

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

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41

42 **Abstract**

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

58 **Introduction**

59 The net effects of plant interactions are the outcomes — often common measurements of plant
60 success such as survival, biomass, or seed production — of many subtle, and often cryptic, processes. These
61 processes include, for example, direct competition for resources (Tilman 1977), facilitation (Callaway 2007),
62 and different modes of indirect interactions (Sotomayor and Lortie 2015; Wootton 1994; Jones and Callaway
63 2007; Aschehoug and Callaway 2014), which can themselves be altered by the abiotic environment (e.g.,
64 Bertness & Callaway 1994; Callaway et al. 2002). Measuring net effects is fundamental to our understanding
65 of the ecology of plants and other sessile organisms (e.g., Connell 1961, 1983; Schoener 1983; Tilman 1996),
66 plant community assembly (Kneitel and Chase 2004; He et al. 2013; Afkhami et al. 2014), and the effects of
67 plant diversity on ecosystem functioning (Cardinale et al. 2012; Tilman et al. 2014; Weisser et al. 2017;
68 Huang et al. 2018). We argue here that failing to partition, or unpack, the processes that underpin net effects
69 limits the development and integration of some key areas of plant ecology.

70 The idea of unpacking net effects might be best communicated by examples. Examining one of these
71 (Callaway et al. 1991) in detail, between 1945 and 1973 roughly 356,000 ha of oak woodlands in California
72 were razed because the oaks were thought to suppress forage for livestock (Bolsinger 1988, in Mensing
73 2006). The hardest hit was a Californian endemic, blue oak (*Quercus douglasii*). However, some studies
74 provided evidence that blue oaks *increased* productivity under their canopies (Holland 1980), creating a
75 conundrum for generalizing about the net effects of blue oaks. Later, this variation in the net effects of blue
76 oaks on the productivity of its understory grasses was quantified, and indeed, net effects were found to range
77 from highly inhibitory to highly facilitative (Callaway et al. 1991). Via sequential experimentation with leaf
78 water potentials, soil nutrients, fine-root distributions, and experiments with soil bioassays and root
79 exclosures, the net effects of individual oaks were then “unpacked”, a term we use throughout to indicate
80 studies that attempt to understand the processes - both biotic and abiotic - driving a net-effect outcome. For
81 *Q. douglasii*, unpacking net effects demonstrated facilitative effects by all *Q. douglasii* canopies via the
82 creation of “fertile islands” (see Eldridge et al. 2024), but also that these facilitative effects depended on
83 whether individual oaks accessed relatively permanent water sources (Callaway et al. 1991). Those that
84 produced few shallow roots together with deep roots had facilitative effects while those that mostly produced
85 dense shallow roots suppressed grasses (also see Aschehoug and Callaway 2014 for a continuation of these
86 experiments). This sequence of experiments unpacked an understanding of the effect of *Q. douglasii* on its
87 understory from “sometimes it suppresses, sometimes it enhances”, to “one phenotype suppresses, and the
88 other phenotype enhances”, explaining conditionality (i.e., context-dependency) and generating further
89 hypotheses.

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

100 **Net effects in SGH and BEF studies**

101 The two conceptual areas of SGH and BEF emerged mostly independently of each other. BEF
 102 research developed mainly in experimentally constructed communities in lowland grasslands and forests. In
 103 contrast, SGH studies focused on how interactions affected plant communities in physically stressful
 104 environments including salt marshes, marine intertidal systems, arctic and alpine tundra, and deserts
 105 (Callaway 2007; Bertness et al. 2024; but see Callaway 1998; Dohn et al. 2012; del Rio et al. 2012; He et al.
 106 2013). Despite this initial isolation, both areas have clearly been highly dependent on the use of net effect
 107 approaches.

108

109 *Stress Gradient Hypothesis (SGH) studies*

110 A key component of the SGH is the balance between plant competition and facilitation, the latter
 111 loosely defined as the beneficial impact of one plant on a neighboring plant (Callaway, 2007). Facilitation
 112 has been examined and quantified by ecologists for decades but moved into mainstream ecological thinking
 113 during the 1990s and 2000s (Hunter and Aarssen 1988; Bertness and Callaway 1994; Callaway et al. 2002).
 114 There is now extensive evidence supporting the SGH, showing both greater relative importance, and at times
 115 intensity (Brooker et al. 2005), of facilitation relative to competition as the environment becomes more
 116 severe (per Bertness and Callaway 1994; Brooker and Callaghan 1998; Brooker et al. 2008; Cavieres et al.
 117 2014; Bertness et al. 2024).

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

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

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

151 *Biodiversity–Ecosystem Functioning (BEF) studies*

152 The study of biodiversity and ecosystem functioning emerged in the early 1990s (Naeem et al. 1994,
153 1995; Tilman 1996; Tilman et al., 1996) with several groundbreaking experiments in which biodiversity was
154 experimentally manipulated. Naeem et al. (1994, 1995) manipulated food webs with four trophic levels in
155 controlled ‘ecotrons’, where species were removed from each trophic level and key functions were measured,

156 such as community respiration. This was then expanded to large field experiments in which plant diversity (a
157 single trophic level) was manipulated; these researchers found that diversity increased both mean community
158 productivity and the temporal stability of that productivity (Tilman 1996). This has now been consistently
159 found across trophic levels, ecosystems, and geographic regions (Allan et al. 2013; Isbell et al. 2015;
160 O'Connor et al. 2016; see also meta-analysis by Balvanera et al. 2006, Chen et al. 2025a, and reviews by
161 Tilman et al. 2014; Ali 2023). Most of this work has focused on productivity or plant growth as the primary
162 metric but has not unpacked net effects to explore variation in the intensity of outcomes.

