

A niche for ecosystem multifunctionality in global change research

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Abstract

Concern about human modification of Earth's ecosystems has recently motivated ecologists to address how global change drivers will impact the simultaneous provisioning of multiple functions, termed ecosystem multifunctionality (EMF). However, metrics of EMF have often been applied in global change studies with little consideration of the information they provide beyond single functions, or how and why EMF may respond to global change drivers. Here, we critically review the current state of this rapidly expanding field and provide a conceptual framework to guide the effective incorporation of EMF in global change research. In particular, we emphasize the need for a priori identification and explicit testing of the biotic and abiotic mechanisms through which global change drivers impact EMF, as well as assessing correlations among multiple single functions because these patterns underlie shifts in EMF. While the role of biodiversity in mediating global change effects on EMF has justifiably received much attention, empirical support for effects via other biotic and physicochemical mechanisms are also needed. Studies also frequently stated the importance of measuring EMF responses to global change drivers to understand the potential consequences for multiple ecosystem services, but explicit links between measured functions and ecosystem services were missing from many such studies. While there is clear potential for EMF to provide novel insights to global change research, predictive understanding will be greatly improved by insuring future research is strongly hypothesis-driven, is designed to explicitly test multiple abiotic and biotic mechanisms, and assesses how single functions and their covariation drive emergent EMF responses to global change drivers.

KEYWORDS

anthropogenic stressors, biodiversity, biotic mechanisms, ecosystem function, ecosystem multifunctionality, ecosystem services, global change, physicochemical mechanisms

1 | INTRODUCTION

Human impact on Earth's biological systems has motivated an era of research into how ecosystems will continue to supply goods and services under various global change scenarios (Naeem, Duffy, & Zavaleta, 2012). Accordingly, an enormous effort has been made to understand how resulting changes in biodiversity will influence ecosystem processes and the likely consequences for human well-being (Cardinale et al., 2012). While this line of research began with examining how experimentally manipulated biodiversity drives variation in single ecosystem functions (Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994; Tilman & Downing, 1994), there has been a significant shift in recent years toward examining the influence of biodiversity on the simultaneous delivery of multiple ecosystem functions, or "ecosystem multifunctionality" (EMF; Manning et al., 2018). Such studies have been often interested in the relationship between random biodiversity loss (i.e., biodiversity is manipulated by removing species at random from the community) and EMF in order to understand the importance of biodiversity per se for EMF (Byrnes, Gamfeldt, et al., 2014a). However, biodiversity typically responds nonrandomly to global change drivers due to differences in species tolerances to environmental change (Elmqvist et al., 2003; Harpole et al., 2016; De Laender et al., 2016). Furthermore, biodiversity is not the only aspect of biological systems that influences ecosystem functions. Indeed, studies have shown physiological (Dillon, Wang, & Huey, 2010) and behavioral responses (e.g., Taylor, 2008) to various global change drivers that can have important consequences for ecosystem functioning (Miner, Sultan, Morgan, Padilla, & Relyea, 2005). In general, incorporating global change drivers into biodiversity–ecosystem function research has received substantial attention (e.g., De Laender et al., 2016), but is only more recently gaining notable traction in EMF research.

Although there has been considerable discussion over the true value of EMF within the context of biodiversity–ecosystem function research (Bradford et al., 2014; Byrnes, Gamfeldt, et al., 2014a; Gamfeldt & Roger, 2017), the potential benefits of studying EMF in terms of gaining a holistic understanding of ecosystem functioning and the supply of relevant ecosystem services have been clearly identified (Manning et al., 2018). Yet, as the concept of EMF becomes increasingly implemented into global change research, it is imperative that researchers explicitly consider whether the assessment of EMF will significantly enhance our understanding of how a given system responds to global change drivers and whether such knowledge can be incorporated into ecosystem services valuation (Díaz et al., 2018) and policy recommendations (e.g., IPBES, 2018). This highlights two pivotal questions that need to be asked when implementing EMF in global change research: 1) is there added knowledge beyond what can be gained by separately examining multiple single ecosystem functions and 2) is it possible to identify explicit hypotheses based on scientific theory about how a given global change driver will impact EMF? By answering yes to both of these questions, researchers can ensure that studies on EMF under global change scenarios will yield unique and valuable insight that will help foster predictive global change research.

Here, we present a conceptual framework to guide the incorporation of EMF in global change research (hereafter GC-EMF research) in order to enhance understanding and predictions of how global environmental change will impact ecosystem performance (Figure 1a). Specifically, we propose that GC-EMF research needs to be strongly hypothesis-driven, whereby the potential underlying biotic (e.g., species richness, functional diversity, physiology) and abiotic (e.g., physical and chemical) mechanisms that mediate the effects of global change drivers on EMF are identified a priori. Furthermore, we propose that the utility of EMF in global change research—beyond that of analyzing individual functions—should be critically assessed on a case-by-case basis and will likely depend on the number and type of functions measured, as well as on the overall interpretability of results. To determine whether GC-EMF research has so far met these important criteria, we conducted a review to assess the status of research addressing the impacts of global change drivers on EMF. We discuss findings from this review within the context of the framework described in Figure 1 and summarize knowledge gained so far from this new and rapidly developing field. Furthermore, we assess the overall value of applying an EMF approach to global change research and discuss important considerations for future GC-EMF studies.

