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Horizontal and vertical diversity jointly shape food web stability against small and large perturbations

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Horizontal and vertical diversity jointly shape food web stability against small and large perturbations

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8 2 **and large perturbations.**
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12 36 designed experiments. SV, FG and MV assisted experiments. QHZ and YXGW analysed all data.
13 37 QHZ and FDL drafted the manuscript, and all authors contributed substantially to revisions.
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42 49 included at the end of the article. Model code will be available on Github.
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3 50 **ABSTRACT**
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6 51 The biodiversity of food webs is composed of horizontal (i.e. within trophic levels) and vertical
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8 52 diversity (i.e. the number of trophic levels). Understanding their joint effect on stability is a
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11 53 key challenge. Theory mostly considers their individual effects and focuses on small
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13 54 perturbations near equilibrium in hypothetical food webs. Here, we study the joint effects of
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16 55 horizontal and vertical diversity on the stability of hypothetical (modelled) and empirical food
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18 56 webs. In modelled food webs, horizontal and vertical diversity increased and decreased
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21 57 stability, respectively, with a stronger positive effect of producer diversity on stability at higher
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23 58 consumer diversity. Experiments with an empirical plankton food-web, where we
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26 59 manipulated horizontal and vertical diversity and measured stability from species interactions
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28 60 and from resilience against large perturbations, confirmed these predictions. Taken together,
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31 61 our findings highlight the need to conserve horizontal biodiversity at different trophic levels
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33 62 to ensure stability.
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63 INTRODUCTION

64 Diversity (i.e., species richness) within food webs is important for sustaining ecosystem
65 functions such as biomass production, energy flow and nutrient uptake (Otto *et al.* 2007;
66 Rooney & McCann 2012; Soliveres *et al.* 2016; Barnes *et al.* 2018; Wang & Brose 2018).
67 Diversity can be characterized in two dimensions (Duffy *et al.* 2007; Srivastava & Bell 2009;
68 Wang & Brose 2018): the number of species within trophic levels (i.e., horizontal diversity)
69 and the number of trophic levels (i.e., vertical diversity). Horizontal and vertical diversity both
70 affect the functioning and stability of food webs, via different mechanisms (Duffy *et al.* 2007).
71 Effects of horizontal diversity are driven by competitive interactions, while effects of vertical
72 diversity are mediated by predation. Horizontal and vertical diversity may interact with each
73 other (Duffy *et al.* 2007). For instance, producer coexistence can be indirectly mediated by
74 consumer diversity (Brose 2008).

75 Until now, the effects of horizontal and vertical diversity on food web stability (i.e., via local
76 stability analysis) have been mostly treated separately (Pimm & Lawton 1977; Duffy *et al.*
77 2007), and mainly using small trophic modules (Pimm & Lawton 1977; McCann *et al.* 1998;
78 Thébault & Loreau 2005). No information is available on their joint effect in multitrophic food
79 webs. Horizontal diversity of consumers is expected to increase stability (McCann *et al.* 1998),
80 because a higher number of consumer species decreases the per capita energy flux in
81 consumer-resource interactions by decreasing the per capita consumption rate (Crowder *et al.*
82 1997; Perna *et al.* 2004; Finke & Denno 2005), hence stabilizing the consumer-resource
83 links (Rip & Mccann 2011; Gilbert *et al.* 2014). Producer diversity can increase stability
84 (McCann 2000) by increasing the potential for niche differentiation among consumers
85 (Novotny *et al.* 2006; Jetz *et al.* 2009; Poisot *et al.* 2013), or again weaken consumer-resource

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3 86 interactions (Berlow 1999; Hillebrand & Cardinale 2004; Edwards *et al.* 2010; Moore & de
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5 87 Ruitter 2012). In contrast, vertical diversity is expected to decrease stability in simple food
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7 88 chains via increasing recovery times (Pimm & Lawton 1977; Morin & Lawler 1995; Post 2002).
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10 89 This negative vertical diversity effect has been evoked as an explanation for the limited
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12 90 number of trophic levels in natural food webs (Pimm & Lawton 1977; Morin & Lawler 1995;
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14 91 McHugh *et al.* 2010; Sabo *et al.* 2010).

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18 92 In natural systems, horizontal and vertical diversity will vary jointly. For example, the decrease
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20 93 of vertical diversity (e.g., the extinction of top predators) could cause cascades that lead to
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22 94 species extinction, lowering horizontal diversity (Crooks & Soulé 1999; Borrvall & Ebenman
23
24 95 2006; Srivastava & Bell 2009). In addition, ecosystem succession and degradation often
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26 96 change both horizontal and vertical diversity (Ferris & Matute 2003; Maharning *et al.* 2009;
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28 97 Yang *et al.* 2018). Hence, it is critical to understand how horizontal (both producer and
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30 98 consumer) and vertical diversity interact and shape food web stability.

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36 99 The individual effects of horizontal and vertical diversity on local stability are often examined
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38 100 by analysing the Jacobian matrix (hereafter 'Jacobian'). This approach assumes that systems
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40 101 are near equilibrium and exposed to small perturbations (May 2001; Allesina & Tang 2012,
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42 102 2015). However, ecosystems are often far away from equilibrium (Allesina & Tang 2015) and
43
44 103 face large perturbations (De Laender *et al.* 2016). This makes it uncertain if stability analyses
45
46 104 based on the Jacobian provide useful information for real-world perturbations (May 2001).
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48
49 105 Alternative stability measures have therefore been proposed (Grimm & Wissel 1997; Arnoldi
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51 106 *et al.* 2016; Donohue *et al.* 2016). Examples include population recovery and resistance
52
53 107 following severe perturbations (Isbell *et al.* 2015; Baert *et al.* 2016; Hillebrand *et al.* 2018) and
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55 108 the coefficient of temporal variation of population dynamics (McCann 2000; Pennekamp *et al.*
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3 109 2018). Recent work indicates that these alternative stability measures may correlate poorly
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5 110 (Ives & Carpenter 2007; Montoya *et al.* 2013; Hillebrand *et al.* 2018; Radchuk *et al.* 2019). For
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7 111 example, temporal stability is positively associated with diversity, while the latter is negatively
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9 112 correlated with resistance (Pennekamp *et al.* 2018).

