018; Guerra et al., 2020). This is particularly worrying as global mismatches between above- and belowground biodiversity have been observed (Cameron et al., 2019), and we can only efficiently protect what we know (Phillips et al., 2017). As a result, there is a discrepancy between the vulnerability and importance of soil ecosystems on the one hand and the scarcity of knowledge on how they are affected by global-change drivers on the other hand (Geisen et al., 2019; Guerra et al., 2021). Thus, we need to better understand the vulnerability of soils to change and the connections between their ecological structure and the processes they support. Only then can we efficiently protect soil biodiversity and ecosystem processes and attempt to effectively mitigate global-change impacts on our soils to maintain ecosystem integrity and multifunctionality.

2 | MULTITROPHIC INTERACTIONS CONNECT STRUCTURE AND FUNCTIONING

Our knowledge on soil ecology has come a long way over the past decades, and we now know a lot about the key players in soil ecosystems and their major interactions (Bardgett & van der Putten, 2014). However, a few remaining key knowledge gaps hinder a more comprehensive understanding of soil-ecosystem responses to global change. First, we would like to see more research going beyond certain taxonomic and trophic groups and single organism size classes and embracing the multidiversity and multitrophic nature of soil ecosystems (Figure 1) (Delgado-Baquerizo et al., 2020). Multitrophic approaches are necessary to account for the cascading nature of how changes at a given trophic level impact the adjacent levels and resonate throughout the entire system (Eisenhauer et al., 2019; Seibold, Cadotte, McIvor, Thorn, & Müller, 2018). Biodiversity change is non-random, as species respond to environmental changes based on their traits, such as trophic level and body size, and interaction partners (Eisenhauer et al., 2019; Hines, 2015). Second, we think that taking an integrative look at both ecological communities and ecosystem processes is required (Bardgett & van der Putten, 2014). It is the interactions between the organisms that connect community structure to ecosystem functioning (Figure 1, “Functions”). Integrated approaches, simultaneously looking at multiple taxa across trophic groups (i.e., multitrophic multidiversity; Allan et al., 2014, Soliveres et al., 2016) and multiple processes (i.e., multifunctionality; Byrnes et al., 2013, Manning et al., 2018), allow for a
mechanistic assessment of how global-change drivers impact ecosystems via direct and indirect effects on communities and functioning (Delgado-Baquerizo et al., 2020; Soliveres et al., 2016). Third, we believe that, to comprehensively study global-change impacts on soil ecosystems, we need to embrace the diversity of pathways through which our ecosystems are provided with the matter and energy required to sustain the biodiversity, complexity and multifunctionality of belowground ecosystems (Barnes et al., 2018). If we are to understand how land use, climate, pollution or invasions impact soil systems, we cannot only focus on either the bacterial, fungal or plant channels (Figure 1, “Energy channels”). Instead, we need to study them all simultaneously and assess the relative matter and energy flow through these channels (De Vries et al., 2012; Geisen, 2016). This way, we will be able to quantify which parts of the above–belowground food web are fuelled by these different resource pools and how this drives their response to global change.

3 | ABOVE–BELOWGROUND INTERACTIONS—MATTER AND ENERGY

It is a well-established paradigm in ecosystem ecology that linking above- and belowground systems and studying their positive and negative feedbacks is key to understanding both their complex interplay and their responses to global change (Bardgett & Wardle, 2010; Scheu, 2001; Wardle et al., 2004). We know that soil ecosystem structure and functioning are directly and indirectly affected by processes predominantly perceived as originating, or applied, above
the ground (Bardgett & Wardle, 2010). In turn, what happens below the ground has important impacts on ecosystem components that might be predominantly perceived, for example, by us humans, as an aboveground process or function (plant primary productivity; Figure 1, “Functions”; Eisenhauer, 2012, van der Putten, Bradford, Brinkman, van de Voorde, & Veen, 2016). The example of nutrient cycles illustrates how tightly linked above- and belowground processes are and how limited our perspective is if we separately study the above- and belowground realms. However, although we know that these linkages exist, ecological research, including food web and energy flux research, too often focuses on only one subsystem, and we reiterate previous calls for more research actively integrating belowground and aboveground compartments (Bardgett & Wardle, 2010; Mulder et al., 2013; Scheu, 2001; Wardle et al., 2004). Rather than merely repeating this generic claim, we advocate a promising approach to advance this field. This approach focuses on the flux of matter and energy between the two systems. Before outlining the advantages of taking an energy-flux approach to study above–belowground interactions, we will first summarize how matter and energy flows of above- and belowground systems might be connected. There are multiple ways of how these precious goods are traded across the soil surface, and we should make an effort to capture more of these interactions in our research.