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

169 Additive partitioning showed that mixtures can do better than the average monoculture because
170 many species produce more yield in mixture than in monoculture (positive CE; $CE = NE$ if all species have
171 equal monoculture yield) or because a single or few species with high monoculture yield become(s)
172 disproportionately dominant in mixture (positive SE). Additive partitioning has shown — amongst other
173 things — that CEs explain roughly half or more of the NE of species richness on biomass (Cardinale et al.
174 2007) and tend to become stronger over time (Marquard et al. 2009; Reich et al. 2012; Huang et al. 2018;
175 Wagg et al. 2022).

176 A key point is that NE is a particular application of the net-effect approach. Additive partitioning of
177 the NE into CE and SE is a step toward understanding underlying processes, but these are still only statistical
178 effects at a lower level within the “unpacking hierarchy”. The biological mechanisms (e.g., plant interactions)
179 are rarely investigated (see Barry et al. 2019), and there are further layers in the unpacking hierarchy. For
180 example, a positive CE can be underpinned by niche partitioning, biotic feedback, or facilitation (Chen et al.
181 2025a). In addition, NEs focus only on biodiversity drivers, whereas other net effects can be driven by both
182 biotic interactions and abiotic drivers.

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

185 Despite BEF and SGH research generally developing in isolation, there are similarities in the heavy
186 reliance of their analytical approaches on net effect metrics. These metrics include log response ratios,
187 mixture overyielding, or indices such as the Relative Interaction Index (RII; Armas et al. 2004). These
188 metrics are then interpreted in terms of their fit to particular mechanistic scenarios, but this risks
189 confirmation bias (Zvereva and Kozlov 2021), in this case specifically the attribution of an observed net
190 effect response to the incorrect underlying process because of preconceptions. These problems are illustrated
191 when we consider that multiple scenarios can be constructed to explain even a single net effect response such
192 as increasing ecosystem functioning with increasing biodiversity (e.g. mixture overyielding), or a switch
193 from negative neighbor effects to positive neighbor effects along a stress gradient (Figure 1). Here we point
194 out that generalization can be improved in cases where net effects are unpacked (Box 1). However, without
195 experiments that independently — as crossed or sequential treatments — manipulate the underpinning
196 processes, unpacking remains difficult and the breadth of possible mechanistic scenarios cannot be
197 constrained. For example, only recently has empirical evidence demonstrated that facilitation can underpin
198 statistically derived CEs and can increase in intensity with physical stress (Wright et al. 2017; Schöb et al.
199 2018; Barry et al. 2019).

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

211

212 **Unpacking supports application**

213 *Intercropping*

214 Unpacking net effects not only aids fundamental and generalizable ecological understanding but also
215 supports the application of that understanding. This point is illustrated well by studies of intercropping,
216 where many processes underlying net effects have been measured, which in turn helps improve the design
217 and management of intercrops. All intercrops involve two or more crop species or genotypes growing
218 together at the same time, in contrast to monocropping and rotation cropping (Vandermeer 1989; Li et al.
219 2021) and to the larger number of largely non-agricultural species used in most BEF experiments. The
220 difference between a crop monoculture and mixture can generate large changes in functions (essentially net
221 effects) including yield — and net outcomes may vary with changes in underpinning processes. Other net
222 effects include sustained yield with reduced inputs (fuel, agrochemicals), suppression of weeds, pests and
223 diseases, improved soil health, and enhanced structural diversity within the crop canopy which in turn
224 supports a healthier invertebrate community and wider biodiversity in the farming landscape (Brandmeier et
225 al. 2021; Gu et al. 2021; Homulle et al. 2022).

226 Interest in the effects of diversity as a driver of net effects has existed for many years in intercrop
227 studies; and more recent studies have assessed variation in intercropping outcomes in the context of abiotic
228 stress. Studying how ecosystem functions such as crop yield or disease shift from monocultures to mixtures
229 is a BEF assessment (see Martin-Guay et al. 2018; Chadfield et al. 2022). Understanding the context
230 dependency of, for example, the facilitative effects of legumes in intercrops on gradients of soil nitrogen
231 availability combine BEF and SGH concepts (Sun et al. 2024). Indeed, early ecological reviews of
232 facilitation (Hunter and Aarssen 1988) drew many of their examples from crop systems and their exploration
233 of net-effect metrics, and the net effect measures used in BEF studies have their roots in measures of crop
234 yield (reviewed by Wagg et al. 2019).

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

241 was due to increased uptake of phosphorus that had been mobilized by organic acids and protons released
242 from faba bean roots. Understanding these effects of root exudates helps to generalize about when
243 intercropping is successful or not, and so to improve the design and management of intercrop systems.

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

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

268

269 *Ecological restoration*

270 Applied ecological restoration is another area which would gain from unpacking net effects.
271 Ecological restoration initiates or accelerates the recovery of degraded ecosystems (Gann et al. 2019) and is
272 beset by variation and conditionality in outcomes (e.g., Emsens et al. 2022; Gerrits et al. 2023). Brudvig et al.
273 (2017) articulated the role of context-dependency in regulating restoration success, suggesting that
274 practitioners consider “...the drivers of variation among existing restoration efforts, [and] experiments to
275 quantify and understand variation in restoration outcomes...”, which in turn would be aided by unpacking
276 net effects.