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13 113 In this paper, we combine models and experiments to examine the joint effect of horizontal
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15 114 and vertical diversity on food web stability. We define stability using two kinds of metric:
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17 115 either based on the assumption of small near equilibrium perturbations, or on biomass and
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19 116 compositional recovery following large perturbations away from equilibrium. To this end, we
20
21 117 first analysed the joint effect of horizontal (the number of producer/consumer species) and
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23 118 vertical diversity (the number of trophic levels) on the Jacobian-based stability of randomly
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25 119 created food webs. Second, we manipulated horizontal and vertical diversity in an experiment
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27 120 with a planktonic food web and quantified their joint effect on stability, measured using
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29 121 empirically established Jacobian matrices. Finally, we quantified the effect of horizontal and
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31 122 vertical diversity on the stability of the same food web, but now measured as resilience
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33 123 following large perturbations caused by two types of chemicals.

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38 124 Overall, our results show for the first time that the positive effect of producer diversity on
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40 125 stability increases with consumer diversity, regardless of vertical diversity. In contrast, vertical
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42 126 diversity always decreased stability. This trend emerged from all analyses and suggests that
43
44 127 conserving diversity within multiple trophic levels is key to promote food web stability.

45 128 **MATERIALS AND METHODS**

46 129 **Model and simulations**

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48 130 We conducted a full factorial design with 24 food web configurations: four levels of horizontal
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50 131 diversity at the first trophic level (producer diversity equalled 6, 7, 8, or 9), three levels of

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3 132 horizontal diversity at the second trophic level (consumer diversity equalled 3, 4, or 5), and
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5 133 two levels of vertical diversity (2 or 3 trophic levels). This design reflects the empirically
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8 134 observed triangularity of food webs (Woodward *et al.* 2005; Turney & Buddle 2016). We
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10 135 deliberately omitted omnivores (species consuming at multiple trophic levels), because
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13 136 omnivores have already been proven to stabilize food webs by creating weak predator-prey
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15 137 interactions (Neutel *et al.* 2002, 2007). Food web connectance (i.e. the number of links divided
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18 138 by the square of the number of species) was set to 0.10 (Dunne *et al.* 2002a, b; Williams *et al.*
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20 139 2002). The links were randomly distributed between adjacent trophic levels.

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23 140 We described community dynamics with generalised Lotka–Volterra equations (Eq. 1)
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25 141 (Emmerson & Yearsley 2004; Gibbs *et al.* 2018; Maynard *et al.* 2018):

$$26 \quad 142 \quad \frac{dN_i}{dt} = N_i(b_i + \sum_j a_{ij}N_j) \quad (1)$$

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29 143 where N_i and N_j are the population density of species i and j , respectively; b_i is the intrinsic
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32 144 per capita growth rate of species i . The b_i is positive for producers, where it represents the
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35 145 density independent growth rate, while b_i is negative for consumers and predators, where it
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38 146 represents a death rate. The a_{ij} is the per capita effect of species j on the growth rate of
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41 147 species i .

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44 148 The growth rate b_i for all producers was equal to 1, which guaranteed that emergent food
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47 149 web patterns were a direct effect of horizontal/vertical diversity, rather than fitness
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50 150 differences among species (Maynard *et al.* 2018). For consumers and predators, we randomly
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53 151 drew b_i from a uniform distribution $U(-0.001, 0)$ while b_i for predators was generated from
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56 152 $U(-0.0001, 0)$ (Eklöf & Ebenman 2006). We ensured that the b_i of predators were less negative
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59 153 than the b_i of consumers, because species at higher trophic levels often have larger body sizes,
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154 and therefore lower mortality rates (Borrvall *et al.* 2000). We ensured that intraspecific

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3 155 competition a_{ii} ($i=j$) was stronger for primary producers (-1) than for consumers and predators
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6 156 (-0.1) (Berg *et al.* 2011; Kadoya *et al.* 2018). Interspecific competitions a_{ij} ($i \neq j$) among
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8 157 producers were sampled from $U(-0.5, 0)$ and set symmetrically to avoid cycling or chaos
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10 158 (Maynard *et al.* 2018)(Eklöf & Ebenman 2006). Consumers competed indirectly by sharing
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13 159 producers, and direct interspecific interactions among consumers were thus set to zero (Eklöf
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15 160 & Ebenman 2006).

161 Finally, the a_{ij} ($i \neq j$), the per capita effect of consumers (or predators) species j on the per capita
162 growth rate of producers (or prey) species i , were sampled from $U(-0.5, 0)$ when a consumer
163 (or predator) only consumed one producer (or prey) (Eklöf & Ebenman 2006). Considering that
164 interaction strengths in natural systems communities often have skewed distributions with
165 mostly weak and only few strong interactions (Borrvall *et al.* 2000), one strong a_{ij} was sampled
166 from $U(-0.4, 0)$ and assigned randomly (Eklöf & Ebenman 2006), if the number of producers
167 (or prey) was larger than one. The weak a_{ij} were sampled from $U(-0.1, 0)$ divided by the
168 number of prey species minus one (Borrvall *et al.* 2000; Borrvall & Ebenman 2006). Hence, the
169 total effect of a consumer (or predator) on all its producers (or prey) a_{ij} always varied between
170 -0.5 and 0, but the average per capita effect of a consumer (or predator) on its producers (or
171 prey) decreased with the number of producers (or prey) (McCann *et al.* 1998; Borrvall *et al.*
172 2000). A rationale for this approach and more details can be found in the *supplementary*
173 *information 1*. The effect of producers (or prey) on consumers (or predators) is given by a_{ji} ,
174 which is positive: $a_{ji} = -k * a_{ij}$, with k representing the efficiency of the resources being
175 converted into consumers, which was set at 0.2 (Borrvall & Ebenman 2006; Eklöf & Ebenman
176 2006).