2 | A LITERATURE REVIEW OF GLOBAL CHANGE IMPACTS ON ECOSYSTEM MULTIFUNCTIONALITY

We performed a literature search in Web of Science using the search term "global change" AND "multifunctionality". Additionally, we compiled all articles that cited key papers in the development of multifunctionality metrics (Byrnes, Gamfeldt, et al., 2014a; Hector & Bagchi, 2007; Maestre et al., 2012) as of August 2018. We screened the titles and abstracts of the resulting 786 papers to identify studies that tested EMF metric responses to global change drivers. We excluded literature that measured multiple ecosystem functions but did not calculate an EMF metric, as well as studies that only manipulated biodiversity directly. We identified 23 studies that present experimental or observational evidence of global change effects on at least one metric of EMF (Table 1). For each study, we assessed whether there was an overall EMF response to the global change driver(s) and examined the biotic and abiotic mechanisms that were either hypothesized or shown (with statistical tests) to be driving the response (Supporting information Table S1). We considered a study to hypothesize a mechanism if it was presented as a formal hypothesis or if it was considered in the introduction or discussion sections.

More than half of the identified studies were published since the beginning of 2017 (Table 1), showing the recent interest in this field of research. The studies calculated a variety of EMF metrics from measurements of 4 to 16 single functions, which were most commonly related to carbon, nitrogen, or phosphorus cycling. In most studies, global change drivers directly or indirectly affected EMF (20 out of 23 studies). The direction and magnitude of these responses were highly variable, which was not surprising given considerable variation in the global change drivers, study systems, functions, and

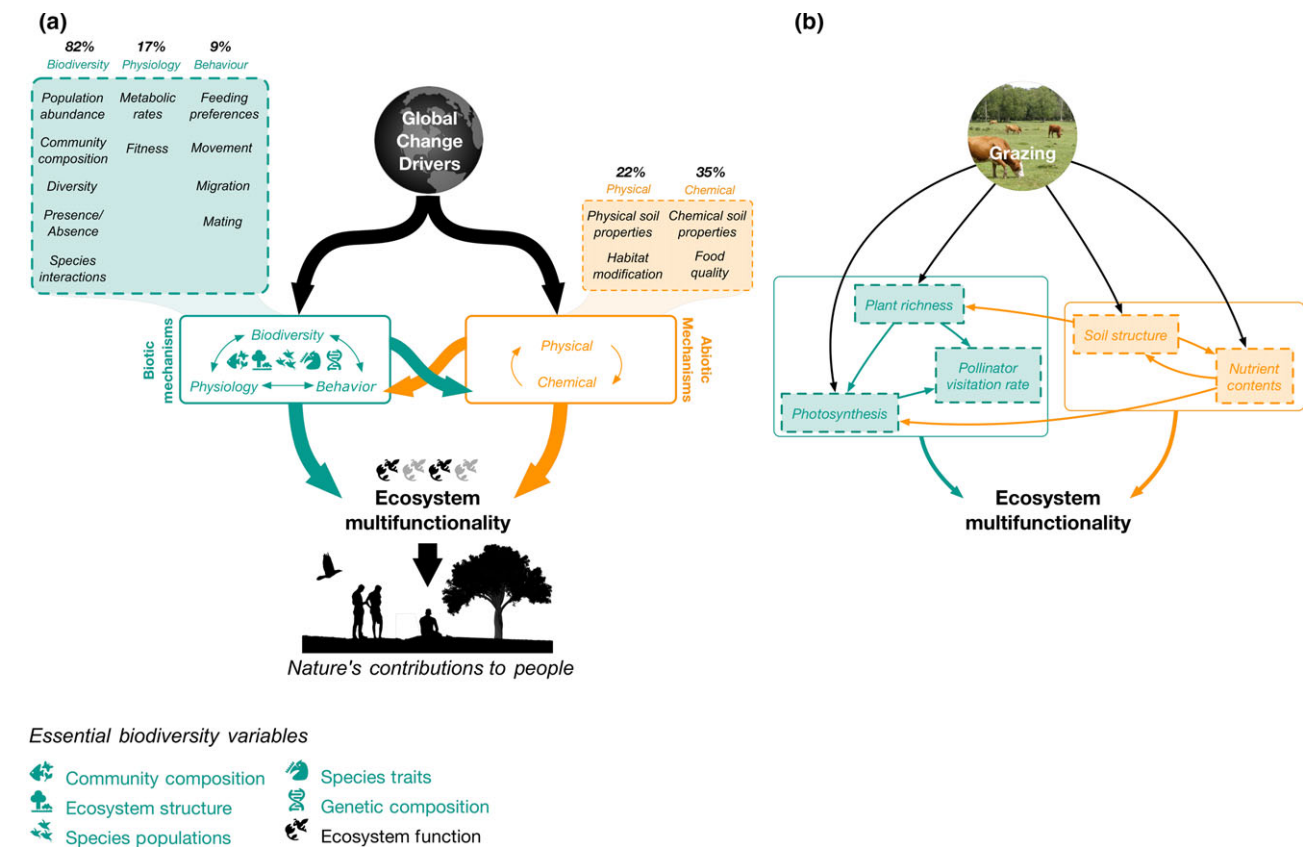


FIGURE 1 (a) Conceptual framework outlining the proposed hypothesis-driven approach to conducting GC-EMF research. Global change drivers influence EMF through an interplay of biotic (green) and abiotic (orange) mechanisms, ultimately influencing nature's contributions to people (NCPs; Díaz et al., 2018). Examples of biotic mechanisms in the biodiversity, physiology, and behavior categories are listed in the green box (top left) and overlap with the essential biodiversity variables that are depicted by the green symbols (Pereira et al., 2013): community composition, ecosystem structure, species populations, species traits, and genetic composition. Abiotic mechanisms may be physical or chemical variables, examples of which are shown in the orange box (top right). The percentages above the boxes indicate the proportion of the reviewed studies that formally tested a mechanism belonging to each respective category (Supporting information Table S1). Mechanisms are expected to frequently interact with each other, both within and between the biotic and abiotic categories. (b) Hypothetical example showing how the framework can be used to explicitly visualize and analyze how biotic and abiotic mechanisms and their interactions mediate grazing impacts on EMF. Grazing directly influences soil structure and nutrient pools through soil compaction and grazers' urine and feces. Additionally, grazing affects plant diversity and physiological rates (e.g., photosynthesis), leading to an indirect effect on the behavior of pollinators. Abiotic and biotic components interact with each other, for example, through the impact of soil compaction on plant roots and nutrient uptake

approaches. Further, there was high variability even within studies; effect size commonly depended on experimental treatment levels and the analytical methods, such as the choice of EMF metric (e.g., averaging or threshold approach; Byrnes, Gamfeldt, et al., 2014a), spatial context (e.g., regions), and temporal context (e.g., seasons) (Supporting information Table S1).

