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# 1 **The community and ecosystem consequences of intraspecific** 2 **diversity: a meta-analysis**

3

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18

19 **ABSTRACT**

20 Understanding the relationships between biodiversity and ecosystem functioning has  
21 major implications. Biodiversity–ecosystem functioning relationships are generally  
22 investigated at the interspecific level, although intraspecific diversity (i.e. within-  
23 species diversity) is increasingly perceived as an important ecological facet of  
24 biodiversity. Here, we provide a quantitative and integrative synthesis testing, across

25 diverse plant and animal species, whether intraspecific diversity is a major driver of  
26 community dynamics and ecosystem functioning. We specifically tested (i) whether the  
27 number of genotypes/phenotypes (i.e. intraspecific *richness*) or the specific identity of  
28 genotypes/phenotypes (i.e. intraspecific *variation*) in populations modulate the structure  
29 of communities and the functioning of ecosystems, (ii) whether the ecological effects of  
30 intraspecific richness and variation are strong in magnitude, and (iii) whether these  
31 effects vary among taxonomic groups and ecological responses. We found a non-linear  
32 relationship between intraspecific richness and community and ecosystem dynamics  
33 that follows a saturating curve shape, as observed for biodiversity–function  
34 relationships measured at the interspecific level. Importantly, intraspecific richness  
35 modulated ecological dynamics with a magnitude that was equal to that previously  
36 reported for interspecific richness. Our results further confirm, based on a database  
37 containing more than 50 species, that intraspecific variation also has substantial effects  
38 on ecological dynamics. We demonstrated that the effects of intraspecific variation are  
39 twice as high as expected by chance, and that they might have been underestimated  
40 previously. Finally, we found that the ecological effects of intraspecific variation are not  
41 homogeneous and are actually stronger when intraspecific variation is manipulated in  
42 primary producers than in consumer species, and when they are measured at the  
43 ecosystem rather than at the community level. Overall, we demonstrated that the two  
44 facets of intraspecific diversity (richness and variation) can both strongly affect  
45 community and ecosystem dynamics, which reveals the pivotal role of within-species  
46 biodiversity for understanding ecological dynamics.

47

48 *Key words:* ecosystem functioning, community, genotype, phenotype, meta-analysis,  
49 biodiversity, eco-evolutionary dynamics.

50	CONTENTS	
51	I. Introduction.....	3
52	II. Materials and methods.....	8
53	(1) Data collection.....	8
54	(2) Meta-analysis.....	10
55	(a) The ecological consequences of intraspecific richness .....	10
56	(b) The ecological consequences of intraspecific variation .....	13
57	(3) Publication bias .....	16
58	III. Results .....	17
59	(1) The intraspecific richness–ecological dynamics relationship .....	17
60	(2) The ecological consequences of intraspecific variation .....	18
61	IV. Discussion .....	19
62	(1) Intraspecific diversity and the dynamics of communities and ecosystems .....	20
63	(2) Research perspectives on the relationships between intraspecific diversity and the	
64	dynamics of communities and ecosystems .....	24
65	V. Conclusions .....	26
66	VI. Acknowledgements.....	27
67	VII. References .....	27
68	VIII. Supporting information .....	39
69		
70		
71	<b>I. INTRODUCTION</b>	
72	Understanding the relationships between biodiversity and ecosystem functioning is an	
73	intensely active field of research informing on the services provided by biodiversity	

74 (Chapin *et al.*, 2000; Loreau, 2000; Hooper *et al.*, 2005; Cardinale *et al.*, 2012).  
75 Biodiversity is generally quantified as the taxonomic, functional and/or phylogenetic  
76 diversity of a species assemblage, and most studies on biodiversity–ecosystem  
77 functioning relationships have to date focused on the interspecific facet of biodiversity  
78 (Naeem *et al.*, 1994; Downing & Leibold, 2002; Hillebrand & Matthiessen, 2009).  
79 However, biodiversity also includes an intraspecific facet that is defined as the  
80 phenotypic, functional and genetic diversity measured within a single species (Odling-  
81 Smee, Laland & Feldman, 2003; Bolnick *et al.*, 2003). During the last two decades,  
82 intraspecific diversity has been demonstrated to account for a non-negligible part of the  
83 total biodiversity measured in plants and animals (Fridley & Grime, 2010; de Bello *et*  
84 *al.*, 2011), representing in some cases up to a quarter of the total variability measured in  
85 communities (Fridley & Grime, 2010; de Bello *et al.*, 2011; Siefert *et al.*, 2015).

86 In parallel, the hypothesis that intraspecific diversity may affect ecological  
87 dynamics at levels higher than the population level (for instance the composition and  
88 the dynamics of communities and/or the dynamics of ecosystem functions) has been  
89 conceptualized (Bolnick *et al.*, 2003, 2011; Hughes *et al.*, 2008; Bailey *et al.*, 2009;  
90 Violle *et al.*, 2012). These conceptual insights have been validated by several key  
91 experiments both in plants and animals (Whitham *et al.*, 2003; Madritch, Greene &  
92 Lindroth, 2009; Matthews *et al.*, 2016; Rudman & Schluter, 2016). For instance, the  
93 experimental manipulation of fish phenotypes from several evolutionarily independent  
94 fish populations has been shown to generate significant changes in both the community  
95 structure of invertebrate prey and the primary productivity of the ecosystem (Harmon *et*  
96 *al.*, 2009; Matthews *et al.*, 2016).

97 Intraspecific diversity can be characterized based on the *richness* of populations,  
98 which corresponds to the differences in the number of genotypes and/or phenotypes

99 composing populations. For instance, populations are often characterized according to  
100 their ‘allelic, genotypic or phenotypic richness’, which is a population parallel of  
101 species richness, a common metric measured at the interspecific level and classically  
102 used to investigate biodiversity–ecosystem function (BEF) relationships (Crutsinger *et*  
103 *al.*, 2006). Intraspecific richness can also affect ecological dynamics hence generating  
104 ‘intraspecific BEF’ (Whitham *et al.*, 2006; Crutsinger *et al.*, 2006). The basic  
105 hypothesis for intraspecific BEF is that increasing the number of genotypes/phenotypes  
106 in a population should alter (either negatively or positively) key ecological functions  
107 such as the decomposition rate of organic matter or the structure of communities. For  
108 instance, experiments manipulating the number of genotypes (from one to 12  
109 genotypes) in plant (*Solidago altissima*) populations have shown that richer populations  
110 contained a higher diversity of invertebrates (Crutsinger *et al.*, 2006). Actually, the  
111 ecological consequences of intraspecific richness should follow a saturating curve (i.e. a  
112 rapid increase followed by a plateau) as often described for BEF observed at the  
113 interspecific level (Hughes *et al.*, 2008). Although rarely tested empirically, this  
114 saturating shape could be due to the combined effects of several mechanisms.  
115 Populations with different richness could have different ecological consequences  
116 because of ecological complementarity among genotypes/phenotypes (i.e. niche  
117 partitioning, facilitation occurring when genotypes use different resources), inhibition  
118 among genotypes/phenotypes (when multiple genotypes are in competition for  
119 resources), or functional redundancy among genotypes/phenotypes that can make  
120 populations ecologically equivalent (Johnson, Lajeunesse & Agrawal, 2006; Hughes *et*  
121 *al.*, 2008). Yet, the shape of the relationship between intraspecific richness and  
122 ecological dynamics has rarely been investigated empirically and to our knowledge has  
123 never been quantified across species.

124           The ecological consequences of intraspecific diversity can also be investigated  
125 through the lens of *variation* in genotypic or phenotypic attributes. Adaptive and non-  
126 adaptive evolutionary processes such as natural selection, plasticity or genetic drift can  
127 generate unique phenotypic differences among populations. These differences can be  
128 associated to key functional processes such as food acquisition or nutrient cycling (e.g.  
129 Grant & Grant, 2006; Rudgers & Whitney, 2006; Lowe, Kovach & Allendorf, 2017),  
130 resulting in both trophic and non-trophic effects of intraspecific variation on ecological  
131 dynamics (Odling-Smee *et al.*, 2003; Whitham *et al.*, 2003; Matthews *et al.*, 2011). For  
132 instance, it has been shown experimentally that plant genotypes differing in their  
133 susceptibility to herbivores harbour different communities of herbivores (Crutsinger,  
134 Cadotte & Sanders, 2009a; Barbour *et al.*, 2009b). Similarly, mesocosm experiments  
135 have shown that differences in diet within predator populations can modify prey  
136 community structure (Post *et al.*, 2008; Harmon *et al.*, 2009; Howeth *et al.*, 2013). Non-  
137 trophic interactions can also have an important role. For instance, differences in the  
138 chemical composition of individuals can result in differences in excretion rate or in leaf  
139 chemistry that can then affect ecosystem functions such as primary production or  
140 nutrient recycling (Lecerf & Chauvet, 2008; El-Sabaawi *et al.*, 2015). Recently, Des  
141 Roches *et al.* (2018) demonstrated that intraspecific variation can affect ecological  
142 dynamics to the same extent as the removal or replacement of a species in the  
143 environment. Although based on a relatively limited number of studies (25 studies on  
144 15 species), their study confirmed the hypothesis that intraspecific variation might be a  
145 non-negligible driver of ecological dynamics.

