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Mini Review

Unpacking net effects in plant ecology: current context and opportunities for progress

Rob W. Brooker [1,*], Andrew Hector [2], Vicky M. Temperton [3], Alexandra J. Wright [4], Beatriz A. Aguirre [5], Kathleen R. Balazs[6], Kathryn E. Barry[7], Bradley J. Butterfield [8], Christopher J. Lortie [9], Gianalberto Losapio [10,11], Shan Kothari [12], Bernhard Schmid [13], Christian Schöb [14,15], Laura Stefan [16], Ragan M. Callaway [17]

[1]The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK
[2]Department of Biology and Leverhulme Centre for Nature Recovery, University of Oxford, Oxford OX1 3RB, UK
[3]Institute of Ecology, School of Sustainability, Leuphana University Lüneburg, 21335 Lüneburg, Germany
[4]Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN 55108, USA
[5]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA
[6]Center for Natural Lands Management, Temecula, CA 92590, USA
[7]Ecology and Biodiversity, Department of Biology, Utrecht University, 3584 CH Utrecht, the Netherlands
[8]Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA
[9]Department of Biology, York University, Toronto, ON M3J 1P3, Canada
[10]Institute of Earth Surface Dynamics, University of Lausanne, CH-1015 Lausanne, Switzerland
[11]Department of Biosciences, University of Milan, 20133 Milan, Italy
[12]Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2E3, Canada
[13]Remote Sensing Laboratories, Department of Geography, University of Zurich, 8057 Zürich, Switzerland
[14]Instituto de Investigación en Cambio Global (IICG-URJC), Universidad Rey Juan Carlos, Calle Tulipán s/n, 28933 Móstoles, Spain
[15]Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Calle Tulipán s/n, 28933 Móstoles, Spain
[16]Cultivation Techniques and Varieties in Arable Farming, Agroscope, 1260 Nyon, Switzerland
[17]Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

***Correspondence:** Rob W. Brooker, Email: rob.brooker@hutton.ac.uk

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Abstract: Does plant ecology have a "net-effect" problem? Net effects are expressed in metrics such as biomass or density that identify an important overarching effect but are produced by a suite of subtle, interacting, and usually unidentified factors, or processes, that vary in intensity. Measuring net effects has led to groundbreaking discoveries in ecology. However, when the relative contributions of subtle interacting processes vary, so do net effects, potentially leading to conflicting conclusions about underlying mechanisms and drivers – both biotic and abiotic – which stymie integration, generalization, and application. To illustrate how unpacking net effects might enable generalization and application, we review the development of the stress gradient hypothesis, where the processes underpinning net effects are often conceptually incorporated, and then key innovations in the field of biodiversity–ecosystem functioning relationships. We then consider how unpacking net effects has enabled progress in the study of intercropping, and how it could contribute to ecological restoration. Finally, we identify where further unpacking of net effects can contribute to addressing apparent paradoxes, and potential experimental approaches to help with this challenge. Measuring net effects has enabled tremendous progress in ecology; but strategically unpacking net effects will improve our ability to generalize more effectively across ecosystems and species.

Keywords: plant interactions, net effects, biodiversity–ecosystem function, stress gradient hypothesis, intercropping, restoration

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INTRODUCTION

The net effects of plant interactions are the outcomes – often common measurements of plant success such as survival, biomass, or seed production – of many subtle, and often cryptic, processes. These processes include, for example, direct competition for resources (Tilman 1977), facilitation (Callaway 2007), and different modes of indirect interactions (Aschehoug & Callaway 2014; Jones & Callaway 2007; Sotomayor & Lortie 2015; Wootton 1994), which can themselves be altered by the abiotic environment (e.g., Bertness & Callaway 1994; Callaway et al. 2002). Measuring net effects is fundamental to our understanding of the ecology of plants and other sessile organisms (e.g., Connell 1961, 1983; Schoener 1983; Tilman 1996), plant community assembly (Afkhami et al. 2014; He et al. 2013; Kneitel & Chase 2004), and the effects of plant diversity on ecosystem functioning (Cardinale et al. 2012; Huang et al. 2018; Tilman et al. 2014; Weisser et al. 2017). We argue here that failing to partition, or unpack, the processes that underpin net effects limits the development and integration of some key areas of plant ecology.

The idea of unpacking net effects might be best communicated by examples. Examining one of these (Callaway et al. 1991) in detail, between 1945 and 1973 roughly 356,000 ha of oak woodlands in California were razed because the oaks were thought to suppress forage for livestock (Bolsinger 1988 in Mensing 2006). The hardest hit was a Californian endemic, blue oak (*Quercus douglasii*). However, some studies provided evidence that blue oaks *increased* productivity under their canopies (Holland 1980), creating a conundrum for generalizing about the net effects of blue oaks. Later, this variation in the net effects of blue oaks on the productivity of its understory grasses was quantified, and indeed, net effects were found to range from highly inhibitory to highly facilitative (Callaway et al. 1991). Via sequential experimentation with leaf water potentials, soil nutrients, fine-root distributions, and experiments with soil bioassays and root exclosures, the net effects of individual oaks were then "unpacked", a term we use throughout to indicate studies that attempt to understand the processes – both biotic and abiotic – driving a net-effect outcome. For *Q. douglasii*, unpacking net effects demonstrated facilitative effects by all *Q. douglasii* canopies via the creation of "fertile islands" (see Eldridge et al. 2024), but also that these facilitative effects depended on whether individual oaks accessed relatively permanent water sources (Callaway et al. 1991). Those that produced few shallow roots together with deep roots had facilitative effects while those that mostly produced dense shallow roots suppressed grasses (also see Aschehoug & Callaway 2014 for a continuation of these experiments). This sequence of experiments unpacked an understanding of the effect of *Q. douglasii* on its understory from "sometimes it suppresses, sometimes it enhances", to "one phenotype suppresses, and the other phenotype enhances", explaining conditionality (i.e., context-dependency) and generating further hypotheses.