3 | ASSESSING THE RATIONALE FOR APPLYING ECOSYSTEM MULTIFUNCTIONALITY TO GLOBAL CHANGE RESEARCH

In order for GC-EMF research to yield meaningful and definitive results, it is essential that studies lay out explicit rationale for quantifying EMF by describing how knowledge will be gained about a system beyond measuring single functions. While most of the reviewed

GC-EMF studies provided such rationale, this differed considerably among studies. The most common motivation was to inform land managers or policy makers (Allan et al., 2015; Bradford et al., 2014; Delgado-Baquerizo et al., 2016). Assessing multiple functions simultaneously has advantages for management because multiple functions are required to deliver the many services that humans require from nature (Manning et al., 2018). Consequently, management recommendations for ecosystem performance based on single functions could be misleading if they respond to global change in contradictory manners (Alsterberg et al., 2017; Constán-Nava, Soliveres, Torices, Serra, & Bonet, 2015). The rationale of other studies was that EMF is important when assessing the role of biodiversity loss as a component of global change, because different sets of species perform different suites of functions (Antiqueira, Petchev, & Romero, 2018; Birkhofer et al., 2018). Similarly, some studies sought to assess if variation in biodiversity can offset the potential negative effects of

TABLE 1 Studies investigating ecosystem multifunctionality (EMF) responses to global change drivers, either observationally (O) or by the application of an experimental manipulation (M)

Global change driver	System	EMF		
		#	effect	Study
Land-use change (LU)				
Land-use intensity	O Grasslands	14	✓	Allan et al. (2015)
Land-use complexity	O Ag. Landscapes	8		Birkhofer et al. (2018)
Land-use intensity	O Subtropical forest	8	✓	Fu et al. (2018)
Grazing intensity	O Grasslands	11	✓	Peco et al. (2017)
Grazing intensity	O Ag. Landscapes	4	✓	Sircely and Naeem (2012)
Habitat diversity	M Marine	4	✓	Alsterberg et al. (2017)
N fertilization ^a	M Grassland	5	✓	Bradford et al. (2014)
Management type	M Grasslands	12	✓	Li et al. (2017)
Land-use intensity	M Ag. Landscapes	12	✓	Luo et al. (2018)
Grazing intensity	M Dryland	5	✓	Zhang et al. (2016)
Climate change (C)				
Degree of aridity	O Drylands	16	✓	Berdugo et al. (2018)
Degree of aridity	O Dryland	5	✓	Delgado-Baquerizo et al., (2016)
Warming ^a	M Aquatic	7	✓	Antiqueira et al. (2018)
Drought	M Stream	5	✓	Pohlon et al. (2013)
Drought	M Peatlands	4	✓	Robroek et al. (2017)
Invasions (I)				
Tree invasion	O Riparian	5	✓	Constán-Nava et al. (2015)
Seaweed invasion	M Intertidal	7	✓	Ramus et al. (2017)
Chemical pollution (P)				
Toxic residues	M Grassy field	4		Manning et al. (2017)
Multiple drivers				
Woody encroachment (LU, C, I)	O Semi-arid rangeland	11	✓	Chandregowda et al. (2018)
Shrub encroachment (LU, C, I)	O Grass/shrubland	10	✓	Quero et al. (2013)
Grazing intensity, aridity (LU, C)	O Drylands	11	✓	Vandendorj et al. (2017)
Nutrient enrichment, toxicants, sedimentation, warming (LU, C, P)	M Marine	6		Alsterberg et al. (2014)
Rainfall frequency, N addition (LU, C)	M Dryland	15	✓	Liu et al. (2017)

Notes. The column “#” specifies the number of individual functions that were measured. The “effect” column indicates whether at least one significant relationship between a global change driver and a metric of EMF was reported. For description of metrics, mechanisms and functions see Supporting information Table S1.

^aCombined or crossed with a biotic community manipulation.

global change on EMF (Liu et al., 2017; Robroek, Jassey, & Hefting, 2017; Zhang, Eldridge, & Delgado-Baquerizo, 2016). Importantly, other studies considered it vital to understand (or just summarize) the complex trade-offs and interactions that occur among global change drivers and multiple functions, for example, when functions are not correlated with each other (Birkhofer et al., 2018; Luo et al., 2018; Manning, Beynon, & Lewis, 2017; Vandendorj, Eldridge, Travers, & Delgado-Baquerizo, 2017; Zhang et al., 2016).

In principle, incorporating EMF was generally appropriate to meet the aims of the reviewed studies, but further clarification of how study designs and individual functions would specifically inform management or policy is required (Manning et al., 2018). A current lack of a strong link between ecosystem functions and services exists, likely because this is highly challenging and requires well-

defined stakeholder objectives (Manning et al., 2018; Box 1). Notable exceptions were studies that considered the ecosystem services that stakeholders are particularly interested in receiving from a given landscape (Allan et al., 2015) or that took a landscape perspective (Alsterberg et al., 2017; Li, Zheng, Xie, Zhao, & Gao, 2017) to better understand how landscape structure can mediate the effects of global change on EMF. While the relevance of some commonly measured material pools and fluxes were easily linked to ecosystem services of interest to stakeholders (e.g., productivity measures), the relevance of many functions or state variables were frequently unaddressed, which strongly limits the ability of some GC-EMF research to make practical recommendations for stakeholders. Improving integration with management and policy is crucial for the future of GC-EMF research, which is becoming increasingly relevant for policy

makers as signposted by its inclusion in the recent IPBES report (IPBES, 2018).