146           Here, we investigated – across various species and ecosystems – the extent to  
147 which both intraspecific richness and intraspecific variation affect the structure of  
148 communities and the functioning of ecosystems, and whether intraspecific diversity is a

149 major driver of ecological dynamics. We reviewed published studies testing the causal  
150 effects of intraspecific diversity on ecological dynamics in two meta-analyses  
151 synthesizing published data across taxa and ecosystems for intraspecific richness and  
152 variation, respectively, and to fulfil three specific objectives. First, we tested the  
153 significance and the shape of the relationship between intraspecific richness and  
154 ecological dynamics. We expected to find a significant saturating relationship between  
155 intraspecific richness and ecological dynamics, because of potential facilitation and  
156 functional redundancy among genotypes and phenotypes (Hughes *et al.*, 2008). Second,  
157 we tested whether manipulating intraspecific richness has similar effects on ecological  
158 dynamics to manipulating interspecific richness, by comparing the ecological effects of  
159 intraspecific richness with those of interspecific richness obtained from experimental  
160 studies manipulating species richness (Duffy, Godwin & Cardinale, 2017). Finally, we  
161 provided a novel and extensive quantitative synthesis testing for the effects of  
162 intraspecific variation on ecological dynamics. Des Roches *et al.* (2018) previously  
163 focused on studies removing or replacing the target species (by which intraspecific  
164 variation was manipulated) to investigate the ecological consequences of intraspecific  
165 variation. This strongly restricted the number of available studies for which effects sizes  
166 could be calculated, and potentially upwardly biased the resulting estimates (Des  
167 Roches *et al.*, 2018). We here relax this restriction by considering all studies  
168 manipulating intraspecific variation, and use a null-model approach to provide a more  
169 accurate relative effect size of intraspecific variation on ecological dynamics. We also  
170 built on this extended data set to partition variance in the ecological consequences of  
171 intraspecific variation according to the type of organism manipulated and the type of  
172 response variable measured. We tested whether the magnitude of the effects of  
173 intraspecific variation on ecological dynamics vary among organism types (primary

174 producers *versus* consumers) and levels of biological organization (community *versus*  
175 ecosystem levels). Because primary producers form the basis of trophic chains, we  
176 expect stronger ecological effects of intraspecific variation in producers than in  
177 consumers. We also expect stronger effects of intraspecific variation on ecosystem  
178 functions than on metrics describing community structure because ecosystem functions  
179 are affected by both trophic and non-trophic effects of biodiversity (Matthews *et al.*,  
180 2014).

181

## 182 **II. MATERIALS AND METHODS**

### 183 **(1) Data collection**

184 We compiled data from published articles quantifying the effects of intraspecific  
185 diversity in a single species on community structure and/or ecosystem functioning. We  
186 focused only on intraspecific diversity that represented the integrative phenotypic effect  
187 of multiple evolutionary processes including selection, drift and/or plasticity. As a  
188 result, we did not consider articles focusing on experimentally induced intraspecific  
189 diversity through induced plastic responses to particular predatory or environmental  
190 cues [for example see Werner & Peacor (2003) for a review]. We reviewed several  
191 experimental studies manipulating intraspecific variation and/or richness within a single  
192 species to test their respective ecological effects. We also reviewed some observational  
193 studies with strong biological hypotheses and adequate design allowing inferring causal  
194 links from intraspecific diversity to ecological dynamics (e.g. Post *et al.*, 2008). Studies  
195 varying intraspecific diversity within a set of multiple species (e.g. Booth & Grime,  
196 2003) were not included in this meta-analysis. The literature search was carried out  
197 using the ISI *Web of Knowledge* and *Scopus* platforms (last accessed 25th July 2018).  
198 We also scrutinized the reference list of each article to obtain additional articles. The

199 following key words were used in various combinations: *community genetics* AND  
200 *intraspecific variation*, *eco-evolutionary dynamics* AND *ecosystem function*, *community*  
201 *genetics* AND *ecosystem function*, and *intraspecific genetic variation* AND *ecosystem*  
202 *function*. We selected articles describing the effects of genotypic and/or phenotypic  
203 richness (intraspecific *richness*) and/or different genotypes/phenotypes (intraspecific  
204 *variation*) in a single target species on community and/or ecosystem dynamics. A total  
205 of 90 studies with available statistics were selected (see online Supporting information,  
206 Appendix S1 and Fig. S1). Among these, 23 studies (100% experimental studies)  
207 focused on intraspecific richness and 75 studies (90% experimental studies, 10%  
208 empirical studies) focused on intraspecific variation.

209 For each study, we recorded the Latin name of the target species and classified them as  
210 primary producers or consumers (including primary and secondary consumers as well as  
211 predators) and according to the major taxonomic categories represented in our data sets:  
212 arthropods (9 species), fishes (6 species), herbaceous plants (14 species), trees (31  
213 species), and fungi (5 species). Overall, this led to 52 species for studies focusing on  
214 intraspecific variation, and 17 species for studies focusing on intraspecific richness. We  
215 recorded seven main response variables related to community structure and ecosystem  
216 functioning. A community is here defined as a group of at least two species, and we  
217 focused on three types of response variables describing the structure of communities:  
218 (1) species abundance: total number of individuals of all species; (2) biomass: total  
219 mass of individuals of all species; (3) community structure: number of species (e.g.  
220 Simpson or Shannon indices), species evenness and/or species richness.

221 Regarding response variables at the ecosystem level, we considered four main  
222 ecosystem functions: (1) decomposition rate: rate at which organic matter is recycled;  
223 (2) elemental cycling: quantity of organic or inorganic materials; (3) primary

224 productivity: measured as several proxies of primary producers: biomass of primary  
225 producers excluding the productivity of the target species, chlorophyll *a* concentration,  
226 daily oxygen production, and photosynthetically active radiation; (4) ecosystem  
227 respiration: rate of oxygen consumption.

228

## 229 **(2) Meta-analysis**

### 230 *(a) The ecological consequences of intraspecific richness*

231 To test for the consequences of intraspecific richness on ecological dynamics, we  
232 focused only on studies investigating the consequences of genotypic richness since this  
233 was the intraspecific diversity facet most commonly manipulated to test for the effects  
234 of intraspecific richness on ecological dynamics. Here, we used the log-transformed  
235 response ratio ( $\ln RR$ ) as an effect size.  $\ln RR$  was computed as:  $\ln \left( \frac{XG}{1G} \right)$ , where  $1G$  is the  
236 average of the response variable measured for the treatment with a single genotype (i.e.  
237 monoculture), and  $XG$  is the average of the response variable measured for each  
238 treatment independently including more than one genotype. For each response variable,  
239  $\ln RR$  increases as the difference in the mean response variable measured in the  
240 treatment with a single genotype and treatments including more than one genotype  
241 increases. We also recorded the difference in the number of genotypes between the  
242 single genotype treatment (monoculture) and all other treatments separately (i.e.  
243 treatments including 2–12 genotypes) as the ‘difference in intraspecific richness’. In our  
244 data set, difference in intraspecific richness therefore varied between one and 11  
245 genotypes. This approach allowed quantifying the ecological consequences of  
246 increasing the number of genotypes for each target species. Since each study generally  
247 assessed the effects of intraspecific richness on more than one response variable, our  
248 data set included a total of 135 assays.

249 We wanted to test the shape and the significance of the relationship between  
250  $\ln RR$  and the difference in intraspecific richness across all case studies. The general  
251 expectation is that ecological differences between treatments increase as differences in  
252 intraspecific richness increase, although this increase may be non-linear (Hughes *et al.*,  
253 2008). We therefore used non-linear mixed-effect models to test the significance and  
254 shape of the relationship between absolute values of  $\ln RR$  ( $|\ln RR|$ ) and differences in  
255 intraspecific richness. More precisely, we modelled this relationship using four different  
256 models to determine the most likely shape of the relationship between  $|\ln RR|$  and  
257 difference in intraspecific richness: (1) a null model (one parameter) was computed for  
258 the null-effect hypothesis (i.e. no significant relationship between  $|\ln RR|$  and difference  
259 in intraspecific richness); (2) a linear model (two parameters) suggesting a positive and  
260 linear relationship between  $|\ln RR|$  and difference in intraspecific richness; (3) a  
261 Michaelis–Menten model (two parameters) in which  $|\ln RR|$  increases with intraspecific  
262 richness, until a plateau is reached (saturating shape); (4) an asymptotic exponential  
263 model (two parameters) with a shape similar to the Michaelis–Menten model, except  
264 that the plateau is reached sooner.