This and other examples demonstrate the benefits of unpacking net effects, but we suggest two areas of plant ecology in particular would benefit by adopting this approach — the stress gradient hypothesis (SGH; Bertness & Callaway 1994; Bertness et al. 2024) and the role of biodiversity in regulating ecosystem functions (BEF). In the rest of this paper we 1) outline the development and aims of these two areas of research and their reliance on approaches that are based on measuring net effects, 2) demonstrate how unpacking can be fruitful where SGH and BEF come together, using intercropping and ecosystem restoration as two examples, 3) consider some apparent paradoxes at the interface of SGH and BEF concepts which can be addressed through unpacking, and 4) suggest some fruitful routes for unpacking net effects in SGH and BEF studies.

NET EFFECTS IN SGH AND BEF STUDIES

The two conceptual areas of SGH and BEF emerged mostly independently of each other. BEF research developed mainly in experimentally constructed communities in lowland grasslands and forests. In contrast, SGH studies focused on how interactions affected plant communities in physically stressful environments including salt marshes, marine intertidal systems, arctic and alpine tundra, and deserts (Bertness et al. 2024; Callaway 2007; but see Callaway 1998; del Rio et al. 2014; Dohn et al. 2013; He et al. 2013). Despite this initial isolation, both areas have clearly been highly dependent on the use of net effect approaches.

Stress Gradient Hypothesis (SGH) studies

A key component of the SGH is the balance between plant competition and facilitation, the latter loosely defined as the beneficial impact of one plant on a neighboring plant (Callaway 2007). Facilitation has been examined and quantified by ecologists for decades but moved into mainstream ecological thinking during the 1990s and 2000s (Bertness & Callaway 1994; Callaway et al. 2002; Hunter & Aarssen 1988). There is now extensive evidence supporting the SGH, showing both greater relative importance, and at times intensity (Brooker et al. 2005), of facilitation relative to competition as the environment becomes more severe (per Bertness & Callaway 1994; Bertness et al. 2024; Brooker & Callaghan 1998; Brooker et al. 2008; Cavieres et al. 2014).

Much of the evidence for the SGH is based on net effects, although these could be unpacked through approaches such as experimentally manipulating variables across gradients, thereby allowing comparisons among studies. For example, Michalet et al. (2014) statistically unpacked changes in net effects along altitudinal gradients due to environmental severity or due to the trait-mediated effects of neighbors. Partitioning net effects among regional temperatures demonstrated weaker net facilitative effects at high elevations in mesic ecosystems with warming temperatures, but stronger net facilitative effects at low elevations in xeric ecosystems. This refined the relatively limited generalized conclusions about the SGH across climates. Such unpacking to understand context-dependency may be crucial for understanding shifts in interactions that are generally consistent with the SGH, but not necessarily uniform across vegetation types, climates, and methodologies (He et al. 2013).

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A major element of SGH studies has been neighbor removal experiments: removing neighbors from around target individuals, but not from around control individuals, and comparing the responses of the targets to the controls (see Fonteyn & Mahall 1978). This assesses the net effects of neighbors, and has provided insight into species interactions in hundreds of studies, but with dozens of different net outcomes. To unpack these outcomes from the initial experiments and generalize, other variables can be manipulated in subsequent sequential experiments, or in multifactorial experiments. These approaches can provide a partial understanding of what caused the variation in net outcomes. Neighbor removal might decrease target growth or increase target mortality, while watering might eliminate this negative impact of neighbor removal, indicating that an element of the interaction between – and net effect of – neighboring plants was protection from drought. This conditionality or context dependency can be critical to predicting changes in net effects in space or time or with environmental change. Neighbor removal experiments have been a backbone of SGH research, but what has been far less common is moving beyond such assessments of net effects to the next level in the "unpacking hierarchy" and pinning down specific causal mechanisms (although see Cavieres et al. 2007; Michalet et al. 2014; Schöb et al. 2013).

Examining net effects of interactions in the context of the SGH can be affected by species turnover and intraspecific trait variation – not simply mean trait values – along gradients, which links interactions among species on gradients to functional ecology, as recognized by Lepš et al. (2011). They found that species turnover provided important insight into the functional composition of communities when disturbance (mowing) varied, whereas intraspecific trait variation was key to community responses when fertilization varied. The bottom line is that parsing net effects can deliver a great deal by integrating factors such as species turnover and intraspecific variation in traits into our understanding of the context-dependency of net effect ecosystem function measurements. It also helps us to apply our knowledge in applied contexts such as crop production and conservation management; a point explored in greater depth later in this paper.

