

## Accepted Manuscript

Title: Think ratio! A stoichiometric view on biodiversity–ecosystem functioning research

Author: Helmut Hillebrand Jane M. Cowles Aleksandra Lewandowska Dedmer B. Van de Waal Christoph Plum



PII: S1439-1791(14)00064-4  
DOI: <http://dx.doi.org/doi:10.1016/j.baae.2014.06.003>  
Reference: BAAE 50791

To appear in:

Received date: 30-1-2014  
Revised date: 28-5-2014  
Accepted date: 8-6-2014

Please cite this article as: Hillebrand, H., Cowles, J. M., Lewandowska, A., Van de Waal, D. B., and Plum, C., Think ratio! A stoichiometric view on biodiversity and ecosystem functioning research, *Basic and Applied Ecology* (2014), <http://dx.doi.org/10.1016/j.baae.2014.06.003>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18

**Think ratio!**

**A stoichiometric view on biodiversity – ecosystem functioning research**

Helmut Hillebrand<sup>1,3,5</sup>, Jane M. Cowles<sup>2</sup>, Aleksandra Lewandowska<sup>3</sup>, Dedmer B. Van de Waal<sup>4</sup>,  
Christoph Plum<sup>1</sup>

1) Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky  
University Oldenburg, Schleusenstrasse 1, 26382 Wilhemshaven, Germany

2) Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology  
Building, 1987 Upper Buford Circle, Saint Paul, MN 55108, USA

3) German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz  
5e, 04103 Leipzig, Germany

4) Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW),  
Droevendaalsesteeg 10, 6708 PB Wageningen, the Netherlands

5) Corresponding author: contact: hillebrand@icbm.de

**19 Abstract**

20 Ecological stoichiometry (ES) has become one of the most pervasive theoretical frameworks in  
21 environmental sciences and biology in the last two decades. ES allows predicting processes on all  
22 organizational levels from subcellular structures to ecosystems by relating the elemental composition  
23 and demand of organisms to the relative availability of resources. However, ES has been rarely used  
24 to understand and predict the relationship between biodiversity and ecosystem functioning (BEF),  
25 although ES would be ideally suited as it makes predictions on both population processes underlying  
26 biodiversity as well as on matter transformations underlying ecosystem processes. Here, we propose  
27 to link the two fields of research on ES and BEF relationships and highlight a number of potential  
28 avenues for further research. First, we cast a stoichiometric view on drivers of biodiversity change.  
29 Second, we address the stoichiometric underpinning of biodiversity-productivity relationships. Third,  
30 we discuss potential interactions between stoichiometry and diversity in a food web context.

**31 Zusammenfassung**

32 Ökologische Stöchiometrie (ecological stoichiometry, ES) hat sich in den letzten beiden Jahrzehnten  
33 zu einer der grundlegenden Theorien der Umweltwissenschaften und der Biologie entwickelt. Durch  
34 den Vergleich von elementarer Zusammensetzung von Organismen und ihren Ressourcenansprüchen  
35 mit der relativen Verfügbarkeit der Ressourcen sagt ES Prozesse auf allen Organisationsebenen von  
36 subzellulären Strukturen bis hin zu Ökosystemen voraus. Allerdings wurde ES bisher selten  
37 angewandt um den Zusammenhang zwischen Biodiversität und Ökosystemfunktion zu verstehen,  
38 obwohl ES ideal dazu geeignet wäre, da es sowohl Vorhersagen zu Prozessen macht, die Biodiversität  
39 beeinflussen, als auch zu Materieflüssen und –transformationen, auf denen wichtige  
40 Ökosystemfunktionen basieren. In diesem Artikel untersuchen wir den Zusammenhang dieser beiden  
41 Forschungsfelder und zeigen zukünftige Forschungsfelder anhand von drei Themen auf: i) die  
42 stöchiometrische Aspekte der Treiber des Biodiversitätswandels, ii) stöchiometrische Grundlagen des  
43 Zusammenhangs zwischen Biodiversität und Produktivität, iii) potentielle Interaktionen zwischen  
44 Biodiversität und Stöchiometrie im Nahrungsnetzkontext.

## 45 **Introduction**

46 The concept of ecological stoichiometry (ES) describes the balance of elements in ecological  
47 processes, the term deriving originally from the mass balance in chemical reactions. ES has a long  
48 history in ecology with early investigations on the constraints of mass balance reaching back to the  
49 19<sup>th</sup> century (Liebig 1840; Lotka 1925; Redfield 1934, 1958). More recently, ES has developed  
50 towards a general ecological framework linking cellular processes, organism physiology, and trophic  
51 interactions to processes within and across ecosystems (Sterner & Elser 2002). It has gained  
52 increasing attention in community ecology in order to explain the consumer responses to prey food  
53 quality (Hillebrand, Borer, Bracken, Cardinale, Cebrian et al. 2009a), resource competition between  
54 consumer species (Hall 2004), and consumer effects on prey nutrient composition via nutrient  
55 recycling (Hillebrand, Frost & Liess 2008).

56 Most work in the field of ecological stoichiometry has focused on the importance of material  
57 imbalances at the interface between consumers and their prey. Cellular elemental composition can  
58 differ greatly especially between herbivorous primary consumers and their autotroph prey due to  
59 their different physiology. Nutrient uptake and carbon fixation in photoautotrophs, like  
60 phytoplankton or vascular plants, mainly depend on the availability of mineral resources and light.  
61 Nutrient assimilation and CO<sub>2</sub> fixation are physiologically separated, such that fluctuations in  
62 resource availability and ratios are partly reflected in autotrophs' elemental composition (Ågren  
63 2004; Hillebrand, Steinert, Boersma, Malzahn, Meunier et al. 2013). Consequently, autotrophs can  
64 exhibit a broad plasticity in elemental composition.

65 In contrast, consumer species show a more confined stoichiometry and relatively high nutrient  
66 contents compared to autotrophs (Elser, Fagan, Denno, Dobberfuhl, Folarin et al. 2000; Persson,  
67 Fink, Goto, Hood, Jonas et al. 2010). As a result, the flexibility in autotrophic cellular elemental ratios  
68 can have major consequences for heterotrophs because maximal growth and reproduction of  
69 consumers depend on optimal elemental concentrations in their food. Therefore, consumers'  
70 demand for essential nutrients and the relatively plastic balance of these nutrients in their prey can

71 create elemental mismatches. In consequence of the simultaneous carbon and nutrient assimilation,  
72 consumers have to cope with excess carbon or nutrient concentrations in their food by regulating  
73 their cellular nutrient content via excretion or respiration, which is commonly known as homeostasis  
74 (Frost, Evans-White, Finkel, Jensen & Matzek 2005; Persson et al. 2010). Moreover, elemental  
75 mismatches alter ingestion rates of consumers, with different consequences at the individual level  
76 (compensatory feeding, avoidance) and the population level (reduced abundance and consumption  
77 through reduced growth efficiency) (Hillebrand et al. 2009a).

78 Thus, consumer species with high nutrient demands can become nutrient limited rather than carbon  
79 limited. As enhanced light availability increases autotroph biomass, grazers are assumed to benefit  
80 from the surplus of the food concentration. However, enhanced light intensities also increase the  
81 carbon:nutrient ratios in autotrophs and thereby alter food quality for heterotrophic grazers, either  
82 reducing quality if the consumers are rather nutrient-limited (Urabe, Kyle, Makino, Yoshida,  
83 Andersen et al. 2002; Urabe & Sterner 1996) or increasing it if nutrients are in excess (Boersma &  
84 Elser 2006). Consequently, elemental imbalance in plant-animal interactions can affect herbivore  
85 performance and elemental recycling efficiency (Sterner et al. 2002; Urabe et al. 2002). Yet, since the  
86 nutritional requirements vary between different taxonomical groups, changes in community  
87 composition and species richness may alter the stoichiometric interactions in food webs.