First, some organisms are simultaneously present in both realms. Plants and generalist predators are probably the most obvious examples of organisms that connect the above- and belowground compartments (Scheu, 2001; Figure 1, “Interactions”). Matter and energy are constantly transferred throughout the plant and across the above-below boundary. Although these plant-internal processes are well known, we think that not enough emphasis has been put on the fact that (a) matter and energy are not only transported within the plant but also taken up and released by the plant in the two different subsystems—creating gradients of resources for a variety of organisms above and below the ground and (b) these goods are then available more or less exclusively to the consumers of only one of the two realms. The energetic role of these permanent links between the two realms seems underappreciated.

Second, some organisms actively use both realms. This can happen on a daily basis, commuting across the soil surface more or less on demand—driven by multiple gradients connected, for example, to resource availability, microclimatic conditions or consumer interactions. These organisms (e.g., the earwig in Figure 1, “Interactions”) take up resources and, at least in part, release them—for example, by defaecating, dying and decomposing, or by being preyed upon—in both realms (Scheu, 2001). Other organisms cross the soil surface at certain points in their ontogeny (e.g., the crane fly in Figure 1, “Interactions”) with a varying relative amount of the time spent in either world. Depending on their inherent role in each ecosystem compartment, including their ontogeny, physiology and trophic role, their energy and matter uptake and release in both realms will vary (Blume et al., 2016). Others predominantly or exclusively spend their life in one of the realms, but rely on matter and energy input from the other realm. Examples range from birds feeding on earthworms to earthworms feeding on leaves (see Figure 1, “Interactions”). To embrace this variety of interactions and its importance for matter and energy flux in joint above-belowground systems, and to combine it with the aspects outlined in the previous section (multitaxa & multitrophic; structure & functioning, energy channels), we need to adopt approaches capable of dealing with this variety of information and designed to inherently connect these multiple levels of organization.

4 | ENERGY FLUX—CONNECTING STRUCTURE AND FUNCTION

Energy-flux approaches have long been used to study soil systems (Hunt et al., 1987; Meehan, 2006; Moore & de Ruiter, 2012). However, given their inbuilt ability to integrate important elements of the above-described aspects, we think that they are clearly not adopted widely enough. We advocate assessing energy flux using the adapted food-web energetics approach (Figure 2; hereafter, for simplicity, referred to as the energy-flux approach) (Barnes et al., 2018; Gauzens et al., 2018; Jochum et al., 2021), which is based on previous work of many others over the past century (de Ruiter et al., 1993; Lindeman, 1942; Meehan, 2006; Moore & de Ruiter, 2012; Odum, 1968). Combining food-web theory (Elton, 1927; Paine, 1980) and metabolic theory (Brown, Gillooly, Allen, Savage, & West, 2004), this approach quantifies the flux of matter and energy through trophic networks using a combination of community, physiological and food-web data and thereby links multitrophic biodiversity to ecosystem functioning (Barnes et al., 2018; Jochum et al., 2021). It combines community data (Who is present?) and metabolic demand of the constituent organisms (How much energy do they need?) with a food web topology (Who feeds on whom?), preferences (How much?) and assimilation efficiencies (How much of the consumed energy is available to the consumer?) (Figure 2). This list may seem daunting, but the only aspect absolutely necessary is the community data (Figure 2a)—everything else can be inferred if necessary (e.g., rough topology based on feeding guilds, body
masses and assimilation efficiencies from the literature, metabolic rates based on body masses, preferences based on relative resource availability, etc.), but of course this comes with a certain degree of uncertainty, which needs to be acknowledged and discussed (Jochum et al., 2021). The approach estimates how much energy flux is needed to maintain the survival of the present community. The result is a metric of total energy flux through the system, as well as a matrix of single fluxes along each food-web link. These can be used to quantify energy and matter flow (Barnes et al., 2014) or, for example, to assess interaction strengths (Kortsch et al., 2021) and food-web stability (Schwarz et al., 2017). Although the theoretical (Barnes et al., 2018), methodological (Jochum et al., 2021), and technical (Gauzens et al., 2018) details have been introduced elsewhere, and several studies have used this approach in various ecosystems (Barnes et al., 2014, 2016, 2020; Kortsch et al., 2021; Schwarz et al., 2017), including soil and litter ecosystems (Barnes et al., 2014; Schwarz et al., 2017), we think that it is still under-represented and largely unknown among soil researchers. In spite of the ubiquitous limitations of research budgets and expertise, we would argue that projects working with multitrophic community data can generally adopt energy-flux approaches. But of course, the resolution of community data, food-web topologies and other aspects can be much improved by available project resources. Below, we will briefly summarize how the approach can be used to integrate the above-presented desirable areas of future research.
First, the approach inherently includes multiple trophic levels as it estimates energy flowing through trophic networks. It can be integrated across many trophic levels and includes a large number of taxa with different trophic roles and size classes—above and below the ground (Figures 1 and 2d)—represented as food-web nodes (Gauzens et al., 2018). This enables us to systematically and mechanistically link, for example, horizontal and vertical diversity to ecosystem functioning (Barnes et al., 2018).