Biodiversity–Ecosystem Functioning (BEF) studies

The study of biodiversity and ecosystem functioning emerged in the early 1990s (Naeem et al. 1994, 1995; Tilman 1996; Tilman et al. 1996) with several groundbreaking experiments in which biodiversity was experimentally manipulated. Naeem et al. (1994, 1995) manipulated food webs with four trophic levels in controlled 'ecotrons', where species were removed from each trophic level and key functions were measured, such as community respiration. This was then expanded to large field experiments in which plant diversity (a single trophic level) was manipulated; these researchers found that diversity increased both mean community productivity and the temporal stability of that productivity (Tilman 1996). This has now been consistently found across trophic levels, ecosystems, and geographic regions (Allan et al. 2013; Isbell et al. 2015; O'Connor et al. 2016; see also meta-analysis by Balvanera et al. 2006; Chen et al. 2025b, and reviews by Ali 2023; Tilman et al. 2014). Most of this work has focused on productivity or plant growth as the primary metric but has not unpacked net effects to explore variation in the intensity of outcomes.

A first step towards unpacking net outcomes in BEF studies was the introduction of a statistical additive partitioning method splitting the net effect of diversity on biomass production (NE) into complementarity effects (CEs) and selection effects (SEs; Loreau & Hector 2001). Hereafter, we refer to net biodiversity effects as NEs, consistent with Loreau & Hector (2001), and to distinguish them from the larger overall group of net effect metrics and approaches which is the focus of this paper (and which can be influenced by more than biodiversity).

Additive partitioning showed that mixtures can do better than the average monoculture because many species produce more yield in mixture than in monoculture (positive CE; CE = NE if all species have equal monoculture yield) or because a single or few species with high monoculture yield become(s) disproportionately dominant in mixture (positive SE). Additive partitioning has shown – amongst other things – that CEs explain roughly half or more of the NE of species richness on biomass (Cardinale et al. 2007) and tend to become stronger over time (Huang et al. 2018; Marquard et al. 2009; Reich et al. 2012; Wagg et al. 2022).

A key point is that NE is a particular application of the net-effect approach. Additive partitioning of the NE into CE and SE is a step toward understanding underlying processes, but these are still only statistical effects at a lower level within the "unpacking hierarchy". The biological mechanisms (e.g., plant interactions) are rarely investigated (see Barry et al. 2019), and there are further layers in the unpacking hierarchy. For example, a positive CE can be underpinned by niche partitioning, biotic feedback, or facilitation (Chen et al. 2025b). In addition, NEs focus only on biodiversity drivers, whereas other net effects can be driven by both biotic interactions and abiotic drivers.

Measuring net effects without unpacking underlying processes limits progress in plant ecology

Despite BEF and SGH research generally developing in isolation, there are similarities in the heavy reliance of their analytical approaches on net effect metrics. These metrics include log response ratios, mixture overyielding, or indices such as the Relative Interaction Index (RII; Armas et al. 2004). These metrics are then interpreted in terms of their fit to particular mechanistic scenarios, but this risks confirmation bias (Zvereva & Kozlov 2021), in this case specifically the attribution of an observed net effect response to the incorrect underlying process because of preconceptions. These problems are illustrated when we consider that multiple scenarios can be constructed to explain even a single net effect response such as increasing ecosystem functioning with increasing biodiversity

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(e.g., mixture overyielding), or a switch from negative neighbor effects to positive neighbor effects along a stress gradient (Fig. 1). Here we point out that generalization can be improved in cases where net effects are unpacked (Box 1). However, without experiments that independently – as crossed or sequential treatments – manipulate the underpinning processes, unpacking remains difficult and the breadth of possible mechanistic scenarios cannot be constrained. For example, only recently has empirical evidence demonstrated that facilitation can underpin statistically derived CEs and can increase in intensity with physical stress (Barry et al. 2019; Schöb et al. 2018; Wright et al. 2017).