4 | TOWARD A MECHANISTIC UNDERSTANDING OF GLOBAL CHANGE IMPACTS ON ECOSYSTEM MULTIFUNCTIONALITY

Key to developing a predictive framework for GC-EMF research is identifying the mechanisms that mediate how EMF responds to global change drivers. We propose that these mechanisms take the form of either biotic or abiotic factors and can be developed into a framework from which clear hypotheses can be formulated and tested (Figure 1a). The biotic mechanisms may be related to aspects of biodiversity, physiology, or behavior, while abiotic mechanisms fall

into the categories of physical or chemical effects (Figure 1a). In any one system, a number of these mechanisms may interact to influence overall EMF responses (Figure 1b). Neither of these broad pathways can be labeled as exclusively “direct” or “indirect” effects on EMF, as this distinction depends on the mechanism. For example, biotic mechanisms such as changes in community composition may be interpreted as indirect effects, while others like changes in physiological rates may be direct if that rate is the actual function of interest (Manning et al., 2006).

In the reviewed GC-EMF literature, we found that the most common explicit hypothesis was that global change would impact EMF through a biodiversity mechanism (Figure 1a; Supporting information Table S1), congruent with the development of EMF within biodiversity–ecosystem function research. The hypothesized and tested biodiversity mechanisms collectively represented multiple biodiversity

BOX 1 Linking multiple ecosystem functions to ecosystem services

There are a great number of functions that can be and have been used in multifunctionality analyses (Allan et al., 2015; Fu, Wu, Duan, Guan, & Huang, 2018; Luo et al., 2018; Supporting information Table S1). However, it can often be unclear how these functions relate to the multiple nature's contributions to people (NCPs; Díaz et al., 2018) that are desired from ecosystems. When initiating a multifunctional analysis aimed at informing the policy or management of a global change driver, researchers, and practitioners should contemplate not only the responses of multiple functions, but also how those responses may relate to the supply of one or more NCPs (Manning et al., 2018). We considered this relationship by classifying all the functions measured by the 23 reviewed papers into broader ecosystem function categories and linking these ecosystem function categories to NCPs using the description and examples provided by Díaz et al. (2018). Additionally, we included a separate category called “ecosystem properties,” which describes measured state variables (e.g., soil pH, biological control, and species richness) that did not belong in any of the ecosystem function categories. These ecosystem properties may be indicators of functions (e.g., species richness may influence productivity) and/or be directly connected to the supply of NCPs (e.g., pathogen regulation).

By linking functions to NCPs, we established that there are numerous plausible relationships between the ecosystem functions that have been considered in the current literature and NCPs (Figure 1: Box 1). It is highly conceivable that most function categories can contribute to one or more NCPs, and that each NCP may be described by one or multiple functions. For variables categorized as ecosystem properties, the connections and implications are even more unclear and often arbitrary. In some cases, these ecosystem properties were related to social and/or cultural services such as esthetic value (e.g., flower cover), recreational opportunities (e.g., hunting), and conservation value (e.g., species richness) (Allan et al., 2015; Birkhofer et al., 2018). However, functions that link to social and cultural services were generally underrepresented in the literature. The ecosystem service-multifunctionality approach described by Manning et al. (2018) is a promising approach that could fill this gap because the ecosystem services required are explicitly defined with stakeholders at the first stage of the analysis. While we used a specific ecosystem service classification (NCPs) to establish these relations, the same conclusions would be drawn from any other classification (e.g., Millennium Ecosystem Assessment, 2005).

Although the links between ecosystem functions and NCPs are generally ill-defined without the context of specific systems or aims, we advocate that future GC-EMF studies constrain the possible links by considering the specific interests of intended stakeholders, such as conservationists or farmers (Manning et al., 2018). Further, these relationships should be spatially explicit. Not all the relationships depicted in Figure 1: Box 1 may be reasonably inferred from current measures of multifunctionality because functions are not usually evaluated at the larger spatial scales most relevant to the supply and demand of NCPs (Manning et al., 2018). Providing theoretical or empirical support for the connection of functions to one or multiple NCPs that are most relevant to the study system will make research more readily applicable to management or policy advice, which was one of the main motivations for performing GC-EMF research according to our literature review. This process can also identify if there is a potential link between multifunctionality and multiple NCPs; as we show here, a collection of similar functions does not necessarily inform only a single NCP and nor do a wide range of functions inherently describe a wide range of NCPs. In this context, future evaluations of how ecosystem multifunctionality relates to the supply of multiple NCPs under different global change scenarios will be a critical step to discern how and where society can benefit from actions to mitigate global change.