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3 177 Per food web configuration, we created 10,000 food webs, yielding 240,000 food webs. For
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6 178 each food web, we calculated stability as follows. First, we calculated equilibrium population
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8 179 density (directly solving the equations $0 = b_i + \sum_j a_{ij} \hat{N}_j$ on Eq. 1) and verified if all equilibrium
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11 180 densities were positive. If this was the case, we retained the particular food web, otherwise
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13 181 we discarded it. For each food web configuration, more than 95% of the generated food webs
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15 182 were feasible with positive equilibrium densities (Table S1). Next, we used these equilibria to
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18 183 compute the Jacobian for this food web. Finally, we quantify stability using the recovery time,
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21 184 defined as the negative reciprocal of the real part of the dominant eigenvalue of the Jacobian,
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23 185 i.e. $(-1/\text{real}(\lambda_{\max}))$ (Pimm & Lawton 1977; Emmerson & Yearsley 2004; Moore & de Ruiter
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25 186 2012). A larger recovery time indicates a lower stability. Finally, we conducted two sensitivity
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28 187 analyses to inspect how our results changed with the selected parameter ranges (Fig S1-3).

188 **Experiments: general conditions**

189 We experimentally tested the effect of horizontal and vertical diversity on the stability of a
190 freshwater plankton food web representative of Dutch ditches. These two experiments, each
191 lasted for 21 days, were performed in 900 mL glass jars, filled with 500 ml WC medium
192 (Guillard & Lorenzen 1972; Frenken *et al.* 2018) and contained in a water bath at constant
193 temperature ($19.9 \text{ }^\circ\text{C} \pm 0.8 \text{ }^\circ\text{C}$) and a light regime of 12h: 12h (light: dark). The light intensity
194 at the surface (measured with a LI-COR LI-250A, LI-COR Biosciences, Lincoln, USA) was 120
195 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, and was created using Ceramalux® Phillips 430 Watt High Pressure Sodium Non-
196 Cycling Lamps. We worked with field-collected organisms (details are in the *supplementary*
197 *information 2*). The total initial bio-volume of producers (algae) and consumers (invertebrate
198 grazers) was always 25 mm^3 and 0.2 mm^3 , respectively, regardless of producer and consumer
199 diversity (richness). For the systems with three trophic levels, we added one individual of

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3 200 predator *Chaoborus* to each system. The predators used in the experiments had mean
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5 201 individual body length 11.21 ± 0.04 mm. In both experiments, we worked with 4 replicates.
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8 202 **Experiment 1: empirical Jacobian matrices**

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11 203 The aim of the experiment was to examine how stability, based on empirically constructed
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13 204 Jacobian matrices varied with horizontal and vertical diversity. We manipulated horizontal
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15 205 diversity, at the first (producers; 1 or 5 species) and second trophic level (consumers; 1 or 4
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17 206 species), and vertical diversity (2 or 3 trophic levels) in a full factorial design (Table S2). At all
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19 207 combinations, we estimated interactions (within and between trophic levels) to characterize
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21 208 the Jacobian on day 21 after the start of the experiment. The off-diagonal elements of this
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23 209 matrix are per capita interactions, which we estimated as the per capita material fluxes
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25 210 between consumers (or predators) and producers (or consumers) (de Ruiter *et al.* 1995;
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27 211 Neutel *et al.* 2007; Schwarz *et al.* 2017). The effect of consumers (or predators) on producers
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29 212 (or consumers) is given by $J_{ji} = -\frac{F_{ij}}{M_j}$, and the effect of producers (or consumers) on
30
31 213 consumers (or predators) is given by $J_{ij} = e_j \frac{F_{ij}}{M_i}$, where F_{ij} is the energy flux from i to j (e.g.
32
33 214 from producers to consumers), e_j is the assimilation efficiency of j , and M_i and M_j (g m^{-2}) are
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35 215 the biomass of i and j , respectively (Schwarz *et al.* 2017). The diagonal elements of the
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37 216 Jacobian are $J_{ii} = -s \frac{X_i}{M_i}$, where X_i is the metabolism of trophic level i , and s is a free parameter
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39 217 between 0 and 1 (Schwarz *et al.* 2017). Because s cannot be determined empirically in complex
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41 218 food webs, we determined the smallest s leading to all eigenvalues of the Jacobian having
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43 219 negative real parts. The value of s represents the stability of the community against small
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45 220 perturbations, assessed based on estimated interactions (Schwarz *et al.* 2017). It is therefore
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47 221 conceptually similar to recovery time (smaller values indicate more stable food webs)
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222 obtained with the model and is referred to as the degree of self-damping. Details on the
 223 calculation of F_{ij} , X_{ij} and M are provided in the *supplementary information 3*.