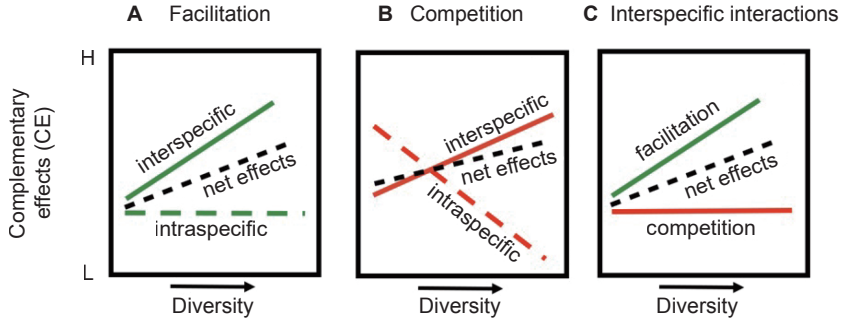


Figure 1: Illustration of the complex nature of interactions uncovered by unpacking net effects. Interactions can be synergistic, non-linear, and multiplicative but here we show linear, additive effects to illustrate the principles of net effects. The relationship between biodiversity and productivity is often examined in BEF studies using calculated CEs. Calculating CEs (and SEs) is a crucial step in unpacking net biodiversity effects (NEs), and provides enhanced mechanistic understanding, but these effects can themselves in turn be driven by changes in underlying processes. As an example, the plots (where the y axis runs L to H = low to high strength) show how, on diversity gradients, increasing CE effects (black dashed line) can be caused by (**A**) increasing interspecific facilitation relative to intraspecific facilitation, (**B**) strongly decreasing negative effects of intraspecific competition with weakly increasing negative effects of interspecific competition, or (**C**) increasing facilitation with constant competition. Note that the relationships are simply illustrating the directional trends in net CE effect and underlying drivers. Metrics such as CE are useful tools, and it can be difficult to move beyond certain levels of the "unpacking hierarchy", but we need to be conscious that many common metrics such as CE are to some extent still measurements of net effects, and that further unpacking is possible. It is also likely that net effects can be the sum (or product) of multiple, interacting variables in addition to diversity and that unpacking will require careful, and ideally, sequential examination for key processes that underpin the responses of net effects.

To be clear, we are not criticizing the usefulness of net effects — much crucial ecological theory is built on net effects. Instead, we highlight that without detailed studies of underlying processes our understanding of cause and effect in appropriate ecological contexts is limited, and it is also more difficult to generalize among studies even of the same conceptual subject. Without unpacking, simplistic interpretations and – perhaps more problematic – an assumption that a measurement of a net effect metric such as RII is in some way a measurement of the actual mechanism makes the search for mechanisms in either BEF, SGH, or many other fields even more difficult. An example of this (in retrospect) overly-simplistic interpretation is the concentration on traits to explain the consequences of biodiversity (van der Plas et al. 2020), which in turn could explain why other processes were initially under-represented in BEF studies, including indirect biotic effects (e.g., via soil biota; Schnitzer et al. 2011), and abiotic facilitation via amelioration of local micro-climate (Wright et al. 2017, 2021).