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

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

291 Priority effects, which derive from the order that species arrive or initiate growth at a site, can be
292 important for basic community organization and applied restoration success (Fukami 2015; Weidlich et al.
293 2021), for example by excluding invasive species (Hess et al. 2020; Wilsey 2021). If we understand better
294 how priority effects arise mechanistically, we could then use them to greater advantage in restoration efforts.
295 However, priority effect research suffers from the same net-effect issues (as illustrated in Figure 1), whereby
296 overall outcomes can be due to negative and positive priority effects that may be additive or neutralizing.

297 Indeed, a priority effect can be considered another example of a net effect. Priority-effect research has
298 traditionally assumed niche preemption to be critical and that negative interactions such as competition drive
299 priority effects, with facilitative interactions receiving less attention (Weidlich et al. 2021). This sets up a
300 key opportunity for sequential experiments, because facilitation is increasingly recognized as playing an
301 important role in processes such as priority effect-driven overyielding (Delory et al. 2021). For example,
302 facilitation-based priority effects can be important in restoration of peatlands, where vigorous growth of
303 some *Sphagnum* species (e.g., *S. magellanicum*) depends on the prior establishment and hummock-forming
304 activities of other species such as *S. fuscum* (Johnson et al. 2014). In turn, the strength of facilitation can be
305 actively manipulated, for example by planting functionally and morphologically diverse combinations of
306 species to foster strong facilitative or niche-partitioning CEs in forest restoration (Huang et al. 2018; Veryard
307 et al. 2023).

308 As in SGH studies, ecosystem engineers, such as nurse plants, play pivotal roles in generating
309 priority effects and shaping communities (Jones et al. 1994; Gómez-Aparicio et al. 2004; Losapio et al. 2021,
310 2024). Their ability to modify microhabitats, buffer environmental stress, and enhance nutrient availability
311 indicate a great potential to improve ecosystem recovery in degraded environments (Byers et al. 2006;
312 Losapio et al. 2024). Some sequential experiments have linked ecotypic variation in nurse plant traits to
313 variation in their community-shaping roles (Michalet et al. 2011). Atkinson et al. (2022) quantified the mean
314 success of restoration projects on biodiversity, a net effect, and variation in success, suggesting that
315 unpacking that variation might be important. The potential sources of variation in biodiversity responses
316 appeared to include prior land use and restoration protocols, indicating “the need for new research
317 confronting the causes of variability in restoration outcomes.” Grman et al. (2013) used variation partitioning
318 to unpack potential mechanistic components of restoration success and found that seed mix characteristics
319 and site age explained a large proportion of variation in net effect metrics of species richness and community
320 composition in restored prairies. These studies show that at least some of the unexplained variation in
321 restoration outcomes can be explained by unpacking net effects, and more importantly improve our ability to
322 generalize and predict the outcome of different restoration protocols.

323 However, despite the promise of manipulating processes such as priority effects and the impacts of
324 ecosystem engineers, ecological restoration may remain limited by a continued focus on net effects. This is
325 true even for well-studied ecosystems such as hay meadows, where we normally still rely on net-effect

326 approaches but need to understand the relative roles of facilitation vs competition and their context-
327 dependency across time, soil types, or precipitation gradients (Weidlich et al. 2018; Delory et al. 2021,
328 Alonso-Crespo et al. 2025). Deepening our understanding of underlying mechanisms by unpacking net
329 effects will benefit restoration, for example by enabling species selection to promote beneficial priority
330 effects in specific communities and through the identification of key environmental factors that can be
331 manipulated to enhance restoration outcomes.

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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 (Wright et al. 2017; Schöb et al. 2018; Barry et al. 2019; Chen et al. 2025a). 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.

360 **Pointers for progress**

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

363 Above, we illustrated the basic principles of sequential experimentation through the study of blue
364 oak impacts on understory forage production. In sequential experimentation (Fisher 1952) an experimenter
365 does not consider “material as wholly passive but instead looks to what may be learnt from it with a view to
366 the improvement and extension of the enquiry.” In other words, each subsequent experiment is informed by
367 the results of the previous one (see Maestre et al. 2003; Baumeister & Callaway 2006). Our use of
368 “sequential” is informal (again see Fisher, 1952) and different than formal sequential statistical analyses (e.g.,
369 Wald 2004). Sequential experiments are successively derived from discoveries, much like the general
370 expectations of repeatedly applying the scientific method. A discovery in a first experiment can lead to and
371 guide a second experiment, and a discovery from that can lead to and guide a third experiment, and so on. A
372 good recent example of this sequential approach is provided by Su et al. (2025) who first found that
373 experimentally planting mixtures of maize cultivars increased productivity - a net effect of overyielding.
374 Second, they found that spatial root segregation in two-cultivar mixtures was greater than would be predicted
375 from each cultivar grown alone, parsing the net effect into cultivar-specific responses. And finally, the extent
376 of the spatial segregation of the roots of different cultivar combinations correlated with grain mass and
377 productivity, connecting the - unpacked - parsed responses into a potentially causal relationship.