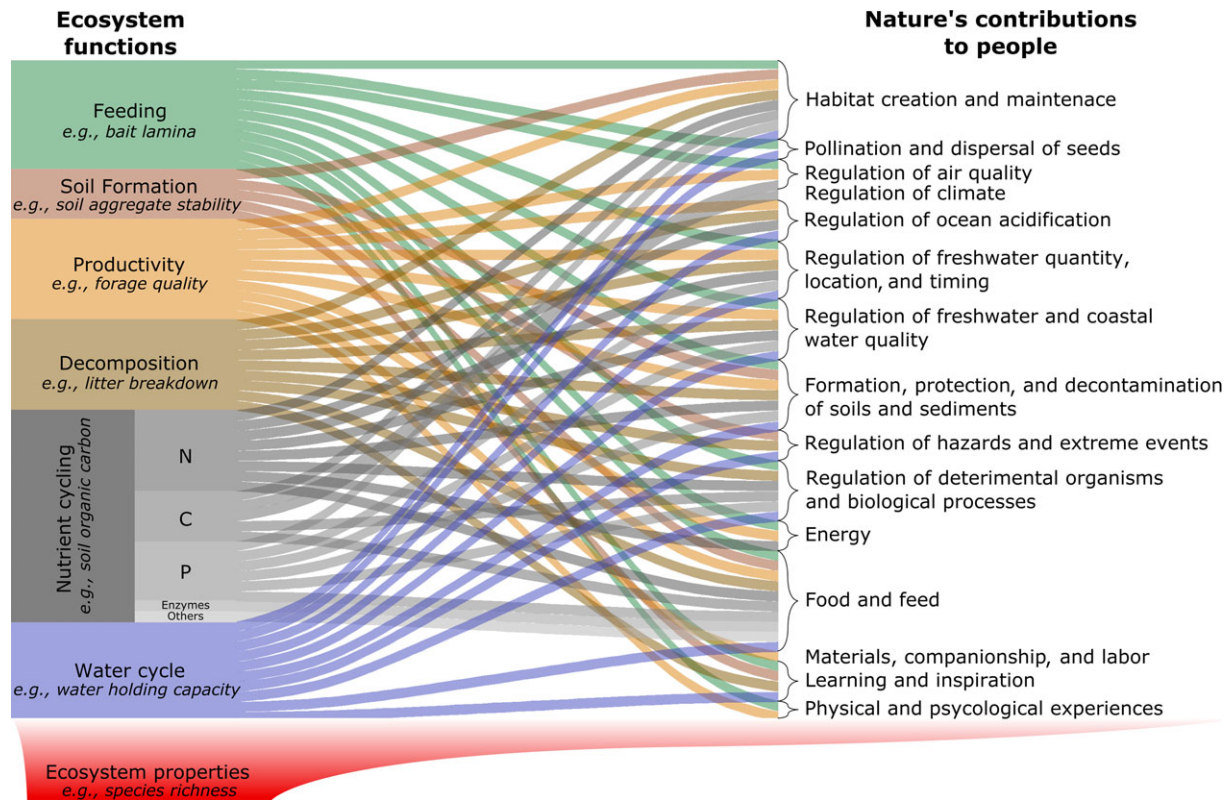


Figure 1: Box 1. The links between measured ecosystem functions and nature's contributions to people (NCPs). All measured functions from the reviewed papers were categorized into broader ecosystem functions (left hand side) and linked to NCPs (right hand side; Díaz et al., 2018). In addition, ecosystem properties were categorized separately and could conceivably be related to NCPs in myriad ways, both directly and indirectly by mediating one or more ecosystem function.

facets (here we refer to "essential biodiversity variables" as defined by Pereira, Ferrier, & Walters, 2013), including reporting the impact of global change on community composition, species and phylogenetic diversity, and trait distributions (Figure 1a). Populations of single species were also considered, such as increased cover of an invasive seaweed that provided habitat structure (Ramus, Silliman, Thomsen, & Long, 2017) or the survival of dung beetles after exposure to veterinary drugs (Manning et al., 2017). Nearly all of the reviewed studies formally tested the mediation of global change effects on EMF by shifts in some aspect of biodiversity (Supporting information Table S1). However, testing EMF responses driven by other major biotic aspects, that is, physiological or behavioral mechanisms, has received far less attention, despite their undoubted importance for mediating global change effects on EMF. One notable example of a physiological mechanism highlighted in the GC-EMF literature is the positive effect of warming on rates of biochemical reactions, which increases the metabolic demand and consumption rate of individual organisms (Antiqueira et al., 2018; Brown, Gillooly, Allen, Savage, & West, 2004). The resultant effects on EMF were expected to emerge through interactions with changes in community

composition due to differences in temperature sensitivity among species and altered trophic interaction strengths (Gruner et al., 2017; Rall, Vucic-Pestic, Ehnes, Emmerson, & Brose, 2009). To the best of our knowledge, however, behavioral mechanisms are mostly unexplored, but could operate for instance by changes in plant cover affecting the foraging activity of organisms (Mattos & Orrock, 2010).

General consideration of how abiotic mechanisms drive EMF responses was fairly common in the reviewed studies, but a more limited set actually tested these mechanisms (Supporting information Table S1). Where present, hypotheses of abiotic mechanisms were most clearly stated in the case of invasive or domestic species that have physical effects on biogeochemical cycling (Constán-Nava et al., 2015; Zhang et al., 2016). For example, in addition to altering local diversity, invasive plants may alter soil or sediment properties, such as water retention, stability, and biogeochemical cycling (Constán-Nava et al., 2015; Quero, Maestre, Ochoa, García-Gómez, & Delgado-Baquerizo, 2013; Ramus et al., 2017). The activities of grazers may also impact soil properties and processes through trampling and dung and urine deposition (Allan et al., 2015; Peco, Navarro, Carmona, Medina, & Marques, 2017; Sircely & Naeem, 2012;

BOX 2 A workflow for generating mechanistic hypotheses of global change effects on ecosystem multifunctionality

Effectively hypothesizing the effects of global change on multifunctionality a priori is challenging due to the combination of multiple ecological and statistical effects that drive multifunctionality responses. Researchers need to disentangle these effects to increase the clarity and mechanistic basis of their GC-EMF hypotheses. This can be achieved with the following workflow, which expands on the presented framework (Figure 1) to explicitly consider the underlying ecological and mathematical interactions in three steps (Figure 1: Box 2). Importantly, these considerations are always based on hypotheses related to single functions and their dependence on biotic and abiotic mechanisms.