In this vein, the approach also intrinsically delivers information on multiple ecosystem functions (Figure 2d), at least if used in a food-web context (but even with very broadly defined nodes such as, for example, predators, herbivores or detritivores (Barnes et al., 2014)). If the food web involves a trophic group such as predators, herbivores or detritivores and their resources, the related ecosystem processes of predation, herbivory and detritivory can be quantified by summing up all fluxes from animal, plant or detritus resources, respectively (Figure 1; “Functions”; Barnes et al., 2018). By linking community data (required for the calculation) to process data (delivered via the energy-flux quantification), the approach naturally requires and provides an integrative eco-system perspective—at least for those aspects that are related to the transport of matter and energy through the living part of the system. Moreover, we can quantify processes that are traditionally hard to measure and thus rarely studied, such as belowground herbivory or predation (Figure 1, “Functions” and Figure 2d). The energy-flux approach elegantly circumvents the issue of how to measure these processes by inferring the minimum energy flux and thus herbivory or predation rates based on the present herbivore or predator communities, respectively.

Being able to look at multiple individual ecosystem processes has value in itself, particularly as they do not need to be measured individually but are simply inferred based on the presence of the respective players and their energy demands. However, using the energy-flux approach, we can not only look at these multiple functions in isolation but we can use the single functions to calculate trophic multifunctionality (Barnes et al., 2018; Potapov, Klärner, Sandmann, Widyastuti, & Scheu, 2019).

The approach can also be used to quantify the importance of specific energy channels in the soil (Figure 1, “Energy channels” and Figure 2d). Importantly, we can not only see how much energy is directly taken out of bacterial, fungal or plant resource pools, but we can go a step further and assess which parts of the entire community are dependent on these resources. Thus, the trophic network and the resulting links of the direct consumers of these resources to higher-trophic level parts of the community enable us to assess the system-wide impact of changes affecting these resources. Instead of simply focusing on the size of the respective resource stocks in the soil systems (i.e., focusing on fungal vs. bacterial biomass), the approach provides quantitative, system-wide information on the relative importance of these energy channels, and how this might vary with climate or land use (Figure 1, “Energy channels”). This is important, because using relative biomass of different resources to infer their relative importance is problematic, given that, for example, low bacterial biomass could either mean that they are not important, or that they are heavily foraged upon and thus cannot develop high biomass.

As established above, above–belowground interactions are important and still often ignored both in aboveground- and belowground-focused research. The energy-flux approach enables us to take into account most of the above-described aspects and to quantify above–belowground linkages. The basic underlying necessity for calculating above–belowground energy flux is a trophic network that connects the above- and belowground worlds. The simultaneous physical presence of plants in both realms is not an issue for the energy-flux approach as we can simply allow consumers in both realms to feed on plants as a resource. For those organisms moving between both realms (earwig in Figure 1, “Interactions”), the approach would focus on where they function as consumers of and a resource for other organisms. Via feeding preferences, those consumers could simply be allowed to satisfy their energetic demands by feeding in both realms. The same is true for consumers living in one but feeding off the other realm. With our trophic network integrating across both realms, such feeding interactions are naturally included. Ontogenetic realm shifts (crane fly in Figure 1, “Interactions”) might best be dealt with by splitting those organisms into different nodes in the trophic network. Although the energy-flux approach is not the only one that allows for jointly studying above- and belowground systems, it represents a promising framework for quantifying the linkages between these subsystems.