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

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

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

407

408 **Conclusions**

409 Net-effect measurements underpin a tremendous amount of progress in ecology. BEF and SGH
410 studies have depended heavily on assessments of net effects for their conceptual frameworks. Both research
411 fields have produced important theory (Lortie and Callaway 2006; He et al. 2013, Tilman et al. 2014, Isbell
412 et al. 2018), but both are also still constrained to some degree by variation and conditionality in outcomes.
413 Unpacking net effects is possible via sequential and multifactorial experimental approaches and cross-study
414 comparisons that explain variation in outcomes (Spehn et al. 2002; He et al. 2013), and that move us to the
415 next level down in mechanistic understanding and towards generalization. We suggest that such unpacking
416 can be optimized through multifactorial and preferably sequential (after Fisher 1952) experiments.

417 Unpacking will provide opportunities to challenge and generalize assumptions concerning dominant
418 mechanisms. In the spirit of De Laender et al. (2016), by explicitly accounting for variation in the abiotic
419 environment, we can better “predict the functioning of ecosystems...”. A deeper understanding of the
420 mechanisms underlying positive biodiversity–ecosystem functioning relationships across environmental
421 gradients will allow us to link BEF results to applied goals such as restoration and food production. Similarly,
422 mechanistic examinations of the processes underlying changes in net plant–plant interactions along
423 environmental gradients will uncover traits, trait combinations, and environmental conditions where different
424 management and restoration approaches can be best applied. Overall, unpacking net effects can provide
425 opportunities to address apparent paradigms and better generalize across the impressive collection of case
426 studies in key fields in plant ecology, and to then apply this knowledge to major global challenges such as
427 food security and the conservation and restoration of ecosystems.

428

429 **Funding**

430 This paper was supported by funding grant IZSEZ0_193944 “Facilitation and biodiversity-ecosystem
431 function research” from the Swiss National Science Foundation.

432

433 **Author contributions**

434 Conceptualisation: Brooker, Hector, Temperton with input from all authors; writing – original draft
435 preparation: Brooker, Callaway, Hector, Temperton, Wright; writing – review and editing: all authors;
436 funding acquisition: Schöb, Wright.

437

438 **Competing interests**

439 The authors declare no competing interests.

440

441 **Acknowledgements,**

442 This paper was supported by funding grant IZSEZ0_193944 “Facilitation and biodiversity-ecosystem
443 function research” from the Swiss National Science Foundation.

444

445 **References**

- 446 Afkhami ME, McIntyre PJ, Strauss SY. 2014. Mutualist - mediated effects on species' range limits across
447 large geographic scales. *Ecology Letters* **17**: 1265-1273.
- 448 Allan E, Weisser WW, Fischer M, Schulze E-D *et al.* 2013. A comparison of the strength of biodiversity
449 effects across multiple functions. *Oecologia* **173**: 223-237.
- 450 Ali A. 2023. Biodiversity–ecosystem functioning research: Brief history, major trends and
451 perspectives. *Biological Conservation* **285**: 110210.
- 452 Alonso - Crespo IM, Temperton VM, Fichtner A, Niemeyer T *et al.* 2025. Exploring priority and year
453 effects on plant diversity, productivity and vertical root distribution: first insights from a grassland
454 field experiment. *Journal of Vegetation Science* **36**: e70026.
- 455 Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant interactions: a new comparative index. *Ecology* **85**:
456 2682-2686.

457 Aschehoug ET, Callaway RM. 2014. Morphological variability in tree root architecture indirectly affects
 458 coexistence among competitors in the understory. *Ecology* **95**: 1731-1736.

459 Atkinson J, Brudvig LA, Mallen - Cooper M, Nakagawa S *et al.* 2022. Terrestrial ecosystem restoration
 460 increases biodiversity and reduces its variability, but not to reference levels: a global
 461 meta - analysis. *Ecology Letters* **25**: 1725-1737.

462 Balvanera P, Pfisterer AB, Buchmann N, He JS *et al.* 2006. Quantifying the evidence for biodiversity effects
 463 on ecosystem functioning and services. *Ecology Letters* **9**: 1146-1156.

464 Barry KE, Mommer L, van Ruijven J, Wirth C, *et al.* 2019. The future of complementarity: disentangling
 465 causes from consequences. *Trends in Ecology & Evolution* **34**: 167-180.

466 Baumeister D., Callaway RM. 2006. Facilitation by *Pinus flexilis* during succession: a hierarchy of
 467 mechanisms benefits other plant species. *Ecology* **87**: 1816-1830.

468 Bertness MD, Callaway RM. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* **9**:
 469 191-193.

470 Bertness MD, Cavieres LA, Lortie CJ, Callaway RM. 2024. Positive interactions and interdependence in
 471 communities. *Trends in Ecology and Evolution* **39**: 1014-1023.

472 Boudreau MA. 2013. Diseases in intercropping systems. *Annual Review of Phytopathology* **51**: 499-
 473 519.

474 Brandmeier J, Reininghaus H, Pappagallo S, Karley AJ *et al.* 2021. Intercropping in high input agriculture
 475 supports arthropod diversity without risking significant yield losses. *Basic and Applied Ecology* **53**:
 476 26-38.

477 Brooker RW, Bennett AE, Cong WF, Daniell TJ *et al.* 2015. Improving intercropping: a synthesis of
 478 research in agronomy, plant physiology and ecology. *New Phytologist* **206**: 107-117.

479 Brooker RW, Callaghan TV. 1998. The balance between positive and negative plant interactions and its
 480 relationship to environmental gradients: a model. *Oikos* **81**: 196-207.

481 Brooker R, Kikvidze Z, Pugnaire FI, Callaway RM *et al.* 2005. The importance of importance. *Oikos* **109**:
 482 63-70.