Step 1: Hypothesize the effects of global change on biotic and abiotic mechanisms. First, consider how global change will affect biotic and abiotic variables that are likely to be important drivers of your suite of functions (or clusters of functions). In most systems, literature searches, pilot studies, or expert opinion can be used to hypothesize the direction and magnitude of disturbance effects (e.g., land-use change) on biotic and abiotic mechanisms (e.g., species richness and water availability, respectively). Further, consider if these biotic and abiotic mechanisms are likely to interact. For example, an invasive species may alter an abiotic variable (e.g., shading) by affecting a biotic variable (e.g., plant cover).

Step 2: Hypothesize the effects of mechanisms on individual functions. Next, consider how these variables are likely to affect each of the focal functions individually. For example, meta-analyses of the biodiversity–ecosystem functioning relationship may provide reasonable estimates for the effect size of a biotic mechanism (e.g., species richness) on a certain function (e.g., productivity). It is important to recognize this step as an implicit intermediate stage between any mechanism and a metric of multifunctionality.

Step 3: Consider how covariation among functions and EMF calculation method influence emergent responses. After defining the ecological effects and interactions, consider the implications of the way these functions are combined mathematically to produce a multifunctionality metric. There are multiple ways to calculate multifunctionality, including the averaging approach and threshold approach, the merits of which are discussed in detail elsewhere (Byrnes, Gamfeldt, et al., 2014a). However, in the context of the current framework, it is crucial to recognize that a combination of covariation among individual functions and the utilized multifunctionality metric will determine the overall effects of global change on EMF (Bradford et al., 2014; Byrnes, Lefcheck, et al., 2014b; Figure 2: Box 2). For example, it is possible that a multifunctionality metric reflects the responses of some single functions but not others (Figure 2: Box 2). An understanding of whether functions respond similarly and a signal of whether this covariation may influence the interpretation of your multifunctionality responses can be quickly garnered from visualizing the covariation among functions using a correlation matrix or network (Berdugo et al., 2018; Birkhofer et al., 2018; Luo et al., 2018).

Completing these three steps will allow the examination of the direct and indirect GC-EMF effects that may be expected given the correlation structure of the hypothesized underlying model. Even though direct effects of global change on EMF do not explicitly consider the intermediate steps, a greater understanding of the relationship is gained by not considering the steps as a black box. The hypothesis generation exercise we present here can be conducted conceptually or through a data simulation exercise. The latter may be especially useful when considering the threshold approach to multifunctionality, because the responses are not always trivial to conceptualize. To aid this, we provide an interactive version of Figure 2: Box 2 as an online application, where hypothesized relationships can be provided by the user and potential multifunctionality responses simulated (<https://shiny.idiv.de/dg45koti/multifun-app/>).

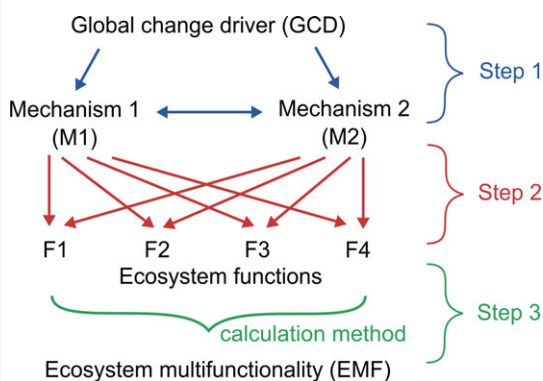


Figure 1: Box 2. Extension of the conceptual framework provided in Figure 1 demonstrating the suggested steps for building mechanistic hypotheses of global change effects on ecosystem multifunctionality. *Step 1* entails defining the effect of a global change driver on mechanisms that may be important for ecosystem functioning (blue arrows). These mechanisms may be biotic and/or abiotic, as illustrated in Figure 1. Two mechanisms are displayed here (M1 and M2), but there may be more and they may influence each other (horizontal blue arrow). At *Step 2*, the hypothesized additive or interactive effects of these mechanisms on individual functions (F1–F4) are defined (red arrows). Finally, *Step 3* involves considering how the method of multifunctionality calculation affects the interpretation of emergent global change effects (green brace).