88 The potential consequences of elemental imbalances for trophic interactions are crucial in the face of  
89 expanding human alteration of the global biogeochemical cycles. During the past decades,  
90 anthropogenic nutrient input into the biosphere has almost doubled due to P-mining and the  
91 industrial manufacture of ammonium (Haber-Bosch-method) for the production of artificial fertilizer  
92 (Rockström, Steffen, Noone, Persson, Chapin et al. 2009; Vitousek, Aber, Howarth, Likens, Matson et  
93 al. 1997). The overall input of N and P and their proportion is changing as a consequence of both,  
94 increasing loads of nitrogen due to enhanced use in agriculture on the one hand, and management  
95 success focused on phosphorus control on the other (Glibert 2012; Grizzetti, Bouraoui & Aloe 2012).  
96 Excess in nutrient enrichment has immense implications for the mass balance of carbon to nutrients

97 in the environment on the one hand (Penuelas, Sardans, Rivas-Ubach & Janssens 2012) and the  
98 relative availability of different nutrients on the other hand, e.g., atmospheric N-deposition has  
99 already been shown to induce secondary P-limitation (Elser, Andersen, Baron, Bergstrom, Jansson et  
100 al. 2009). The ratio of elements then constrains the energy and nutrient flow through consumer-  
101 resource interactions and thus biogeochemical cycling in ecosystems (Cherif & Loreau 2013; Glibert,  
102 Kana & Brown 2013).

103 The basic principles of the above mentioned predictions are based on experiments which have  
104 focused on linear food chains with single species on different trophic levels. Hence, the effects  
105 resulting from species interactions within trophic levels and between multiple species across trophic  
106 levels have often been excluded from studies on ecological stoichiometry. However, species diversity  
107 may substantially influence organisms' stoichiometry and mediate the stoichiometric interactions  
108 between consumers and their prey. For phytoplankton communities, species richness altered  
109 autotroph stoichiometry by affecting carbon assimilation and nutrient uptake in unequal  
110 proportions, leading to increasing C:nutrient ratios with increasing diversity (Striebel, Behl & Stibor  
111 2009; Striebel, Spörl & Stibor 2008). Similar effects of biodiversity on vascular plant stoichiometry  
112 have been demonstrated in a long-term grassland experiment (Abbas, Ebeling, Oelmann, Ptacnik,  
113 Roscher et al. 2013).

114 These results suggest that there is a potentially strong, but mostly ignored relationship between ES  
115 and a second dominant field of ecological research addressing the relationship between biodiversity  
116 and ecosystem functioning (BEF). Triggered by rapid changes in species composition in many  
117 communities worldwide, BEF research analyses the potential importance of biodiversity for  
118 ecosystem processes such as biomass production, nutrient uptake efficiency, ecosystem stability and  
119 resistance. Most of the BEF studies so far have focused on the relation between biodiversity and  
120 productivity within trophic levels in a variety of ecosystems (Cardinale, Duffy, Gonzalez, Hooper,  
121 Perrings et al. 2012; Cardinale, Matulich, Hooper, Byrnes, Duffy et al. 2011). Duffy et al (2007)  
122 suggested that consequences of altering biodiversity in complex natural ecosystems have to be

123 analyzed in vertical and horizontal dimensions, where vertical means across trophic levels, and  
124 horizontal means within trophic levels. Indeed, recent studies considering diversity effects on the  
125 vertical scale have shown that changes in species richness alter ecosystem processes both within and  
126 across trophic levels (Bruno, Boyer, Duffy & Lee 2008; Filip, Muller, Hillebrand & Moorthi 2012;  
127 Gamfeldt, Hillebrand & Jonsson 2005; Long, Bruno & Duffy 2007).

128 Despite the considerable progress made in this field, many of the relevant studies have manipulated  
129 diversity directly and focused on a biomass-related ecosystem function (productivity, transfer  
130 between trophic levels, decomposition) (Hillebrand & Matthiessen 2009c). These functions are  
131 strongly related to carbon use, whereas the efficiency of using other elements has been less well  
132 investigated in the BEF context. In this opinion paper, we argue that thinking in ratios helps  
133 understanding the relationships between species coexistence and species performance, and thus  
134 enables a more mechanistic view of biodiversity effects in ecosystems. Therefore, we approach i) the  
135 drivers of biodiversity change, ii) the relationship between diversity and productivity, and iii) diversity  
136 effects in food webs from a stoichiometric perspective. These considerations are conceived as  
137 starting points for further research and discussion, not as a review of the respective bodies of  
138 literature. Thus, we strongly focus on recent advances and potential gaps in understanding the  
139 explicit link between ES and BEF, whereas much of the basic literature within these two fields of  
140 research will not be reviewed here.

141

#### 142 **A stoichiometric view on drivers of biodiversity change**

143 The pressure on global biodiversity continues to increase despite increased efforts to mitigate human  
144 impact, resulting in decreasing indicators of the status of biodiversity (Butchart et al. 2010). Some of  
145 these pressures already exceed what has been called “planetary boundaries for a safe-operating  
146 space for humanity” (Rockström et al. 2009). Many of these drivers of biodiversity decline seem to be  
147 reflective of increasing “amounts” of human pressure, including land conversion to agriculture,  
148 pollution, climate change, and increasing availability of resources for primary producers. Increasing

149 quantities of these pressures are often associated with increasing negative impact on biodiversity.  
150 The negative consequences for biodiversity may not only be mechanistically explained by the  
151 “absolute amounts”, but also by the “relative amounts (or ratios)” at which these pressures occur.  
152 The best example for this argument derives from the human domination of elemental cycles and  
153 consequences of eutrophication for biodiversity. Nutrient enrichment is one of the main drivers of  
154 biodiversity change. Experimental evidence shows that fertilization generally increases dominance of  
155 a limited number of species in autotroph communities (i.e., reduces evenness), but can have  
156 differential impact on species richness depending on ecosystem type and nutrient supply (Hillebrand,  
157 Gruner, Borer, Bracken, Cleland et al. 2007). Analyzing chronic nutrient deposition in long-term  
158 experiments and observational data, a decline in species richness with increasing nutrient supply has  
159 been observed in many systems such as grasslands (Dupre, Stevens, Ranke, Bleeker, Pepler-Lisbach  
160 et al. 2010; Stevens, Dise, Mountford & Gowing 2004; Wassen, Olde Venterink, Lapshina &  
161 Tanneberger 2005) or coastal ecosystems (Lotze, Lenihan, Bourque, Bradbury, Cooke et al. 2006).  
162 Increasing amounts of nutrients tend to reduce biodiversity more and thus we often relate  
163 biodiversity loss to the amount of fertilization (Fig. 1A). However, the concentration levels achieved  
164 in fertilized systems are rarely high enough to be toxic and thus to be directly responsible for species  
165 loss. Instead, nutrient enrichment does primarily act on biodiversity by altering resource ratios and  
166 thereby competition.

