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A multitrophic, eco-evolutionary perspective on biodiversity–ecosystem functioning research

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84	Contents	
85	1. What are the key achievements of BEF research?	XX
86	1.1. A short history of BEF research	XX
87	1.2. A new BEF era provides novel insights	XX
88	1.3. Identification of BEF mechanisms	XX
89	1.4. BEF in multitrophic communities	XX
90	1.5. BEF implications for ecosystem services	XX
91		
92	2. What are the key challenges of future BEF research?	XX
93	2.1. Non-random biodiversity change across trophic levels	XX
94	2.2. Predicting the strength of BEF relationships across environmental contexts	XX
95	2.3. Spatial scaling of BEF relationships	XX
96	2.4. Eco-evolutionary implications of multitrophic BEF	XX
97	2.5. FAIR data and beyond	XX
98	2.6. Operationalize BEF insights for ecosystem management, society, and	
99	decision making	XX
100		
101	3. Concluding remarks	XX
102	4. Acknowledgements	XX
103	5. References	XX
104		

105 **Abstract**

106 Concern about the functional consequences of unprecedented loss in biodiversity has
107 prompted biodiversity–ecosystem functioning (BEF) research to become one of the most
108 vibrant fields of ecological research in the past 25 years. Hundreds of experiments have
109 manipulated biodiversity as an independent variable and found compelling support that
110 the functioning of ecosystems increases with the diversity of their ecological communities.
111 This research has also identified some of the underlying mechanisms of BEF relationships,
112 some context-dependencies of the strength of relationships, as well as implications for
113 various ecosystem services that mankind depends on. In this paper, we argue that a
114 multitrophic and eco-evolutionary perspective of biotic interactions in random and non-
115 random biodiversity change scenarios is key to advance future BEF research and to
116 address some of its most important remaining challenges. We discuss that the study and
117 the quantification of multitrophic interactions in space and time facilitates scaling up from
118 small-scale biodiversity manipulations and ecosystem function assessments to
119 management-relevant spatial scales across ecosystem boundaries. We specifically consider
120 multitrophic conceptual frameworks to understand and predict the context-dependency of
121 BEF relationships. Moreover, we highlight the importance of the eco-evolutionary
122 underpinnings of multitrophic BEF relationships. We outline that FAIR data and
123 reproducible processing will be key to advance this field of research by making it more
124 integrative. Finally, we show how these BEF insights may be implemented for ecosystem
125 management, society, and policy. Given that human well-being critically depends on the
126 multiple services provided by diverse, multitrophic communities, integrating the
127 approaches of evolutionary ecology, community ecology, and ecosystem ecology in future
128 BEF research will be key to refine conservation targets and develop sustainable
129 management strategies.

1. What are the key achievements of BEF research?

„The community is indeed the hierarchical level where the basic characteristics of life – its diversity, complexity, and historical nature – are perhaps the most daunting and challenging. [...] however, most of the theoretical insights that have been gained about the effects of biodiversity on ecosystem functioning come from approaches developed in community ecology.“

Michel Loreau (2000)

Human activities influence virtually all ecosystems around the globe through a large variety of environmental alterations (MEA, 2005). Habitat destruction (Maxwell et al., 2016), changing and intensified land use (Gossner et al., 2016; Newbold et al., 2015), climate change (Urban et al., 2016), and invasion of exotic species (Murphy and Romanuk, 2014; van Kleunen et al., 2015; Vitousek et al., 1997; Wardle et al., 2011) are some of the most significant drivers of biodiversity change (Maxwell et al., 2016). Subsequent changes in ecological communities raise substantial ethical and aesthetic concerns as well as questions regarding the functioning of altered ecosystems (Hooper et al., 2005; Isbell et al., 2017a; Naeem et al., 2012). Biodiversity-ecosystem functioning (BEF) research has revealed strong positive effects of biodiversity on various ecosystem functions, and has begun to link these effects to underlying mechanisms. Positive BEF relationships can be observed at different spatial (Cardinale et al., 2012; Hautier et al., 2018; Isbell et al., 2011; Roscher et al., 2005; Thompson et al., 2018; van der Plas et al., 2016) and temporal scales (Guerrero-Ramírez et al., 2017; Reich et al., 2012; Zavaleta et al., 2010), and can be multi-dimensional on both the predictor (i.e., multidiversity) and response side (multifunctionality) (e.g., Hector and Bagchi, 2007; Meyer et al., 2018; Schuldt et al., 2018; Soliveres et al., 2016a).

One of the most important conclusions of BEF research is that the strength of BEF relationships is strongly context-dependent. BEF relationships have been shown to depend on climatic conditions (Fridley, 2002; Ratcliffe et al., 2017), local site conditions (Eisenhauer et al., 2018; Reich et al., 2001), and disturbance and management regimes (Guerrero-Ramírez et al., 2017; Kardol et al., 2018; Weigelt et al., 2009), which interact with biodiversity (Guerrero-Ramírez and Eisenhauer, 2017; but see Craven et al., 2016). Accordingly, mechanisms underlying biodiversity effects have been found to differ from one community to the next. Before discussing how the *status quo* can inspire future research to address some of the most important challenges in BEF research and ecology in general, we provide an overview of key achievements of past BEF work.

1.1. A short history of BEF research

Prior to the era of BEF research, nature conservation efforts targeted biodiversity separately from ecosystem functioning. On the one hand, the goal of conservation was to prevent species extinctions (Mace, 2014). On the other hand, ecosystems were protected and managed to conserve and maximize their functions and services (such as forests for groundwater recharge, erosion control, or recreation), but without explicit consideration of their diversity (Costanza et al., 1997). Thus, there was a consensus that it was important to protect different species and certain functions,

172 but these aims were, and still are in many places of the world, regarded as poorly connected, as well
173 as insufficiently linked to ecological theory. BEF research helped to provide an empirical
174 underpinning for these inherently related objects, thus adding an important justification for
175 conserving biodiversity that went beyond ethical and aesthetic motivations (Dallimer et al., 2012;
176 Potthast, 2014).

177

178 Early observations of natural communities inspired the notion that biodiversity may be a key
179 determinant of the functioning of ecosystems (Darwin and Wallace, 1858; Elton, 1958;
180 McNaughton, 1977; Schulze and Mooney, 1994). This idea was supported by theoretical models
181 (Loreau, 1998; Tilman et al., 1997a; Yachi and Loreau, 1999) and experiments (Hooper et al., 2005;
182 O'Connor et al., 2017). In fact, over the past 25 years, BEF research has led us to recognize that
183 the identity and combinations of species are powerful drivers of ecosystem processes and thus
184 central properties of ecosystems (Hooper et al., 2005; Isbell et al., 2017a; Schulze and Mooney,
185 1994; Tilman et al., 2014; Weisser et al., 2017).

186

187 More specifically, prior to the mid-1990s, ecosystem ecologists focused more on abiotic factors,
188 such as geology and climate, than biotic factors, such as species diversity and species interactions
189 (Hobbie 1992). Early topical questions were related to the environmental determinants of
190 biodiversity (**Figure 1**; van der Plas, 2019). The search for answers to these fundamental questions
191 in biodiversity yielded major scientific achievements, such as Darwin's theory of evolution (Darwin,
192 1859), Mendel's rules of heredity (Mendel, 1866), Hutchinson's concept of the ecological niche
193 (Hutchinson, 1957), and MacArthur and Wilson's theory of island biogeography (MacArthur and
194 Wilson, 1967; summarized in Craven et al. *under review*). Still today, the exploration of the
195 determinants of biodiversity is a crucial field in ecology (e.g., Adler et al., 2011), which is important
196 to some of the most pressing challenges of mankind, particularly given the unprecedented rate of
197 anthropogenic environmental change.

198

199 While the importance of species diversity to ecosystem functioning was recognized more than 150
200 years ago; e.g., Darwin and Wallace (1858) stated “... *it has been experimentally shown that a plot of land*
201 *will yield a greater weight if sown with several species and genera of grasses, than if sown with only two or three*
202 *species*”, this recognition of the importance of biodiversity fell into oblivion (Hector and Hooper,
203 2002). In fact, one of the first experiments of the 20th century reporting on BEF relationships was
204 originally designed to study how different concentrations of nitrogen drive plant diversity (Tilman
205 and Downing, 1994). However, when these plant communities were unexpectedly hit by an
206 extreme drought, it became evident that the response to the extreme event and the stability of the
207 ecosystem function ‘plant productivity’ depended on the species richness of the community
208 (Tilman and Downing, 1994). This study showed a positive biodiversity-stability relationship, but
209 was criticized because it did not manipulate biodiversity as an independent factor, meaning that
210 stability of plant biomass production was likely (co-)determined by the nitrogen treatment (Givnish
211 et al., 1994; Huston, 1997). After the first ‘wave’ of scientific debate, Grime (1997) concluded that
212 “...*neither evolutionary theory nor empirical studies have presented convincing evidence that species diversity and*
213 *ecosystem function are consistently and causally connected*”.

214

215 This debate stimulated a series of controlled experiments that directly manipulated biodiversity
216 aiming to quantify the effect of plant species richness on ecosystem functioning under controlled
217 environmental conditions (*e.g.*, Díaz et al., 2003; Ebeling et al., 2014; Hector et al., 1999; Hooper
218 et al., 2005; Naeem et al., 1994; Niklaus et al., 2001; O'Connor et al., 2017; Roscher et al., 2004;
219 Tilman et al., 1997b; Wardle and Zackrisson, 2005; **Figure 1**). The results were surprisingly clear:
220 community biomass production, in particular, increased with an increasing number of plant species
221 (Hooper et al., 2005). Subsequent debates (*e.g.*, Eisenhauer et al., 2016; Wardle, 2016) and
222 adjustments of experimental designs provided compelling evidence that BEF relationships could
223 occur irrespective of the inclusion of certain species, functional groups, or combinations of species
224 (Eisenhauer et al., 2016; Huang et al., 2018; van Ruijven and Berendse, 2003; Wilsey and Polley,
225 2004).

226

227 Subsequently, BEF research became more integrative in terms of scientific disciplines by realizing
228 that a whole-ecosystem perspective, including *e.g.* multitrophic interactions and element cycles, is
229 required to explore the mechanistic underpinnings and implications of biodiversity change
230 (Roscher et al., 2004; Schuldt et al., 2018). Nonetheless, these experiments have also provoked
231 debate over their realism. Randomly-assembled communities may not mirror real-world assembly
232 and disassembly (Leps, 2004; Wardle, 2016), which are determined by the simultaneous interplay
233 of abiotic and biotic filters in time and space (Götzenberger et al., 2012). Some recent experiments
234 thus shifted their focus from the number of species to the functional and phylogenetic dissimilarity
235 of species assemblages (Cadotte, 2013; Dias et al., 2013; Ebeling et al., 2014; Ferlian et al., 2018;
236 Scherer-Lorenzen et al., 2007) or have implemented non-random biodiversity loss scenarios (*e.g.*,
237 Bracken et al., 2008; Bruelheide et al., 2014; Schläpfer et al., 2005).