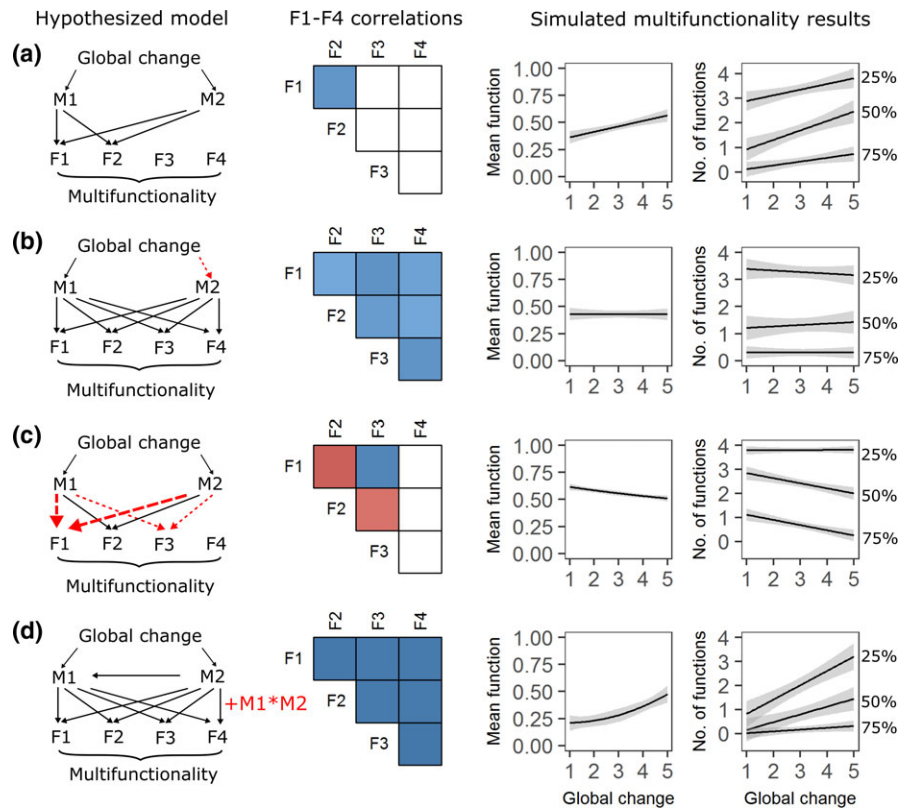


Figure 2: Box 2. Examples of using the framework to generate GC-EMF hypotheses and assess how interaction structures influence the emergent effects of global change drivers on different metrics of multifunctionality. The path diagrams (left column) show the hypothesized effects of global change on biotic and/or abiotic mechanisms (M1 and M2) and their subsequent effects on single functions (F1-F4). Solid black and dashed red lines show positive and negative effects, respectively, while line thickness indicates effect strength. The middle column displays a correlation matrix for F1-F4, where blue and red squares indicate positive and negative correlations, respectively (at significance level $p = 0.05$). The plots on the right show a simulation of the direct effect of global change on EMF that emerges from the defined correlation structure. The left plot shows average multifunctionality, and the right plot shows the number of functions that are above the 25%, 50%, and 75% thresholds. The underlying data were generated using the interactive version of this figure (<https://shiny.idiv.de/dg45koti/multifun-app/>). Rows show (a) a case where the two mechanisms affect some functions but not others, producing an overall positive GC-EMF effect; (b) a case where a global change driver influences mechanisms in opposing ways, negating any EMF responses even though all functions are positively correlated; (c) a case where strong effects on one function can drive EMF responses even if other functions respond in the opposite direction; (d) a case where adding interactive effects of M1 and M2 on F1-F4 to the additive models in cases a-c can produce complex responses.

Vandendorj et al., 2017; Zhang et al., 2016), resulting in altered EMF (Figure 1b).

In general, however, hypotheses were often highly generic statements and clear expectations for how and why global change may affect metrics of EMF through the alteration of single functions by biotic or abiotic mechanisms were scarce (but see e.g., Zhang et al., 2016; Vandendorj et al., 2017). Beyond hypotheses focusing on the mechanisms that modulate responses of specific functions to global change drivers, more consideration of the expected trade-offs or covariation among functions is required, as these patterns drive emergent responses of EMF. For example, a

shift in land-use change to accommodate grazing may decrease certain biotic variables, such as plant taxa richness and photosynthesis rates, but increase an abiotic driver of functioning, such as soil nutrient content (Figure 1b). Together, these responses may have potentially predictable impacts on aggregate measures of EMF. Current studies have laid important groundwork to begin understanding these patterns (e.g., Berdugo, Kéfi, Soliveres, & Maestre, 2018; Birkhofer et al., 2018; Luo et al., 2018), and future studies should strive to develop clear mechanistic hypotheses about the relationships that underlie responses for GC-EMF research to become a more predictive field of science (Box 2).

5 | DISENTANGLING THE MECHANISMS OF GLOBAL CHANGE EFFECTS ON MULTIFUNCTIONALITY

Central to identifying key factors for managing EMF under different global change scenarios is elucidating the relative importance of different biotic and abiotic mechanisms for mediating EMF responses to global change drivers (Allan et al., 2015; Zhang et al., 2016). However, this is often highly challenging due to the complex and potentially interacting mechanisms. For instance, there is support for the notion that global change impacts can induce cascades of interacting abiotic and biotic mechanisms, whereby one affects the other to yield net changes in EMF (as denoted by horizontal arrows between abiotic and biotic mechanisms in Figure 1). For example, Manning et al. (2017) hypothesized that a reduction in dung beetle abundance by pesticide use could in turn reduce dung incorporation into the soil and ultimately alter soil physical properties. Identifying these potentially complex interactions among biotic and abiotic mechanisms will greatly enhance our understanding of how global change will ultimately impact EMF. Where resources exist to measure a set of biotic and abiotic variables that may represent the most important mechanisms, complex interactions between abiotic factors, biotic factors, and multifunctionality may be effectively teased apart with a combination of appropriate statistical methods (Luo et al., 2018). These include approaches such as random forest analysis, which is suited to datasets with complex interaction structure and nonlinear responses (Cutler et al., 2007) and structural equation modeling (SEM), which is ideal for testing and separating multiple hypothesized relationships (Grace et al., 2012).

Indeed, nearly half of the reviewed studies explicitly investigated the relative role of different mechanisms with a SEM approach. In some cases, abiotic-mediated effects on EMF were generally stronger (though these were often not explicitly defined and more typically shown as “direct effects”; Constán-Nava et al., 2015; Peco et al., 2017; Zhang et al., 2016), while biodiversity-mediated effects were important in other cases (Delgado-Baquerizo et al., 2016; Liu et al., 2017; Luo et al., 2018). Such discrepancies among studies are likely due to the different types of mechanisms tested, as well as variation in the measurement of EMF and the global change drivers in question. This was clearly demonstrated in a number of the studies, whereby the relative strength of global change effects *via* abiotic or biotic mechanisms on multifunctionality was dependent on the global change driver, set of measured ecosystem functions, multifunctionality metric, or the spatiotemporal context considered (Allan et al., 2015; Alsterberg et al., 2017; Antikeira et al., 2018; Peco et al., 2017; Vandandorj et al., 2017).