483 Brooker RW, Maestre FT, Callaway RM, Lortie CL *et al.* 2008. Facilitation in plant communities: the past,
 484 the present, and the future. *Journal of Ecology* **96**: 18-34.

485 Brudvig LA. 2017. Toward prediction in the restoration of biodiversity. *Journal of Applied Ecology*, **54**:
486 1013-1017.

487 Byers JE, Cuddington K, Jones CG, Talley TS *et al.* 2006. Using ecosystem engineers to restore ecological
488 systems. *Trends in Ecology & Evolution* **21**: 493-500.

489 Callaway, R.M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern
490 Rocky Mountains, USA. *Oikos* **82**: 561-573.

491 Callaway RM. 2007. *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht,
492 The Netherlands.

493 Callaway RM, Brooker RW, Choler P, Kikvidze Z *et al.* 2002. Positive interactions among alpine plants
494 increase with stress. *Nature* **417**: 844-848.

495 Callaway RM, Nadkarni NM, Mahall BE. 1991. Facilitating and interfering effects of *Quercus douglasii* in
496 central California. *Ecology* **72**: 1484-1499.

497 Cardinale BJ, Wright JP, Cadotte MW, Carroll IT *et al.* 2007. Impacts of plant diversity on biomass
498 production increase through time because of species complementarity. *Proceedings of the National*
499 *Academy of Sciences* **104**: 18123-18128.

500 Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU *et al.* 2012. Biodiversity loss and its impact on humanity.
501 *Nature* **486**: 59-67.

502 Cavieres LA, Badano EI, Sierra-Almeida A, Molina-Montenegro MA. 2007. Microclimatic modifications of
503 cushion plants and their consequences for seedling survival of native and non-native herbaceous
504 species in the high Andes of central Chile. *Arctic, Antarctic, and Alpine Research* **39**: 229-236.

505 Cavieres LA, Brooker RW, Butterfield BJ, Cook BJ. *et al.* 2014. Facilitative plant interactions and climate
506 simultaneously drive alpine plant diversity. *Ecology Letters* **17**: 193-202.

507 Chadfield VGA, Hartley SE, Redeker KR. 2022. Associational resistance through intercropping reduces
508 yield losses to soil-borne pests and diseases. *New Phytologist* **235**: 2393-2405.

509 Chen C, Bongers FJ, Schmid B, Ma K. *et al.* 2025b. Ecosystem consequences of functional diversity in
510 forests and implications for restoration. *New Phytologist* **247**: 1081-1097.

511 Chen C, Xiao W, Chen HYH. 2025a. Meta-analysis reveals global variations in plant diversity effects on
512 productivity. *Nature* **638**: 435–440.

513 Connell JH. 1961. The influence of interspecific competition and other factors on the distribution of the
514 barnacle *Chthamalus stellatus*. *Ecology* **42**: 710-723.

515 Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from
516 field experiments. *The American Naturalist* **122**: 661-696.

517 De Laender F, Rohr JR, Ashauer R, Baird DJ *et al.* 2016. Reintroducing environmental change drivers in
518 biodiversity–ecosystem functioning research. *Trends in Ecology & Evolution* **31**: 905-915.

519 Del Río M, Schütze G, Pretzsch H. 2014. Temporal variation of competition and facilitation in mixed species
520 forests in Central Europe. *Plant Biology* **16**: 166-176.

521 Delory BM, Schempp H, Spachmann SM, Störzer L *et al.* 2021. Soil chemical legacies trigger species-
522 specific and context-dependent root responses in later arriving plants. *Plant, Cell and Environment* **44**:
523 1215-1230.

524 Dohn J, Dembélé F, Karembé M, Moustakas A *et al.* 2013. Tree effects on grass growth in savannas:
525 competition, facilitation and the stress - gradient hypothesis. *Journal of Ecology* **101**: 202-209.

526 Eldridge D, Ding J, Dorrough J, Delgado-Baquerizo M *et al.* 2024. Hotspots of biogeochemical activity
527 linked to aridity and plant traits across global drylands. *Nature Plants* **10**: 760-770.

528 Emsens WJ, de Weyer M, Fuentes I, Liezner Y *et al.* 2022. Strong conditionality in plant-fungal community
529 assembly after soil inoculation in post-agricultural grasslands. *Soil Biology and Biochemistry* **166**:
530 108580.

531 Engbersen N, Brooker RW, Stefan L, Studer B *et al.* 2021. Temporal differentiation of resource capture and
532 biomass accumulation as a driver of yield increase in intercropping. *Frontiers in Plant Science* **12**:
533 668803.

534 Farmer EE, Ryan CA. 1990. Interplant communication: airborne methyl jasmonate induces synthesis of
535 proteinase inhibitors in plant leaves. *Proceedings of the National Academy of Sciences* **87**: 7713-7716.

536 Fisher RA. 1952. Sequential experimentation. *Biometrics* **8**: 183-187.

537 Fonteyn PJ, Mahall BE. 1978. Competition among desert perennials. *Nature* **275**: 544-545.

538 Fukami T. 2015. Historical contingency in community assembly: integrating niches, species pools, and
539 priority effects. *Annual Review of Ecology, Evolution, and Systematics* **46**: 1-23.

540 Gann GD, McDonald T, Walder B, Aronson J *et al.* 2019. International principles and standards for the
541 practice of ecological restoration. *Restoration Ecology* **27(S1)**: S1-S46.

542 Gerrits GM, Waenink R, Aradottir AL, Buisson E *et al.* 2023. Synthesis on the effectiveness of soil
543 translocation for plant community restoration. *Journal of Applied Ecology* **60**: 714-724.