167 Increasing nutrient deposition increases the chance that another resource becomes limiting for  
168 organisms and that competition for this resource intensifies (Fig. 1B). In plant assemblages, the  
169 competition for resources along a gradient of N-deposition switches from most (if not all) species  
170 being N-limited at very low N-availability towards light as the dominant limiting resource at high N-  
171 deposition as fertilized biomass production reduces light availability. Different resources (N, K, P,  
172 light, water) potentially limit different species at intermediate N-deposition, as species exhibit trade-  
173 offs in their demand and experience limitation by different concentrations. In a stoichiometric view,  
174 enrichment of one resource imbalances the supply ratios of resources such that all species are



175 limited by the same resource and thus the potential for coexistence decreases (Fig. 1C, see also  
176 Ptacnik, Moorthi & Hillebrand 2010). This prediction directly refers to Tilman's resource-ratio based  
177 theory of competition (Tilman 1982), and is also congruent with Chesson's ideas of stabilizing and  
178 equalizing mechanisms for coexistence (Chesson 2000), when extreme resource supply ratios  
179 prevent trade-offs in resource use from stabilizing coexistence. Furthermore, equalizing mechanisms  
180 also become less likely to maintain coexistence under these imbalanced conditions, as the alteration  
181 of fitness ratios through, e.g. minor fluctuations in resource supply become less plausible.

182 A global study on grasslands revealed that the negative effect of nutrient enrichment on plant  
183 diversity indeed is related to the increase in light limitation induced by fertilization (Borer, Seabloom,  
184 Gruner, Harpole, Hillebrand et al. 2014). This mechanism for biodiversity loss with fertilization has  
185 been described as the destruction of resource niches (Harpole & Tilman 2007) leading to faster  
186 competitive extinction. For pelagic systems, a similar argument has been forwarded as nutrient-load  
187 hypothesis, which also described the reduction in biodiversity as a consequence of eutrophication  
188 resulting from a shift in competition for multiple mineral resources towards competition for a single  
189 resource, light (Brauer, Stomp & Huisman 2012). Field studies on spatial diversity patterns in  
190 different systems indeed revealed that grassland biodiversity peaks at intermediate N:P ratios  
191 (Wassen et al. 2005) and that phytoplankton diversity is maximized when multiple resources are  
192 potentially limiting (Interlandi & Kilham 2001).

193 One prediction from these studies would be that the consequences of nitrogen enrichment on  
194 species extinction is mitigated if the access to other resources would be balanced (Fig. 1D). Recently,  
195 this idea has been tested by analyzing the effects of N-enrichment with and without amendment of  
196 other resources. In fact, the negative effects of N-deposition on grassland biodiversity were mitigated  
197 by addition of understory light supply (Hautier, Niklaus & Hector 2009) or increased atmospheric CO<sub>2</sub>  
198 supply (Reich 2009). Likewise, herbivores can alleviate fertilization effects on plant diversity if they  
199 enhance light availability (Borer et al. 2014). Thus, understanding the consequences of  
200 eutrophication on biodiversity requires ratio-based thinking to unravel the underlying mechanisms.

201

202 **A stoichiometric view on biodiversity – productivity relationships**

203 Scientists have tried to reveal the mechanisms underlying the biodiversity-productivity relationship  
204 by focusing either on how diversity is affected by the available resources, or alternatively, how  
205 diversity influences the uptake of resources and the conversion into new biomass. Here we argue  
206 that the explicit consideration of resource ratios enhances understanding how biodiversity affects  
207 productivity and at the same time is affected by productivity. To the latter argument, recent  
208 evidence amounts that there is no simple bivariate relationship that describes how the rate of  
209 primary production directly constraints biodiversity. Neither meta-analyses (Mittelbach, Steiner,  
210 Scheiner, Gross, Reynolds et al. 2001; for a critical discussion of this meta-analysis see Whittaker  
211 2010) nor global assessments of the productivity-biodiversity relationship in grasslands (Adler,  
212 Seabloom, Borer, Hillebrand, Hautier et al. 2011) find a strong direct effect of productivity on  
213 biodiversity. The first argument that biodiversity-driven productivity needs a stoichiometric  
214 viewpoint is based on the fact that organisms (and thus biodiversity) integrate different elemental  
215 pathways, such that the assimilation of one element depends on the availability of other elements  
216 (Frost et al. 2005), e.g. N-rich transport proteins for uptake or P-rich ribosomes for growth.  
217 Biodiversity effects on productivity thus reflect multi-element resource use efficiency and the ratio of  
218 available resources should be an important determinant of these effects.

219 Two articles by Cardinale and co-authors paved the way to apply the stoichiometric approach to the  
220 BEF framework. A model on resource supply and resource use in metacommunities showed that  
221 more species coexist at higher levels of supply if resource ratios are balanced and that this enhanced  
222 coexistence leads to more efficient transformation of available resources into biomass production  
223 (Gross & Cardinale 2007). In an empirical test of this model, Cardinale et al. (2009) found the  
224 predicted patterns between resource supply, biodiversity and resource use in microalgal  
225 communities. They concluded that producer biodiversity responded to the potential productivity  
226 (resource availability and ratios), but biodiversity itself affected the realized productivity (resource

227 use efficiency = actual biomass production). Thereby, biodiversity can be the cause and consequence  
228 of productivity at the same time in their multivariate productivity-diversity model.

229 To illustrate this idea, let us consider resource use efficiency (RUE) for single and multiple resources  
230 for an assemblage of primary producers. RUE describes the efficiency at which organisms can convert  
231 resources into biomass and for producers typically refers to the amount of carbon produced per unit  
232 of available resource. Productivity generally shows a saturation function with resource availability in  
233 a system limited by a single resource, whereas RUE peaks at intermediate availability. More  
234 specifically, RUE first increases as the resource becomes less limiting, but then decreases as the  
235 resource becomes available in excess (Fig. 2A). In such a system, the species with the highest RUE will  
236 largely determine the attained biomass production, and additional biodiversity will not necessarily  
237 enhance this ecosystem function. By contrast, biodiversity will alter productivity in an environment  
238 allowing for multiple resource limitation. Trade-offs in the acquisition of different resources (i.e. high  
239  $RUE_{R1}$  vs. high  $RUE_{R2}$ ) may not only affect the probability of coexistence (see Fig. 1C), but also the  
240 traits of species maintaining biomass production and the overall production of biomass (Fig. 2B). If  
241 relative resource availability fluctuates over time, highest productivity is maintained by diverse  
242 assemblages exhibiting functional turnover, i.e. the replacement of dominant species with different  
243 RUE optima drives community biomass dynamics under different supply ratios. Corroborating these  
244 ideas, only diverse plots in the long-term Jena-Experiment maintained high productivity over time as  
245 more species were able to significantly sustain productivity (Allan, Weisser, Weigelt, Roscher, Fischer  
246 et al. 2011).

247 Using a large data set on phytoplankton, a further iteration of this concept explicitly considered the  
248 amount and the ratios of multiple resources by combining different model frameworks including  
249 species energy theory, resource ratio theory and BEF (Cardinale, Hillebrand, Harpole, Gross & Ptacnik  
250 2009, see their Fig. 1). Across almost 500 lakes in Norway, resource availability (amount and ratios)  
251 affected both biodiversity and biomass production of phytoplankton, and biodiversity was  
252 additionally positively related to productivity. Subsequently, this productivity-stoichiometry-diversity

253 (PSD) framework (for nutrients and phytoplankton illustrated in Fig. 3) was experimentally tested  
254 with phytoplankton communities, which corroborated major predictions of the concept (Gamfeldt &  
255 Hillebrand 2011; Hillebrand & Lehmpfuhl 2011), as resource amounts and ratios affected both  
256 biodiversity and productivity, and biodiversity furthermore affected biomass via changed resource  
257 use efficiency.