224 **Experiment 2: large perturbations**

225 The objective of this experiment was to examine how horizontal and vertical diversity affected
 226 the stability against large perturbations. Here, we applied functional and compositional
 227 resilience as stability metrics. We manipulated the same experimental factors as in
 228 experiment 1, and added one additional factor: pesticide exposure (absent or present). We
 229 performed this experiment twice, once using the insecticide chlorpyrifos ($1 \mu\text{g l}^{-1}$), and once
 230 using the herbicide linuron ($100 \mu\text{g l}^{-1}$), selectively targeting consumers and producers,
 231 respectively (Wijngaarden *et al.* 1996; Daam *et al.* 2009). Experimental procedures were
 232 identical to the experiment 1. Information on chemical administration is provided in
 233 *supplementary information 4*. We measured community biomass, community composition
 234 (using the same methods as for experiment 1 and on days 6 and 21 day) and stability. To
 235 measure stability we first measured functional resilience (the recovery rate of total biomass)
 236 as (Isbell *et al.* 2015; Baert *et al.* 2016):

$$237 \text{ functional resilience} = \frac{|B_{\text{control},6} - B_{\text{stress},6}|}{|B_{\text{control},21} - B_{\text{stress},21}|} \quad (2)$$

238 where $B_{\text{control},6}$, $B_{\text{control},21}$, $B_{\text{stress},6}$ and $B_{\text{stress},21}$ represent the total biomass in the control (no
 239 pesticide) and exposure (pesticide present) on days 6 and 21. Functional resilience is >1 if
 240 biomass differences between the control and stress treatment decrease between day 6 and
 241 21, and <1 otherwise. Larger values mean faster recovery.

242 Next, we measured compositional resilience (compositional recovery) as (Baert *et al.* 2016;
 243 Hillebrand *et al.* 2018):

$$\text{compositional resilience} = \left(\overbrace{1 - \frac{\sum_i |N_{i\text{control},21} - N_{i\text{stress},21}|}{\sum_i N_{i\text{control},21} + \sum_i N_{i\text{stress},21}}}_{BC_{21}} \right) - \left(\overbrace{1 - \frac{\sum_i |N_{i\text{control},6} - N_{i\text{stress},6}|}{\sum_i N_{i\text{control},6} + \sum_i N_{i\text{stress},6}}}_{BC_6} \right) \quad (3)$$

Compositional resilience can be considered an abundance-based change of Bray-Curtis similarity between day 6 (BC_6) and day 21 (BC_{21}) (Baert *et al.* 2016; Hillebrand *et al.* 2018), where N_i is abundance of species i . Positive values reflect that compositions of the control and disturbed communities converge between day 6 and day 21, while negative values imply compositional divergence. Again, larger values mean faster recovery.

Analysis of simulated and empirical data

To the simulated data, we applied linear regression to estimate the effect of producer, consumer, and vertical diversity, and their pairwise interactions, on the recovery time. To interpret potential effects on recovery time, we also tested for diversity effects on average interaction strengths, defined as the square root of the average of all the off-diagonal elements in the interaction matrix $J_{ij} (i \neq j)$ with total species T i.e., $\left(\frac{\sum_{i \neq j} J_{ij}^2}{T(T-1)} \right)$ (May 2001; Moore & de Ruiter 2012), again using linear regression.

To the data from experiment 1, we applied linear mixed models to test for the effect of producer, consumer, and vertical diversity, and their pairwise interactions, on the degree of self-damping, as calculated from the estimated interactions. We used species identity as a random effect to exclude the potential confounding effect of species identity.

To understand possible effects of diversity on the degree of self-damping, we examined diversity effects on three variables underlying the degree of self-damping: consumer biomass, the energy flux into consumers, and interaction strengths. We did so by first applied the mixed model to test for the effect of producer, consumer, and vertical diversity, and their pairwise

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3 266 interactions (again with species identity as a random effect) on these three variables. Next,
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5 267 we constructed linear regression models to examine the relationship between (1) consumer
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8 268 biomass and energy flux into consumers, (2) energy flux into consumers and the absolute
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10 269 value of interaction strength of consumers to producers, and finally (3) the absolute value of
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13 270 interaction strength of consumers to producers and degree of self-damping (minimum s).
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15 271 Again, we used mixed models with species identity as a random effect, and included
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18 272 interactions between horizontal and vertical diversity. We adopted the same approach for
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20 273 predator biomass, energy flux into predator, and absolute value of interaction strength of
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23 274 predator to consumer. However, note that by definition, vertical diversity here was always
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25 275 three, so we could only analyse the effects of horizontal diversity.

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28 276 To the data from experiment 2, we again used linear mixed-effects models (species identity
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30 277 was again a random effect) to test for the effect of producer, consumer, and vertical diversity
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33 278 and their pairwise interactions on the two measures of recovery (Eq. 2 and 3). Because these
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35 279 measures depend on how total biomass changed with time, we also included sampling time
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38 280 and chemical concentrations into the analysis of total biomass. All models were fitted with the
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40 281 lme4 package in R (Bates *et al.* 2014).

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44 45 283 **RESULTS**

46 47 48 284 **Model simulations**

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51 285 Producer and consumer diversity both promoted stability, i.e., decreased recovery time (Fig.
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53 286 1). The positive effect of producer diversity on stability increased with increasing consumer
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56 287 diversity, and this trend was not qualitatively changed by vertical diversity. Vertical diversity
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58 288 on itself always decreased stability. Stability was highest at high horizontal (producer and
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3 289 consumer) diversity and low vertical diversity, and lowest at low horizontal diversity and high
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5 290 vertical diversity (Fig. 1a,b), indicating that high horizontal diversity can compensate the
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8 291 stability loss caused by vertical diversity. These results were robust to changing all parameters
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10 292 simultaneously from their reference value by -20% and +20% (Fig. S1). Outside of this range,
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12
13 293 the model results were sensitive to the conversion efficiency k (Fig. S2), where larger k
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15 294 destabilized the food webs and switched the diversity-stability relationship, as expected (Rip
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18 295 & Mccann 2011; Barbier & Loreau 2019). When fixing the conversion efficiency k to its
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20 296 reference value, the model results were robust to changes of up to -60% and +60% of all
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23 297 parameters except k (Fig. S3).