238

239 Non-random changes in biodiversity and the notion that the strength of BEF relationships is
240 context-dependent (Baert et al., 2018; Guerrero-Ramírez et al., 2017; Ratcliffe et al., 2017) have led
241 contemporary BEF research to re-introduce non-random and indirect manipulations of
242 biodiversity using environmental change drivers, such as various climate variables, management
243 intensity, chemical pollutants, and nutrient enrichment, as well as observations along
244 environmental gradients (De Laender et al., 2016; Everwand et al., 2014; Grace et al., 2016; Isbell
245 et al., 2013a; **Figure 1**). Although empirical evidence is limited to date, the findings of, *e.g.*, Duffy
246 et al. (2017) and Isbell et al. (2013a) substantiate the general predictions from BEF experiments by
247 demonstrating that the repeatedly-reported discrepancies in results between experimental and real-
248 world BEF studies may, in fact, be due to multiple interacting or unrecognized drivers typically
249 operating in real-world systems (De Laender et al., 2016; Eisenhauer et al., 2016; Loreau, 1998).

250

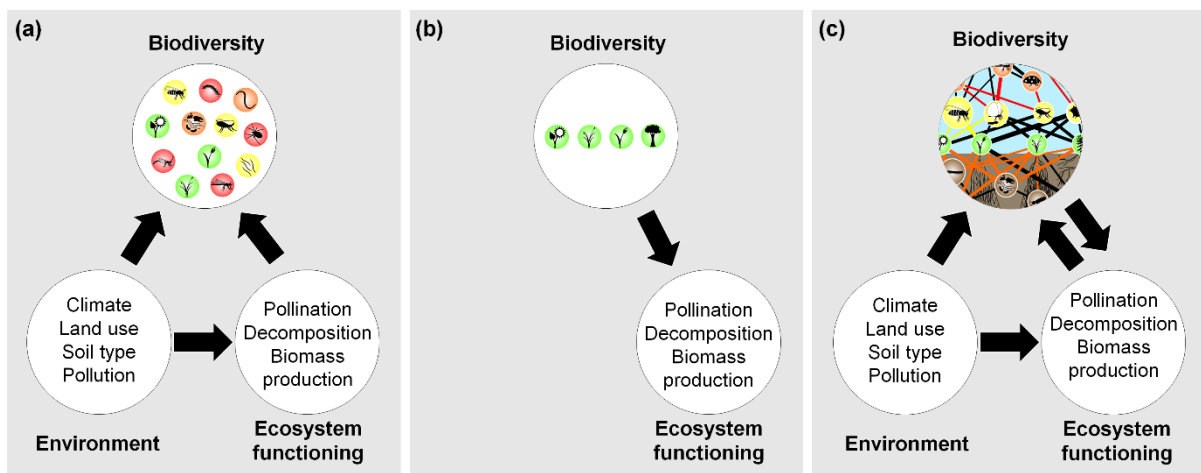
251

252 **1.2. A new BEF era provides novel insights**

253 In the last ~10 years, multiple review papers on BEF relationships have comprehensively
254 summarized the major achievements and novel insights by BEF research (*e.g.*, Cardinale et al., 2012;
255 Dirzo et al., 2014; Hooper et al., 2005; Isbell et al., 2017a; Loreau et al., 2001; Naeem et al., 2012;
256 Scherer-Lorenzen, 2014; Tilman et al., 2014; van der Plas, 2019; Weisser et al., 2017). Briefly, this
257 research has shown the importance of biodiversity (from microorganisms to trees, but mostly of
258 primary producers) in driving the functioning of ecosystems, with functions ranging from very

259 specific ones, such as the molecular transformation of organic compounds, to highly integrated
 260 ones, such as primary productivity. Positive BEF relationships arise from phenotypically- and
 261 genetically-based differences or trade-offs in species characteristics that drive the evolutionary
 262 diversification of niches (and the niches created by other species) through selective pressures, such
 263 that there is no single species or few species that perform(s) the different functions in exactly the
 264 same way or contribute(s) to all of the different functions (Turnbull et al., 2016). Another essential
 265 trade-off is the one between plasticity and specialization; *i.e.*, if a species could be so plastic that it
 266 could do everything that all other species can do, then there would be no need for diversity and
 267 division of labor. Consequently, it has been shown that the conservation of species diversity is
 268 necessary to sustain long-term functioning (Guerrero-Ramírez et al., 2017; Meyer et al., 2016; Reich
 269 et al., 2012) and multifunctionality of ecosystems (Allan et al., 2013; Hector and Bagchi, 2007; Isbell
 270 et al., 2011; Lefcheck et al., 2015; Meyer et al., 2018; Schuldt et al., 2018).

271



272

273 **Figure 1 | The evolution of biodiversity research.** Main foci of biodiversity–ecosystem functioning
 274 research over time (Chapin et al., 2000; De Laender et al., 2016; Eisenbauer et al., 2016; Isbell et al., 2013a;
 275 van der Plas, 2019). While studying the environmental drivers of different facets of biodiversity and ecosystem
 276 functioning (only some examples given) has been an important subdiscipline in ecological research for many decades
 277 (*i.e.*, community ecology) (a), in the mid-1990s, researchers started to manipulate biodiversity (mostly at the producer
 278 level; mostly random biodiversity loss scenarios) as an independent variable (functional biodiversity research or BEF
 279 research) (b). More recently, ecologists started focusing on the complex interplay between anthropogenically driven
 280 environmental gradients, non-random biodiversity change across trophic levels in food webs (c) (see also **Figure 2**),
 281 and the consequences for ecosystem function (*e.g.*, Barnes et al., 2018; De Laender et al., 2016; Mori et al., 2013;
 282 Sobral et al., 2017; Soliveres et al., 2016a) (c). Figure modified after van der Plas (2019).

283

284 While BEF research has mostly focused on uncovering the links between species richness and
 285 ecosystem function, showing that some particular species or functional groups have a
 286 disproportionately strong contribution to BEF relationships, variation at different levels of
 287 ecological organization (genetic diversity, phylogenetic species diversity, functional diversity) can
 288 have comparable effects on ecosystem functioning (*e.g.*, Hughes et al., 2008). In contrast to earlier
 289 assumptions (Cardinale et al., 2011), there seems to be low functional redundancy of coexisting
 290 species (Reich et al., 2012), particularly so across environmental contexts (Isbell et al., 2011), and
 291 therefore, at larger spatial scales, which is a finding that corresponds to coexistence theory
 292 (Turnbull et al., 2016). Thus, there is increasing awareness of the mechanistic links between traits

293 involved in coexistence and resource use and traits affecting emerging properties and processes in
294 ecosystems (Bannar-Martin et al., 2018; Chesson et al., 2001; Mouquet et al., 2002; Turnbull et al.,
295 2013, 2016); although empirical evidence for the role of response and effect traits in ecosystem
296 functioning still is limited (*e.g.*, Paine et al., 2015; Yang et al., 2018).

297

298

299 **1.3. Identification of BEF mechanisms**

300 BEF research has identified a list of (non-mutually exclusive) mechanisms that contribute to
301 enhancing ecosystem functioning with increasing biodiversity (*e.g.*, increased biotope space
302 describing the number of different ecological niches, more efficient resource use, multitrophic
303 interactions, facilitation; Hooper et al., 2005; Weisser et al., 2017; reviewed by Barry et al. 2018).
304 Mathematical approaches and experimental treatments were established to disentangle different
305 facets of biodiversity effects (*e.g.*, complementarity effect, selection effect, and species asynchrony;
306 Fox, 2005; de Mazancourt et al., 2013; Isbell et al., 2018; Loreau and Hector, 2001; but see Barry
307 et al., *In press* for missing empirical evidence for more efficient resource use at high biodiversity).
308 More recent research has provided insights into the niche dynamics. This means that species'
309 realized niches change over time according to their competitive environment and their interaction
310 network that are both dynamic in time and space (Hofstetter et al., 2007). As a consequence, this
311 might lead to increasing biodiversity effects on certain ecosystem functions over time (Allan et al.,
312 2011; Huang et al., 2018; Isbell et al., 2011; Meyer et al., 2016; Reich et al., 2012; Zuppinger-Dingley
313 et al., 2014).

314

315 In fact, previous studies, particularly short-term studies, may have underestimated the strength of
316 biodiversity-ecosystem functioning relationships by missing these longer-term effects (Eisenhauer
317 et al., 2012; Finn et al., 2013; Schmid et al., 2008). Among those is the important finding of
318 strengthening complementarity effects (calculated based on Loreau and Hector, 2001) of species-
319 rich communities over time (Cardinale et al., 2007; Huang et al., 2018; Reich et al., 2012; but see
320 Kardol et al., 2018). These complementarity effects may be driven by several underlying
321 mechanisms. For example, at low biodiversity, negative density-dependent effects of pests and
322 pathogens may contribute to the deterioration of community functions in comparison to more
323 diverse communities (Eisenhauer et al., 2012; Guerrero-Ramírez et al., 2017; Maron et al., 2011;
324 Schnitzer et al., 2011; Schuldt et al., 2017b; Weisser et al., 2017). In contrast, species-rich
325 communities may support more mutualistic interactions (*e.g.*, Wright et al., 2014; Schuldt et al.,
326 2017b), which may increase ecosystem functioning over time (Eisenhauer et al., 2012). These two
327 mechanisms are not mutually exclusive (Guerrero-Ramírez et al., 2017), and different ecosystem
328 functions show varying relative importance of the two mechanisms at the same time (Meyer et al.,
329 2016). Despite these first promising insights into potential explanations of complementarity effects,
330 the underlying ecological and evolutionary mechanisms remain elusive.

331

332

333 **1.4. BEF in multitrophic communities**

334 BEF research has demonstrated that biodiversity change at one trophic level cascades to other
335 trophic levels. For example, plant diversity increases the diversity of above- and belowground
336 consumer communities (“*biodiversity begets biodiversity*”; e.g., Ebeling et al., 2018; Eisenhauer et al.,
337 2013; Haddad et al., 2009; Scherber et al., 2010; Thebault and Loreau, 2003), and independent
338 biodiversity changes at more than one trophic level interactively affect ecosystem functions (e.g.
339 Coulis et al., 2015; Eisenhauer et al., 2012; Gessner et al., 2010; Handa et al., 2014). Relatedly, it
340 has been shown that complex, multitrophic communities affect the relationship between
341 biodiversity and multiple ecosystem functions (Schuldt et al., 2018; Soliveres et al., 2016a; Wang et
342 al., *In press*). For instance, across a land-use intensity gradient in German grasslands, the diversity
343 of primary producers, herbivorous insects, and microbial decomposers were particularly important
344 predictors of plant biomass and forage quality (Soliveres et al., 2016a). For Chinese subtropical
345 forests, it was shown that individual ecosystem functions central to energy and nutrient flows across
346 trophic levels are more strongly affected by the diversity of heterotrophs promoting decomposition
347 and nutrient cycling, and by plant functional-trait diversity and composition, than by tree species
348 richness (Schuldt et al., 2018). In managed Inner Mongolian grasslands, diversifying livestock by
349 mixing both sheep and cattle promoted multidiversity (including the diversity of plants, insects, soil
350 microbes, and nematodes) and multifunctionality (including plant biomass, insect abundance,
351 nutrient cycling, and soil carbon) (Wang et al., *In press*).