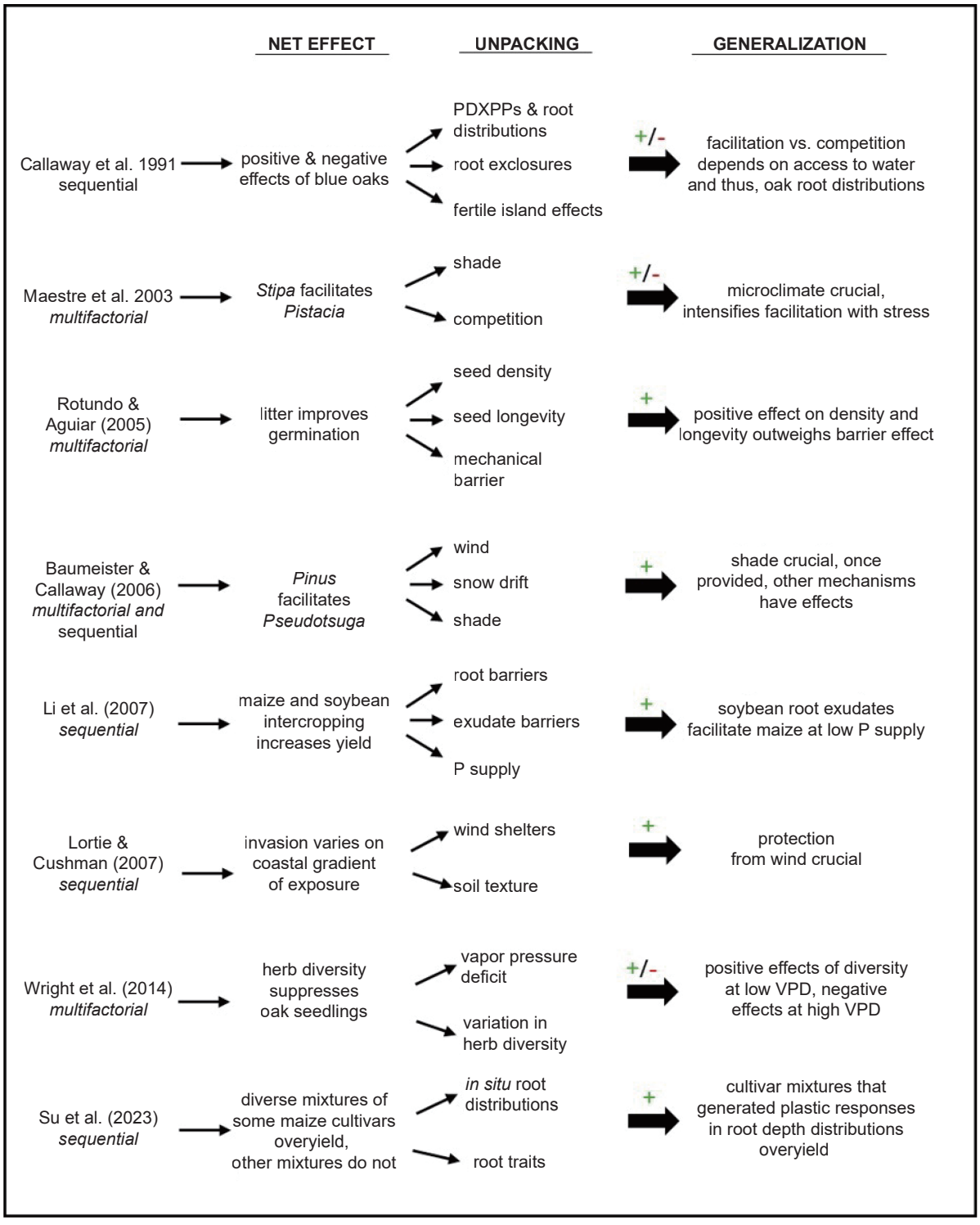
UNPACKING SUPPORTS APPLICATION

Intercropping

Unpacking net effects not only aids fundamental and generalizable ecological understanding but also supports the application of that understanding. This point is illustrated well by studies of intercropping, where many processes underlying net effects have been measured, which in turn helps improve the design and management of intercrops. All intercrops involve two or more crop species or genotypes growing together at the same time, in contrast to monocropping and rotation cropping (Li et al. 2021; Vandermeer 1989) and to the larger number of largely non-agricultural species used in most BEF experiments. The difference between a crop monoculture and mixture can generate large changes in functions (essentially net effects) including yield — and net outcomes may vary with changes in underpinning processes. Other net effects include sustained yield with reduced inputs (fuel, agrochemicals), suppression of weeds, pests and diseases, improved soil health, and enhanced structural diversity within the crop canopy which in turn supports a healthier invertebrate community and wider biodiversity in the farming landscape (Brandmeier et al. 2021; Gu et al. 2021; Homulle et al. 2022).

Interest in the effects of diversity as a driver of net effects has existed for many years in intercrop studies; and more recent studies have assessed variation in intercropping outcomes in the context of abiotic stress. Studying how ecosystem functions such as crop yield or disease shift from monocultures to mixtures is a BEF assessment (see Chadfield et al. 2022; Martin-Guay et al. 2018). Understanding the context dependency of, for example, the facilitative effects of legumes in intercrops on gradients of soil nitrogen availability combine BEF and SGH concepts (Sun et al. 2024). Indeed, early ecological reviews of facilitation (Hunter & Aarssen

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Box 1: Examples of unpacking net effects. Examples of studies in which net effects have been unpacked and how this had led to generalization. Note that PDXPPs are predawn xylem pressure potentials. +, - symbols above large arrows show general trends in the unpacked results: +/− shows partitioning yielding predictable shifts from competition and facilitation; the + symbols show where a facilitative mechanism was identified.

1988) drew many of their examples from crop systems and their exploration of net-effect metrics, and the net effect measures used in BEF studies have their roots in measures of crop yield (reviewed by Wagg et al. 2019).

Studies of intercropping have unpacked processes driving net effects (Boudreau 2013; Li et al. 2007; reviews by Li et al. 2014 and Brooker et al. 2015). Some of the most fascinating examples of unpacked processes in intercropping studies, often explored through sequential experimental approaches, are related to root exudates. For example, Li et al. (2016) found that exudates from maize (*Zea mays*) stimulated nodulation and N-fixation by faba bean (*Vicia faba*), and this correlated

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with increases in yield. In similar experiments, Li et al. (2007) found that maize yield increased when intercropped with faba bean and that this was due to increased uptake of phosphorus that had been mobilized by organic acids and protons released from faba bean roots. Understanding these effects of root exudates helps to generalize about when intercropping is successful or not, and so to improve the design and management of intercrop systems.

Other studies have also linked BEF concepts – in particular the context dependency of beneficial effects – to intercropping. For example, Su et al. (2023) showed that crop diversity increased stability in production over time more in climatically stressful conditions, primarily through facilitation, than in benign environments. Engbersen et al.'s (2021) and Schmutz & Schöb's (2023) mesocosm-based studies of crop mixtures demonstrated the potential role of temporal as well as spatial niche differentiation, foundational in BEF studies, in driving yield increase in intercropping. Schöb et al. (2023) found that ecological processes discovered in BEF studies also operate in crop systems, and SGH-type responses have also been found in intercropping systems. For example, maize benefited more from growing in three-species polycultures under low moisture conditions (Ramirez & Wright 2023). Natarajan & Willey (1986) reported that positive effects in intercropped systems increased as water stress increased. Shi et al. (2023) found that the benefits from intercropping peanuts (*Arachis hypogaea*) and sorghum (*Sorghum bicolor* (L.) Moench) were greater when salt stress was higher. Nyawade et al. (2019) found that different combinations of intercropped species improved yield on an elevational gradient in Kenya, but this was dependent on matching crop species to each environment. For instance, in nitrogen and phosphorus gradients, the facilitative effect of intercropped white lupine on wheat varied from strong when nutrients were low to weak when nutrients were high.