There are several reasons to be cautious about using EMF metrics to infer mechanisms driving ecosystem change without carefully considering *a priori* hypotheses. In some cases, the hypothesized abiotic mechanisms were unable to be confirmed because the intermediate physical or chemical state variables were not measured. This typically resulted in studies concluding that these effects were “direct,” which may, in fact, subsume many unexplored indirect abiotic or biotic mechanisms. For instance, grazers may affect the function

of water infiltration through the direct effects of trampling on soil compaction, but this cannot be attributed without measures of soil density. A future priority should be designing studies to test hypothesized physicochemical pathways alongside biotic mechanisms that can be explicitly explored using analytical tools, such as SEM. Current results also highlight the importance of carefully considering which aspects of biodiversity are measured (Fu et al., 2018; Li et al., 2017). Indeed, Allan et al. (2015) note that direct effects in a SEM will be overestimated, if the selected biotic measures do not sufficiently capture the underlying drivers of EMF. For example, community evenness may be more important than richness in mediating global change effects (Li et al., 2017), though one may falsely conclude that richness is the key mediating mechanism, if evenness is not additionally included in such an analysis. There is also a risk that unexplained variation in EMF is channeled into seemingly direct effects, when in fact EMF is responding to some unmeasured biotic mechanism. Zhang et al. (2016) hypothesized this as a potential reason for finding direct global change effects in their structural equation model, because plausible direct mechanisms were lacking. While it is not feasible to forecast and measure all important variables everywhere, these potential issues should be considered when interpreting results to identify mechanisms. Potential missing variables may be identified from previous studies and included in future efforts to assess how global change drivers alter EMF.

6 | INSIGHTS FROM SINGLE AND MULTIPLE FUNCTIONS: SEEING THE FOREST AND THE TREES

Finally, we consider whether global change effects have been interpreted differently through the lens of EMF versus single functions. Nearly all studies in our review presented data on both single functions and their aggregate EMF metric. This approach was well justified; often the single functions underlying the multifunctionality metrics did not respond in a consistent manner. For instance, Constán-Nava et al. (2015) report that single functions related to phosphorus cycling responded in the opposite direction to single functions related to carbon cycling and productivity. Thus, metrics of multifunctionality often qualitatively reflected the positive or negative responses of some single functions, while other single functions showed an opposite response or no response (Alsterberg et al., 2017; Antikeira et al., 2018; Bradford et al., 2014; Ramus et al., 2017). The inverse was also observed, whereby global change drivers affected some single functions but not others, producing no discernible overall effects on EMF (Alsterberg, Sundback, & Gamfeldt, 2014; Manning et al., 2017). In contrast, others found that nearly all single functions responded in the same manner, which was inevitably reproduced in the multifunctionality metric (Chandregowda, Murthy, & Bagchi, 2018; Luo et al., 2018; Quero et al., 2013).

When functions respond dissimilarly, EMF metrics (particularly the averaging approach) can be misleading, potentially obscuring the responses of individual functions and masking causal relationships

(Bradford et al., 2014; Box 2). We argue that there are clear benefits to simultaneously considering both single functions and multifunctionality. For instance, invasion by shrubs is generally perceived to have a negative impact on a landscape when considering only grass cover, but this is not necessarily the case under an integrated perspective; shrubs actually increase a range of functions such as soil carbon and nitrogen content (Chandregowda et al., 2018). Multifunctionality can be viewed analogously to metrics of biotic communities. While a single number representing diversity or evenness does not provide the full story, neither does the abundance of one particular species. Ultimately, the most appropriate response variable will depend on the range of stakeholders involved (Box 1; Manning et al., 2018). Thus, although EMF metrics may enhance our ability to generalize about the total functioning of a system when individual functions are particularly numerous or respond in a similar fashion (Allan et al., 2015; Meyer et al., 2018), the additional presentation of single functions is strongly recommended in all cases.

Clear presentation of the multiple functions will allow insight to how global change may drive the coupled or uncoupled responses of single functions (or clusters of single functions), and how this may be related to the performance of different species or other components of biodiversity. One effective approach is reporting correlation matrices or networks of the single functions under different conditions or treatments (Berdugo et al., 2018; Birkhofer et al., 2018). Ultimately, there appear to be no clear thresholds where EMF is an effective response variable in GC-EMF research; this likely depends on the goal of the research and the number, identity, and covariation of the measured functions. For few functions that represent similar broad categories of functioning (e.g., soil formation or biomass production), it may be more informative to present all functions separately, while for many functions or clusters of functions, EMF can be a more tractable and informative response, particularly if there are interactions among biological processes.

7 | CONCLUSIONS






Our review of rapidly expanding GC-EMF research revealed extensive effects of global changes on EMF. We propose that in order to understand and predict global change effects on EMF, the underlying biotic and abiotic mechanisms need to be identified. While various mechanisms were tested in the reviewed studies, the presence and relative strength of biotic- and abiotic-mediated effects were highly variable, both within and among studies. This suggests that the suite of hypotheses, functions, and analytical methods may need to be assessed on a case-by-case basis. Nonetheless, this does not preclude future GC-EMF research from applying the general framework presented here, with an aim of advancing toward the formation of a more predictive field. Specifically, such studies will (a) develop concrete, a priori hypotheses about how global change will affect emergent EMF by considering covariation among single functions; (b) measure appropriate intermediate variables to statistically test underlying mechanisms; and (c) critically assess the implications of EMF responses in concert with single functions or

groups of single functions. Further, where researchers wish to inform policy or management with multifunctionality, they should relate the measured functions to specific stakeholder interests. Together, these guidelines will increase our basic understanding and interpretability of GC-EMF research and its application to ensure continued supply of ecosystem services under the ever-increasing challenges of global change.

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