544 Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA *et al.* 2004. Applying plant facilitation to forest
545 restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* **14**: 1128-
546 1138.

547 Grman E, Bassett T, Brudvig LA. 2013. Confronting contingency in restoration: management and site
548 history determine outcomes of assembling prairies, but site characteristics and landscape context have
549 little effect. *Journal of Applied Ecology* **50**: 1234-1243.

550 Gu C, Bastiaans L, Anten NP, Makowski D *et al.* 2021. Annual intercropping suppresses weeds: a meta-
551 analysis. *Agriculture, Ecosystems & Environment* **322**: 107658.

552 He Q, Bertness MD, Altieri AH. 2013. Global shifts towards positive species interactions with increasing
553 environmental stress. *Ecology Letters* **16**: 695-706.

554 Hess MCM, Buisson E, Fontes H, Bacon L *et al.* 2020. Giving recipient communities a greater head start and
555 including productive species boosts early resistance to invasion. *Applied Vegetation Science* **23**: 340-
556 352.

557 Holland VL. 1980. Effect of blue oak on rangeland forage production in central California. Pages 314-318 in
558 T.R. Plumb. Ecology Management and Utilization of California Oaks. United States Department of
559 Agriculture General Technical Report PSW-44, Number 319.

560 Homulle Z, George TS, Karley AJ. 2022. Root traits with team benefits: understanding belowground
561 interactions in intercropping systems. *Plant Soil* **471**: 1-26.

562 Hong P, Schmid B, De Laender F, Eisenhauer N *et al.* 2022. Biodiversity promotes ecosystem functioning
563 despite environmental change. *Ecology Letters* **25**: 555-569.

564 Huang HY, Chen CY, Castro-Izaguirre N, Baruffol M *et al.* 2018. Impacts of species richness on
565 productivity in a large-scale subtropical forest experiment. *Science* **362**: 80-83.

566 Hunter AF, Aarssen LW. 1988. Plants helping plants. *Bioscience* **38**: 34-40.

567 Isbell, F, Craven D, Connolly J, Loreau M *et al.* 2015. Biodiversity increases the resistance of ecosystem
568 productivity to climate extremes. *Nature* **526**: 574-577.

569 Isbell F, Cowles J, Dee LE, Loreau M *et al.* 2018. Quantifying effects of biodiversity on ecosystem
570 functioning across times and places. *Ecology Letters* **21**:763-778.

571 Johnson MG, Granath G, Tahvanainen T, Pouliot R *et al.* 2014. Evolution of niche preference in *Sphagnum*
572 peat mosses. *Evolution* **69**: 90-103.

573 Jones CG, Callaway RM. 2007. The third party. *Journal of Vegetation Science* **18**: 771-776.

574 Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373-386.

575 Karban R, Baldwin IT, Baxter KJ, Laue G *et al.* 2000. Communication between plants: induced resistance in
576 wild tobacco plants following clipping of neighboring sagebrush. *Oecologia* **125**: 66–71.

577 Karban R, Shiojiri K, Huntzinger M, McCall AC. 2006. Damage - induced resistance in sagebrush: volatiles
578 are key to intra - and interplant communication. *Ecology*, **87**: 922-930.

579 Karban R, Wetzel WC, Shiojiri K, Ishizaki S *et al.* 2014. Deciphering the language of plant communication:
580 volatile chemotypes of sagebrush. *New Phytologist* **204**: 380-385.

581 Karban R, Wetzel WC, Shiojiri K, Pezzola E *et al.* 2016. Geographic dialects in volatile communication
582 between sagebrush individuals. *Ecology* **97**: 2917-2924.

583 Kneitel JM, Chase JM. 2004. Trade - offs in community ecology: linking spatial scales and species
584 coexistence. *Ecology letters* **7**: 69-80.

585 Lepš J, de Bello F, Šmilauer P, Doležal J (2011) Community trait response to environment: disentangling
586 species turnover vs intraspecific trait variability effects. *Ecography* **34**: 856–863.

587 Li B, Li Y, Wu H, Zhang F *et al.* 2016. Root exudates drive interspecific facilitation by enhancing
588 nodulation and N₂ fixation. *Proceedings of the National Academy of Sciences* **113**: 6496-6501.

589 Li L, Li SM, Sun JH, Zhou LL *et al.* 2007. Diversity enhances agricultural productivity via rhizosphere
590 phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of*
591 *Sciences* **104**: 11192-11196.

592 Li L, Tilman D, Lambers H, Zhang FS. 2014. Plant diversity and overyielding: insights from belowground
593 facilitation of intercropping in agriculture. *New Phytologist* **203**: 63-69.

594 Li XF, Wang ZG, Bao XG, Sun JH *et al.* 2021. Long-term increased grain yield and soil fertility from
595 intercropping. *Nature Sustainability* **4**: 943-950.

596 Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature*
597 **412**: 72-76.

598 Lortie CJ, Callaway RM. 2006. Re-analysis of meta-analysis: support for the stress gradient hypothesis.
599 *Journal of Ecology* **94**: 7-16.

600 Lortie CJ, Cushman JH. 2007. Effects of a directional abiotic gradient on plant community dynamics and
601 invasion in a coastal dune system. *Journal of Ecology* **95**: 468-481.

602 Losapio G, Norton Hasday E, Espadaler X, Germann C *et al.* 2021. Facilitation and biodiversity jointly drive
603 mutualistic networks. *Journal of Ecology* **109**: 2029-2037.