265 All models cited above included article ID and the monoculture ID (i.e. the monoculture  
266 treatment to which each other treatment of richness was compared for a given response  
267 variable within each study) as random terms to account for non-independence of effect  
268 sizes (Noble *et al.*, 2017), and the inverse of the sample size as a weighting parameter  
269 giving greater weight to articles including more replicates. Models were compared using  
270 the Akaike information criterion (AIC) and we retained (as “best models”) all models  
271 that fell within a  $\Delta AIC < 4$  (Burnham & Anderson, 2002). We also calculated for each  
272 model the Akaike weight that provides a conditional probability for each model to be  
273 best supported by the data (Burnham & Anderson, 2002).

274 We then compared the magnitude (absolute effect size) of ecological effects of  
275 intraspecific and interspecific richness. We extracted from each study and for each  
276 response variable the  $\ln RR$  corresponding to the most extreme levels of genotypic  
277 richness ( $x_{\max}$ ) manipulated in each study ( $N = 63 \ln RR$ ). These values were  
278 subsequently compared to published  $\ln RR$  values calculated following a similar method  
279 for experiments ( $N = 35$ ) manipulating interspecific richness (Duffy *et al.*, 2017).  
280 Because absolute effect sizes follow a folded-normal distribution, we used an ‘analyse  
281 and transform’ approach (*sensu* Morrissey, 2016*a,b*) to estimate the absolute means of  
282 effect sizes. This approach consists first of estimating the mean and variance of  $\ln RR$   
283 (using non-absolute values), and then deriving the mean absolute value from these  
284 estimates. To do so, we estimated the mean of  $\ln RR$  for interspecific and intraspecific  
285 richness, respectively, using two independent intercepts models with  $\ln RR$  as the  
286 response variable, article ID as the random effect and the inverse of the sample size as  
287 the weighting parameter. These intercepts models were implemented using the  
288 MCMCglmm package in R (Hadfield, 2010). Markov chain Monte Carlo (MCMC)  
289 chains were run on  $15 \times 10^5$  iterations, with a burn-in interval of  $3 \times 10^4$ , a thinning  
290 interval of  $1 \times 10^3$ , and an inverse-Wishart prior ( $V = 1$  and  $\eta = 0.002$ ). Finally, the  
291 estimated means’  $\ln RR$  values were converted into absolute-magnitude  $|\ln RR|$  values  
292 (following Morrissey, 2016*b*), and we compared the magnitudes of the ecological  
293 effects of interspecific and intraspecific richness based on visual inspection of 95%  
294 percentile intervals (PIs).

295 Finally, to compare the ecological consequences of intraspecific richness  
296 between levels of biological organization, we performed the same ‘analyse and  
297 transform’ approach described above. We used a linear mixed-effect model  
298 (implemented in the MCMCglmm package in R, and parameterized similarly than

299 above) with the  $\ln RR$  as the dependent variable, the inverse of the sample size as the  
300 weighting parameter, article ID and monoculture ID as random factors, and with the  
301 level of biological organization (community *versus* ecosystem response variables)  
302 treated as a fixed effect. The type of organism was not included in this analysis given  
303 that studies on intraspecific richness focused almost exclusively on primary producers  
304 (with two exceptions on fungi).

305

306 *(b) The ecological consequences of intraspecific variation*

307 Given that most studies (86%) did not include a control (i.e. a treatment without the  
308 target species), we compared the strength of effects among all unique genotypes and/or  
309 phenotypes that were considered in each study. Studies generally compared the  
310 consequences of 2–10 different unique genotypes and/or phenotypes (i.e. 2–10  
311 treatments, with each treatment corresponding to a unique genotype/phenotype) on  
312 community and/or ecosystem dynamics; we gathered from each study the statistic ( $t$ ,  $F$ ,  
313  $\chi^2$ , Pearson's  $r$ , Spearman's  $r$ ,  $R^2$  or Hedges'  $g$ ) associated with the between-  
314 treatments comparison (i.e. the variation of the phenotypes/genotypes). The higher the  
315 absolute value of the statistic, the higher the community and ecosystem consequences  
316 due to the variation of genotypes and/or phenotypes. The value of each statistic was  
317 converted into a correlation coefficient ( $r$ ) ranging from 0 to 1 (see Table S1 for the  
318 formulae used). We did not use the direction of the statistic (i.e. positive or negative)  
319 because this depended upon the ecological response variable that was considered, which  
320 complicates comparisons on the direction of effects. The Z-Fisher transformation then  
321 was used to obtain a standardized effect size using the formula:  $Zr = 0.5 \ln \frac{(1+r)}{(1-r)}$ . For  
322 each  $Zr$  value, we calculated the corresponding standard error as  $se_{Zr} = \frac{1}{\sqrt{n-3}}$   
323 (Nakagawa & Cuthill, 2007). Since each study generally focused on more than one

324 response variable, we obtained a total of 502 observed  $Zr$  values, each corresponding to  
325 the effect size of intraspecific variation observed within one species on a single  
326 response variable. The mean global  $Zr$  or mean effect size observed ( $MES_{obs}$ ) and its  
327 95% confidence interval (CI) were calculated using an intercept-only model. This  
328 intercept-only model was run as a mixed model with no fixed effect, article ID as the  
329 random effect and  $se_{Zr}$  included as a weighting parameter to give more weight to  
330 studies with a larger sample size (Koricheva, Gurevitch & Mengersen, 2013).

331 Because  $Zr$  ranged between 0 and  $+\infty$ , the CIs of the  $MES_{obs}$  do not theoretically  
332 overlap 0, which makes it difficult to assess the significance of the strength of the  
333  $MES_{obs}$ . We therefore used a null-model approach to test if  $MES_{obs}$  was significantly  
334 different from that expected under the null hypothesis, i.e. the true effect of intraspecific  
335 variation in all studies was zero. We resampled each statistic (e.g.  $t$ ,  $F$ ) from each  
336 empirical study in their respective null distribution with the adequate degree of freedom.  
337 This resampled set of statistics ( $N = 502$ ) was transformed into  $Zr$  as described above to  
338 create a set of resampled  $Zr$  values. We used this set of resampled  $Zr$  values to fit an  
339 intercept-only model with no fixed effect, the corresponding article ID as a random term  
340 and  $se_{Zr}$  included as a weighting parameter (as for  $MES_{obs}$ ). The mean global  
341 resampled  $Zr$  ( $MES_{res}$ ) was extracted from the model, and we repeated this resampling  
342 procedure 1000 times to obtain 1000 values of  $MES_{res}$ . This resampled distribution of  
343 1000  $MES_{res}$  approximates the range of possible MES values expected if the null  
344 hypothesis was true. Finally, we calculated the probability of  $MES_{obs}$  to be larger than  
345 expected under this null hypothesis using a one-tailed test (Manly, 1997).

346 We then compared the median of effect sizes ( $MES_{common}$ ) of studies that were in  
347 common between our extended data set and that used by Des Roches *et al.* (2018) (i.e.  
348 15 studies that were used both in our meta-analysis and that of Des Roches *et al.*) to a

349 selection of 15 studies randomly sampled from our extended data set (i.e. 75 studies in  
350 our extended data set). We calculated the median effect size for the subset of random  
351 studies ( $MES_{ran}$ ) and repeated this resampling procedure 1000 times to obtain 1000  
352 values of  $MES_{ran}$ . We then compared  $MES_{common}$  to each  $MES_{ran}$  value to calculate the  
353 probability that  $MES_{common}$  was higher than a random subset of 15 studies taken from  
354 the whole data set (Manly, 1997).

355 We then investigated the variability in effect sizes ( $Zr$ ) and the potential  
356 moderators. We analysed the heterogeneity in effect sizes across articles using the  $I^2$   
357 statistic, which was calculated using an intercept model with the article ID as the  
358 random effect and  $se_{Zr}$  as the weighting parameter (Higgins & Thompson, 2002; Senior  
359 *et al.*, 2016). Finally, we tested whether effect sizes ( $Zr$ ) differed among organism types  
360 with intraspecific variation manipulation, and among the ecological response variables  
361 considered. We hence computed meta-regressions based on linear mixed-effect models  
362 with  $Zr$  values (for all 75 studies and 502 measures) as the dependent variable, and  
363 organism type or ecological response variable as fixed effects. The article ID was  
364 included as a random effect, and  $se_{Zr}$  was included as a weighting parameter. Four  
365 models were run to assess the differences of effect sizes (*i*) between organism types  
366 classified as consumers or primary producers, and (*ii*) between detailed taxonomic  
367 categories (arthropods, fishes, herbaceous plants and trees). We then tested whether the  
368 effect sizes of intraspecific variation differed among ecological response variables (*iii*)  
369 classified as community or ecosystem variables, and (*iv*) classified according to more  
370 detailed categories (abundance, biomass, community structure, decomposition, nutrient  
371 cycling, primary productivity and respiration of the ecosystem).