All these examples of processes and shifts on gradients illustrate how and when certain net effects occur and provide opportunities for generalization (Box 1), and how unpacking net effects increases (agro)ecological knowledge which in turn aids the design and management of intercrops. Further studies that identify species or genotypes for management or breeding to enhance facilitation and to reduce the competitive impacts of neighbors may be important next steps, and the traits selected can be informed by studies that unpack the net effects of intercropping. More broadly, evidence from intercropping studies indicates that net effects are indeed influenced by competing and different processes at different times and places, and that understanding this context-dependency contributes to our understanding of net effects and our application of that understanding.

Ecological restoration

Applied ecological restoration is another area which would gain from unpacking net effects. Ecological restoration initiates or accelerates the recovery of degraded ecosystems (Gann et al. 2019) and is beset by variation and conditionality in outcomes (e.g., Emsens et al. 2022; Gerrits et al. 2023). Brudvig (2017) articulated the role of context-dependency in regulating restoration success, suggesting that practitioners consider "…the drivers of variation among existing restoration efforts, [and] experiments to quantify and understand variation in restoration outcomes…", which in turn would be aided by unpacking net effects.

A good example of tailoring restoration to understanding the context dependency of net ecological outcomes focuses on biodiversity in grasslands. Mowing or grazing generally increases species diversity (Maron & Jefferies 2001; Smith et al. 2018), but not always (Socher et al. 2013), and this variation in net effects may be due to differences in soil fertility. Low soil nutrient concentrations or aridity can increase the intensity of facilitation (Callaway 2007) by legumes (Mulder et al. 2002; Temperton et al. 2007), which may either enhance or counteract the effects of mowing and grazing.

Unpacking net effects among natives and invasives can also be insightful. Nagy et al. (2022) reported that mowing to suppress the European invader *Solidago gigantea* yielded effects from almost complete suppression to increasing *Solidago* density by up to five times. Taking initial steps to unpacking this variation using sequential experiments, they first showed that the native *Tanacetum vulgare* strongly suppressed *Solidago*, but only in the absence of mowing. In a second experiment, in mowing treatments, *Tanacetum* facilitated the invader. While representing the early stages of unpacking net effects, this example – along with those given above – illustrates the potential for unpacking to explain variation of outcomes in restoration and conservation management, which can then inform improved approaches.

Priority effects, which derive from the order that species arrive or initiate growth at a site, can be important for basic community organization and applied restoration success (Fukami 2015; Weidlich et al. 2021), for example by excluding invasive species (Hess et al. 2020; Wilsey 2021). If we understand better how priority effects arise mechanistically, we could then use them to greater advantage in restoration efforts. However, priority effect research suffers from the same net-effect issues (as illustrated in Fig. 1), whereby overall outcomes can be due to negative and positive priority effects that may be additive or neutralizing. Indeed, a priority effect can be considered another example of a net effect. Priority-effect research has traditionally assumed niche preemption to be critical and that negative interactions such as competition drive priority effects, with facilitative interactions receiving less attention (Weidlich et al. 2021). This sets up a key opportunity for sequential experiments, because facilitation is increasingly recognized as playing an important role in processes such as priority effect-driven overyielding (Delory et al. 2021). For example, facilitation-based priority effects can be important in restoration of peatlands, where vigorous growth of some *Sphagnum* species (e.g., *S. magellanicum*) depends on the prior establishment and hummock-forming activities of other species such as *S. fuscum* (Johnson et al. 2015). In turn, the strength of facilitation can be actively manipulated, for example by planting functionally and morphologically diverse combinations of species to foster strong facilitative or niche-partitioning CEs in forest restoration (Huang et al. 2018; Veryard et al. 2023).

As in SGH studies, ecosystem engineers, such as nurse

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plants, play pivotal roles in generating priority effects and shaping communities (Gómez-Aparicio et al. 2004; Jones et al. 1994; Losapio et al. 2021, 2024). Their ability to modify microhabitats, buffer environmental stress, and enhance nutrient availability indicate a great potential to improve ecosystem recovery in degraded environments (Byers et al. 2006; Losapio et al. 2024). Some sequential experiments have linked ecotypic variation in nurse plant traits to variation in their community-shaping roles (Michalet et al. 2011). Atkinson et al. (2022) quantified the mean success of restoration projects on biodiversity, a net effect, and variation in success, suggesting that unpacking that variation might be important. The potential sources of variation in biodiversity responses appeared to include prior land use and restoration protocols, indicating "the need for new research confronting the causes of variability in restoration outcomes." Grman et al. (2013) used variation partitioning to unpack potential mechanistic components of restoration success and found that seed mix characteristics and site age explained a large proportion of variation in net effect metrics of species richness and community composition in restored prairies. These studies show that at least some of the unexplained variation in restoration outcomes can be explained by unpacking net effects, and more importantly improve our ability to generalize and predict the outcome of different restoration protocols.

However, despite the promise of manipulating processes such as priority effects and the impacts of ecosystem engineers, ecological restoration may remain limited by a continued focus on net effects. This is true even for well-studied ecosystems such as hay meadows, where we normally still rely on net-effect approaches but need to understand the relative roles of facilitation vs competition and their context-dependency across time, soil types, or precipitation gradients (Alonso-Crespo et al. 2025; Delory et al. 2021; Weidlich et al. 2018). Deepening our understanding of underlying mechanisms by unpacking net effects will benefit restoration, for example by enabling species selection to promote beneficial priority effects in specific communities and through the identification of key environmental factors that can be manipulated to enhance restoration outcomes.