604 Losapio G, Genes L, Knight CJ, McFadden TN *et al.* 2024. Monitoring and modelling the effects of
605 ecosystem engineers on ecosystem functioning. *Functional Ecology* **38**: 8-21.

606 Maestre FT, Bautista S, Cortina J. 2003. Positive, negative, and net effects in grass–shrub interactions in
607 Mediterranean semiarid grasslands. *Ecology* **84**: 3186-3197.

608 Marquard E, Weigelt A, Roscher C, Gubsch M *et al.* 2009. Positive biodiversity–productivity relationship
609 due to increased plant density. *Journal of Ecology* **97**: 696-704.

610 Maron JL, Marler M. 2008. Effects of native species diversity and resource additions on invader impact.
611 *American Naturalist* **172**: S18–S33.

612 Martin-Guay MO, Paquette A, Dupras J, Rivest D. 2018. The new green revolution: sustainable
613 intensification of agriculture by intercropping. *Science of the Total Environment* **615**: 767-772.

614 Mensing, S. (2006). The history of oak woodlands in California, part II: the native American and historic
615 period. *The California Geographer* **46**:1-31.

616 Michalet R, Schöb C, Lortie CJ, Brooker RW. *et al.* 2014. Partitioning net interactions among plants along
617 altitudinal gradients to study community responses to climate change. *Functional Ecology* **28**: 75-86.

618 Michalet R, Xiao S, Touzard B, Smith DS. *et al.* 2011. Phenotypic variation in nurse traits and community
619 feedbacks define an alpine community. *Ecology Letters* **14**: 433-443.

620 Montgomery, D. C. 2017. *Design and analysis of experiments* (Ninth ed.): Hoboken, NJ: John Wiley & Sons,
621 Inc.

622 Mulder CPH, Uliassi DD, Doak DF. 2001. Physical stress and diversity-productivity relationships: the role
623 of positive interactions. *Proceedings of the National Academy of Sciences* **98**: 6704-6708.

624 Mulder CPH, Jumpponen A, Högberg P, Huss-Danell K. 2002. How plant diversity and legumes affect
625 nitrogen dynamics in experimental grassland communities. *Oecologia* **133**: 412-421.

626 Naeem S, Thompson LJ, Lawler SP, Lawton JH *et al.* 1994. Declining biodiversity can alter the performance
627 of ecosystems. *Nature* **368**: 734-37.

628 Naeem S, Thompson LJ, Lawler SP, Lawton JH *et al.* 1995. Empirical evidence that declining species
629 diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal*
630 *Society of London Series B* **347**: 249-62.

631 Nagy DU, Rauschert ES, Callaway RM, Henn T *et al.* 2022. Intense mowing management suppresses
632 invader, but shifts competitive resistance by a native to facilitation. *Restoration Ecology* **30**: e13483.

633 Natarajan M, Willey RW. 1986. The effects of water stress on yield advantages of intercropping
634 systems. *Field Crops Research* **13**: 117-131.

635 Nyawade SO, Karanja NN, Gachene CK, Gitari HI *et al.* 2019. Intercropping optimizes soil temperature and
636 increases crop water productivity and radiation use efficiency of rainfed potato. *American Journal of*
637 *Potato Research* **96**: 457-471.

638 O'Connor MI, Gonzalez A, Byrnes JEK, Cardinale BJ *et al.* 2016. A general biodiversity-function
639 relationship is mediated by trophic level. *Oikos* **126**: 18-31.

640 Ramirez C, Wright AJ. 2023. Microclimate and growth advantages in the 'Three sisters' planting food
641 system in an urban garden. *Plant and Soil* **506**: 541-553.

642 Reich PB, Tilman D, Isbell F, Mueller K *et al.* 2012. Impacts of biodiversity loss escalate through time as
643 redundancy fades. *Science* **336**: 589-592.

644 Rotundo JL, Aguiar MR. 2005. Litter effects on plant regeneration in arid lands: a complex balance between
645 seed retention, seed longevity and soil-seed contact. *Journal of Ecology* **93**: 829-838.

646 Schnitzer SA, Klironomos JN, HilleRisLambers J, Kinkel LL *et al.* 2011. Soil microbes drive the classic
647 plant diversity–productivity pattern. *Ecology* **92**: 296-303.

648 Schmutz A, Schöb C. 2023. Crops grown in mixtures show niche partitioning in spatial water uptake.
649 *Journal of Ecology*, **111**: 1151-1165.

650 Schöb C, Armas C, Guler M, Prieto I *et al.* 2013. Variability in functional traits mediates plant interactions
651 along stress gradients. *Journal of Ecology* **101**: 753-762.

652 Schöb C, Engbersen N, López-Angulo J, Schmutz A *et al.* 2023. Crop Diversity Experiment: towards a
653 mechanistic understanding of the benefits of species diversity in annual crop systems. *Journal of Plant*
654 *Ecology* **16**: rtad016.

655 Schöb C, Brooker RW, Zuppinger-Dingley D. 2018. Evolution of facilitation requires diverse communities.
656 *Nature Ecology and Evolution* **2**: 1381-1385.

657 Schoener TW. 1983. Field experiments on interspecific competition. *The American Naturalist* **122**: 240-285.

658 Shi X, Zhou Y, Guo P, Ren J *et al.* 2023. Peanut/sorghum intercropping drives specific variation in peanut
659 rhizosphere soil properties and microbiomes under salt stress. *Land Degradation & Development* **34**:
660 736-750.