372

### 373 (3) Publication bias

374 For both intraspecific variation and intraspecific richness, we assessed potential  
375 publication bias by combining Egger's regressions and funnel plots (Egger *et al.*, 1997).  
376 Egger's regressions and funnel plots were computed using the residuals of meta-  
377 regressions related effect sizes to the main modifiers (i.e. the explanatory variables) and  
378 a measure of study size (the inverse of  $se_{Zr}$  and sample size for intraspecific variation  
379 and intraspecific richness, respectively; Horvathova, Nakagawa & Uller, 2012;  
380 Nakagawa & Santos, 2012). Typically, for intraspecific variation we ran an Egger's  
381 regression model including the residuals of the meta-regression linking intraspecific  
382 variation to the modifiers as a response variable and the inverse of  $se_{Zr}$  as the  
383 explanatory variable. A similar approach was used for intraspecific richness. The  
384 intercept  $\alpha$  and the slope  $\beta$  of the Egger's regressions are expected not to differ  
385 significantly from zero if the data sets are not biased towards significant results. Finally,  
386 funnel plots were produced as a scatterplot linking the residuals described above to the  
387 respective measure of the study size. An unbiased data set is expected to generate a  
388 funnel plot in which articles with larger sample sizes will be close to the mean effect  
389 size, whereas articles with small sample sizes will show more variance around the mean  
390 effect size (Horvathova *et al.*, 2012; Nakagawa & Santos, 2012).

391 Overall, and after accounting for important modifiers we found that there was  
392 no strong visual sign of publication bias, neither for intraspecific variation nor for  
393 intraspecific richness (Fig. S2). This visual inspection of funnel plots was confirmed by  
394 the Egger's regressions since parameter values were not significant for intraspecific  
395 variation ( $\alpha = 0.015$ ,  $P = 0.404$ ;  $\beta = -0.001$ ,  $P = 0.501$ ) or for intraspecific richness ( $\alpha =$   
396  $-0.001$ ,  $P = 0.914$ ;  $\beta < 0.001$ ,  $P = 0.961$ ).

397 All statistical analyses were performed using the R environment (R core team,  
398 2013, Appendix S2). The nlme package (Pinheiro *et al.*, 2014) was used to compute  
399 linear and non-linear mixed-effect models, unless specified otherwise.

400

### 401 **III. RESULTS**

402 All articles ( $N = 90$ ) selected for investigating the effects of intraspecific richness and  
403 intraspecific variation were published between 2000 and 2018, and 74% used primary  
404 producers as target species (Fig. 1). The first studies focusing on consumers were  
405 published in 2008, using fish (60%), arthropods (32%), and fungi (8%) as model  
406 species.

407

#### 408 **(1) The intraspecific richness–ecological dynamics relationship**

409 As expected, we found a significant, positive and non-linear relationship between  
410 intraspecific richness and ecological dynamics that approximated a saturating curve  
411 (Fig. 2A). The AIC selection procedure revealed that one out of the four tested models  
412 was highly likely to be supported by the data (i.e. 99% chance of being the best fitting  
413 model according to the Akaike weight and  $\Delta AIC > 15.721$  for the other models, Table  
414 1). The model that best supported the data was the exponential asymptotic model,  
415 suggesting that the relationship between intraspecific richness and changes in  
416 community structure and ecosystem functioning (i.e. effect size:  $\ln RR$ ) likely followed a  
417 saturating shape (Fig. 2A).

418 We further found that the ecological effects of intraspecific richness were similar  
419 to the ecological effects induced by interspecific richness (Fig. 2B). Indeed, the two  
420 distributions largely overlapped and the estimated means were similar (intraspecific  
421 richness  $|\ln RR| = 0.132$ , PI = 0.048–0.216; interspecific richness  $|\ln RR| = 0.134$  PI =

422 0.012–0.462). The ecological effects of intraspecific richness tended to be higher,  
423 although the difference was not significant, for community metrics ( $|\ln RR| = 0.156$ , PI =  
424 0.070–0.242) than for ecosystem metrics ( $|\ln RR| = 0.045$ , PI = 0.004–0.137) (see Fig. S3  
425 for details of ecological metrics).

426

## 427 **(2) The ecological consequences of intraspecific variation**

428 We extended the meta-analysis performed by Des Roches *et al.* (2018) to 52 species (15  
429 species were used in Des Roches *et al.*, 2018). We found that that the observed effect  
430 size of intraspecific variation on community structure and ecosystem dynamics was  
431 significant, and was twice as large as the resampled effect size expected under the null  
432 expectation ( $MES_{obs} = 0.521$ , 95% confidence interval (CI) = 0.444–0.598;  $MES_{null} =$   
433 0.259, CI = 0.258–0.259; resampled test,  $P < 0.001$ ; see Figs 3 and S4).

434 We tested the extent to which the more restricted data set of Des Roches *et al.*  
435 (2018) was representative of our extended data set, or whether it was upwardly biased  
436 as expected by Des Roches *et al.* (2018). We found that that effect sizes for studies in  
437 common with the Des Roches *et al.* (2018) data set ( $MES_{common} = 0.299$ , 95% percentile  
438 interval (PI) = 0.033–1.092) were not significantly different from the distribution of  
439 effect sizes measured in our extended data set ( $MES_{ran} = 0.418$ , PI = 0.255–0.616;  
440 resampling test,  $P = 0.118$ ; Fig. S5), and in fact showed a tendency to be downwardly  
441 biased.

442 Finally, a relatively low heterogeneity in effect size ( $Zr$ ) was detected across  
443 articles ( $I^2 = 0.151$ ). The ecological effects induced by intraspecific variation were  
444 stronger when primary producers rather than consumers were manipulated ( $F = 3.968$   
445 d.f. = 1, 425,  $P = 0.047$ ; Fig. 4A). Nonetheless, the strongest ecological effects of  
446 intraspecific variation tended to be observed in arthropods and herbaceous species,

447 whereas the smallest effects were observed in fish and tree species ( $F = 2.475$  d.f. = 3,  
448 417,  $P = 0.061$ ; Fig. 4A). Irrespective of organism type, the effects of intraspecific  
449 variation were significantly stronger when the response variables were measured at the  
450 ecosystem level rather than at the community level ( $F = 7.295$ , d.f = 1, 425,  $P = 0.007$ ;  
451 Fig. 4B). The strongest effects were detected when response variables concerned  
452 nutrient cycling and the assembly of community, whereas the lowest effects were found  
453 for general measures of abundance and density of species ( $F = 2.725$ , d.f = 6, 417,  $P =$   
454 0.013; Fig. 4B).

455

#### 456 **IV. DISCUSSION**

457 Intraspecific diversity is increasingly recognized as an important facet of biodiversity  
458 that can affect all biological levels (Bailey *et al.*, 2009). Several studies have  
459 experimentally tested the ecological effects of intraspecific diversity, and we here  
460 provide the first global and quantitative estimates of the consequences of intraspecific  
461 richness and variation on community structure and ecosystem functioning. We  
462 demonstrated for the first time that the intraspecific BEF followed – as theoretically  
463 expected – a non-linear saturating curve with a plateau at 4–6 genotypes per population.  
464 Importantly, we demonstrated also for the first time that intraspecific richness affects  
465 community and ecosystem dynamics with a magnitude comparable to that of  
466 biodiversity measured at the species level. We further confirmed and extended the result  
467 that genotypic and/or phenotypic variation observed between populations can have non-  
468 negligible effects on community structure and ecosystem functions, and we  
469 demonstrated that previous estimates (Des Roches *et al.*, 2018) of these ecological  
470 effects of intraspecific variation actually tended to be underestimated. Finally, our  
471 exhaustive quantitative survey identified that the ecological consequences of

472 intraspecific variation differ among biological level of organization, and among  
473 organism types. These findings provide novel and integrative insights, as well as  
474 multiple research perspectives, into the ecological role of intraspecific diversity.