UNPACKING TO AID INTEGRATION

We noted that recent empirical evidence has demonstrated that facilitation operates as a separate process within complementarity effects (CEs, above) and can increase in intensity with abiotic stress (Barry et al. 2019; Chen et al. 2025b; Schöb et al. 2018; Wright et al. 2017). This perspective is starting to bridge the general gap between BEF and SGH concepts and is vital because an integrated approach is necessary to further generalization and to address key applied issues.

Without such integration and a move away from reliance on net effects, apparent paradoxes can occur. As an example of this, consider that complementarity effects (CE) in many studies have been shown to increase in complex and resource-rich environments (Tilman et al. 2014), and that (as mentioned above) facilitation has been shown to be a component of CEs. But consider also that facilitation, both as a component of CEs, and more widely based on general principles of the SGH, is expected to increase in more severe environments (Wright et al. 2017). This appears to be contradictory. A potential explanation is that in more productive environments CEs are more dependent on niche complementarity (in other words, the avoidance of competition) and the relative role of facilitation declines. But for there to be a general increase in CEs in complex and resource-rich environments, the positive effects of increasing niche complementarity on CEs must outweigh the declining effect of facilitation. This is a critical prediction because if activities such as intercropping or restoration are intended for resource-rich environments, to maximize CEs the focus should be on the niche complementarity of components. In contrast, in stressful environments the focus should be on maximizing facilitative processes. Such a mechanism might go some way to explaining the difficulties of understanding BEF effects through the analysis of plant traits, as per van der Plas et al. (2020; but see Chen et al. 2025a, b).

Such a formulation integrates SGH and BEF concepts with potential applied benefits, but to the best of our knowledge has not been considered widely in the literature or explored in detail by any targeted experiments. Its exploration would be dependent upon understanding the underlying processes regulating CEs across environmental gradients and not simply an assessment of the net effects of neighbors which would simply show positive CEs in both stressful abiotic and beneficial resource-complex environments.

POINTERS FOR PROGRESS

Given the wide-ranging potential benefits for unpacking of net effects, what are the routes open to plant ecologists? We have mentioned a few options and now explore them in more detail.

Above, we illustrated the basic principles of sequential experimentation through the study of blue oak impacts on understory forage production. In sequential experimentation (Fisher 1952) an experimenter does not consider "material as wholly passive but instead looks to what may be learnt from it with a view to the improvement and extension of the enquiry." In other words, each subsequent experiment is informed by the results of the previous one (see Baumeister & Callaway 2006; Maestre et al. 2003). Our use of "sequential" is informal (again see Fisher 1952) and different than formal sequential statistical analyses (e.g., Wald 2004). Sequential experiments are successively derived from discoveries, much like the general expectations of repeatedly applying the scientific method. A discovery in a first experiment can lead to and guide a second experiment, and a discovery from that can lead to and guide a third experiment, and so on. A good recent example of this sequential approach is provided by Su et al. (2023) who first found that experimentally planting mixtures of maize cultivars increased productivity – a net effect of overyielding. Second, they found that spatial root segregation in two-cultivar mixtures was greater than would be predicted from each cultivar grown alone, parsing the net effect into cultivar-specific responses. And finally, the extent of the spatial segregation of the roots of different cultivar

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combinations correlated with grain mass and productivity, connecting the – unpacked – parsed responses into a potentially causal relationship.

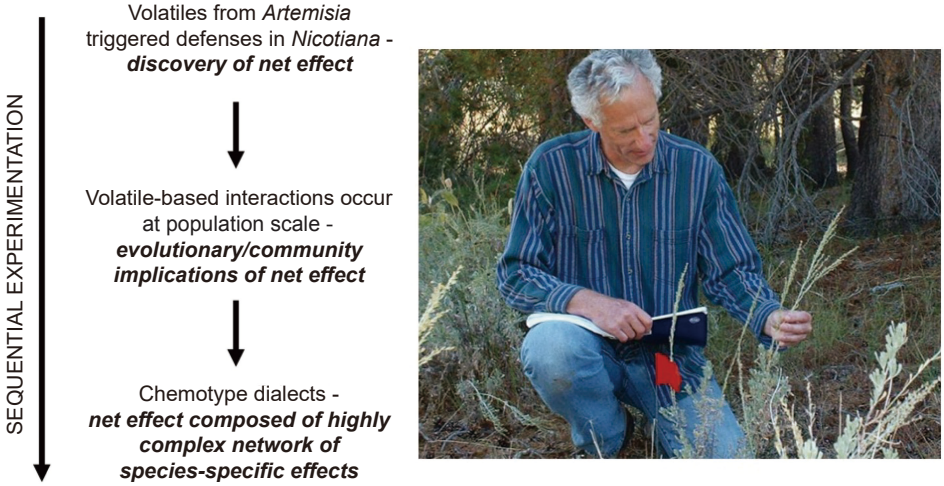
On the other hand, "multifactorial experiments", which are much more common in the literature, test two or more factors and their interactions simultaneously to unpack net effects. Multifactorial experiments with the goal of unpacking net effects in BEF studies are highly demanding in design, implementation, and logistics, but there are good examples. Maron & Marler (2008) took a multifactorial approach, with diversity treatments crossed with water supply treatments, and showed that higher native diversity suppressed invasion by the non-native *Centaurea stoebe*, but that this resistance was context-dependent, being higher at low water supply, and indicating that high resource supply exacerbated the competitive advantage of the invader (also see Mulder et al. 2001). Net effects were measured as the biomass of invading *C. stoebe*, which was dramatically reduced by native diversity in all treatments, but water supply substantially affected the intensity of native resistance.