258 These studies strongly suggest that resource ratios not only affect coexistence and thus biodiversity,  
259 but also mediate how biodiversity affects ecosystem processes. Further mechanistic insight into  
260 these relationships has to be based on functional traits and the link between physiology and  
261 biogeochemistry (Glibert et al. 2013). Besides trade-offs in the acquisition of various resources,  
262 producers also exhibit physiological trade-offs in the uptake and utilization of a single resource, e.g.,  
263 between resource uptake rates and affinities (Angert, Huxman, Chesson & Venable 2009; Litchman,  
264 Klausmeier, Schofield & Falkowski 2007). A high affinity (low half-saturation constant) for a resource  
265 likely facilitates a high RUE, which is particularly favorable at limiting resource conditions, whereas  
266 growth rates may rather scale to maximum uptake rates (Litchman et al. 2007). Thus, physiological  
267 trade-offs in traits associated to the acquisition of various resources will yield a variety of RUEs which  
268 may help explaining the distribution of producer diversity along resource ratio gradients and  
269 ultimately biodiversity-productivity relationships.

270

#### 271 **A stoichiometric view on vertical biodiversity effects**

272 Diversity effects on elemental ratios may propagate through the food web and may additionally be  
273 altered by the diversity of adjacent trophic levels. BEF research has seen major breakthroughs in  
274 understanding the consequences of altered diversity at one trophic level (e.g. primary producers) for  
275 biomass, process rates or diversity at other trophic levels (e.g. consumers) (Griffin, Byrnes &  
276 Cardinale 2013) or decomposers (Srivastava, Cardinale, Downing, Duffy, Jouseau et al. 2009).  
277 However, the consequences of changing diversity at any given trophic level for stoichiometric  
278 constraints across trophic levels are still poorly understood, both from a bottom-up and a top-down

279 perspective. In this section we focus on the plant-herbivore link, which has received the largest  
280 attention in this respect, but explicitly encourage future studies exploring stoichiometric top-down  
281 effects by predators or decomposers, e.g. via nutrient recycling.

282 One bottom-up example is the observation that a more diverse phytoplankton prey community  
283 mitigates the negative effects of increased CO<sub>2</sub>-availability on a herbivore (Urabe & Waki 2009).  
284 Increasing CO<sub>2</sub>-availability increased the C:nutrient ratio of phytoplankton and thereby reduced food  
285 quality for zooplankton and their growth rate (Urabe, Togari & Elser 2003). These stoichiometric  
286 effects on the consumer were mitigated in a more diverse phytoplankton assemblage (Urabe et al.  
287 2009). Increasing phytoplankton diversity has also been shown to enhance performance of  
288 zooplankton (Gamfeldt et al. 2005; Striebel, Singer, Stibor & Andersen 2012). Complementarity in  
289 food quality is one potential mechanism for this trophic overyielding (Striebel et al. 2012), when  
290 more species allow more balanced ingestion of multiple essential resources, whether they are  
291 elements or organic molecules.

292 From a top-down perspective, consumer diversity affects consumption rates and consumer biomass  
293 production (Griffin et al. 2013). However, little is known of how this relates to the stoichiometry of  
294 nutrient recycling, which has rarely been addressed in a diversity context (Hillebrand, Gamfeldt,  
295 Jonsson & Matthiessen 2009b).

296 The influence of resource supply and balance on diversity effects across trophic levels increases the  
297 complexity of the relationship between biodiversity and ecosystem functions, resulting in multiple  
298 pathways linking resource availability, resource use efficiency and diversity across trophic levels (as  
299 described in Fig. 3). Such systems become experimentally less tractable, albeit there is obviously a  
300 large need to incorporate stoichiometric drivers of biodiversity and functioning in multitrophic  
301 studies.

302 As an illustrative example for this need, increasing temperatures and rising global CO<sub>2</sub> concentrations  
303 may interact synergistically to enhance the change in global phytoplankton C:N:P ratios (Finkel,  
304 Beardall, Flynn, Quigg, Rees et al. 2010). Increasing CO<sub>2</sub> levels are observed to increase

305 phytoplankton C:nutrient ratios (Bellerby, Schulz, Riebesell, Neill, Nondal et al. 2008; Burkhardt &  
306 Riebesell 1997; Losh, Morel & Hopkinson 2012) and can shift phytoplankton communities towards N<sub>2</sub>  
307 fixing cyanobacteria (Agawin, Rabouille, Veldhuis, Servatius, Hol et al. 2007). Further increases of  
308 phytoplankton C:nutrient ratios were observed with rising temperature combined with phosphorus  
309 limitation (De Senerpont Domis, Elser, Gsell, Huszar, Ibelings et al. 2013) and with warming-induced  
310 strengthened stratification reducing nutrient flux from the deep ocean to the surface (Taucher,  
311 Schulz, Dittmar, Sommer, Oschlies et al. 2012, Sardans, Rivas-Ubach & Penuelas 2012). Increased  
312 C:nutrient ratios due to enhanced CO<sub>2</sub> levels may provoke shifts in zooplankton community  
313 composition towards less nutrient demanding species (van de Waal, Verschoor, Verspagen, van Donk  
314 & Huisman 2010). Such stoichiometric signals can transfer to higher trophic levels, also beyond the  
315 herbivore-autotroph link (Boersma, Aberle, Hantzsche, Schoo, Wiltshire et al. 2008; Malzahn,  
316 Clemmesen, Wiltshire, Laakmann & Boersma 2007; Schoo, Aberle, Malzahn & Boersma 2010; Schoo,  
317 Malzahn, Krause & Boersma 2013). Thus, food web dynamics in a more CO<sub>2</sub>-rich world may be  
318 triggered directly by changes in food quality at the producer level, or indirectly by changing  
319 composition and diversity at the producer or consumer level (Fig. 3). These pathways are potentially  
320 interconnected, leading to synergistic or antagonistic interactions, and it is often difficult to extract  
321 the relative contribution of direct mechanisms and diversity-mediated indirect mechanisms  
322 (Hillebrand et al. 2009c). One possible way to compare direct and indirect mechanisms of changing  
323 diversity-ecosystem functioning relationship in complex ecosystems is combining manipulative  
324 multitrophic experiments with modelling approaches including both biodiversity and the  
325 stoichiometry of elements.

326

## 327 **Summary**

328 ES and BEF are two highly successful scientific frameworks, which to a large degree have developed  
329 separately. Here, we show that they can complement each other by (i) providing a mechanistic basis  
330 for changes in biodiversity and in biodiversity effects on ecosystem processes, and (ii) highlighting

331 differences between single species responses to global change and responses in multispecies  
332 communities. Explicitly considering the relative availability of multiple resources instead of simple  
333 bivariate relationships between resources and species will enhance our understanding of  
334 anthropogenic impacts in Earth's ecosystems. Resource ratios will not be the only aspect needed to  
335 understand BEF relationships within and across trophic levels - other metabolic constraints such as  
336 the importance of essential molecules (e.g. essential fatty acids) or structural defense compounds  
337 may be as important – but incorporating resource ratios may strongly increase our ability to predict  
338 functional consequences of biodiversity change.

339

#### 340 **Acknowledgements**

341 This work has been triggered by Teja Tschardt through an invitation for this article and  
342 substantiated by the JenaExperiment research group (DFG FOR, DFG Hi848/11-2). CP has been  
343 funded by DFG (Hi 848/7-1). The final manuscript is a joint effort of the working group StoichFun and  
344 an outcome of a workshop supported by sDiv, the Synthesis Centre for Biodiversity Sciences - a unit  
345 of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the  
346 German Research Foundation (FZT 118).