475

#### 476 **(1) Intraspecific diversity and the dynamics of communities and ecosystems**

477         Although the form of the relationship between intraspecific richness and  
478 ecological consequences has already been discussed conceptually (Hughes *et al.*, 2008),  
479 our meta-analysis provides for the first time a qualitative and quantitative assessment of  
480 intraspecific BEF measured experimentally. Specifically, although considering mostly  
481 primary producers, our results demonstrated that an increase in intraspecific richness  
482 resulted in a non-linear (saturating) increase in the magnitude of its effects on ecological  
483 dynamics. This finding supports the idea that ecological divergence between an  
484 environment hosting populations composed of a single genotype and an environment  
485 hosting populations composed of multiple genotypes increases until a plateau is reached  
486 as the number of genotypes increases. This result echoes the BEF as defined at the  
487 interspecific level (Reiss *et al.*, 2009; Cadotte, Carscadden & Mirotnick, 2011) and  
488 suggests that the saturating shape might arise from similar mechanisms occurring at the  
489 intraspecific and interspecific levels (Johnson *et al.*, 2006; Hughes *et al.*, 2008). More  
490 specifically, the initial linear increase is assumed to be due to complementarity and  
491 facilitation among genotypes, whereas the plateau likely occurs due to functional  
492 redundancy among genotypes (Johnson *et al.*, 2006). Redundant genotypes probably  
493 display functionally similar traits since two genotypes do not necessarily generate two  
494 functionally different traits (e.g. through synonymous mutations or trait convergences).  
495 Thus manipulating trait richness rather than genotypic richness, or more precisely  
496 manipulating functional effect traits [i.e. traits with ecological effects (Violle *et al.*,

497 2007)], in future experiments should allow us to explore the mechanisms underlying the  
498 intraspecific biodiversity–ecological dynamics relationship.

499 We found that effect sizes for intraspecific richness were very similar to values  
500 reported recently reported for experimental interspecific BEF, indicating that the  
501 ecological effects of varying phenotypic/genotypic richness within populations are close  
502 to those induced by varying species richness within communities. This finding raises  
503 several questions regarding the general relationships among intraspecific diversity,  
504 community structure, ecosystem functioning and common abiotic constraints. A large  
505 body of literature has demonstrated that intraspecific genetic diversity and species  
506 diversity (a measure of community structure) might co-vary because of common  
507 environmental drivers and/or reciprocal causal relationships between intraspecific  
508 genetic diversity and species diversity [i.e. the species–genetic diversity correlation  
509 (SGDC) framework (Vellend & Geber, 2005; Vellend, 2005)]. Because most studies  
510 considered in our meta-analysis are experimental, our findings confirm that intraspecific  
511 diversity can directly influence the structure of communities irrespective of the abiotic  
512 environments, hence adding weight to the SGDC framework. Additionally, we suggest  
513 expanding the SGDC framework since intraspecific diversity can also affect ecosystem  
514 functioning. This suggests that intraspecific diversity, community structure and  
515 ecosystem functioning may actually be tightly linked in a tripartite relationship. A major  
516 future challenge will be to tease apart the causal relationships linking these three  
517 components within a common abiotic environment. These relationships might be direct  
518 (e.g. intraspecific diversity directly affects community structure), indirect (e.g.  
519 intraspecific diversity indirectly affects ecosystem functions through its direct effect on  
520 community structure such as the trophic cascade), and/or due to the parallel effects of  
521 common abiotic drivers (e.g. temperature directly affects intraspecific diversity,

522 community structure and ecosystem functions). As has been done recently for the BEF  
523 (Grace *et al.*, 2016; Duffy *et al.*, 2016) and the SGDC (Fourtune *et al.*, 2016; Lamy *et*  
524 *al.*, 2017) frameworks, we argue that a future important step will be to combine  
525 powerful statistical methods (e.g. path analysis; Shipley, 2000; Grace, 2006) with  
526 appropriate experimental designs to disentangle causal relationships between  
527 intraspecific diversity, community structure, ecosystem functions and their common  
528 environment.

529 We further demonstrated that intraspecific variation has significant ecological  
530 effects across a large set of species (52 species and 75 articles), hence confirming and  
531 refining a previous estimate based on a more restricted species set (Des Roches *et al.*,  
532 2018). By more than tripling the number of species being investigated in this meta-  
533 analysis, we extend the conclusion to a greater taxonomic set that intraspecific variation  
534 is involved in shaping ecological dynamics, and that the ecological effects of  
535 intraspecific variation might be more common than expected. Moreover, we  
536 demonstrated that previous estimates (Des Roches *et al.*, 2018) were not upwardly  
537 biased (as expected from their focus on a non-random species pool), but were well  
538 within the range of estimates we report here and actually tended to be slight  
539 underestimates. Our finding hence strongly supports the idea that adaptive and non-  
540 adaptive processes can lead to unique populations differentially and significantly  
541 affecting ecological systems.

542 Although our conclusions held true for many species, the ecological effects of  
543 intraspecific variation were not homogeneous across species, and this was partly  
544 explained by their trophic level. Indeed, and according to expectations, the ecological  
545 effects of intraspecific variation were stronger when the target species was a primary  
546 producer than when it was a consumer. Several non-exclusive mechanisms might

547 explain this result. For instance, many primary producers considered here provide a  
548 habitat for many invertebrate species (Southwood, Brown & Reader, 1979) (this is not  
549 the case for the consumer species), and this habitat can be modulated by changes in  
550 plant structure. The relative biomass of primary producers is higher than that of  
551 consumers, thus primary producers could generate stronger effects on communities and  
552 ecosystems than consumers simply because of this biomass effect. However, a more  
553 detailed analysis showed that the effects of intraspecific variation tended to be stronger  
554 for arthropod and herbaceous species than for fish (and to a lesser extent tree) species.  
555 This suggests that the trophic level of a species may not be the only predictor of the  
556 ecological effects of intraspecific diversity, and we argue that future work should aim to  
557 test specifically why intraspecific variation matters more for some species than others.

558         Finally, the effects of intraspecific variation were globally higher for ecosystems  
559 than for communities, hence generalizing across organism and ecosystem types a  
560 previous conclusion for freshwater consumer species (Palkovacs *et al.*, 2015). We can  
561 speculate that this difference arises because intraspecific variation acts on community  
562 dynamics through trophic mechanisms, whereas ecosystem functions can be modulated  
563 through both trophic and non-trophic interactions [e.g. excretion rate or leaf chemistry  
564 (Vanni, 2002; Schmitz *et al.*, 2014)]. For instance, a consumer species that shows  
565 intraspecific variation in resource selectivity and/or consumption rate could affect both  
566 the community structure and productivity of its resource (Harmon *et al.*, 2009). Non-  
567 trophic mechanisms such as variability in organismal stoichiometry could reinforce the  
568 effect of the consumer species on several ecosystem functions [e.g. primary production  
569 or soil mineralization (Schmitz, Hawlena & Trussell, 2010; Hawlena *et al.*, 2012)].  
570 Alternatively, changes in ecosystem functions might be due to both direct effects of  
571 intraspecific diversity and indirect effects of intraspecific diversity mediated through

572 changes in community structure, which may overall strengthen the effects of  
573 intraspecific diversity at the ecosystem level. However, a more detailed analysis  
574 revealed that much variation exists between sub-categories of response variables (Fig.  
575 4B), and that the dichotomy between variables measured at the community and  
576 ecosystem levels is not straightforward. Although providing the first attempts to  
577 separate variance in the ecological effects of intraspecific variation into its component  
578 parts, our findings call for further studies on various taxa and in different ecosystems in  
579 order to understand fully the ecological effects of intraspecific diversity.

580

581 **(2) Research perspectives on the relationships between intraspecific diversity and**  
582 **the dynamics of communities and ecosystems**

583 We highlight several research avenues that may greatly enhance our understanding of  
584 the relationships between intraspecific diversity and the dynamics of communities and  
585 ecosystems.

586 Our review demonstrates that the ecological effect size of intraspecific diversity varies  
587 among species and that this interspecific variance in effect size can be partly explained  
588 by the type of organism (i.e. primary producer or consumer). However, species  
589 composing a community also vary according to abundance, role in the ecosystem (e.g.  
590 keystone species; Paine, 1969), body size (or height for plants), life-history strategy  
591 (e.g.  $r$ - $K$  strategy), recent history (e.g. whether the species is non-native), functional  
592 characteristics (e.g. stoichiometry, metabolism), etc. The next challenge will be to  
593 partition this interspecific variance in effect size better by determining the species  
594 characteristics that best predict the strength of effect sizes; this is a pre-requisite to  
595 design coherent conservation plans at the intraspecific level (Mimura *et al.*, 2016).

596           Intraspecific diversity is often manipulated with respect to a single target  
597 species. However, in nature, species are interacting and we argue that future studies  
598 should manipulate intraspecific diversity within multiple interacting species to reflect  
599 natural conditions, and to allow partitioning the relative importance of intraspecific  
600 diversity between interacting (and potentially co-evolving) species.