25 298 **Experiment 1: empirical Jacobian matrices**

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28 299 Producer, consumer, and vertical diversity all affected food web stability. In line with the
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30 300 model predictions, both producer and consumer diversity increased food web stability (i.e.,
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32
33 301 decreasing the degree of self-damping) and the impact of producer diversity on stability
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36 302 increased with increasing consumer diversity. Also in line with the model results, vertical
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38 303 diversity on itself decreased stability (Fig. 2a,b). Stability was highest at high horizontal (both
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41 304 producer and consumer) diversity and low vertical diversity, and was lowest at low horizontal
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43 305 diversity (producer and consumer) and high vertical diversity (Fig. 2a,b).

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46 306 The effects of horizontal and vertical diversity on stability were associated with effects on
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49 307 consumer biomass, energy fluxes, and interaction strengths between trophic levels. Consumer
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51 308 biomass increased with producer and consumer diversity but decreased with vertical diversity
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54 309 (Fig. 2c,d). Diversity did not affect predator biomass (Table S3).

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57 310 Interactions of producer, consumer, and vertical diversity affected the energy flux into
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59 311 consumers (Fig. 2e,f). At high vertical diversity (i.e., 3), horizontal diversity of either producers

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3 312 or consumers increased the energy flux into consumers (Fig. 2f). This higher energy flux was
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5 313 associated with higher consumer biomass (Fig. 3a). Under low vertical diversity (i.e., 2),
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7 314 however, horizontal diversity decreased the energy flux (Fig. 2e), while increasing consumer
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9 315 biomass (Fig. 3a). We found no effect of diversity on the energy flux into predators (Table S3).
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11 316 The interaction strength of consumers to producers was influenced by interactions of
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13 317 producer, consumer, and vertical diversity. Horizontal diversity decreased the interaction
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15 318 strength, whereas vertical diversity increased it (Fig. 2g,h). The interaction strength was
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17 319 lowest at high horizontal and low vertical diversity, but highest at low horizontal and high
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19 320 vertical diversity (Fig. 2g,h), where the interaction strength was positively correlated with the
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21 321 energy flux into consumers (Fig. 3b). No significant diversity effects were detected on the
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23 322 interaction strength of predators to consumers (Table S3). Finally, the interaction strength of
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25 323 consumers to producers was positively correlated with the degree of self-damping (Fig. 3c),
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27 324 indicating that strong interactions decreased food web stability.
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36 325 **Experiment 2: large perturbations**

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39 326 In line with the results obtained with the Jacobian method for simulated and empirical food
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41 327 web data, producer and consumer diversity both increased stability (i.e. functional resilience)
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43 328 against severe perturbations and the positive effect of producer diversity was stronger when
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45 329 consumer diversity was high (Fig. 4a-d). Again, vertical diversity decreased stability (Fig. 4a-d).
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47 330 Therefore, functional resilience was highest at high horizontal diversity and low vertical
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49 331 diversity, and it was lowest when horizontal diversity was low and vertical diversity was high
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51 332 (Fig. 4a-d). We found qualitatively identical results for stability measured by the compositional
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53 333 resilience (Fig. 5a-d), even though the interactive effect of producer and consumer diversity
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55 334 was weaker for the case of herbicide exposure.
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3 335 The effects of horizontal and vertical diversity on the functional and compositional resilience
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5 336 were associated with effects on total biomass (sum across all trophic levels) and composition,
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7 337 respectively. Total biomass showed signs of recovery after exposure to the herbicide and
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9 338 insecticide, but horizontal diversity increased the biomass recovery rate while vertical
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11 339 diversity decreased it. This result can be understood from the smaller effect the pesticides had
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13 340 on the horizontally more diverse communities (Fig. S4a-d and Fig. S5a-d). Indeed, this smaller
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15 341 effect translates to the numerator and especially denominator of Eq.2 being smaller at higher
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17 342 horizontal diversity, making their ratio (i.e. functional resilience) inevitably larger. The
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19 343 opposite occurred for vertical diversity, which increased biomass differences (Fig. S4e,f and
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21 344 Fig. S5e,f) and therefore decreased the recovery rate.

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23 345 On average, the composition of the exposed and control communities was more similar on
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25 346 day 21 than on day 6, indicating compositional recovery. Horizontal and vertical diversity had
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27 347 also opposite effects on compositional recovery. Because producer abundance accounted for
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29 348 more than 97% of the whole community, the effects of horizontal and vertical diversity on
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31 349 compositional recovery can be understood by focusing on the producer community.

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33 350 The herbicide directly decreased the abundance of sensitive producers (*Desmodesmus*
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35 351 *pannonicum*, *Chlorella vulgaris* and *Selenastrum capricornutum*, Fig. S6a) on day 6, but did not
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37 352 change consumer composition (Fig. S6c,d). A greater producer diversity caused an insurance
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39 353 effect as tolerant producers (e.g., *Scenedesmus obliquus* in Fig. S6a) became dominant, which
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41 354 caused compositional differences between the control and the herbicide-treated systems.
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43 355 This difference translates to the last term of Eq.3 (BC_6) being smaller at higher producer
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45 356 diversity (no composition changes on day 21), making the difference between BC_{21} and BC_6
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47 357 (i.e., compositional resilience) inevitably greater. We also found that the magnitude of this
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3 358 insurance effect was increased by consumer diversity, but decreased by vertical diversity,
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6 359 which respectively increased and decreased compositional recovery (Fig. S6a-d).
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9 360 The insecticide directly decreased the abundance of sensitive consumers (i.e., *Daphnia pulex*,
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11 361 and *Moina macrocopa* in Fig. S7a), and tolerant species (e.g., *Daphnia lumholtzi* in Fig. S7a)
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13 362 became dominant. The dominance of tolerant species had indirect, top-down, effects on its
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15 363 preferred algae (*Scenedesmus acutus*, *C. vulgaris* and *S. capricornutum*), which increased the
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17 364 abundance of non-preferred algae (*D. pannonicum*), compensating the loss of the preferred
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19 365 algae (Fig. S7c). Again, this represents an insurance effect, but this time driven by consumer
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21 366 diversity. This mechanism caused composition to be more different between control and
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23 367 insecticide-exposed systems on day 6 (no composition discrepancy on day 21), which again
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25 368 translated to the last term of Eq.3 (BC_6) being smaller at higher consumer diversity, making
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27 369 the difference between BC_{21} and BC_6 (i.e. compositional resilience) inevitably greater. This
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29 370 insurance effect was again increased by producer diversity, but decreased by vertical diversity,
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31 371 which increase and decrease compositional recovery, respectively (Fig. S7a-d).
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41 373 **DISCUSSION**