347

#### 348 **References**

349 Abbas, M., Ebeling, A., Oelmann, Y., Ptacnik, R., Roscher, C., Weigelt, A., Weisser, W.W., Wilcke, W.,  
350 & Hillebrand, H. (2013). Biodiversity Effects on Plant Stoichiometry. *PLOS ONE*, 8, e58179.

351 Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S.,  
352 O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., Brown, C.S., Buckley, Y.M.,  
353 Calabrese, L.B., Chu, C.J., Cleland, E.E., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I.,  
354 Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S., Hagenah, N.,  
355 Lambers, J.H.R., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre,  
356 K.J., Lambrinos, J.G., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore,

357 J.L., Morgan, J.W., Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M.,  
358 Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P., & Yang, L.H. (2011).  
359 Productivity Is a Poor Predictor of Plant Species Richness. *Science*, *333*, 1750-1753.

360 Agawin, N.S.R., Rabouille, S., Veldhuis, M.J.W., Servatius, L., Hol, S., van Overzee, H.M.J., & Huisman,  
361 J. (2007). Competition and facilitation between unicellular nitrogen-fixing cyanobacteria and non-  
362 nitrogen-fixing phytoplankton species. *Limnology and Oceanography*, *52*, 2233-2248.

363 Ågren, G.I. (2004). The C : N : P stoichiometry of autotrophs - theory and observations. *Ecology*  
364 *Letters*, *7*, 185-191.

365 Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., & Hillebrand, H. (2011). More diverse  
366 plant communities have higher functioning over time due to turnover in complementary dominant  
367 species. *Proceedings of the National Academy of Sciences*, *108*, 17034-17039.

368 Angert, A.L., Huxman, T.E., Chesson, P., & Venable, D.L. (2009). Functional tradeoffs determine  
369 species coexistence via the storage effect. *Proceedings of the National Academy of Sciences of the*  
370 *United States of America*, *106*, 11641-11645.

371 Bellerby, R.G.J., Schulz, K., Riebesell, U., Neill, C., Nondal, G., Johannessen, T., & Brown, K.R. (2008).  
372 Marine ecosystem community carbon and nutrient uptake stoichiometry under varying ocean  
373 acidification during the PeECE III experiment. *Biogeosciences*, *5*, 1517-1527.

374 Boersma, M., Aberle, N., Hantzsche, F.M., Schoo, K.L., Wiltshire, K.H., & Malzahn, A.M. (2008).  
375 Nutritional limitation travels up the food chain. *International Review of Hydrobiology*, *93*, 479-488.

376 Boersma, M., & Elser, J.J. (2006). Too much of a good thing: On stoichiometrically balanced diets and  
377 maximal growth. *Ecology*, *87*, 1325-1330.

378 Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler, P.B.,  
379 Alberti, J., Anderson, T.M., Bakker, J.D., Biederman, L., Blumenthal, D., Brown, C.S., Brudvig, L.A.,  
380 Buckley, Y.M., Cadotte, M., Chu, C., Cleland, E.E., Crawley, M.J., Daleo, P., Damschen, E.I., Davies,  
381 K.F., DeCrappeo, N.M., Du, G., Firn, J., Hautier, Y., Heckman, R.W., Hector, A., HilleRisLambers, J.,  
382 Iribarne, O., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Leakey, A.D.B., Li, W., MacDougall, A.S.,



383 McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Mortensen, B., O'Halloran, L.R., Orrock,  
384 J.L., Pascual, J., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan,  
385 L.L., Williams, R.J., Wragg, P.D., Wright, J.P., & Yang, L.H. (2014). Herbivores and nutrients control  
386 grassland plant diversity via light limitation. *Nature*, *508*, 517-520.

387 Brauer, V.S., Stomp, M., & Huisman, J. (2012). The Nutrient-Load Hypothesis: Patterns of Resource  
388 Limitation and Community Structure Driven by Competition for Nutrients and Light. *American*  
389 *Naturalist*, *179*, 721-740.

390 Bruno, J.F., Boyer, K.E., Duffy, J.E., & Lee, S.C. (2008). Relative and interactive effects of plant and  
391 grazer richness in a benthic marine community. *Ecology*, *89*, 2518-2528.

392 Burkhardt, S., & Riebesell, U. (1997). CO<sub>2</sub>-availability affects elemental composition (C:N:P) of the  
393 marine diatom *Skeletonema costatum*. *Marine Ecology Progress Series*, *155*, 67-76.

394 Cardinale, B.J., Bennett, D.M., Nelson, C.E., & Gross, K. (2009). Does productivity drive diversity or  
395 vice versa? A test of the multivariate productivity-diversity hypothesis in streams. *Ecology*, *90*, 1227-  
396 1241.

397 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace,  
398 G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A.,  
399 Srivastava, D.S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59-67.

400 Cardinale, B.J., Hillebrand, H., Harpole, W.S., Gross, K., & Ptacnik, R. (2009). Separating the influence  
401 of resource 'availability' from resource 'imbalance' on productivity-diversity relationships. *Ecology*  
402 *Letters*, *12*, 475-487.

403 Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P.,  
404 O'Connor, M.I., & Gonzalez, A. (2011). The functional role of producer diversity in ecosystems.  
405 *American Journal of Botany*, *98*, 572-592.

406 Cherif, M., & Loreau, M. (2013). Plant - herbivore - decomposer stoichiometric mismatches and  
407 nutrient cycling in ecosystems. *Proceedings of the Royal Society B-Biological Sciences*, *280*.

- 408 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and*  
409 *Systematics*, 31, 343-366.
- 410 De Senerpont Domis, L., Elser, J.J., Gsell, A.S., Huszar, V.L.M., Ibelings, B.W., Jeppesen, E., Kosten, S.,  
411 Mooij, W.M., Roland, F., Sommer, U., Van Donk, E., Winder, M., & Lurling, M. (2013). Plankton  
412 dynamics under different climatic conditions in space and time. *Freshwater Biology*, 58, 463-482.
- 413 Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thebault, E., & Loreau, M. (2007). The  
414 functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, 10,  
415 522-538.
- 416 Dupre, C., Stevens, C.J., Ranke, T., Bleeker, A., Pepller-Lisbach, C., Gowing, D.J.G., Dise, N.B., Dorland,  
417 E., Bobbink, R., & Diekmann, M. (2010). Changes in species richness and composition in European  
418 acidic grasslands over the past 70 years: the contribution of cumulative atmospheric nitrogen  
419 deposition. *Global Change Biology*, 16, 344-357.
- 420 Elser, J.J., Andersen, T., Baron, J.S., Bergstrom, A.K., Jansson, M., Kyle, M., Nydick, K.R., Steger, L., &  
421 Hessen, D.O. (2009). Shifts in Lake N:P Stoichiometry and Nutrient Limitation Driven by Atmospheric  
422 Nitrogen Deposition. *Science*, 326, 835-837.
- 423 Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S.J., Kilham,  
424 S.S., McCauley, E., Schulz, K.L., Siemann, E., & Sterner, R.W. (2000). Nutritional constraints in  
425 terrestrial and freshwater food webs. *Nature*, 408, 578-580.
- 426 Filip, J., Muller, L.L., Hillebrand, H., & Moorthi, S. (2012). Nutritional mode and specialization alter  
427 protist consumer diversity effects on prey assemblages. *Aquatic Microbial Ecology*, 66, 257-269.
- 428 Finkel, Z.V., Beardall, J., Flynn, K.J., Quigg, A., Rees, T.A.V., & Raven, J.A. (2010). Phytoplankton in a  
429 changing world: cell size and elemental stoichiometry. *Journal of Plankton Research*, 32, 119-137.
- 430 Frost, P.C., Evans-White, M.A., Finkel, Z.V., Jensen, T.C., & Matzek, V. (2005). Are you what you eat?  
431 Physiological constraints on organismal stoichiometry in an elementally imbalanced world. *Oikos*,  
432 109, 18-28.