601           Ecosystems are interconnected through cross-ecosystem fluxes of matter  
602 (Loreau, Mouquet & Holt, 2003). For instance, freshwater ecosystems such as rivers  
603 receive a large amount of material from surrounding terrestrial ecosystems [e.g. dead  
604 leaves falling from trees (Bartels *et al.*, 2012)]. A major future challenge would be to  
605 assess the relative effects of intraspecific diversity on allochthonous ecosystems *versus*  
606 autochthonous ecosystems; for example testing whether the consequences of intraspecific  
607 diversity manipulation in a fish species are greater in associated aquatic ecosystems than  
608 on nearby terrestrial ecosystems [see Jackrel & Wootton (2014), Crutsinger *et al.*  
609 (2014)*b* and Rudman *et al.* (2015) for attempts to quantify across-ecosystem effects of  
610 intraspecific diversity]. This is an important next step to quantify in a more integrative  
611 way the importance of intraspecific diversity in natural systems.

612           Previous studies have mainly assessed the consequences of intraspecific  
613 diversity by considering the genetic or the phenotypic characteristics of organisms as a  
614 whole. However, some traits have been shown to be more important for ecological  
615 dynamics than others; this is the case for functional effect traits that are defined as traits  
616 with an ecological impact [e.g. excretion rate or leaf nutrient content (Violle *et al.*,  
617 2007; Díaz *et al.*, 2013)]. We suggest that direct manipulation of the functional trait  
618 diversity of individuals within a species, rather than their genotypic or phenotypic  
619 diversity as a whole would be a powerful means to understanding the mechanisms by  
620 which intraspecific diversity acts on ecological dynamics.

621           Although we emphasize that intraspecific diversity is an essential component of  
622 the community and ecosystem facets of ecological dynamics, comparisons with the  
623 effects of other major ecological constraints (e.g. temperature, interspecific biodiversity,  
624 human disturbance) have rarely been conducted (but see Burkle *et al.*, 2013; El-Sabaawi  
625 *et al.*, 2015). To evaluate and quantify the importance of intraspecific diversity in  
626 natural systems better, it is important to assess the relative contributions of intraspecific  
627 diversity and other determinants of ecosystem functioning. This will be an essential step  
628 in confirming that intraspecific variation is a key determinant, and not just a random  
629 signal in complex systems.

630

## 631 **V. CONCLUSIONS**

632 (1) This study provides empirical evidence that the ecological effects of intraspecific  
633 richness increase asymptotically, paralleling well-known patterns observed at the  
634 interspecific level (Loreau, 2000; Hooper *et al.*, 2005) and confirming previous  
635 hypotheses (Hughes *et al.*, 2008).

636 (2) We found that experimental manipulations of intraspecific richness caused  
637 community and ecosystem differentiations as large as those generated by interspecific  
638 richness. This suggests that variation in richness within populations can have similar  
639 ecological consequences to variation in richness among species.

640 (3) We also demonstrated that variation in phenotypes or genotypes within species is an  
641 important driver of community and ecosystem dynamics. These major ecological effects  
642 of intraspecific diversity held true for a range of organisms including plants and  
643 animals, although much remains to be tested.

644 (4) Overall these findings demonstrate that intraspecific diversity - beyond its  
645 importance for species to adapt to environmental changes - is an important facet of

646 biodiversity for understanding and predicting the ecological dynamics of communities  
647 and ecosystems, reinforcing the need for a better appraisal of the causes and  
648 consequences of intraspecific diversity in natural populations and for improved  
649 conservation plans.

650

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657

## 658 VII. REFERENCES

659

660 ABBOTT, J.M., GROSBERG, R.K., WILLIAMS, S.L. & STACHOWICZ, J.J. (2017). Multiple  
661 dimensions of intraspecific diversity affect biomass of eelgrass and its  
662 associated community. *Ecology* **98**, 3152–3164.

663 BAILEY, J.K., SCHWEITZER, J.A., UBEDA, F., KORICHEVA, J., LEROY, C.J., MADRITCH,  
664 M.D., REHILL, B.J., BANGERT, R.K., FISCHER, D.G., ALLAN, G.J. & WHITHAM,  
665 T.G. (2009). From genes to ecosystems: a synthesis of the effects of plant  
666 genetic factors across levels of organization. *Philosophical Transactions of the  
667 Royal Society B: Biological Sciences* **364**, 1607–1616.

668 BARBOUR, M.A., FORTUNA, M.A., BASCOMPTE, J., NICHOLSON, J.R., JULKUNEN-TIITTO,  
669 R., JULES, E.S. & CRUTSINGER, G.M. (2016). Genetic specificity of a plant–  
670 insect food web: Implications for linking genetic variation to network  
671 complexity. *Proceedings of the National Academy of Sciences* **113**, 2128–2133.

672 BARBOUR, R.C., FORSTER, L.G., BAKER, S.C., STEANE, D.A. & POTTS, B.M. (2009a).  
673 Biodiversity consequences of genetic variation in bark characteristics within a  
674 foundation tree species. *Conservation Biology* **23**, 1146–1155.

675 BARBOUR, R.C., O’REILLY-WAPSTRA, J.M., DE LITTLE, D.W., JORDAN, G.J., STEANE,  
676 D.A., HUMPHREYS, J.R., BAILEY, J.K., WHITHAM, T.G. & POTTS, B.M. (2009b).  
677 A geographic mosaic of genetic variation within a foundation tree species and its  
678 community-level consequences. *Ecology* **90**, 1762–1772.

- 679 BARBOUR, R.C., STORER, M.J. & POTTS, B.M. (2009c). Relative importance of tree  
680 genetics and microhabitat on macrofungal biodiversity on coarse woody debris.  
681 *Oecologia* **160**, 335–342.
- 682 BARRIOS-GARCIA, M.N., RODRIGUEZ-CABAL, M.A., RUDGERS, J.A. & CRUTSINGER,  
683 G.M. (2016). Soil fertilization does not alter plant architectural effects on  
684 arthropod communities. *Journal of Plant Ecology*, rtw087.
- 685 BARTELS, P., CUCHEROUSSET, J., STEGER, K., EKLÖV, P., TRANVIK, L.J. & HILLEBRAND,  
686 H. (2012). Reciprocal subsidies between freshwater and terrestrial ecosystems  
687 structure consumer resource dynamics. *Ecology* **93**, 1173–1182.
- 688 BASSAR, R.D., MARSHALL, M.C., LOPEZ-SEPULCRE, A., ZANDONA, E., AUER, S.K.,  
689 TRAVIS, J., PRINGLE, C.M., FLECKER, A.S., THOMAS, S.A., FRASER, D.F. &  
690 REZNICK, D.N. (2010). Local adaptation in Trinidadian guppies alters ecosystem  
691 processes. *Proceedings of the National Academy of Sciences* **107**, 3616–3621.
- 692 BOLNICK, D.I., AMARASEKARE, P., ARAÚJO, M.S., BÜRGER, R., LEVINE, J.M., NOVAK,  
693 M., RUDOLF, V.H., SCHREIBER, S.J. & URBAN, M.C. (2011). Why intraspecific  
694 trait variation matters in community ecology. *Trends in ecology & evolution* **26**,  
695 183–192.
- 696 BOLNICK, D.I., SVANBÄCK, R., FORDYCE, J.A., YANG, L.H., DAVIS, J.M., HULSEY, C.D.  
697 & FORISTER, M.L. (2003). The ecology of individuals: incidence and  
698 implications of individual specialization. *The American Naturalist* **161**, 1–28.
- 699 BOOTH, R.E. & GRIME, J.P. (2003). Effects of genetic impoverishment on plant  
700 community diversity. *Journal of Ecology* **91**, 721–730.
- 701 BURKLE, L.A., SOUZA, L., GENUNG, M.A. & CRUTSINGER, G.M. (2013). Plant genotype,  
702 nutrients, and G X E interactions structure floral visitor communities. *Ecosphere*  
703 **4**.
- 704 BURNHAM, K.P. & ANDERSON, D.R. (2002). *Model selection and multimodel inference:*  
705 *a practical information-theoretic approach*. Springer, New York.
- 706 BUSTOS-SEGURA, C., POELMAN, E.H., REICHEL, M., GERSHENZON, J. & GOLS, R.  
707 (2017). Intraspecific chemical diversity among neighbouring plants correlates  
708 positively with plant size and herbivore load but negatively with herbivore  
709 damage. *Ecology Letters* **20**, 87–97.
- 710 CADOTTE, M.W., CARSCADDEN, K. & MIROTCHEV, N. (2011). Beyond species:  
711 functional diversity and the maintenance of ecological processes and services.  
712 *Journal of Applied Ecology* **48**, 1079–1087.
- 713 CAMPOS-NAVARRETE, M.J., MUNGUÍA-ROSAS, M.A., ABDALA-ROBERTS, L., QUINTO, J.  
714 & PARRA-TABLA, V. (2015). Effects of tree genotypic diversity and species  
715 diversity on the arthropod community associated with big-leaf mahogany.  
716 *Biotropica* **47**, 579–587.
- 717 CARDINALE, B.J., DUFFY, J.E., GONZALEZ, A., HOOPER, D.U., PERRINGS, C., VENAIL, P.,  
718 NARWANI, A., MACE, G.M., TILMAN, D., WARDLE, D.A., KINZIG, A.P., DAILY,