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44 374 Our model and empirical results show for the first time that horizontal diversity and vertical
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46 375 diversity jointly affect stability. Specifically, the effect of producer diversity was stronger when
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48 376 consumer diversity was higher, regardless of vertical diversity. Vertical diversity consistently
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50 377 decreased stability. Taken together, these results suggest that food webs that are horizontally
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52 378 diverse at various trophic levels, but contain relatively few trophic levels will be more stable.
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54 379 These conclusions are broadly supported. First, both model simulations and two independent
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56 380 experiments with natural food webs yield consistent results. Second, we applied both
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3 381 Jacobian-based stability assessments that assume small perturbations and population
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5 382 equilibrium, but also alternative stability measures following large perturbations.
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8 383 The results from the simulations and empirical food webs (experiment 1) indicate that, under
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10 384 the assumption of small perturbations and population at equilibrium, horizontal and vertical
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12 385 diversity affect food web stability by changing (average) interaction strength. The individual
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14 386 and joint effects of producer and consumer diversity as well as the effect of vertical diversity,
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16 387 as found through modelling, can be understood from changing average interaction strengths
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18 388 (Fig. S8). The results from experiment 1 can be explained by biomass changes and energy flows
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20 389 between trophic levels, which finally change interaction strengths between trophic levels. We
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22 390 show that the well-known positive (and negative) effects of horizontal (and vertical) diversity
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24 391 on consumer biomass (Duffy 2002; Cardinale *et al.* 2003) underpin these proposed effects.
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26 392 The positive interactive effects of producer and consumer diversity on consumer biomass
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28 393 reflects a greater niche differentiation among producers and consumers, optimising consumer
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30 394 biomass (Cardinale *et al.* 2006; Tilman *et al.* 2014; Barnes *et al.* 2018). The negative effect of
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32 395 vertical diversity on biomass reflects predation on consumers. It should be noted that, in this
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34 396 study, we only added a single predator individual. Given that natural systems are controlled
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36 397 by predator populations (Cardinale *et al.* 2003; Snyder *et al.* 2008; Griffin *et al.* 2013), biomass
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38 398 depression by vertical diversity can be higher than reported here.
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48 399 Increasing the biomass of a focal trophic group generally increases the energy flux into this
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50 400 group (Otto *et al.* 2007; Ehnes *et al.* 2011; Barnes *et al.* 2014). At high vertical diversity (i.e.,
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52 401 3), we found a positive interactive effect of producer and consumer diversity on consumer
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54 402 biomass, which was indeed positively associated with energy fluxes into consumers. However,
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56 403 the positive association between biomass and energy flux can be overruled by other factors
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3 404 such as body size structure (Barnes *et al.* 2014, 2018). Under low vertical diversity (i.e., 2), we
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6 405 detected that high consumer biomass was negatively correlated with the energy fluxes to
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8 406 consumers. We found some support that individual body mass distributions could explain this
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10 407 result (Fig. S9). The treatments with high consumer biomass had a higher proportion of large
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13 408 individuals, which have slower metabolic rates, and thus generate lower energy fluxes, than
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15 409 small organisms.

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18 410 High energy flux between trophic levels can increase interaction strength (McCann 2000; Rip
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21 411 & Mccann 2011; Schwarz *et al.* 2017; Kadoya *et al.* 2018), which in turn decreases food web
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23 412 stability (McCann 2000; Rip & Mccann 2011; Ushio *et al.* 2018). We found that the large energy
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26 413 flux into consumers indeed increased the interaction strength between consumers and
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28 414 producers, which led to lower stability. More specifically, producer and consumer diversity
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30 415 positively interacted to decrease interaction strength, which increased food web stability.
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33 416 Vertical diversity increased the interaction strength and decreased stability.

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36 417 Taken together, interactive effects of producer and consumer diversity can change consumer
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38 418 biomass and the energy flux into consumers, leading to weak interactions and increased
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41 419 stability. Vertical diversity, in contrast, makes for strong links which will decrease stability.

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44 420 Pesticide effects on community biomass were a direct result of effects on community
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46 421 composition, and were buffered by horizontal diversity. This buffering effect has been shown
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48 422 before for competitive systems (Gonzalez & Loreau 2009; Isbell *et al.* 2015; Baert *et al.* 2016).