352

353 Perspectives papers have suggested to integrate BEF- and food-web theory to advance the
354 understanding of causal relationships between complex communities and multiple ecosystem
355 functions (Barnes et al., 2018; Duffy et al., 2007; Hines et al., 2015b; Thompson et al., 2012).
356 Moreover, multitrophic interactions may play a decisive role in shaping BEF relationships *via*
357 diversity-induced species plasticity in physiology, morphology, and micro-evolutionary processes
358 (Mraja et al., 2011; Zuppinger-Dingley et al., 2014). However, even though one of the first
359 biodiversity experiments manipulated multitrophic biodiversity in terrestrial ecotrons (Naeem et
360 al., 1994), multitrophic BEF research in terrestrial ecosystems is still in its infancy, and the majority
361 of existing studies focus on aquatic systems (Lefcheck et al., 2015; O’Connor et al., 2017; Seibold
362 et al., 2018; Stachowicz et al., 2007, 2008a).

363

364

365 **1.5. BEF implications for ecosystem services**

366 Beyond its focus on ecosystem functioning, BEF research has also shown that biodiversity is
367 important for a wide range of potential ecosystem services (Allan et al., 2015; Balvanera et al., 2006,
368 2014; Cardinale et al., 2012; Isbell et al., 2017a, b). These cover provisioning, regulating, and also
369 cultural services, underpinned by supporting services and includes, e.g., forage production (Binder
370 et al., 2018; Finn et al., 2013), wood production (Liang et al., 2016), soil carbon storage for climate
371 regulation (Fornara and Tilman, 2008; Lange et al., 2015), soil erosion control (Berendse et al. 2015;
372 Pérès et al., 2013), water quality regulation (Scherer-Lorenzen et al., 2003), natural attenuation of
373 pollutants in soil (Bandowe et al., 2019), pollination (Ebeling et al., 2008), and pest control (Hertzog
374 et al., 2017) or herbivory reduction (Civitello et al., 2015; Schuldt et al., 2017b).

375

376 Moreover, BEF research has stressed the role of multifunctionality, including the simultaneous
377 provisioning of many functions at one location (Hector and Bagchi, 2007; Lefcheck et al., 2015;

378 Schuld et al., 2018) and across environmental contexts (Isbell et al., 2015a; Eisenhauer et al., 2018),
379 as well as single functions in different settings (Isbell et al., 2011). However, this research has also
380 highlighted that biodiversity does not necessarily enhance all ecosystem services at the same time
381 (Cardinale et al., 2012), and trade-offs have been observed among different services (Meyer et al.,
382 2018). Moreover, studies simultaneously exploring a range of functions remain scarce, poorly
383 represent the whole range of services provided by ecosystems, and are often disconnected from
384 the utilitarian value of the (agro-)ecosystem (Manning et al., 2018; Swift et al., 2004; van der Plas et
385 al., 2018). Nonetheless, these achievements represent first important steps towards operationalizing
386 BEF insights for society and policy makers (Manning et al., 2018) and will help to incorporate the
387 importance of biodiversity for ecosystem-service provision in political discussions around the globe
388 (including, *e.g.*, halting biodiversity loss is included among sustainable development goals, changes
389 to the European Common Agricultural Policy; IPBES reports, <https://www.ipbes.net/>).

390

391

392 **2. What are the key challenges of future BEF research?**

393

394 *“The central problem in understanding and measuring biological diversity is that we still have a lot of work to do.*
395 *And while we are taking inventory, the shelves are already being cleared.”*

396

Christian Wirth (2013)

397

398 Congruent to the statement above, biodiversity research is a field under time pressure. Biodiversity
399 change can alter the functioning of ecosystems in dramatic ways and at an unprecedented pace,
400 which will have important consequences for the provision of ecosystem services (Balvanera et al.,
401 2006; Cardinale et al., 2012) and human health (Civitello et al., 2015; Lozupone et al., 2012; Wall et
402 al., 2015). Some of the related key challenges of BEF research have been described in previous
403 review papers (*e.g.*, Cardinale et al., 2012; Hooper et al., 2005; Isbell et al., 2017a), and the plethora
404 of (meta-)studies and mechanistic insights that were derived in the last years has helped to refine
405 existing and ask novel questions in BEF research. Here, we argue that taking a multitrophic
406 (Eisenhauer, 2017; Seibold et al., 2018) and eco-evolutionary perspective (Tilman and Snell-Rood,
407 2014; Zuppinger-Dingley et al., 2014) of biotic interactions will advance this field of research by
408 adding important mechanisms. Despite the broad consensus on the significance of BEF
409 relationships, the underlying ecological and evolutionary mechanisms are not well understood,
410 which impedes the transition from a description of patterns to a predictive science. Importantly,
411 the focus should now not only be on generalizable patterns, but more on the context-dependency
412 of BEF relationships (Baert et al., 2018; Craven et al., 2016; Eisenhauer et al., 2018; Fridley, 2002;
413 Guerrero-Ramírez et al., 2017; Jousset et al., 2011; Kardol et al., 2018; Ratcliffe et al., 2017; Schuld
414 et al., 2017a). Understanding why and how the strength of biodiversity effects varies with
415 environmental conditions and at which spatial scales different mechanisms operate will be key to
416 operationalizing BEF insights for ecosystem management, society, and decision making. We will
417 discuss these research frontiers in the following sections.

418

419

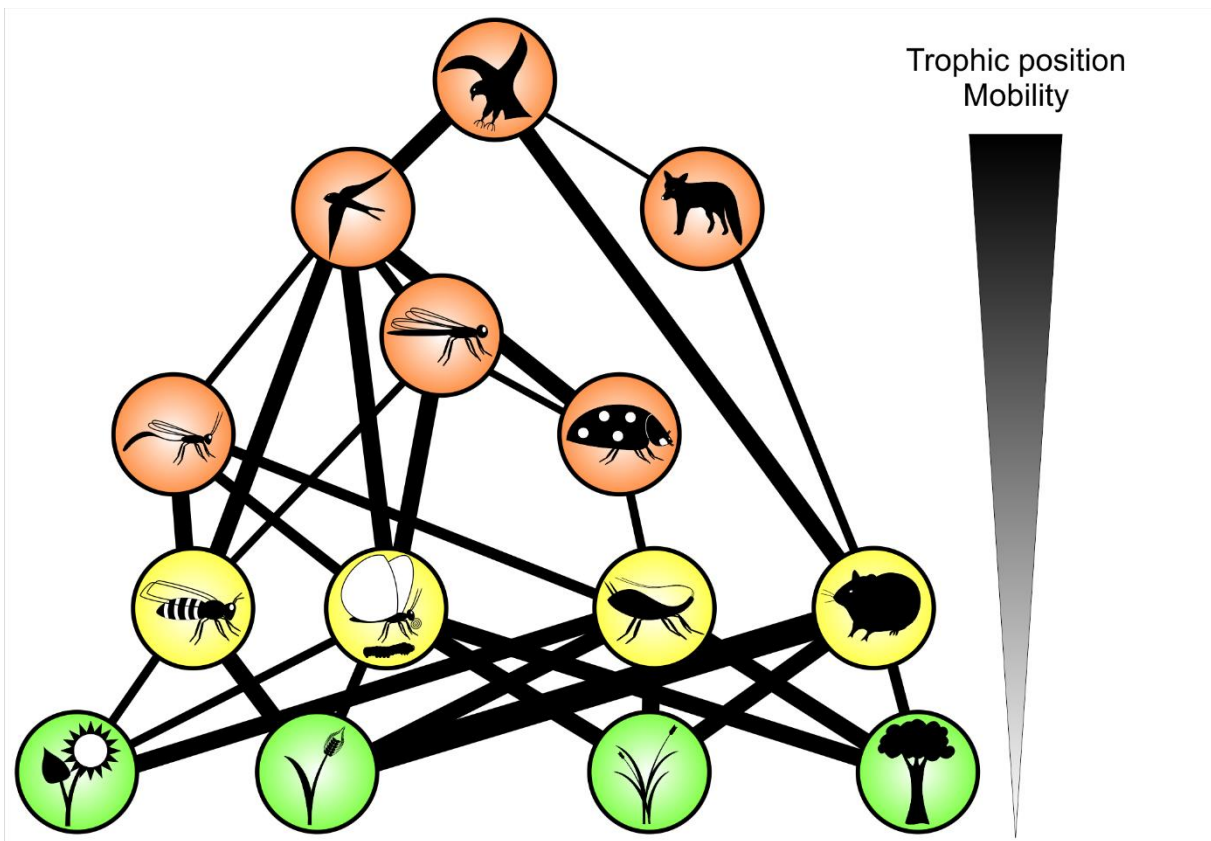
2.1. Non-random biodiversity change across trophic levels

“What escapes the eye... is a much more insidious kind of extinction: the extinction of ecological interactions.”

Daniel Janzen (1974)

Real-world biodiversity change (both invasions and extinctions) can be highly non-random (Haddad et al., 2008; Wardle, 2016). Thus, future BEF research has to investigate how non-random biodiversity loss affects ecosystem functioning in real-world ecosystems (Isbell et al., 2017a, b). Addressing this question is particularly important in order to facilitate the application of BEF results to agriculture, forestry, and biodiversity conservation. At the same time, this is a very challenging task as biodiversity change and species turnover may be hard to predict due to multiple co-occurring and interacting global-change drivers (Scherber, 2015; Tylianakis et al., 2008) and their context-dependent effects on species and their interactions (Bowler et al., 2018; Schmid and Hector, 2004). Furthermore, it might be promising to look more closely into the many published studies using random extinction scenarios, as some of them might by chance resemble extinction patterns that are actually observed in nature and provide opportunities for re-analysis. At the same time, the existing literature needs to be synthesized to derive a better understanding of trait-specific extinction risks of different taxonomic groups (Cardillo et al., 2005; Kotiaho et al., 2005; Seibold et al., 2015).

Another aspect of non-random species loss that has attracted increasing scientific attention over the last years is the role of rare species for community functioning. Across ecosystems, the large majority of species are rare and thus prone to extinction (Jousset et al., 2017; Soliveres et al., 2016b; Suding et al., 2005). In contrast to the mass-ratio hypothesis, which assumes that locally abundant species drive ecosystem functioning (Grime, 1998), many studies have shown that rare species can have disproportionately strong impacts on ecosystems (Allan et al., 2013; Connolly et al., 2013; Klein et al., 2003; Lyons et al., 2005; Mouillot et al., 2013; Soliveres et al., 2016b). Future experiments thus need to investigate the role of rare species and their interactions with common species, and compare „real-world“, non-random extinction scenarios with random extinction scenarios. Such an experiment was, for example, established in the subtropical BEF-China experiment, where two non-random extinction scenarios were included: one is based on local rarity and one on specific leaf area (SLA) of tree species, mimicking habitat loss through fragmentation and climate change, two current and likely future key drivers of change in Chinese subtropical forest communities (Bruehlheide et al., 2014).