- 719 G.C., LOREAU, M., GRACE, J.B., LARIGAUDERIE, A., ET AL. (2012). Biodiversity  
720 loss and its impact on humanity. *Nature* **486**, 59–67.
- 721 CHAPIN, S.F., ZAVALA, E.S., EVINER, V.T., NAYLOR, R.L., VITOUSEK, P.M.,  
722 REYNOLDS, H.L., HOOPER, D.U., LAVOREL, S., SALA, O.E., HOBBIE, S.E., MACK,  
723 M.C. & DÍAZ, S. (2000). Consequences of changing biodiversity. *Nature* **405**,  
724 234–242.
- 725 CHISLOCK, M.F., SARNELLE, O., OLSEN, B.K., DOSTER, E. & WILSON, A.E. (2013).  
726 Large effects of consumer offense on ecosystem structure and function. *Ecology*  
727 **94**, 2375–2380.
- 728 CLASSEN, A.T., CHAPMAN, S.K., WHITHAM, T.G., HART, S.C. & KOCH, G.W. (2007).  
729 Genetic-based plant resistance and susceptibility traits to herbivory influence  
730 needle and root litter nutrient dynamics. *Journal of Ecology* **95**, 1181–1194.
- 731 COOK-PATTON, S.C., MCART, S.H., PARACHNOWITSCH, A.L., THALER, J.S. &  
732 AGRAWAL, A.A. (2011). A direct comparison of the consequences of plant  
733 genotypic and species diversity on communities and ecosystem function.  
734 *Ecology* **92**, 915–923.
- 735 CORNELISSEN, J.H.C., PEREZ-HARGUINDEGUY, N., GWYNN-JONES, D., DIAZ, S.,  
736 CALLAGHAN, T.V. & AERTS, R. (2000). Autumn leaf colours as indicators of  
737 decomposition rate in sycamore (*Acer pseudoplatanus L.*). *Plant and Soil* **225**,  
738 33–38.
- 739 CRAWFORD, K.M. & RUDGERS, J.A. (2013). Genetic diversity within a dominant plant  
740 outweighs plant species diversity in structuring an arthropod community.  
741 *Ecology* **94**, 1025–1035.
- 742 CRUTSINGER, G.M., CADOTTE, M.W. & SANDERS, N.J. (2009a). Plant genetics shapes  
743 inquiline community structure across spatial scales. *Ecology Letters* **12**, 285–  
744 292.
- 745 CRUTSINGER, G.M., CARTER, B.E. & RUDGERS, J.A. (2013). Soil nutrients trump  
746 intraspecific effects on understory plant communities. *Oecologia* **173**, 1531–  
747 1538.
- 748 CRUTSINGER, G.M., COLLINS, M.D., FORDYCE, J.A., GOMPERT, Z., NICE, C.C. &  
749 SANDERS, N.J. (2006). Plant genotypic diversity predicts community structure  
750 and governs an ecosystem process. *Science* **313**, 966–968.
- 751 CRUTSINGER, G.M., COLLINS, M.D., FORDYCE, J.A. & SANDERS, N.J. (2008a).  
752 Temporal dynamics in non-additive responses of arthropods to host-plant  
753 genotypic diversity. *Oikos* **117**, 255–264.
- 754 CRUTSINGER, G.M., REYNOLDS, W.N., CLASSEN, A.T. & SANDERS, N.J. (2008b).  
755 Disparate effects of plant genotypic diversity on foliage and litter arthropod  
756 communities. *Oecologia* **158**, 65–75.
- 757 CRUTSINGER, G.M., RODRIGUEZ-CABAL, M.A., RODDY, A.B., PEAY, K.G., BASTOW,  
758 J.L., KIDDER, A.G., DAWSON, T.E., FINE, P.V.A. & RUDGERS, J.A. (2014a).

- 759 Genetic variation within a dominant shrub structures green and brown  
760 community assemblages. *Ecology* **95**, 387–398.
- 761 CRUTSINGER, G.M., RUDMAN, S.M., RODRIGUEZ-CABAL, M.A., MCKOWN, A.D., SATO,  
762 T., MACDONALD, A.M., HEAVYSIDE, J., GERALDES, A., HART, E.M., LEROY,  
763 C.J. & EL-SABAawi, R.W. (2014b). Testing a ‘genes-to-ecosystems’ approach to  
764 understanding aquatic-terrestrial linkages. *Molecular Ecology* **23**, 5888–5903.
- 765 CRUTSINGER, G.M., SANDERS, N.J. & CLASSEN, A.T. (2009b). Comparing intra- and  
766 inter-specific effects on litter decomposition in an old-field ecosystem. *Basic  
767 and Applied Ecology* **10**, 535–543.
- 768 DE BELLO, F., LAVOREL, S., ALBERT, C.H., THUILLER, W., GRIGULIS, K., DOLEZAL, J.,  
769 JANECEK, S. & LEPS, J. (2011). Quantifying the relevance of intraspecific trait  
770 variability for functional diversity. *Methods in Ecology and Evolution* **2**, 163–  
771 174.
- 772 DE GRAAFF, M.-A., SIX, J., JASTROW, J.D., SCHADT, C.W. & WULLSCHLEGER, S.D.  
773 (2013). Variation in root architecture among switchgrass cultivars impacts root  
774 decomposition rates. *Soil Biology & Biochemistry* **58**, 198–206.
- 775 DES ROCHES, S., POST, D.M., TURLEY, N.E., BAILEY, J.K., HENDRY, A.P., KINNISON,  
776 M.T., SCHWEITZER, J.A. & PALKOVACS, E.P. (2018). The ecological importance  
777 of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.
- 778 DES ROCHES, S., SHURIN, J.B., SCHLUTER, D. & HARMON, L.J. (2013). Ecological and  
779 evolutionary effects of stickleback on community structure. *PLoS ONE* **8**,  
780 e59644.
- 781 DÍAZ, S., PURVIS, A., CORNELISSEN, J.H.C., MACE, G.M., DONOGHUE, M.J., EWERS,  
782 R.M., JORDANO, P. & PEARSE, W.D. (2013). Functional traits, the phylogeny of  
783 function, and ecosystem service vulnerability. *Ecology and Evolution* **3**, 2958–  
784 2975.
- 785 DOWNING, A.L. & LEIBOLD, M.A. (2002). Ecosystem consequences of species richness  
786 and composition in pond food web. *Nature* **416**, 837–841.
- 787 DUFFY, J.E., GODWIN, C.M. & CARDINALE, B.J. (2017). Biodiversity effects in the wild  
788 are common and as strong as key drivers of productivity. *Nature* **549**, 261–264.
- 789 DUFFY, J.E., LEFCHECK, J.S., STUART-SMITH, R.D., NAVARRETE, S.A. & EDGAR, G.J.  
790 (2016). Biodiversity enhances reef fish biomass and resistance to climate  
791 change. *Proceedings of the National Academy of Sciences* **113**, 6230–6235.
- 792 EGGER, M., SMITH, G.D., SCHNEIDER, M. & MINDER, C. (1997). Bias in meta-analysis  
793 detected by a simple graphical test. *Bmj* **315**, 629–634.
- 794 EL-SABAawi, R.W., BASSAR, R.D., RAKOWSKI, C., MARSHALL, M.C., BRYAN, B.L.,  
795 THOMAS, S.N., PRINGLE, C., REZNICK, D.N. & FLECKER, A.S. (2015).  
796 Intraspecific phenotypic differences in fish affect ecosystem processes as much  
797 as bottom-up factors. *Oikos* **124**, 1181–1191.