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51 423 Our findings suggest that this effect also holds for food webs. Importantly, we found that – in
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53 424 our system where producers were the largest community – this effect occurs both when the
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56 425 pesticide directly affects producers and when it affects producers indirectly by depressing
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58 426 consumers.
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3 427 We are cognizant of our study's limitations. First, in our experiments, we only considered two
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6 428 levels per horizontal and vertical diversity treatment. Previous studies have shown that food
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8 429 webs with higher horizontal (producer or consumer) diversity have larger niche differentiation
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10 430 and lower consumption rate (Duffy *et al.* 2007; Edwards *et al.* 2010). We therefore expect the
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12 431 positive effect of producer diversity on stability to be stronger than reported here. Second,
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14 432 natural systems often vary not only in species richness but also in how species biomasses are
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16 433 distributed. Our results may therefore change when considering alternative diversity indices
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18 434 (e.g., Shannon's index in Kato *et al.* (2018)). However, a combination of Shannon's index and
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20 435 species richness may provide a deeper insight in future work. Third, our model assumed
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22 436 pairwise interactions and neglected potential higher-order interactions, i.e. pairwise
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24 437 interactions being modulated by a third species, which have been found to stabilize
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26 438 communities (Bairey *et al.* 2016; Grilli *et al.* 2017; Mayfield & Stouffer 2017; Letten & Stouffer
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28 439 2019). We expect that adding high-order interactions will reinforce the positive effect of
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30 440 horizontal diversity we found here, but weaken the negative effect of vertical diversity on
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32 441 stability. Finally, our results cannot be extrapolated to food webs that include omnivores.
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34 442 Previous studies indeed showed that complex food webs with omnivores potentially hold
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36 443 many stabilizing weak links (Neutel *et al.* 2002, 2007), making the destabilizing effect of
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38 444 vertical diversity we report here possibly weaker. Recent studies demonstrated that the
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40 445 presence of omnivores can alter the relationship between vertical diversity and primary
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42 446 productivity in complex food webs (Wang *et al.* 2019).
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52 447 Our results show that different aspects of biodiversity may affect stability in different ways,
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54 448 through effects on biomass, energy fluxes, and eventually interaction strengths. How our
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56 449 results scale up to more complex food webs is an outstanding question, but our findings
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58 450 suggest that the benefits of horizontal diversity can in theory overcompensate the negative
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3 451 effects of vertical diversity. Our results show that conserving horizontal diversity across
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6 452 trophic levels (multiple horizontal biodiversity) can offer a solution to maintain both
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8 453 functioning and stability of natural ecosystems with high vertical diversity.
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For Review Only

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3 618 **FIGURE LENGENDS**
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6 619 **Figure 1.** Model simulations illustrating the interactive effects of horizontal (producer and
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8 620 consumer) and vertical diversity on recovery time (a lower recovery time indicates a greater
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11 621 stability).

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14 622 **Figure 2.** The interactive effects of horizontal (producer and consumer) and vertical diversity
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16 623 on stability (the degree of self-damping) (a, b), on consumer biomass (c, d), on energy flux
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18 624 from producers to consumers (e, f), and on the absolute value of interaction strength of
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20 625 consumers to producers (g, h). Plotted are sample mean \pm one s.d. Detailed statistical results
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23 626 are listed in Table S4.

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27 627 **Figure 3.** Relationships between consumer biomass (g m^{-2}) and energy flux from producers
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29 628 to consumers ($\text{g c m}^{-2} \text{ h}^{-1}$) (a), between the energy flux from producers to consumers (g c m^{-2}
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31 629 h^{-1}) and the absolute value of interaction strength of consumers to producers (b), and
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33 630 between the absolute value of interaction strength of consumers to producers and the
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35 631 degree of self-damping (c).

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40 632 **Figure 4.** The interactive effects of horizontal (producer and consumer) and vertical diversity
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42 633 on the functional resilience after herbicide (a, b) and insecticide (c, d) exposure. Plotted are
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44 634 sample mean \pm one s.d. Detailed statistical results are listed in Table S5.

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48 635 **Figure 5.** The interactive effects of horizontal (producer and consumer) and vertical diversity
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50 636 on the compositional resilience after herbicide (a, b) and insecticide (c, d) exposure. Plotted
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52 637 are sample mean \pm one s.d. Detailed statistical results are listed in Table S5.

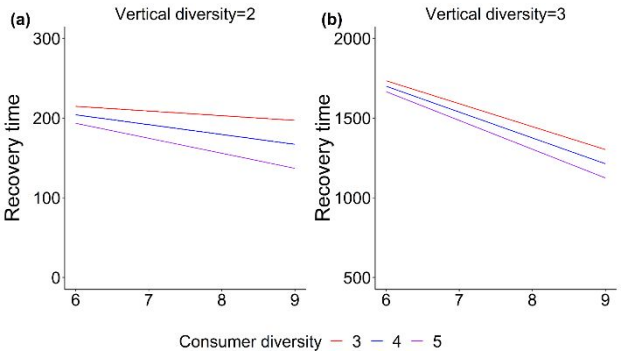
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639 **FIGURES**

640 **Figure 1**

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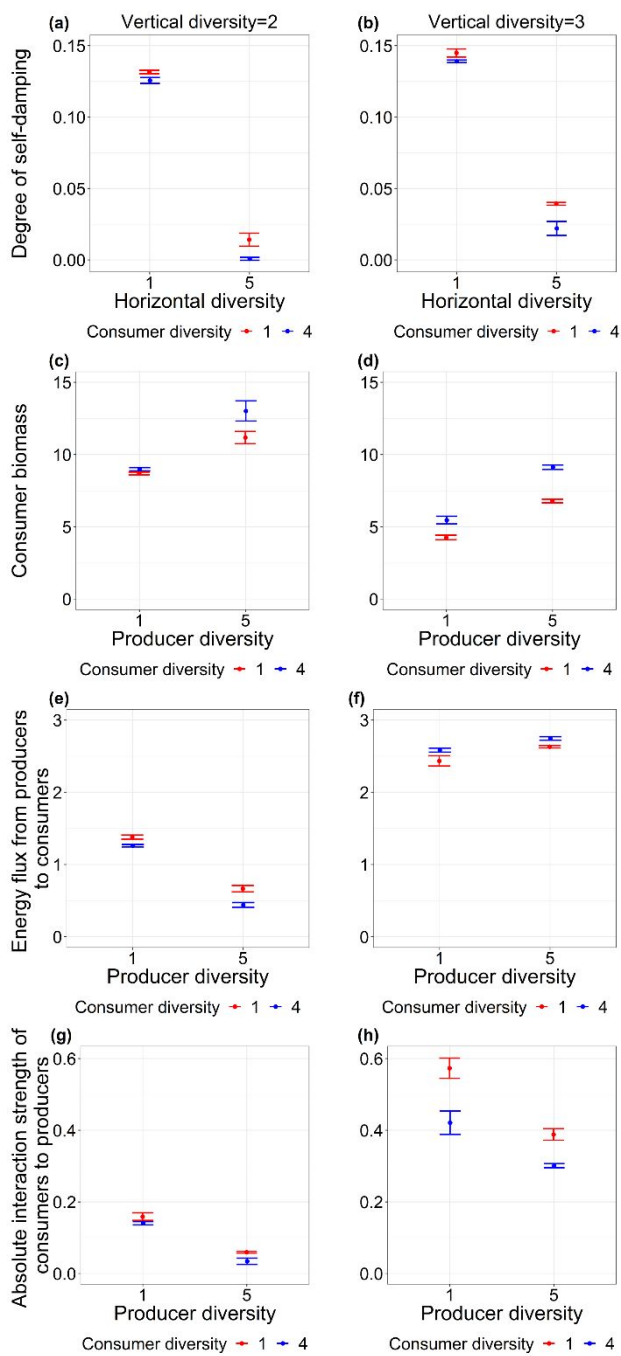
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645 **Figure 2**