455

456 **Figure 2 | A multitrophic perspective on biodiversity-ecosystem functioning research.**

457 *Mobility tends to increase with increasing trophic position in ecological networks, and some work suggests that the*
 458 *vulnerability to environmental change does too (Hines et al., 2015a; Voigt et al., 2003), although species at all*
 459 *trophic levels may be vulnerable to changing environments based on their specific life-history traits. This means that*
 460 *the previous focus of BEF experiments on the primary producer level does not necessarily reflect that this is the most*
 461 *vulnerable trophic level to environmental change. This simple aboveground food web serves as the basis for other figures*
 462 *in this paper. It illustrates that species within complex communities are connected by feeding links that can represent*
 463 *ecosystem functions and services (see also Figure 3).*

464

465

466 Both high trophic level and high body mass have been associated with vulnerability to extinction
 467 (with many related traits; **Figure 2**; e.g., Dirzo et al., 2014; Voigt et al. 2003), but vulnerability to
 468 environmental change occurs at all trophic levels according to species' life history traits. Thus, the
 469 focus of previous terrestrial BEF experiments on manipulating the primary producer level does
 470 not necessarily reflect that this is the most vulnerable trophic level to environmental change.
 471 Although early BEF research already considered multiple trophic levels (Naeem et al., 1994), the
 472 understanding of how multitrophic communities change their diversity and how this affects their
 473 functioning in terrestrial ecosystems remains limited (Eisenhauer et al., 2013; Haddad et al., 2009;
 474 Scherber et al., 2010). Moreover, terrestrial BEF research so far has virtually neglected the fact that
 475 primary producers do not function in isolation, but in a complex network of multitrophic, and also
 476 non-trophic interactions (**Figure 2**; Duffy, 2002; Hines et al., 2015b; Seabloom et al., 2017; Sobral
 477 et al., 2017; Tiede et al., 2016).

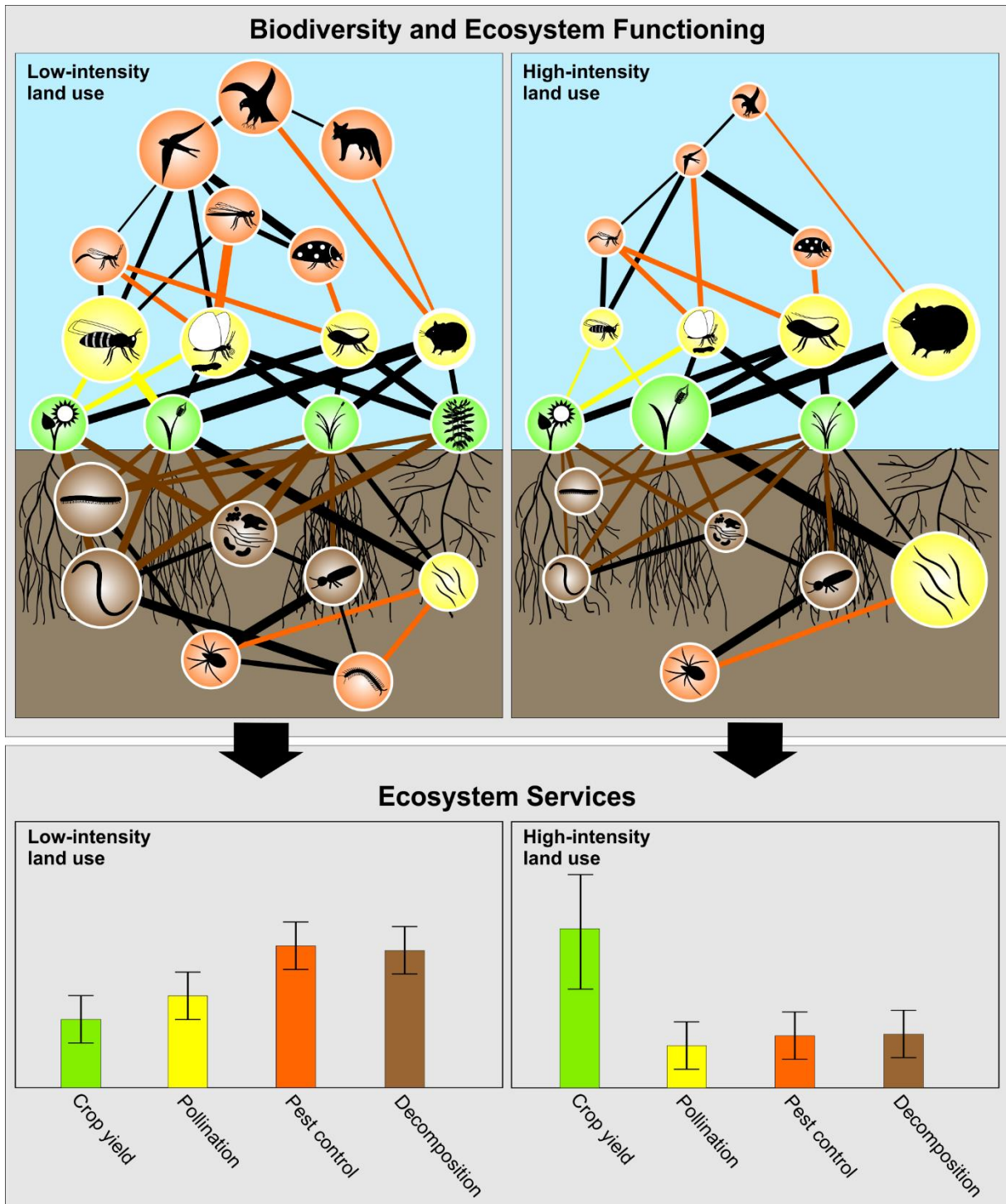
478

479 In complex food webs, the strength of different ecosystem functions is tightly coupled to the
480 community size structure describing how the body masses of species and individuals are distributed
481 across trophic levels (Brose et al., 2017; Dossena et al., 2012). For instance, subtle shifts in the body
482 mass structure of top consumer populations can induce strong trophic cascades with pronounced
483 effects on primary production (Jochum et al., 2012). Consistently, analyses of complex food-web
484 models demonstrated that primary production may be more tightly coupled to the trophic level
485 and body mass of the top consumer than to total or plant diversity (Wang and Brose, 2018). Thus,
486 ecological networks are an important tool that can be used to evaluate links that drive trade-offs
487 between multiple ecosystem functions (*Figure 3*; Brose et al., 2017; Hines et al., 2015b).

488

489 In fact, there is strong empirical evidence that, across ecosystems, the diversity at higher trophic
490 levels is important for providing multiple ecosystem functions and services (Barnes et al., 2018;
491 Bruno et al., 2006, 2008; Gessner et al., 2010; Hines et al., 2015b; Lefcheck et al., 2015; Schneider
492 et al., 2012, 2016; Schuldt et al., 2018; Soliveres et al., 2016a; Wang et al., 2019). This was, for
493 example, shown by manipulating stream-living macroinvertebrates and investigating their effect on
494 decomposition (Cardinale et al., 2002; Handa et al., 2014), or by manipulating the diversity of aphid
495 natural enemies and investigating pest control (Cardinale et al., 2003). Biodiversity changes at
496 higher trophic levels of aquatic ecosystems have been shown to exert cascading effects on the
497 biomass production at lower levels (Duffy et al., 2007; Worm and Duffy, 2003). This finding was
498 generalized by models of complex food webs, in which increased animal diversity led not only to
499 higher herbivory but also, counter-intuitively, to higher primary production by plants (Schneider et
500 al., 2016). This surprising finding is explained by systematic trait shifts in the plant communities
501 that are induced by the increased top-down pressure (Schneider et al., 2016). These results
502 contribute to the general notion that biodiversity changes across trophic levels can have complex
503 indirect effects, which strongly calls for a multitrophic whole-ecosystem perspective for
504 mechanistically understanding BEF relationships (Barnes et al., 2018; Brose and Hillebrand, 2016;
505 Eisenhauer, 2017; Hines et al., 2015b; Seibold et al., 2018; Thompson et al., 2012; Worm and Duffy,
506 2003).

507



508

509 **Figure 3 | Multitrophic communities drive ecosystem multifunctionality.** This scheme depicts
 510 relationships between the diversity of species in aboveground-belowground networks and the management of multiple
 511 ecosystem services. Management decisions, such as intensifying agricultural practices (right part of the figure), that
 512 focus on maximizing one ecosystem service, such as crop yield, can limit the other ecosystem services provided in
 513 complex food webs (e.g., pest control is reduced, indicated by higher biomass of aphid and vole). Note that the stability
 514 of delivering the focal service decreases in this example (larger error bar in crop yield) at high land-use intensity (Isbell
 515 et al., 2017b). Socio-political context related to human population density and stakeholder interests can influence
 516 feedbacks between ecosystem services and the management of complex ecosystems. Importantly, ecosystem services are
 517 not solely provided by single nodes in the food web, but by the interaction among multiple nodes (colors of example

518 *links between nodes in upper part, correspond to ecosystem service bar colors in lower part). Redrawn after Hines et*
519 *al. (2015b).*

520

521 Ultimately, the understanding of real-world BEF relationships requires coupling multitrophic
522 biodiversity change and indirect effects among species addressed at local habitat scales with spatio-
523 temporal upscaling to the landscape level. However, research on multitrophic interactions and
524 quantitative food-web changes in space and time is little developed so far (but see, *e.g.*, Grass et al.,
525 2018; Tscharrntke et al., 2012). Across ecosystems, the increase in the number of interactions
526 between species is predictably linked to the simultaneous increase in the number of species (Brose
527 et al., 2004). This connection between species-area and link-area relationships facilitates the
528 prediction of food-web complexity at the landscape level, but upscaling of BEF relationships would
529 also require integrating the identities or traits of species and their interactions into models. In this
530 vein, behavior- and trait-based allometric random walk models (Hirt et al., 2018), as well as
531 extensions of the classic theory of island biogeography that account for effects of the species'
532 trophic levels (Gravel et al., 2011) or body masses (Jacquet et al., 2017), have great potential to
533 become important cornerstones of novel BEF upscaling approaches (see also section "Spatial
534 scaling of BEF relationships").

535

536 In order to account for the finding of substantial species turnover and biotic homogenization due
537 to human activities (Dornelas et al., 2014; Hautier et al., 2018; van der Plas et al., 2016), future BEF
538 experiments may also include both species gains and losses (Mori et al., 2018; Wardle et al., 2011)
539 across different trophic levels. Integrating trophic complexity will be key to account for cascading,
540 facilitative, and competitive effects in order to understand how biodiversity affects whole-
541 ecosystem functioning (Barnes et al., 2018), regardless of the direction of biodiversity change (loss
542 or gain; Wardle, 2016). Moreover, biotic homogenization across trophic levels may have important
543 implications for the stable provisioning of multiple ecosystem services (Gossner et al., 2016; van
544 der Plas et al., 2016) as synchrony in responses across species may compromise ecosystem
545 functioning (Craven et al., 2018; de Mazancourt et al., 2013). Higher synchrony among species in
546 space and time may be particularly deleterious for ecosystems with ongoing global change as
547 predicted by the temporal and spatial insurance hypotheses of biodiversity (Loreau et al., 2003a;
548 Yachi and Loreau, 1999).