A recent meta-analysis by Hong et al. (2022) of 46 multifactorial experiments manipulating species richness and key environmental variables, including warming, drought, fertilization, and carbon dioxide, demonstrated their outstanding potential for unpacking net effects in BEF studies. A challenge for multi-factorial experiments, however, is that they require knowledge of the system that may not be available before an experiment is conducted and thus may be less effective than sequential experiments in unpacking net effects (see Fisher 1952). In his book on experimental design, Montgomery (2017) supports this point, arguing "A single comprehensive experiment requires the experimenters to know the answers to a lot of questions, and if they are wrong, the results will be disappointing." In other words, new clues that emerge from initial experiments are difficult to explore with multifactorial experiments.

Given the benefits of sequential experiments, the obvious question is why are they not more common? One possibility is that such studies *are* undertaken but are not easy to spot because each step is published as a separate paper and often in different journals (see Box 2), in contrast to some classic studies of plant ecology which received sequential multi-part publication in a single journal (see for example Willis et al. 1959a, b). However, we suggest the issue is not a lack of visibility for sequential studies. We can imagine instead a scenario where sequential experiments take longer to conclude and sequential funding is hard to come by, and so complex experiments are planned to attempt to address multiple questions in a single study while funding is available. We also suggest that big and complex experiments are more attractive to the reviewers of funding applications than sequential studies in which five-year plans cannot be spelled out in year one. It would be ironic if this is in fact partially responsible for slowing progress.

CONCLUSIONS

Net-effect measurements underpin a tremendous amount of progress in ecology. BEF and SGH studies have depended heavily on assessments of net effects for their conceptual



Box 2: Volatile communication among *Artemisia tridentata* shrubs: an example of unpacking. Throughout this commentary, we focus on single publications that unpack net effects in sequential and multifactorial experiments. However, there are many examples of sequential experiments in different publications. One of the best examples of this is provided by Rick Karban (see photo; photo credit Mikaela Huntzinger; used with permission) and colleague's research on volatile communication among *Artemisia tridentata* shrubs. Motivated by volatile-based interactions reported by Farmer & Ryan (1990; R. Karban, *pers. com.*), they found that volatiles from damaged *A. tridentata* served as a warning, triggering defensive responses in *Nicotiana attenuata* (Karban et al. 2000), but the big picture consequences of this communication were not clear. Next, Karban et al. (2006) showed that volatile-based communication among *Artemisia* occurred over much larger distances, establishing it as meaningful within populations, but raising questions about the evolutionary ramifications of warning competitors. This led to the discovery of different chemotypes within populations and dialects that limited communication among unrelated individuals (Karban et al. 2014, 2016). If the net effect of volatile communication was simply measured among large numbers of *Artemisia* individuals, the conclusion would have been that sometimes plants communicate using volatiles and sometimes they do not. Of course, none of this implies "intent" by either interacting species, but discovering dialects unpacked the initial conclusion and demonstrated an unexpected level of generality for volatile communication.

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frameworks. Both research fields have produced important theory (He et al. 2013; Isbell et al. 2018; Lortie & Callaway 2006; Tilman et al. 2014), but both are also still constrained to some degree by variation and conditionality in outcomes. Unpacking net effects is possible via sequential and multifactorial experimental approaches and cross-study comparisons that explain variation in outcomes (He et al. 2013; Spehn et al. 2002), and that move us to the next level down in mechanistic understanding and towards generalization. We suggest that such unpacking can be optimized through multifactorial and preferably sequential (after Fisher 1952) experiments. Unpacking will provide opportunities to challenge and generalize assumptions concerning dominant mechanisms. In the spirit of De Laender et al. (2016), by explicitly accounting for variation in the abiotic environment, we can better "predict the functioning of ecosystems …". A deeper understanding of the mechanisms underlying positive biodiversity–ecosystem functioning relationships across environmental gradients will allow us to link BEF results to applied goals such as restoration and food production. Similarly, mechanistic examinations of the processes underlying changes in net plant–plant interactions along environmental gradients will uncover traits, trait combinations, and environmental conditions where different management and restoration approaches can be best applied. Overall, unpacking net effects can provide opportunities to address apparent paradigms and better generalize across the impressive collection of case studies in key fields in plant ecology, and to then apply this knowledge to major global challenges such as food security and the conservation and restoration of ecosystems.

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Competing Interests

The authors declare no competing interests.

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