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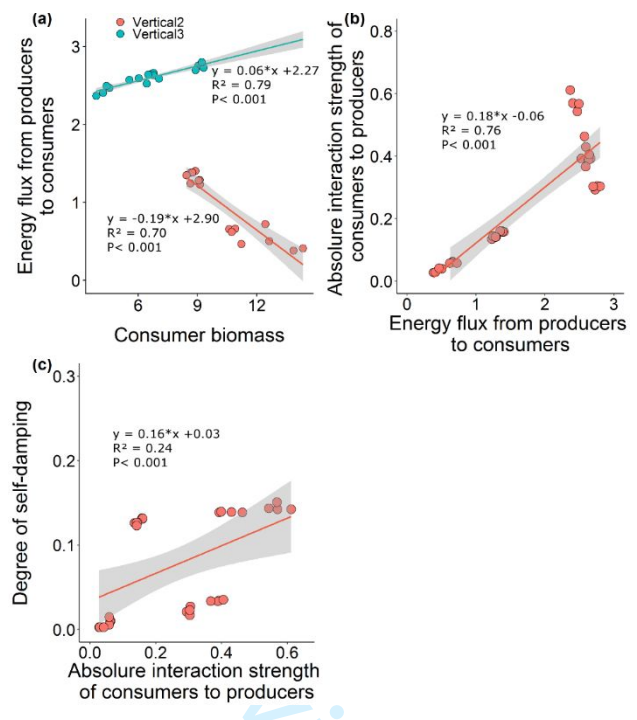
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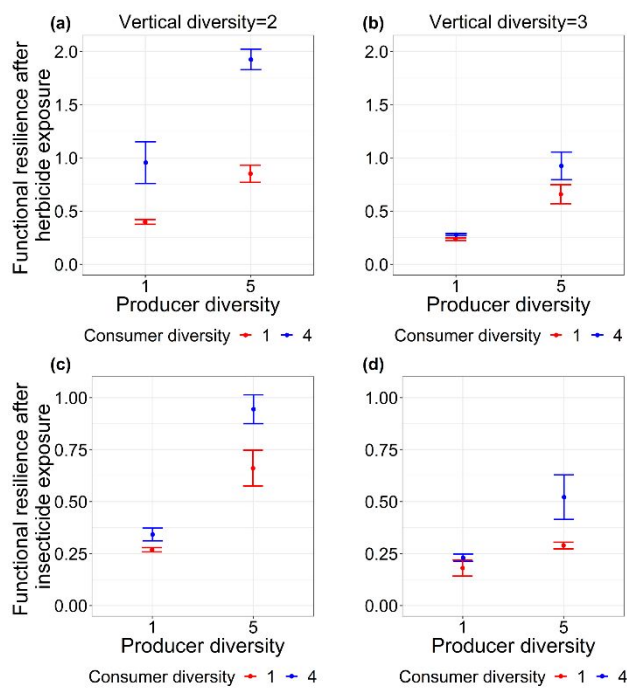
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Figure 3



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657 **Figure 4**
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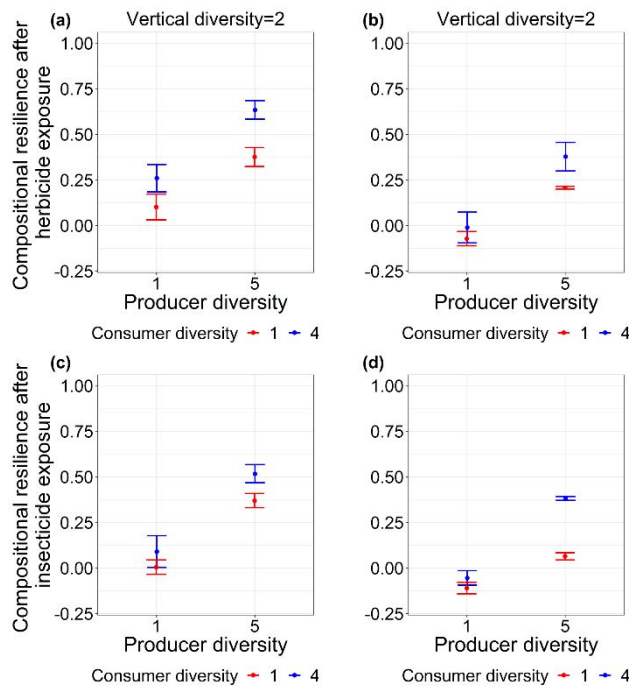


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662 **Figure 5**



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