One of the most pressing challenges of ecosystem research is to assess and mitigate the impacts of global change on Earth’s ecosystems. Based on the ability of the energy-flux approach to involve multитrophic communities, multiple ecosystem processes and energy channels, and be integrated across the above–belowground boundary, it is highly suited to quantify the impacts of various global-change drivers on soil ecosystems (Figure 1, “Energy channels”). Even among other energy-flux approaches, the adapted food-web energetics approach is comparably well suited to deal with such changes for a number of reasons. First, the approach is based on the quantification of metabolic rates—ideally of individuals—which are directly affected by temperature and body mass (amongst other things). This means that, in contrast to approaches looking
at biomass-turnover rates without involving the energetic value or demand of this (resource or consumer) biomass, the adapted food-web energetics approach naturally captures important aspects of the environment and also of climate change. The warmer it is, the more energy is needed to keep the community alive (Brown et al., 2004). Additionally, we know that warming and other global-change factors, such as direct exploitation (fishing, harvesting), can alter community body-size structures (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011; Sheridan & Bickford, 2011), which, via the effect of body mass on metabolic rates (Brown et al., 2004), is also inherently captured in the approach. This is important because a certain amount of consumer biomass can have substantially different metabolic needs, simply because smaller consumers need more energy per unit biomass (Brown et al., 2004; Jochum et al., 2021). In addition to metabolic rates, assimilation efficiencies are also impacted by temperature, with more energy being transferred across consumer gut walls at higher temperatures (Lang et al., 2017).

Although most of these effects are well known and described in the literature, other impacts are expected, but we do not (yet) have the data to directly apply them in our energy-flux assessments. Changing nutrient availability, chemical pollution or precipitation also impact important aspects of the energy-flux calculation, such as metabolic rates and assimilation efficiencies (Jeyasingh, 2007; Jochum et al., 2017). Given the availability of such relationships, they could easily be included.

In addition, some global-change impacts directly influence ecological communities, such as their taxonomic and functional composition or their trophic pyramid. Land-use change and intensity, climate change, biological invasions, pollution and other factors directly alter communities (Díaz et al., 2019, FAO et al., 2020, Geisen et al., 2019). These changes directly impact who is present, who eats whom and how much, all of which can be accounted for in energy-flux assessments.

Finally, there is one aspect that seems largely underrepresented and often ignored in ecological research on food webs and energy flux (but see exceptions; Schmitz, Hawlena, & Trussell, 2010). This is if and how trophic interactions (food-web topology) and feeding preferences (relative importance of different trophic links) change across natural or global-change gradients with changing abiotic and biotic conditions. Commonly, food webs are taken as static networks and investigators apply the same network of feeding interactions across gradients of, for example, plant species richness, across seasons, or before and after an invasion. However, hardly anyone believes that these links and preferences actually are static. We simply lack the tools to efficiently track who eats whom across these gradients and seasons and between experimental treatments. Luckily, these tools are getting more advanced and more widely available, which enables their use together with the energy-flux approach—a powerful combination that will advance our ability to quantify global-change impacts on communities and ecosystems.

5 | CONNECTING ENERGY FLUX WITH OTHER CUTTING-EDGE METHODS

As we have seen, our assessment of community and food-web ecology depends on the available tool box enabling us to identify who is present (community assessment), who eats whom (food-web topology), and how much (feeding preferences). Improvements in these aspects can heavily influence the amount and detail of input information for the energy-flux approach (Figure 2c), with consequences for the resulting conclusions.

First, we need to know who is present in the focal community (Figure 2a,b). Although there are various well-established methods to assess soil communities, there have recently been considerable breakthroughs moving the field forward. One of the most important ones is the use of metabarcoding in assessing the biodiversity and identity of organisms in a given system (Decaëns, 2021). The method can provide an unprecedented amount and detail of information on the present community. Unfortunately, in addition to the high cost of fully adopting this method (to date), there is still no standardized approach allowing for a quantitative assessment of absolute or at least relative species abundances (Deagle et al., 2019; Sousa et al., 2019). However, this information is necessary to obtain meaningful energy-flux metrics. As there are several approaches suggested to overcome this barrier (Deagle et al., 2019, Sousa et al., 2019), the issue is likely to be resolved soon, so that metabarcoding can be combined with the energy-flux approach. In addition, there are technical novelties allowing for a real-time assessment of soil fauna organisms, including their body size, such as the EDAPHOLOG system (Dombos et al., 2016). Together, these novelties have the power to revolutionize the temporal and spatial resolution of soil-fauna community and energy-flux assessments—given that their methodological disadvantages can be overcome and their cost will be further reduced.