549

550 The explicit quantification of fluxes of energy and matter in BEF experiments would greatly
551 facilitate the integration of different trophic levels (Barnes et al., 2014, 2018; Lindeman, 1942;
552 Stocker et al., 1999; Wilsey and Polley, 2004). Rates of fluxes may actually be more sensitive and
553 may show faster responses to variations in biodiversity than pools (Meyer et al., 2016; but see Liu
554 et al., 2018 for a counter example). Evidence for this, however, is scarce (but see Allan et al., 2013;
555 Niklaus et al., 2016) and deserves further attention, particularly so in long-term (Huang et al., 2018;
556 Meyer et al., 2016), and multitrophic experiments (Eisenhauer, 2017). One such example is an
557 Ecotron study with intact soil monoliths from the Jena Experiment (Milcu et al., 2014). This
558 experimental set-up under controlled conditions allowed quantifying the effects of plant diversity
559 on ecosystem carbon fluxes and uptake efficiency of plants. Indeed, it was observed that increasing
560 plant species and functional diversity led to higher gross and net ecosystem carbon uptake rates,
561 and effects were partly mediated by the leaf area index and the diversity of leaf nitrogen
562 concentrations of the plant community (Milcu et al., 2014).

563

564 Going a step further, assessing energy flux dynamics in ecological networks provides the theoretical
565 underpinning of multitrophic BEF relationships, which is why the quantification of energy fluxes
566 in food webs may be a powerful tool for studying ecosystem functioning in multitrophic systems
567 ranging from biodiversity experiments to real-world ecosystems (Barnes et al., 2018). By combining
568 food-web theory with BEF theory (Hines et al., 2015b), whole community energy-flux assessment
569 enables investigators to quantify many different types of multitrophic ecosystem processes without
570 having to measure them all separately (Barnes et al., 2018). Energy flux can then be used as a
571 common currency to compare certain types of processes (e.g., herbivory or predation) across
572 different ecosystem types (Barnes et al., 2018); however, energy-flux calculations need to be
573 validated by actual process measurements (e.g., Schwarz et al., 2017), which in complex ecosystems
574 such as grasslands and forests poses a serious challenge.

575

576

577 **2.2. Predicting the strength of BEF relationships across environmental** 578 **contexts**

579

580 *“The idea that the mechanisms underpinning species coexistence are the same as those that link biodiversity with*
581 *ecosystem functioning can be traced all the way back to Darwin’s principle of divergence...”*

582

Lindsay Turnbull et al. (2013)

583

584 The strength and sign of BEF relationships have been reported to differ among studies as well as
585 among biotic and environmental contexts (e.g., Baert et al., 2018; Fridley, 2002; Guerrero-Ramírez
586 et al., 2017; Jousset et al., 2011; Jucker et al., 2016; Kardol et al., 2018; Ratcliffe et al., 2017; Steudel
587 et al., 2012; but see Craven et al., 2016). We still have scant knowledge about how and why effects
588 of the diversity and composition of communities on ecosystem functions vary. How context-
589 dependent are BEF relationships, and what biotic and abiotic factors drive this context-
590 dependency?

591

592 There have been several empirical attempts to study BEF relationships under different
593 environmental contexts, such as the BIODEPTH experiment across eight European countries
594 (Hector et al., 1999), the COST Agroddiversity experimental network across 31 sites in Europe and
595 Canada (Finn et al., 2013; Kirwan et al., 2007), the global network of tree diversity experiments in
596 TreeDivNet (Grossman et al., 2018; Paquette et al., 2018), the global Nutrient Network (Borer et
597 al., 2014, 2017), the global meta-analyses in drylands (Maestre et al., 2012) and forests (Liang et al.,
598 2016), the BioCON experiment in Cedar Creek studying effects of elevated CO₂ concentrations
599 and N deposition (Reich et al., 2001), the BAC experiment in Cedar Creek exploring warming
600 effects (Cowles et al., 2016; Pennekamp et al., 2018; Thakur et al., 2017), the two sites of the BEF-
601 China experiment (Huang et al., 2018), and the Jena drought experiment (Vogel et al., 2012).
602 Moreover, in the Jena Experiment (Roscher et al., 2004), researchers have applied a large number
603 of subplot treatments to study if plant diversity effects are contingent upon management intensity
604 (Weigelt et al., 2009), above- and belowground consumers (Eisenhauer et al., 2011), and plant

605 invasion (Petermann et al., 2010; Roscher et al., 2009; Steinauer et al., 2016). Although some studies
606 report BEF relationships in plant diversity experiments to be consistent across abiotic and biotic
607 contexts (e.g., Craven et al., 2016; O'Connor et al., 2017; Thakur et al., 2015), there is substantial
608 variability within and across studies depending on the point in time of the measurement (Kardol
609 et al., 2018; Reich et al., 2012; Wright et al., 2015), the biodiversity effect investigated (Craven et
610 al., 2016), and the trophic level and complexity of the studied community (Mulder et al., 1999;
611 O'Connor et al., 2017; Seabloom et al., 2017).

612

613 In response to some of the initial debates regarding the validity of BEF relationships across
614 environmental contexts (e.g., Givnish et al., 1994; Tilman and Downing, 1994), previous BEF
615 research has focused heavily on completely removing any 'confounding' effects of abundance,
616 biomass, and environmental gradients, in order to isolate and quantify 'true' biodiversity effects. It
617 is, however, important to understand biodiversity effects in the context of other co-varying factors
618 to better predict scenarios of ecosystem function given species gains or losses (which covary with
619 many other factors; Wardle, 2016). Future research should thus aim at understanding the functional
620 role of biodiversity in dynamic ecosystems that are not at competitive equilibrium (Brose and
621 Hillebrand, 2016; Leibold et al., 2004) as well as in affecting multiple dimensions of stability under
622 changing environmental conditions (Donohue et al., 2016; Pennekamp et al., 2018). Such
623 information is, for instance, urgently needed to inform predictive BEF models and to provide
624 tailored management recommendations in consideration of local environmental conditions
625 (Guerrero-Ramírez et al., 2017).

626

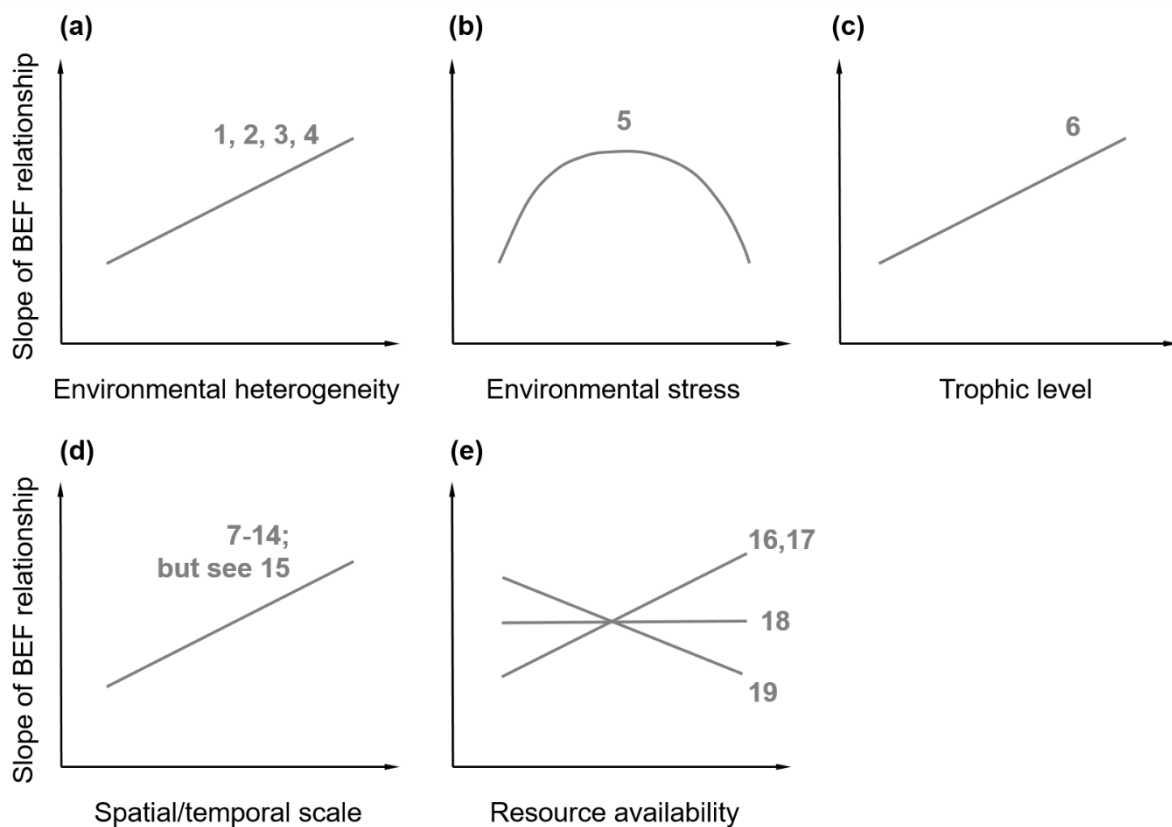
627 Conceptual advances are likely to be achieved by utilizing niche and coexistence theory to
628 understand the context-dependency of BEF relationships (Turnbull et al., 2016). Environmental
629 change often affects the composition of communities by altering the environmental conditions,
630 modifying available niche space directly (Harpole et al., 2016) and/or indirectly through altered
631 biotic interactions (Turnbull et al., 2016). For instance, the addition of nutrients has been repeatedly
632 shown to favor the growth of certain plant species with high nutritional demands and fast uptake
633 strategies (Clark et al., 2007; Harpole and Tilman, 2007; Harpole et al., 2016). Increased plant
634 growth of some species, in turn, induces the shading of other species, which then disappear because
635 their niche requirements are no longer met (Hautier et al., 2009). The resulting loss of species then
636 undermines potential other ecosystem functions beyond productivity of the depauperate plant
637 communities (Isbell et al., 2013a).

638

639 The same mechanisms that permit the coexistence of different species, namely niche differences,
640 also are the key for the complementary resource use and resultant overyielding (Loreau, 2004;
641 Tilman et al., 1997b; Turnbull et al., 2013, 2016; Vandermeer, 1981) and transfer of energy across
642 trophic levels (Barnes et al., 2014). Niche differentiation and facilitation within (Cardinale et al.,
643 2007; Reich et al., 2012; Wright et al., 2017) and across trophic levels (Ferlian et al., 2018; Poisot et
644 al., 2013) are often found to be the main mechanisms behind positive BEF relationships. As a
645 consequence, changes of the environmental conditions that influence the co-existence of species
646 are also likely to affect the strength of BEF relationships. In support of this notion, positive BEF
647 relationships have been shown to be strongest in complex resource environments (**Figure 4**) and
648 to become non-significant or even negative in homogenous resource environments (Eisenhauer et
649 al., 2013; Hodapp et al., 2016; Jousset et al., 2011; Mouquet et al., 2002; Norberg et al., 2001).