- 433 Gamfeldt, L., & Hillebrand, H. (2011). Effects of Total Resources, Resource Ratios, and Species  
434 Richness on Algal Productivity and Evenness at Both Metacommunity and Local Scales. *PLOS ONE*, *6*.
- 435 Gamfeldt, L., Hillebrand, H., & Jonsson, P.R. (2005). Species richness changes across two trophic  
436 levels simultaneously affect prey and consumer biomass. *Ecology Letters*, *8*, 696-703.
- 437 Glibert, P.M. (2012). Ecological stoichiometry and its implications for aquatic ecosystem  
438 sustainability. *Current Opinion in Environmental Sustainability*, *4*, 272-277.
- 439 Glibert, P.M., Kana, T.M., & Brown, K. (2013). From limitation to excess: the consequences of  
440 substrate excess and stoichiometry for phytoplankton physiology, trophodynamics and  
441 biogeochemistry, and the implications for modeling. *Journal of Marine Systems*, *125*, 14-28.
- 442 Griffin, J.N., Byrnes, J.E.K., & Cardinale, B.J. (2013). Effects of predator richness on prey suppression:  
443 a meta-analysis. *Ecology*, *94*, 2180-2187.
- 444 Grizzetti, B., Bouraoui, F., & Aloe, A. (2012). Changes of nitrogen and phosphorus loads to European  
445 seas. *Global Change Biology*, *18*, 769-782.
- 446 Gross, K., & Cardinale, B.J. (2007). Does species richness drive community production or vice versa?  
447 Reconciling historical and contemporary paradigms in competitive communities. *American*  
448 *Naturalist*, *170*, 207-220.
- 449 Hall, S.R. (2004). Stoichiometrically explicit competition between grazers: Species replacement,  
450 coexistence, and priority effects along resource supply gradients. *American Naturalist*, *164*, 157-172.
- 451 Harpole, W.S., & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension.  
452 *Nature*, *446*, 791-793.
- 453 Hautier, Y., Niklaus, P.A., & Hector, A. (2009). Competition for Light Causes Plant Biodiversity Loss  
454 After Eutrophication. *Science*, *324*, 636-638.
- 455 Hillebrand, H., Borer, E.T., Bracken, M.E.S., Cardinale, B.J., Cebrian, J., Cleland, E.E., Elser, J.J., Gruner,  
456 D.S., Harpole, W.S., Ngai, J.T., Sandin, S., Seabloom, E.W., Shurin, J.B., Smith, J.E., & Smith, M.D.  
457 (2009a). Herbivore metabolism and stoichiometry each constrain herbivory at different  
458 organizational scales across ecosystems. *Ecology Letters*, *12*, 516-527.

- 459 Hillebrand, H., Frost, P., & Liess, A. (2008). Ecological stoichiometry of indirect grazer effects on  
460 periphyton nutrient content. *Oecologia*, *155*, 619-630.
- 461 Hillebrand, H., Gamfeldt, L., Jonsson, P.R., & Matthiessen, B. (2009b). Consumer diversity indirectly  
462 changes prey nutrient content. *Marine Ecology Progress Series*, *380*, 33-41.
- 463 Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai,  
464 J.T., Seabloom, E.W., Shurin, J.B., & Smith, J.E. (2007). Consumer versus resource control of producer  
465 diversity depends on ecosystem type and producer community structure. *Proceedings of the National  
466 Academy of Sciences of the United States of America*, *104*, 10904-10909.
- 467 Hillebrand, H., & Lehmpfuhl, V. (2011). Resource Stoichiometry and Consumers Control the  
468 Biodiversity-Productivity Relationship in Pelagic Metacommunities. *American Naturalist*, *178*, 171-  
469 181.
- 470 Hillebrand, H., & Matthiessen, B. (2009c). Biodiversity in a complex world: consolidation and progress  
471 in functional biodiversity research. *Ecology Letters*, *12*, 1405-1419.
- 472 Hillebrand, H., Steinert, G., Boersma, M., Malzahn, A.M., Meunier, C.L., Plum, C., & Ptacnik, R. (2013).  
473 Goldman revisited: Faster growing phytoplankton has lower N:P and lower stoichiometric flexibility.  
474 *Limnology and Oceanography*, *58*, 2076-2088.
- 475 Interlandi, S.J., & Kilham, S.S. (2001). Limiting resources and the regulation of diversity in  
476 phytoplankton communities. *Ecology*, *82*, 1270-1282.
- 477 Liebig, J.v. (1840). *Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie*.  
478 Braunschweig (D): Vieweg.
- 479 Litchman, E., Klausmeier, C.A., Schofield, O.M., & Falkowski, P.G. (2007). The role of functional traits  
480 and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level.  
481 *Ecology Letters*, *10*, 1170-1181.
- 482 Long, Z.T., Bruno, J.F., & Duffy, J.E. (2007). Biodiversity mediates productivity through different  
483 mechanisms at adjacent trophic levels. *Ecology*, *88*, 2821-2829.

- 484 Losh, J.L., Morel, F.M.M., & Hopkinson, B.M. (2012). Modest increase in the C:N ratio of N-limited  
485 phytoplankton in the California Current in response to high CO<sub>2</sub>. *Marine Ecology Progress Series*, 468,  
486 31-42.
- 487 Lotka, A.J. (1925). *Elements of Physical Biology*. Baltimore (USA): Williams and Wilkins Company.
- 488 Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby,  
489 M.X., Peterson, C.H., & Jackson, J.B.C. (2006). Depletion, degradation, and recovery potential of  
490 estuaries and coastal seas. *Science*, 312, 1806-1809.
- 491 Malzahn, A.M., Clemmesen, C., Wiltshire, K.H., Laakmann, S., & Boersma, M. (2007). Comparative  
492 nutritional condition of larval dab *Limanda limanda* and lesser sandeel *Ammodytes marinus* in a  
493 highly variable environment. *Marine Ecology-Progress Series*, 334, 205-212.
- 494 Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R.,  
495 Dodson, S.I., & Gough, L. (2001). What is the observed relationship between species richness and  
496 productivity? *Ecology*, 82, 2381-2396.
- 497 Penuelas, J., Sardans, J., Rivas-Ubach, A., & Janssens, I.A. (2012). The human-induced imbalance  
498 between C, N and P in Earth's life system. *Global Change Biology*, 18, 3-6.
- 499 Persson, J., Fink, P., Goto, A., Hood, J.M., Jonas, J., & Kato, S. (2010). To be or not to be what you eat:  
500 Regulation of stoichiometric homeostasis among autotrophs and heterotrophs. *Oikos*, 119, 741-751.
- 501 Ptacnik, R., Moorthi, S.D., & Hillebrand, H. (2010). Hutchinson Reversed, or Why There Need to Be So  
502 Many Species. *Advances in Ecological Research*, 43, 1-43.
- 503 Redfield, A.C. (1934). On the proportions of organic derivations in sea water and their relation to the  
504 composition of plankton. In: R.J. Daniel (Ed.), *James Johnstone Memorial Volume* (pp. 176-192).  
505 Liverpool: University Press of Liverpool.
- 506 Redfield, A.C. (1958). The biological control of the chemical factors in the environment. *American*  
507 *Scientist*, 46, 205-221.
- 508 Reich, P.B. (2009). Elevated CO<sub>2</sub> Reduces Losses of Plant Diversity Caused by Nitrogen Deposition.  
509 *Science*, 326, 1399-1402.