Next, we need to assess who eats whom (Figure 2) (Brose & Scheu, 2014). There is a multitude of traditional approaches to this issue, for example direct observation (Thakur, Künte, Griffin, & Eisenhauer, 2017), feeding trials (Snyder & Wise, 1999), morphological gut content analysis (Anderson & Healey, 1972; Jochum, Schneider,
Crowe, Brose, & O’Gorman, 2012), and obtaining the required information from the literature, or inferring it via trait-based link derivation rules (Gravel et al., 2013; Hines et al., 2019). In soil ecosystems, where direct observations are naturally more difficult to obtain given the visual barrier and small body size of many constituent species, food-web ecologists have traditionally used additional methods for assessing trophic relationships and energy channels. These include the analysis of stable isotopes (e.g., Potapov et al. 2018) and fatty acids (Ferlian et al., 2012; Ruess et al., 2005). First advances have been made to follow the signature of basal resources across multiple trophic levels (Pollierer et al., 2019; Pollierer & Scheu, 2021). However, although these methods provide a rather general picture of energy channels, their ability to provide species-specific trophic interaction data is limited. By contrast, molecular gut content analysis (Eitzinger et al., 2019; Günther, Rall, Ferlian, Scheu, & Eitzinger, 2014) and metabarcoding (Sousa et al., 2019) can provide higher taxonomic-level or even species-specific information on trophic interactions (Tiede et al., 2016). If applied more frequently, these methods could revolutionize the assessment of energy flux in community and ecosystem ecology by providing an unprecedented trophic detail of the focal community.

Next, we ideally combine our network topology with quantitative information on consumer preferences (Figure 2). This is important, because consumers do not necessarily feed on different resources based on their relative abundance or availability (passive preferences) but regularly exert active preferences (Eitzinger et al., 2019) that might additionally vary with environmental conditions (Gauzens et al., 2021). There is available theory and empirical evidence for consumers choosing their resources based on energetic (Pyke, Pulliam, & Charnov, 1977) or stoichiometric constraints (Hall, 2009; Ott, Rall, & Brose, 2012). To gain a more in-depth view on the specific constraints of the focal consumer community, metabarcoding and other DNA-based gut content analysis techniques could provide valuable insights, if they delivered more quantitative information (Deagle et al., 2019). In the absence of reliable standard methods to obtain quantitative gut content results from single individuals, analysing multiple consumers and using the proportion of consumer-resource matches across all consumers as a proxy for preference would be an option (Eitzinger et al., 2019). For the lower trophic levels feeding on plant-based, bacterial and fungal resources (at least the latter of which are often summarized under these broader categories in food-web studies), we can use a combination of fatty acid analysis of the resource pool (soil) and the consumer body tissue to assess relative resource contributions to consumer diet (Ferlian et al., 2012, Ruess et al., 2005). Recently, this approach has been taken one step further to disentangle different types of fungi as food resources via analysing the stable-isotope composition of amino acids in consumer body tissue (Pollierer & Scheu, 2021). Given that a recent study simultaneously using multiple techniques to assess the trophic niche of soil organisms found that their results were complementary rather than redundant, it seems that using a combination of techniques might be the way to go for soil food webs (Potapov, Pollierer, Salmon, Sustr, & Chen, 2020). In summary, the described techniques and their expected methodological updates promise exciting pathways to overcome the issue of quantifying what is being eaten, in what relative proportion, and how this might change across natural and anthropogenically introduced environmental gradients.

6 | EPILOGUE

In this article, we present a number of key aspects that need to be taken into account when studying the causes and consequences of changes in soil communities, particularly studying multitaxa, multitrophic communities, their interactions, and how they are linked to ecosystem processes and multifunctionality. We stress the need to and the power of quantifying above–belowground interactions in soil biodiversity and ecosystem functioning research. To do so, we highlight the food-web energetics approach to calculating energy flux through trophic networks as particularly well suited to tackle multiple research frontiers simultaneously. Finally, we outline how this powerful approach can be further strengthened by combining it with novel, high-throughput, molecular techniques and technical advancements in the assessment of soil communities, their trophic interactions, and consumer preferences (Figure 2). This will enable us to establish more realistic and more sensitive assessments of how changes in soil communities translate into changes in ecosystem functioning. We encourage the readers to further explore the options and push the boundaries of this approach to better understand and protect the soil ecosystems that represent the basis for human well-being.

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**AUTHOR CONTRIBUTIONS**

**Malte Jochum**: Conceptualization; methodology; visualization; writing - original draft; writing-review & editing.

**Nico Eisenhauer**: Conceptualization; funding acquisition; methodology; supervision; visualization; writing - original draft; writing-review & editing.

**DATA AVAILABILITY STATEMENT**

There is no data related to this manuscript.

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