650 Hodapp et al. (2016) generalized this to resource supply heterogeneity landscapes and showed that
 651 strongly positive effects of richness on ecosystem function occur only if 1) species differ in traits,
 652 2) environments show heterogeneity, and 3) dispersal allows effective species sorting. Research on
 653 algal model communities in relatively structured environments (flow habitats and disturbance
 654 regimes) has shown that communities with more species take greater advantage of the niche
 655 opportunities in a given environment, and this allows diverse systems to better perform ecosystem
 656 functions (Cardinale, 2011; Stachowicz et al., 2007, 2008a). Taken together, these results indicate
 657 that environmental heterogeneity promotes complementarity effects (see, e.g., Wacker et al., 2008)
 658 and thus steeper BEF relationships (**Figure 4**), suggesting that habitat homogenization may
 659 compromise positive biodiversity effects on ecosystems.

660



661

662 **Figure 4 | Context-dependent biodiversity-ecosystem functioning (BEF) relationships;**
 663 *examples include (a) environmental heterogeneity, (b) environmental stress, (c) trophic level, (d) spatial and temporal*
 664 *scale, and (e) resource availability. Although the proposed relationships are supported by some studies (examples*
 665 *given, no comprehensive list of studies), a thorough understanding of the context-dependency of BEF and the*
 666 *underlying mechanisms is elusive. Thus, the depicted relationships should be regarded as working hypotheses for future*
 667 *research. See also Bardgett and Wardle (2010) (Fig. 5.3 and references therein) for a similar conceptualization of*
 668 *the context-dependency of BEF relationships that are mostly based on observational studies and removal experiments,*
 669 *rather than on random biodiversity manipulation experiments, as done here. For panel (b), we followed the definition*
 670 *by Chase and Leibold (2003), stating that “stressful niche factors limit the per capita population growth rate of the*
 671 *focal population, but are not influenced by changes in the population size.”*

672 **1:** Stachowicz et al. (2008b), **2:** Griffin et al. (2009), **3:** Cardinale (2011), **4:** Jousset et al. (2011), **5:** Baert et
 673 al. (2018), **6:** Lefcheck et al. (2015), **7:** Cardinale et al. (2007), **8:** Eisenbauer et al. (2010), **9:** Cardinale et al.
 674 (2011), **10:** Isbell et al. (2011), **11:** Reich et al. (2012), **12:** Thakur et al. (2015), **13:** Meyer et al. (2016), **14:**

675 *Guerrero-Ramírez et al. (2017), 15: Kardol et al. (2018), 16: Reich et al. (2001), 17: Fridley (2002), 18: Craven*
676 *et al. (2016), 19: Zhang and Zhang (2006).*

677

678 To study the context-dependence of BEF relationships, different site-specific conditions for
679 biodiversity effects, including environmental stress and resource availability (**Figure 4**), will need
680 to be disentangled (Baert et al., 2018; Guerrero-Ramírez et al., 2017). Global networks of
681 experiments using standardized methods (Lefcheck et al., 2016; Grossman et al., 2018; Meyer et
682 al., 2015) and syntheses of data are needed and have proven to be extremely powerful in detecting
683 global biodiversity(-function) patterns and underlying mechanisms (*e.g.*, Nutrient Network; Borer
684 et al., 2014, 2017; Grace et al., 2016). Notably, such standardized assessments are particularly
685 important for quantifying multitrophic interactions across environmental gradients (Kambach et
686 al., 2016; Roslin et al., 2017) that are intimately linked with ecosystem function (Eisenhauer et al.,
687 2019). For instance, different tree diversity experiments around the globe collaborate in the
688 framework of TreeDivNet (Paquette et al., 2018; Verheyen et al., 2016) and allow for countering
689 criticisms related to realism, generality, and lack of mechanistic explanation in their work
690 (Grossman et al., 2017; Paquette et al., 2018). However, empirical work and syntheses should not
691 be restricted to certain ecosystems, but should span across ecosystem types (*e.g.*, aquatic and
692 terrestrial; Balvanera et al., 2006; Cardinale et al., 2011; Handa et al., 2014; Lefcheck et al., 2015;
693 Ruiz-González et al., 2018; Schuldt et al., *Under review*). Recent modeling (*e.g.*, Baert et al., 2018) and
694 empirical work (*e.g.*, Guerrero-Ramírez et al., 2017) provide exciting working hypotheses for future
695 research (**Figure 4**).

696

697

698 **2.3. Spatial scaling of BEF relationships**

699

700 *“Biodiversity loss substantially diminishes several ecosystem services by altering ecosystem functioning and stability,*
701 *especially at the large temporal and spatial scales that are most relevant for policy and conservation.”*

702

Forest Isbell et al. (2017a)

703

704 To date, BEF relationships have mostly been investigated at small scales (*e.g.*, in microcosms,
705 mesocosms, or small plots; Cardinale et al., 2011), raising the question “*How does the BEF relationship*
706 *change with spatial scale?*” (Barnes et al., 2016; Isbell et al., 2017a; Thompson et al., 2018). Accordingly,
707 Mori et al. (2018) recently stressed the need for unification of beta-diversity and among-patch
708 ecosystem-function theory. The focus on small-scale studies may also be one reason for described
709 mismatches between local-scale observational and experimental BEF studies and conclusions
710 drawn for management-relevant scales (Oehri et al., 2017; van der Plas et al., 2016). Thus, future
711 research needs to bridge the gap between results from local-scale BEF experiments and real-world
712 relevant scales in order to understand whether and how biodiversity effects are important at the
713 landscape scale (Cardinale et al., 2012; Isbell et al., 2017a; Thompson et al., 2018). There is empirical
714 evidence suggesting that the importance of biodiversity in driving ecosystem functions increases as
715 more spatial contexts are considered (Grace et al., 2016; Hautier et al., 2018; Isbell et al., 2011; Mori
716 et al., 2016; Thompson et al., 2018), stressing the role of environmental heterogeneity in driving
717 the strength and mechanisms of BEF relationships (Cardinale, 2011; Griffin et al., 2009). One

718 solution may be the development of spatial upscaling algorithms to relate local BEF findings to
719 patterns at the landscape scale. Using such an approach, Barnes et al. (2016), however, showed that
720 the relative importance of biodiversity for ecosystem functions decreased with increasing spatial
721 scale. This is in line with contradicting findings on fragmentation-biodiversity studies when
722 focusing on patches or landscapes (Fahrig et al., 2019). There currently is a fundamental debate
723 about the mechanisms behind fragmentation, namely the habitat amount *versus* the connectivity
724 effect, indicating the challenge of upscaling local mechanisms (Fahrig, 2017). Hence, the
725 mechanisms dominating biodiversity and functions might differ between small and large spatial
726 scales (Loreau et al., 2003a, b). This indicates the need for future research on this topic, particularly
727 if we are to integrate knowledge from BEF experiments in ecosystem service modelling and other
728 spatial mapping exercises.

729

730 While BEF experiments have been ‘stuck’ in plots and buckets, meta-community theory has been
731 dealing with species appearance and disappearance without an explicit link to ecosystem
732 functioning (Bannar-Martin et al., 2018; Leibold et al., 2004, 2017; but see Loreau et al., 2003b).
733 Thus, species pools and their turnover and dynamics need to be incorporated into BEF research
734 (Bannar-Martin et al., 2018; Wardle, 2016) to consider the links between community
735 assembly/coexistence mechanisms (*e.g.*, dispersal, demographic stochasticity, niches/traits) and
736 ecosystem functioning (Hillebrand et al., 2018). One step towards this goal may be to identify trade-
737 offs in spatial and temporal scales at which diversity maximizes single and multiple ecosystem
738 functions. In fact, considering multitrophic consumer networks that link different landscape
739 patches and ecosystem compartments through the flux of energy across trophic levels (Barnes et
740 al., 2014) might be a promising approach to facilitate the upscaling of local processes to landscape-
741 level function (**Figure 5**; Barnes et al., 2018). For instance, future research efforts on land-use
742 change and restoration could be targeted towards manipulating biodiversity at different spatial
743 scales and exploring whole-ecosystem consequences within and across different patches and
744 compartments. Another option are disturbances acting at the landscape scale. They offer excellent
745 options for BEF studies at larger spatial scales, but research plans have to be made long before
746 such disturbances happen (Lindenmayer et al., 2010).

747

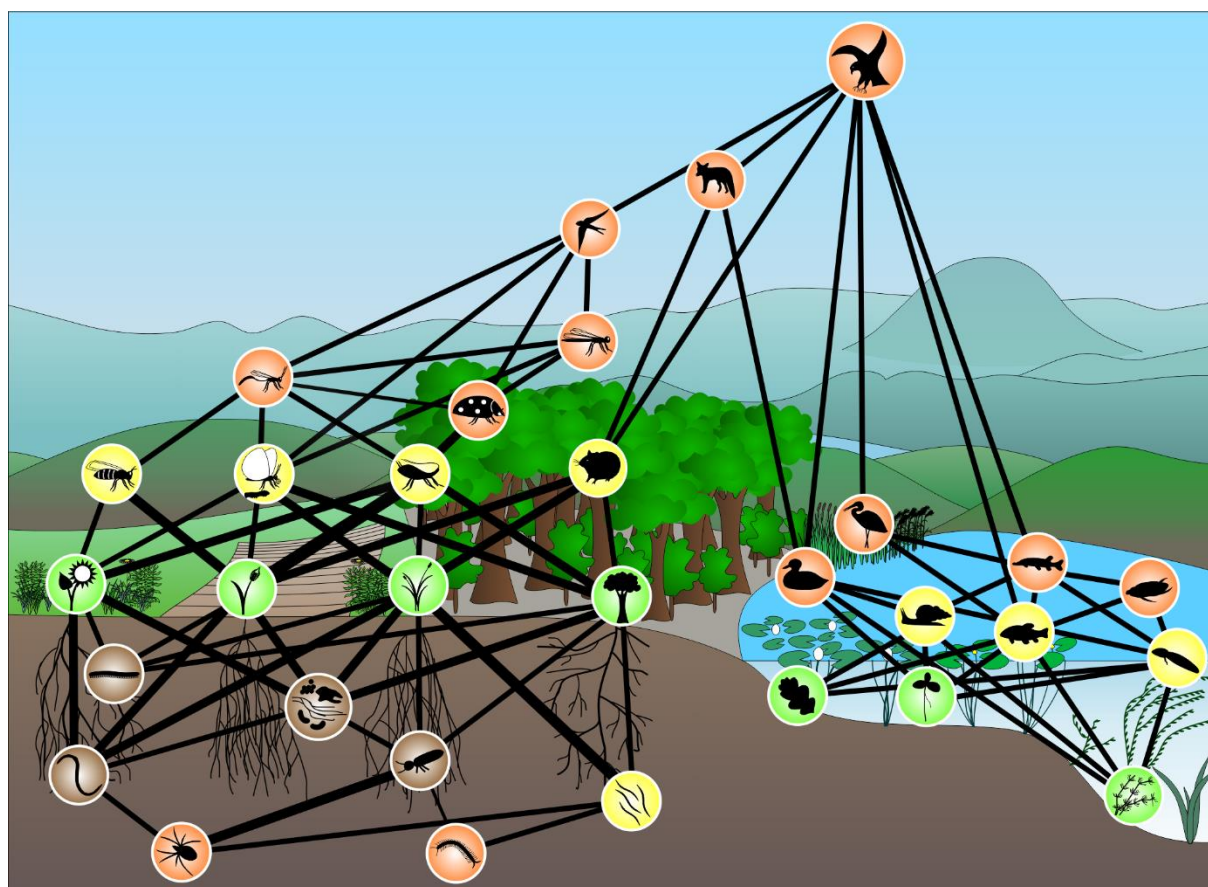
748 Dispersal may promote the functioning of ecosystems in two ways (Leibold et al., 2017; Loreau et
749 al., 2003a; Thompson and Gonzalez, 2016). First, species dispersal and community assembly
750 processes may allow species to track local environmental changes by shifting in space, which may
751 then preserve biodiversity and ensure high ecosystem functioning (Leibold et al., 2017; Loreau et
752 al., 2003a; Thompson and Gonzalez, 2016). Second, source–sink dynamics may allow species to
753 persist in suboptimal environments, thus increasing local biodiversity over time, although this does
754 not necessarily promote functioning (Leibold et al., 2017). Species-sorting dynamics also provide
755 spatial insurance, so that compensatory dynamics stabilize the fluctuations of each function
756 through time at the regional, but not necessarily at the local scale (Loreau et al., 2003a; Thompson
757 and Gonzalez, 2016). Relatedly, spatial network modularity has a buffering effect in perturbed
758 experimental metapopulations, protecting some local subpopulations from the perturbation
759 (Gilarranz et al., 2017) or providing empty patches for recolonization, ultimately stabilizing the
760 metapopulation (Fox et al., 2017). Adding to this complex picture, there is experimental evidence
761 suggesting that also habitat isolation and matrix quality influence biodiversity and ecosystem
762 functioning (Spiesman et al., 2018). Thus, the fragmentation and connectivity of habitat patches as