- 510 Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer,  
511 M., Folke, C., Schellnhuber, H.J., Nykvist, B., de Wit, C.A., Hughes, T., van der Leeuw, S., Rodhe, H.,  
512 Sorlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J.,  
513 Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., & Foley, J.A. (2009). A safe operating  
514 space for humanity. *Nature*, *461*, 472-475.
- 515 Schoo, K.L., Aberle, N., Malzahn, A.M., & Boersma, M. (2010). Does the nutrient stoichiometry of  
516 primary producers affect the secondary consumer *Pleurobrachia pileus*? *Aquatic Ecology*, *44*, 233-  
517 242.
- 518 Schoo, K.L., Malzahn, A.M., Krause, E., & Boersma, M. (2013). Increased carbon dioxide availability  
519 alters phytoplankton stoichiometry and affects carbon cycling and growth of a marine planktonic  
520 herbivore. *Marine Biology*, *160*, 2145-2155.
- 521 Srivastava, D.S., Cardinale, B.J., Downing, A.L., Duffy, J.E., Jouseau, C., Sankaran, M., & Wright, J.P.  
522 (2009). Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology*, *90*,  
523 1073-1083.
- 524 Sterner, R.W., & Elser, J.J. (2002). *Ecological stoichiometry*. Princeton: Princeton University Press.
- 525 Stevens, C.J., Dise, N.B., Mountford, J.O., & Gowing, D.J. (2004). Impact of nitrogen deposition on the  
526 species richness of grasslands. *Science*, *303*, 1876-1879.
- 527 Striebel, M., Behl, S., & Stibor, H. (2009). The coupling of biodiversity and productivity in  
528 phytoplankton communities: consequences for biomass stoichiometry. *Ecology*, *90*, 2025-2031.
- 529 Striebel, M., Singer, G., Stibor, H., & Andersen, T. (2012). "Trophic overyielding": Phytoplankton  
530 diversity promotes zooplankton productivity. *Ecology*, *93*, 2719-2727.
- 531 Striebel, M., Spörl, G., & Stibor, H. (2008). Light-induced changes of plankton growth and  
532 stoichiometry: Experiments with natural phytoplankton communities. *Limnology and Oceanography*,  
533 *53*, 513-522.
- 534 Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press.

- 535 Urabe, J., Kyle, M., Makino, W., Yoshida, T., Andersen, T., & Elser, J.J. (2002). Reduced light increases  
536 herbivore production due to stoichiometric effects of light/nutrient balance. *Ecology*, *83*, 619-627.
- 537 Urabe, J., & Sterner, R.W. (1996). Regulation of herbivore growth by the balance of light and  
538 nutrients. *Proceedings of the National Academy of Sciences of the United States of America*, *93*, 8465-  
539 8469.
- 540 Urabe, J., Togari, J., & Elser, J.J. (2003). Stoichiometric impacts of increased carbon dioxide on a  
541 planktonic herbivore. *Global Change Biology*, *9*, 818-825.
- 542 Urabe, J., & Waki, N. (2009). Mitigation of adverse effects of rising CO<sub>2</sub> on a planktonic herbivore by  
543 mixed algal diets. *Global Change Biology*, *15*, 523-531.
- 544 van de Waal, D.B., Verschoor, A.M., Verspagen, J.M.H., van Donk, E., & Huisman, J. (2010). Climate-  
545 driven changes in the ecological stoichiometry of aquatic ecosystems. *Frontiers in Ecology and the*  
546 *Environment*, *8*, 145-152.
- 547 Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.E., Schlesinger,  
548 W.H., & Tilman, D. (1997). Human alterations of the global nitrogen cycle: Sources and  
549 consequences. *Ecol Appl*, *7*, 737-750.
- 550 Wassen, M.J., Olde Venterink, H., Lapshina, E.D., & Tanneberger, F. (2005). Endangered plants persist  
551 under phosphorus limitation. *Nature*, *437*, 547-550.
- 552 Whittaker, R.J. (2010). Meta-analyses and mega-mistakes: calling time on meta-analysis of the  
553 species richness-productivity relationship. *Ecology*, *91*, 2522-2533.

554

555

556

557 Figure legends

558 Fig. 1: Stoichiometric view on eutrophication as a driver of biodiversity change. (A) Increasing  
559 amount of N-deposition is predicted to decrease biodiversity. Positive effects of N-deposition on  
560 biodiversity may occur at very low productivity, but do not change our argumentation. (B) The  
561 negative effect of N-deposition has been linked to increasing competition for single other resources.  
562 (C) Highest biodiversity is predicted to occur at intermediate resource ratios. (D) N-deposition alone  
563 therefore decreases biodiversity by imbalanced resource supply, whereas increasing N and light  
564 together will not lead to biodiversity loss (biodiversity indicated by shading, dark grey shades = high  
565 biodiversity, light grey = low biodiversity). Please note that potential productivity would increase  
566 from the lower left to the upper right corner of the diagram (see text for details).

567 Fig. 2: Relationships between biomass production, resource use efficiency (RUE) and resource  
568 availabilities with (A) a single resource, and (B) multiple resources. Black line is biomass production,  
569 grey lines indicate RUE with dark grey for resource 1 (R1) and light grey for resource 2 (R2). See the  
570 main text for more detail.

571 Fig. 3: Conceptual summary of the stoichiometric relationship between biodiversity and ecosystem  
572 functioning within and across trophic levels. It can be predicted that overall supply and balance of  
573 essential resources affect autotroph biomass and diversity. Biodiversity then affects realized  
574 productivity (biomass) via resource use efficiency (RUE; biomass per unit resource), and as this  
575 diversity effect differs between elements, this also alters stoichiometric nutrient incorporation. At  
576 the next trophic level, richness, the rate of ingestion and the secondary production are affected by  
577 the richness, biomass and stoichiometry of the producer level. Additionally, also here consumer  
578 diversity can affect realized secondary production by enhancing resource use efficiency (biomass  
579 produced per prey biomass available) and also change chemical composition of biodiversity. This can  
580 lead to altered nutrient recycling ratios and rates, feeding back into the available resource  
581 stoichiometry. Please note that this description is simplistic, it ignores e.g. higher trophic levels and  
582 decomposers.