661 Smith AL, Barrett RL, Milner RN. 2018. Annual mowing maintains plant diversity in threatened temperate
662 grasslands. *Applied Vegetation Science* **21**: 207-218.

663 Socher SA, Prati D, Boch S, Müller J *et al.* 2013. Interacting effects of fertilization, mowing and grazing on
664 plant species diversity of 1500 grasslands in Germany differ between regions. *Basic and Applied*
665 *Ecology* **14**: 126-136.

666 Sotomayor DA, Lortie CJ. 2015. Indirect interactions in terrestrial plant communities: emerging patterns and
667 research gaps. *Ecosphere* **6**: 103.

668 Spehn EM, Scherer-Lorenzen M, Schmid B, Hector A *et al.* 2002. The role of legumes as a component of
669 biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos* **98**: 205-218.

670 Su Y, Yu R, Xu H, Sun J *et al.* 2023. Crop cultivar mixtures stabilize productivity, partly via facilitation,
671 when conditions are less benign. *Field Crops Research* **302**: 109046.

672 Sun T, Zhou J, Fu Y, Wu L *et al.* 2024. Soil nitrogen availability mediates the positive effects of
673 intercropping on soil organic carbon at global scales. *Soil and Tillage Research* **239**: 106063.

674 Temperton VM, Mwangi PN, Scherer-Lorenzen M, Schmid B *et al.* 2007. Positive interactions between
675 nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment.
676 *Oecologia* **151**: 190-205.

677 Tilman D. 1977. Resource competition between plankton algae: an experimental and theoretical approach.
678 *Ecology* **58**: 338-348.

679 Tilman D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* **77**: 350-363.

680 Tilman D, Wedin D, Knops JMH. 1996. Productivity and sustainability influenced by biodiversity. *Nature*
681 **379**: 718-20.

682 Tilman D, Isbell F, Cowles JM. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology,*
683 *Evolution, and Systematics* **45**: 471-493.

684 Vandermeer JH. 1989. *The Ecology of Intercropping*. Cambridge University Press, United Kingdom

685 Van der Plas F, Schröder-Georgi T, Weigelt A, Barry K *et al.* 2020. Plant traits alone are poor predictors of
686 ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution* **4**: 1602-1611.

687 Veryard R, Wu J, O'Brien MJ, Anthony R *et al.* 2023. Positive effects of tree diversity on tropical forest
688 restoration in a field-scale experiment. *Science Advances* **9**: p.eadf0938.

689 Wagg C, Barry KE, O'Brien MJ, McKenzie-Gopsill A *et al.* 2019. Not even wrong: Comment by Wagg *et al.*
690 *Ecology* **100**: e02805.

691 Wagg C, Roscher C, Weigelt A, Vogel A *et al.* 2022. Biodiversity–stability relationships strengthen over
692 time in a long-term grassland experiment. *Nature Communications* **13**: 7752.

693 Wald A. 2004. *Sequential analysis*. Courier Corporation.

694 Weidlich EW, Nelson CR, Maron JL, Callaway RM *et al.* 2021. Priority effects and ecological restoration.
695 *Restoration Ecology* **29**: e13317.

696 Weisser WW, Roscher C, Meyer ST, Ebeling A *et al.* 2017. Biodiversity effects on ecosystem functioning in
697 a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic and Applied*
698 *Ecology* **23**: 1-73.

699 Willis AJ, Folkes BF, Hope-Simpson JF, Yemm EW. 1959a. Branton Burrows: The dune system and its
700 vegetation. Part I. *Journal of Ecology* **47**: 1-24.

701 Willis AJ, Folkes BF, Hope-Simpson JF, Yemm EW. 1959b. Branton Burrows: The dune system and its
702 vegetation. Part II. *Journal of Ecology* **47**: 249-288.

703 Wilsey B. 2021. Restoration in the face of changing climate: importance of persistence, priority effects, and
704 species diversity. *Restoration Ecology* **29**: e13132.

705 Wootton JT. 1994. The nature and consequences of indirect effects in ecological communities. *Annual*
706 *Review of Ecology and Systematics* **25**: 443-466.

707 Wright AJ, Barry KE, Lortie CJ, Callaway RM. 2021. Biodiversity and ecosystem functioning: Have our
708 experiments and indices been underestimating the role of facilitation? *Journal of Ecology* **109**: 1962-
709 1968.

710 Wright A, Schnitzer SA, Reich PB. 2014. Living close to your neighbors: the importance of both
711 competition and facilitation in plant communities. *Ecology* **95**: 2213-2223.

712 Wright AJ, Wardle DA, Callaway RM, Gaxiola A. 2017. The overlooked role of facilitation in biodiversity
713 experiments. *Trends in Ecology & Evolution* **32**: 383-390.

714 Zvereva EL, Kozlov MV. 2021. Biases in ecological research: attitudes of scientists and ways of control.
715 *Scientific Reports* 11: **226**.

716

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

733 **Box 1. Examples of Unpacking Net Effects**

734 Examples of studies in which net effects have been unpacked and how this had led to generalization. +, -
735 symbols above large arrows show general trends in the unpacked results: +/- shows partitioning yielding
736 predictable shifts from competition and facilitation; the + symbols show where a facilitative mechanism was
737 identified.

738

739 **Box 2. Volatile communication among *Artemisia tridentata* shrubs: an example of unpacking**

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

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