763 well as the mobility of taxa driving meta-community dynamics are likely to be of great importance,
764 yet understudied in BEF research (Gonzalez et al., 2017).

765

766 Most terrestrial ecosystems have soft boundaries highly permeable for many species. Accordingly,
767 different ecosystems should not be regarded in isolation but in the context of surrounding
768 ecosystems. For instance, biodiversity effects on adjacent ecosystems should be studied to explore
769 the links between ecosystems (e.g., by linking aquatic ecosystems, forests, agricultural fields, etc.)
770 and the role of ‘source’ and ‘sink’ dynamics in fluxes of elements, energy, organisms, biomass, and
771 information between adjacent ecosystems (Gounand et al., 2018; Knight et al., 2005). Here, the
772 investigation of key organisms linking different ecosystems may be particularly relevant to move
773 from the plot scale to the landscape scale (Barnes et al., 2018; **Figure 5**) as well as to define
774 conservation priorities and corresponding management practices.

775



776

777 **Figure 5 | Complex communities link different habitats**, a consideration that may facilitate the
778 upscaling of BEF. Conceptual illustration of how multitrophic interactions across ecosystem boundaries can link
779 different ecosystem types and compartments, including above- and belowground compartments, forests and grasslands,
780 as well as terrestrial and aquatic ecosystems. Links between different network modules in these subsystems provide
781 stability of trophic dynamics, matter and energy flow across system boundaries and provide stability of ecosystem
782 function and service delivery (Barnes et al., 2018).

783

784

2.4. Eco-evolutionary implications of multitrophic BEF

“Nothing in evolution or ecology makes sense except in the light of the other.”

Fanie Pelletier et al. (2009)

Ecology and evolution are sometimes thought of as acting at different timescales, which might explain why evolutionary processes have rarely been considered in past BEF research. However, a growing body of literature shows that evolutionary processes can be rapid and of relevance at what is commonly considered ecological timescales (Carroll et al., 2007; Hendry, 2016), such that a strict time-scale separation is no longer useful. Furthermore, the study of the molecular basis of adaptation has experienced a boost due to recent technological developments (Bosse et al., 2017; Savolainen et al., 2013; Stapley et al., 2010; Wuest and Niklaus, 2018). BEF research may greatly benefit from embracing the rich and growing body of knowledge on micro-evolutionary processes, population genetics, and the molecular basis of adaptation, because adaptation and evolutionary processes are likely to contribute to the dynamic nature of BEF relationships (e.g., Tilman and Snell-Rood, 2014; Zuppinge-Dingley et al., 2014; van Moorsel et al., 2018). However, such eco-evolutionary processes can only be studied in the few long-term experiments worldwide that have been run for multiple generations of the organisms studied.

Undoubtedly, members of an ecological community impose selection pressures onto each other. For example, changing phenotypes have been reported in a number of plant species in response to manipulated biodiversity gradients (Lipowsky et al., 2011, 2012; Schoeb et al., 2018; Zuppinge-Dingley et al., 2014, 2016). Phenotypic changes may allow different coexisting species to use resources in more dissimilar and complementary ways, thereby reducing competition, maximizing growth, and favoring stable coexistence (Tilman and Snell-Rood, 2014; Zuppinge-Dingley et al., 2014). Yet, we know too little about the relative importance of phenotypic plasticity, transgenerational epigenetic processes (Schmid et al., 2018), and genuine evolutionary adaptation that simultaneously contribute to phenotypic changes (Hoffman and Sgrò, 2011; Zuppinge-Dingley et al., 2014). Such knowledge is important, however, in order to estimate how lasting and/or reversible the effects are.

There are a number of ways in which micro-evolutionary processes may help to understand and predict BEF relationships. For example, a significant role of the comparatively slow process of evolutionary adaptation may explain the observation of strengthening BEF relationships over time in grassland experiments (Tilman and Snell-Rood, 2014; Zuppinge-Dingley et al., 2014). Furthermore, micro-evolutionary dynamics may lead to positive feedback loops that can affect ecosystem functioning. Natural selection is usually expected to reduce genetic variance, but genetic variation provides the raw material for future adaptation (Mousseau and Roff, 1987). Frequent changes in the selective regime may thus jeopardize populations' persistence (Hoffman and Sgrò, 2011). Phenotypic plasticity, in contrast, may buffer populations against changing selection regimes (Charmantier et al., 2008). Taking into account the relative importance of phenotypic plasticity and micro-evolutionary adaptation will be essential for the understanding of how adaptation processes affect BEF relationships.

829 Selection in communities is not a one-way route, since members of a community mutually influence
830 each other (Jousset et al., 2016; Tilman and Snell-Rood, 2014). Two conditions seem to be
831 particularly relevant in the context of community assembly. First, functionally similar and/or
832 related species will be selected for character displacement and niche differentiation, thereby
833 promoting specialization, coexistence, and ecosystem processes (Harmon et al., 2009; Tilman and
834 Snell-Rood, 2014). The genetic and evolutionary mechanisms of such processes have rarely been
835 studied in BEF research. Second, species may co-evolve together with their antagonists like
836 pathogens. Here, the species involved differ substantially in generation time. Pathogens may adapt
837 and change quickly, imposing persistent and likely fluctuating selection pressure on host species.
838 Indeed, several studies showed that negative plant-soil feedback effects can induce a decrease in
839 plant growth in monoculture (*e.g.*, Hendriks et al., 2013; Maron et al., 2011; Schnitzer et al., 2011).
840 On the other hand, prolonged time in monocultures in the Jena Experiment has converted negative
841 into positive net plant-soil feedback effects (Zuppinger-Dingley et al., 2016), which could be partly
842 due to the accumulation of plant growth promoting rhizobacteria (Latz et al., 2012). Deteriorating
843 monocultures over time indicates that Janzen-Connell effects, the accumulation of species-specific
844 plant antagonists, may play an important role in BEF relationships (Petermann et al., 2008).
845 Zuppinger-Dingley et al. (2014) proposed that a respective selection pressure should be particularly
846 pronounced in low-diversity plant communities (see also van Moorsel et al., 2018). In contrast,
847 accumulation of such species-specific plant antagonists in high-diversity plant communities would
848 be impeded because of lower host densities (Civitello et al., 2015; Hantsch et al., 2013, 2014;
849 Rottstock et al., 2014). Taken together, these lines of evidence suggest that dissimilar host-pathogen
850 interactions at low *versus* high biodiversity may impose different selection pressures on community
851 members, both at the level of plant species and genotypes (Roscher et al., 2007).

852

853 Genetic diversity within species offers the raw material for future adaptations (Jousset et al., 2016),
854 even if some of the variation may not be utilized under current conditions (Paaby and Rockman,
855 2014). Genetic variation, thus, serves as a genetic insurance for population persistence and
856 ultimately for sustained ecosystem functioning and multifunctionality. It is vital to understand the
857 processes that affect intra-specific diversity in communities differing in species diversity (Vellend
858 and Geber, 2005). Genetic diversity depends on the effective population size, which in turn is
859 determined by census size, reproductive system, spatial structure, and the intensity and shape of
860 natural selection. Strong directional and stabilizing selection both tend to reduce genetic diversity.
861 The potential cascading effects of community diversity on population diversity and eventually intra-
862 specific and phylogenetic diversity are poorly studied (but see Crutsinger et al., 2006; Hughes et al.,
863 2008; Zeng et al., 2017). In fact, there has been a recent interest in how populations assemble with
864 respect to functional diversity, but also phylogenetic diversity. Species differ partly due to divergent
865 directional selection. Under the premise that phylogenetic distance contains a signal of divergent
866 selection for (unknown) functional traits, phylogenetic distance can be used as a proxy for
867 functional diversity (Cadotte et al., 2008). However, such genetic conservatism may be highly
868 variable among traits, for instance among leaf and root traits of plants (*e.g.*, Valverde-Barrantes et
869 al., 2017). Therefore a combination of traits and stepwise phylogeny has been proposed (Cadotte,
870 2013) and successfully applied in multitaxon studies (Thorn et al., 2016). Translating these
871 challenges that have mostly been addressed for herbaceous plants to higher trophic levels, it is also
872 relevant to explore how much phylogenetic diversity is represented within multitrophic
873 communities for applied conservation aspects.

874

875 The field of ecological genetics has seen a great expansion in opportunities by the rapid
876 development of next-generation sequencing technologies (Savolainen et al., 2013). It is now
877 possible to sequence and assemble the genome of just about any species at manageable cost, which
878 allows the study of the genomics of previous non-model organisms in natural conditions (Ellegren,
879 2014; Savolainen et al., 2013; Stapley et al., 2010). Genotyping-by-sequencing techniques allow the
880 study of genetic polymorphisms without much cost- and labor-intensive development of genetic
881 markers and gives an unbiased view on population-wide genetic diversity (Narum et al., 2013).
882 There are many ways how these new technologies can be employed in a BEF context. A particularly
883 exciting avenue is the study of co-evolutionary dynamics in multi-species systems up to the
884 community level. Genomic and transcriptomic methods may allow to uncover the genetic
885 architecture of functional trait variation (Schielzeth and Husby, 2014). Moreover, population
886 genomics allows studying the population structure and inbreeding patterns at high resolution across
887 multiple species. Ultimately, such knowledge will help to link the diversity at the genome level to
888 ecosystem-level processes (Wuest and Niklaus, 2018) and to explore the role of species interactions
889 driving these interlinkages.