Figure 1

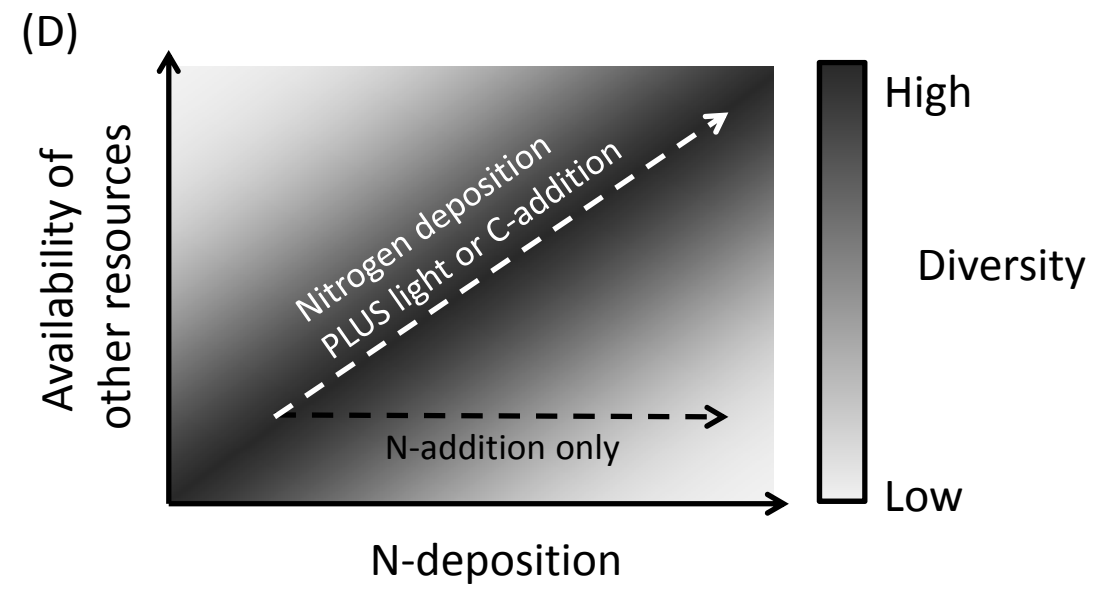
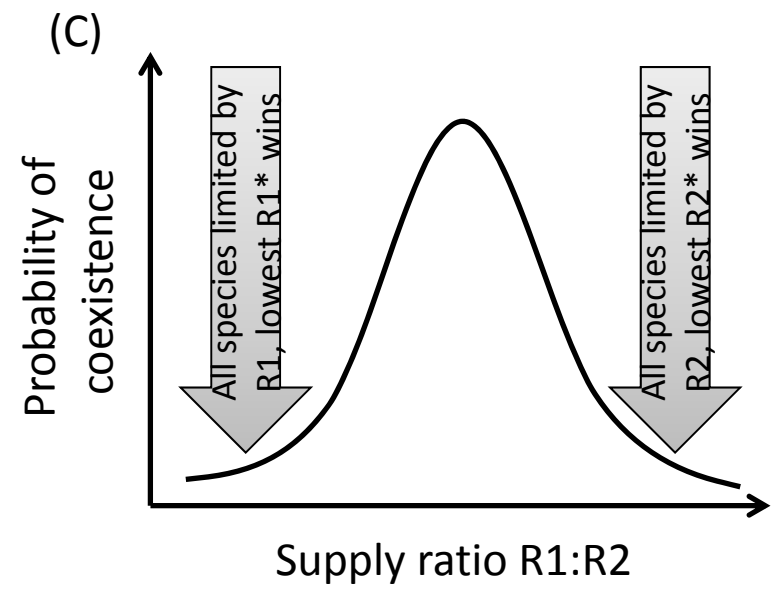
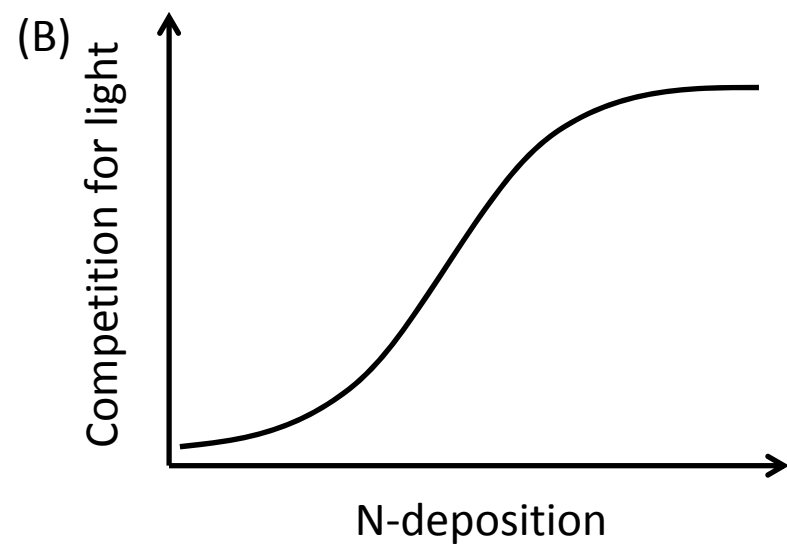
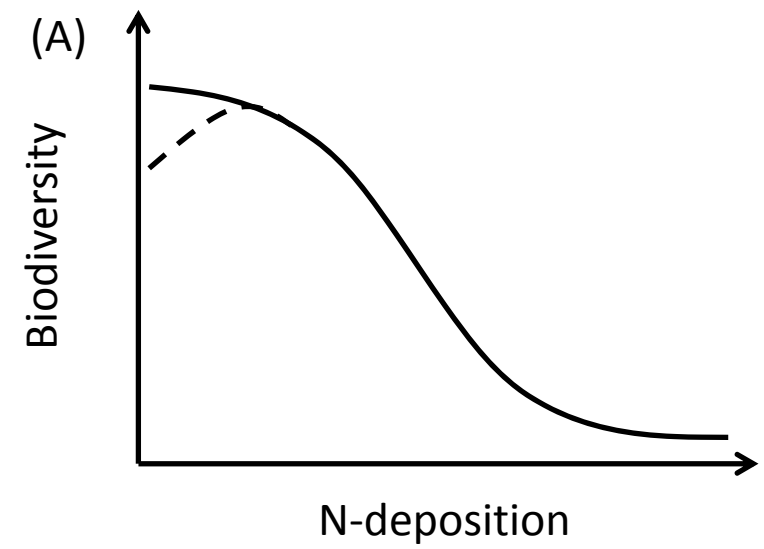


Figure 2

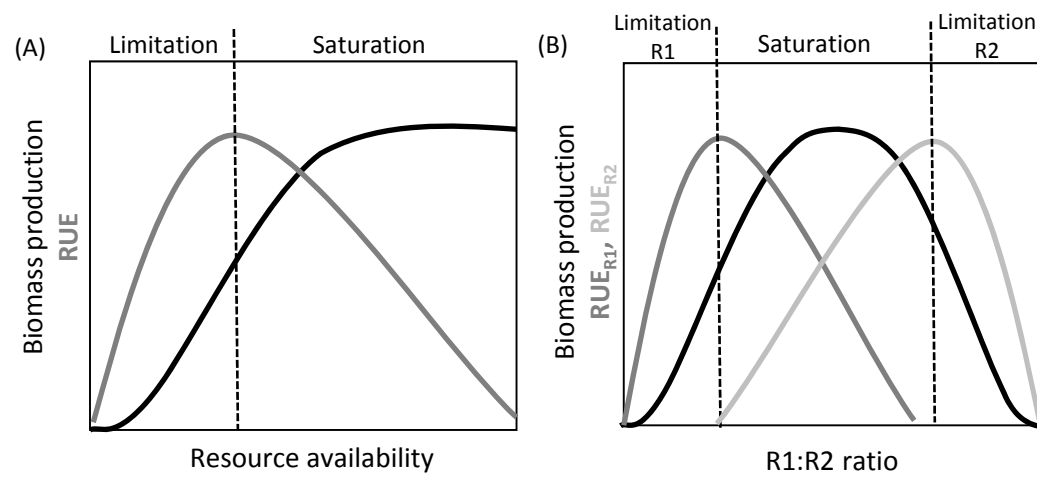


Figure 3