890

891

892 **2.5. FAIR data and beyond**

893

894 *The grand challenge for biodiversity informatics is to develop an infrastructure to allow the available data to be*
895 *brought into a coordinated coupled modelling environment able to address questions relating to our use of the*
896 *natural environment that captures the variety, distinctiveness and complexity of all life on Earth.*

897

Alex Hardisty et al. (2013).

898

899 Data plays an increasingly important role for BEF research (Trogisch et al., 2017). As for other
900 subdisciplines of biodiversity research, this results in a need for improved biodiversity informatics
901 along all steps of the data lifecycle from data collection to data analysis and publication (Hardisty
902 et al., 2013). Due to the availability of novel methods like high-throughput sequencing, automatic
903 monitoring, and remote sensing, more and more data are being produced. Often, the amount of
904 data collected exceeds available resources for manually processing this data. Recently established
905 methods in machine learning, in particular deep neural networks, have the potential to alleviate this
906 problem (see Brust et al., 2017 and Ryo and Rillig, 2017 for successful examples). Currently,
907 however, the applicability of these methods is restricted by their need for large sets of labeled
908 training data. Further development of methods to reduce the need for training data and/or semi-
909 automatically label data are needed. Additionally, better tools for data quality assurance and
910 improvement are needed, such as comprehensive data quality frameworks (Morris et al., 2018;
911 Veiga et al., 2017). These are not yet part of commonly used data management platforms though.

912

913 Answering important questions in BEF research often requires data that covers large temporal and
914 spatial scales. Few projects run long enough or cover a wide enough geographical range to be able
915 to collect all the data needed themselves. Thus, BEF research relies on data reuse and sharing -

916 both within projects and across projects. This necessitates BEF data being preserved following the
917 FAIR principles (Wilkinson et al., 2016): data should be findable, accessible, interoperable, and re-
918 usable. This urgent need was described even before the term FAIR was coined (Hampton et al.,
919 2013). For data to be findable, it needs to be described with rich metadata. While suitable
920 annotation schemas exist for some types of biodiversity data (e.g., ABCD for collection data or
921 Darwin Core for occurrence data), they are still lacking for more complex BEF data. The Easy
922 Annotation Scheme for Ecology (Pfaff et al., 2017) or BioSchemas (<http://bioschemas.org>; Gray
923 et al., 2017), for instance, aim to alleviate this problem. In addition to better annotation schemes,
924 better tools to reduce the human effort in creating these annotations are needed. First examples
925 for such approaches in other disciplines show the general feasibility (Rodrigo et al., 2018).

926

927 The best described dataset will not be found, if no appropriate search engines exist. Even though
928 Google recently launched a dataset search, in general, this topic is not yet well researched and poses
929 a number of fundamental challenges (Chapman et al., 2019). Besides finding relevant data,
930 integrating this data is a challenging and labor-intensive task. Both tasks could be made considerably
931 easier by the usage of semantic web technologies, in particular the usage of ontologies (Gruber,
932 1993) and compliance to the linked open data principles (Bizer et al., 2008). This is also addressed
933 in the parts of the FAIR principles related to interoperability and reusability. Finally, there is
934 growing awareness, that preserving data alone is not sufficient for reproducibility. Rather, analysis
935 tools and workflows need to be preserved as well (Hardisty et al., 2019). Culturally, a shift is needed
936 to incentivise proper data management and sharing. However, there are warnings stating that a
937 raise in openly available datasets might create the illusion of ‘a free lunch for all’ and that this system
938 will collapse, if the considerable effort that goes into providing datasets is not properly
939 acknowledged (Escribano et al., 2018).

940

941

942 **2.6. Operationalize BEF insights for ecosystem management, society,** 943 **and decision making**

944

945 *“A mix of governance options, policies and management practices is available for public and private actors in*
946 *Europe and Central Asia, but further commitment is needed to adopt and effectively implement them to address the*
947 *drivers of change, to safeguard biodiversity and to ensure nature’s contributions to people for a good quality of life.”*

948

IPBES (2018)

949

950 With the rising human population size and subsequent ecosystem service demands, there is an
951 increasing need for bringing the ecological, fundamental BEF knowledge into action in order to
952 develop applications for sustainable agroecosystems (Isbell et al., 2017a, b). Will ecosystems be
953 managed in an ecologically sustainable way or will increasing demands be temporarily compensated
954 by higher management intensity only to be followed by long-term depletion of agriculturally used
955 soils? Indeed, recent studies have pinpointed many potential benefits of increased biodiversity in
956 agroecosystems and production forests (Isbell et al., 2017b; Gerard et al., 2017; Liang et al., 2016;
957 Martin-Guay et al., 2018; Pretty, 2018). These conclusions are supported by a long history of

958 intercropping literature that highlights the importance of increasing biodiversity in space and time
959 to maintain crop yields (e.g., Darwin, 1859; Trenbath, 1974; Vandermeer, 1990). In this context,
960 BEF research has the potential to apply the multifunctionality concept (Byrnes et al., 2014; Hector
961 and Bagchi, 2007) to move beyond considering multifunctionality a suite of independent functions,
962 but rather to consider synergies and trade-offs among different ecosystem services (**Figure 3**, Allan
963 et al., 2015; Binder et al., 2018; Giling et al., 2018; Hines et al., 2015b; Manning et al., 2018; Meyer
964 et al., 2018). Biodiversity potentially provides a partial substitute for many costly and non-
965 sustainable agricultural management practices, such as the application of fertilizers, pesticides,
966 imported pollinators, and irrigation (Finger and Buchmann, 2015; Isbell et al., 2017b; Tilman et al.,
967 2006; Weigelt et al., 2009).

968 .

969 There is increasing concern that the ongoing loss of biodiversity may affect and diminish the
970 provision of ecosystem services in the future (Cardinale et al., 2012; IPBES, 2018; Manning et al.,
971 2018; Ricketts et al., 2016; Wall et al., 2015). While some key ecological processes may be well
972 understood, such patterns can be difficult to translate into quantitative relationships suitable for
973 use in an ecosystem service context. There is a need to derive quantitative ‘pressure-response
974 functions’ linking anthropogenic pressures with ecosystem functions that underpin key climate,
975 water-quality, and food-regulating services. This requires the joint analysis of the complex,
976 sometimes conflicting or interactive, effects of multiple anthropogenic pressures on different
977 ecosystem functions and the role of biodiversity as a mediating factor determining how
978 anthropogenic pressures translate into changes in ecosystem services. Challenges relate to the
979 differing spatial scales and configuration of anthropogenic pressures and ecosystem service
980 beneficiaries, and uncertainties associated with the time lags between anthropogenic pressures and
981 ecosystem responses (Isbell et al., 2015b). Accordingly, future research needs to employ a
982 quantitative, multi-parameter approach to assess the nature of linkages between biodiversity,
983 ecosystem processes, and ecosystem services (Giling et al., 2018; Manning et al., 2018) within and
984 across ecosystem boundaries (Barnes et al., 2018). This involves the effects of anthropogenic
985 pressures on these linkages, including reversal of pressures through conservation and restoration
986 management, and likely threshold or hysteresis functions (Isbell et al., 2013a).

987

988 Results from the last decade of BEF research tend to suggest that we need to conserve a large
989 proportion of existing species, rather than few selected species, to maximize ecosystem service
990 provisioning across spatial and temporal scales (Isbell et al., 2011; Meyer et al., 2018; Reich et al.,
991 2012; Winfree et al., 2018; but see Kleijn et al., 2015). BEF research has to accept the challenge to
992 embrace socio-ecological systems with their different drivers and interaction networks (e.g.,
993 including humans; Bohan et al., 2016; Dee et al., 2017). This means, for instance, building BEF
994 experiments based on communities realized under (more) realistic land-use regimes regarding
995 current and future stakeholder priorities. Here, e.g., disturbances, restoration projects, and changes
996 in management due to different financial incentives may offer real-world replicated experiments.
997 Scientists will have to more deliberately collaborate with national or federal agencies to develop
998 strategies to become engaged in such projects early enough.

999

1000 Fully embracing socio-ecological processes can only happen at larger scales and adds several layers
1001 of complexity to research projects (Thompson et al., 2018). For operationalizing this goal, food
1002 web network theory can meet social network theory to develop combined assessments (Dee et al.,

1003 2017). It will be important to identify vulnerabilities in the network(s) and critical bottlenecks to
1004 perform opportunity and risk assessments. Knowledge about risk factors can then inform where
1005 and when to best employ management interventions. Ultimately, BEF outcomes have to be
1006 translated to show policymakers and the general public the value of biodiversity, including
1007 consequences of biodiversity decline for human well-being and health, as well as economic aspects,
1008 such as jobs, revenues, and the global climate and economy. As one of the few existing examples,
1009 Liang et al. (2016) recently estimated that the value of biodiversity in maintaining commercial forest
1010 productivity alone (~US\$166 billion to 490 billion per year) is more than twice what it would cost
1011 to implement effective global conservation (but see Dorman et al., 2019). Moreover, to date, few
1012 biodiversity studies have expressed the impact of biodiversity loss on the global warming potential
1013 (Isbell et al., 2015b) – a metric accessible to policy makers and commonly used in the IPCC reports
1014 to compare whether the greenhouse gas balance of ecosystems has a net warming or cooling effect
1015 on climate (IPCC, 2014). Thus, studies linking biodiversity change with global warming potential
1016 would not only be of great fundamental value, but could also lead to insights that are of great value
1017 for the society at large, and that could be disseminated through e.g. IPBES discussions and reports.

1018

1019 **3. Concluding remarks**

1020 The BEF research field faces the critical challenge to simultaneously develop a more mechanistic
1021 understanding of BEF relationships and their context-dependencies as well as to scale up from the
1022 plot-level mechanisms and processes to management-relevant spatial and temporal scales in order
1023 to operationalize BEF insights for ecosystem management, society, and decision making. Here, we
1024 argue that further exploring trophic (e.g., Barnes et al., 2018) and non-trophic interactions (e.g.,
1025 competition, facilitation; Ferlian et al., 2018) in multitrophic communities will be key to investigate
1026 the consequences of non-random biodiversity change as well as the eco-evolutionary
1027 underpinnings and implications of BEF relationships. As a consequence, the study of biotic
1028 interactions needs to consider the interaction history of the involved organisms (Zuppinger-
1029 Dingley et al., 2014). Evolutionary history may integrate information about past trophic and non-
1030 trophic interactions and thus determine the functioning of species in complex communities. As
1031 such, this knowledge may not only be essential to mechanistically understand BEF relationships,
1032 but also to develop applications for sustainable agroecosystems (Isbell et al., 2017a; Wang et al.,
1033 2019), advance ecological restoration to maintain ecosystem functioning (Kettenring et al., 2014),
1034 and sustain the integrity of Earth's ecosystems.

1035

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1055

1056

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