- 798 FARKAS, T.E., MONONEN, T., COMEAULT, A.A., HANSKI, I. & NOSIL, P. (2013).  
799 Evolution of camouflage drives rapid ecological change in an insect community.  
800 *Current Biology* **23**, 1835–1843.
- 801 FORTUNE, L., PAZ-VINAS, I., LOOT, G., PRUNIER, J.G. & BLANCHET, S. (2016).  
802 Lessons from the fish: a multi-species analysis reveals common processes  
803 underlying similar species-genetic diversity correlations. *Freshwater Biology* **61**,  
804 1830–1845.
- 805 FRIDLEY, J.D. & GRIME, J.P. (2010). Community and ecosystem effects of intraspecific  
806 genetic diversity in grassland microcosms of varying species diversity. *Ecology*  
807 **91**, 2272–2283.
- 808 FRYXELL, D.C., ARNETT, H.A., APGAR, T.M., KINNISON, M.T. & PALKOVACS, E.P.  
809 (2015). Sex ratio variation shapes the ecological effects of a globally introduced  
810 freshwater fish. *Proceedings of the Royal Society B: Biological Sciences* **282**,  
811 20151970.
- 812 GENUNG, M.A., LESSARD, J.-P., BROWN, C.B., BUNN, W.A., CREGGER, M.A.,  
813 REYNOLDS, W.N., FELKER-QUINN, E., STEVENSON, M.L., HARTLEY, A.S.,  
814 CRUTSINGER, G.M., SCHWEITZER, J.A. & BAILEY, J.K. (2010). Non-additive  
815 effects of genotypic diversity increase floral abundance and abundance of floral  
816 visitors. *Plos One* **5**, e8711.
- 817 GOITOM, E., KILSDONK, L.J., BRANS, K., JANSEN, M., LEMMENS, P. & DE MEESTER, L.  
818 (2018). Rapid evolution leads to differential population dynamics and top-down  
819 control in resurrected *Daphnia* populations. *Evolutionary Applications* **11**, 96–  
820 111.
- 821 GRACE, J.B. (2006). *Structural equation modeling and natural systems*. Cambridge  
822 University Press.
- 823 GRACE, J.B., ANDERSON, T.M., SEABLOOM, E.W., BORER, E.T., ADLER, P.B., HARPOLE,  
824 W.S., HAUTIER, Y., HILLEBRAND, H., LIND, E.M., PÄRTEL, M., BAKKER, J.D.,  
825 BUCKLEY, Y.M., CRAWLEY, M.J., DAMSCHEN, E.I., DAVIES, K.F., ET AL. (2016).  
826 Integrative modelling reveals mechanisms linking productivity and plant species  
827 richness. *Nature* **529**, 390–393.
- 828 GRANT, P.R. & GRANT, B.R. (2006). Evolution of character displacement in darwin's  
829 finches. *Science* **313**, 224–226.
- 830 HADFIELD, J.D. (2010). MCMC methods for multi-response generalized linear mixed  
831 models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1–22.
- 832 HARMON, L.J., MATTHEWS, B., DES ROCHES, S., CHASE, J.M., SHURIN, J.B. &  
833 SCHLUTER, D. (2009). Evolutionary diversification in stickleback affects  
834 ecosystem functioning. *Nature* **458**, 1167–1170.
- 835 HARRISON, J.G., PHILBIN, C.S., GOMPERT, Z., FORISTER, G.W., HERNANDEZ-ESPINOZA,  
836 L., SULLIVAN, B.W., WALLACE, I.S., BELTRAN, L., DODSON, C.D., FRANCIS, J.S.,  
837 SCHLAGETER, A., SHELEF, O., YOON, S.A. & FORISTER, M.L. (2018).  
838 Deconstruction of a plant-arthropod community reveals influential plant traits

- 839 with nonlinear effects on arthropod assemblages. *Functional Ecology* **32**, 1317–  
840 1328.
- 841 HAWLENA, D., STRICKLAND, M.S., BRADFORD, M.A. & SCHMITZ, O.J. (2012). Fear of  
842 predation slows plant-litter decomposition. *Science* **336**, 1434–1438.
- 843 HIGGINS, J.P.T. & THOMPSON, S.G. (2002). Quantifying heterogeneity in a meta-  
844 analysis. *Statistics in Medicine* **21**, 1539–1558.
- 845 HILLEBRAND, H. & MATTHIESSEN, B. (2009). Biodiversity in a complex world:  
846 consolidation and progress in functional biodiversity research. *Ecology Letters*  
847 **12**, 1405–1419.
- 848 HINES, J., REYES, M., MOZDER, T.J. & GESSNER, M.O. (2014). Genotypic trait variation  
849 modifies effects of climate warming and nitrogen deposition on litter mass loss  
850 and microbial respiration. *Global Change Biology* **20**, 3780–3789.
- 851 HOOPER, D.U., CHAPIN, F.S., EWEL, J.J., HECTOR, A., INCHAUSTI, P., LAVOREL, S.,  
852 LAWTON, J.H., LODGE, D.M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H.,  
853 SYMSTAD, A.J., VANDERMEER, J. & WARDLE, D.A. (2005). Effects of  
854 biodiversity on ecosystem functioning: a consensus of current knowledge.  
855 *Ecological Monographs* **75**, 3–35.
- 856 HORVATHOVA, T., NAKAGAWA, S. & ULLER, T. (2012). Strategic female reproductive  
857 investment in response to male attractiveness in birds. *Proceedings of the Royal*  
858 *Society B: Biological Sciences* **279**, 163–170.
- 859 HOWETH, J.G., WEIS, J.J., BRODERSEN, J., HATTON, E.C. & POST, D.M. (2013).  
860 Intraspecific phenotypic variation in a fish predator affects multitrophic lake  
861 metacommunity structure. *Ecology and Evolution* **3**, 5031–5044.
- 862 HUANG, J., LIU, M., CHEN, X., CHEN, J., LI, H. & HU, F. (2015). Effects of intraspecific  
863 variation in rice resistance to aboveground herbivore, brown planthopper, and  
864 rice root nematodes on plant yield, labile pools of plant, and rhizosphere soil.  
865 *Biology and Fertility of Soils* **51**, 417–425.
- 866 HUGHES, A.R. (2014). Genotypic diversity and trait variance interact to affect marsh  
867 plant performance. *Journal of Ecology* **102**, 651–658.
- 868 HUGHES, A.R., INOUE, B.D., JOHNSON, M.T.J., UNDERWOOD, N. & VELLEND, M.  
869 (2008). Ecological consequences of genetic diversity. *Ecology Letters* **11**, 609–  
870 623.
- 871 INGRAM, T., SVANBÄCK, R., KRAFT, N.J.B., KRATINA, P., SOUTHCOTT, L. & SCHLUTER,  
872 D. (2012). Intraguild predation drives evolutionary niche shift in threespine  
873 stickleback. *Evolution* **66**, 1819–1832.
- 874 ITO, M. & OZAKI, K. (2005). Response of a gall wasp community to genetic variation in  
875 the host plant *Quercus crispula*: a test using half-sib families. *Acta Oecologica*  
876 **27**, 17–24.

- 877 JACKREL, S.L. & WOOTTON, J.T. (2014). Local adaptation of stream communities to  
878 intraspecific variation in a terrestrial ecosystem subsidy. *Ecology* **95**, 37–43.
- 879 JOHNSON, M.T. & AGRAWAL, A.A. (2005). Plant genotype and environment interact to  
880 shape a diverse arthropod community on evening primrose (*Oenothera biennis*).  
881 *Ecology* **86**, 874–885.
- 882 JOHNSON, M.T.J., LAJEUNESSE, M.J. & AGRAWAL, A.A. (2006). Additive and interactive  
883 effects of plant genotypic diversity on arthropod communities and plant fitness.  
884 *Ecology Letters* **9**, 24–34.
- 885 JOHNSON, M.T.J., VELLEND, M. & STINCHCOMBE, J.R. (2009). Evolution in plant  
886 populations as a driver of ecological changes in arthropod communities.  
887 *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**,  
888 1593–1605.
- 889 KAGIYA, S., YASUGI, M., KUDOH, H., NAGANO, A.J. & UTSUMI, S. (2018). Does  
890 genomic variation in a foundation species predict arthropod community structure  
891 in a riparian forest? *Molecular Ecology* **27**, 1284–1295.
- 892 KANAGA, M.K., LATTA, L.C., MOCK, K.E., RYEL, R.J., LINDROTH, R.L. & PFRENDER,  
893 M.E. (2009). Plant genotypic diversity and environmental stress interact to  
894 negatively affect arthropod community diversity. *Arthropod-Plant Interactions*  
895 **3**, 249–258.
- 896 KATANO, O. (2011). Effects of individual differences in foraging of pale chub on algal  
897 biomass through trophic cascades. *Environmental Biology of Fishes* **92**, 101–  
898 112.
- 899 KORICHEVA, J., GUREVITCH, J. & MENGERSEN, K. (2013). *Handbook of meta-Analysis*  
900 *in ecology and evolution*. Princeton University press, Princeton, New Jersey.
- 901 KOTOWSKA, A.M., CAHILL JR, J.F. & KEDDIE, B.A. (2010). Plant genetic diversity  
902 yields increased plant productivity and herbivore performance. *Journal of*  
903 *Ecology* **98**, 237–245.
- 904 LAGERSTROM, A., NILSSON, M.-C. & WARDLE, D.A. (2013). Decoupled responses of  
905 tree and shrub leaf and litter trait values to ecosystem retrogression across an  
906 island area gradient. *Plant and Soil* **367**, 183–197.
- 907 LAMY, T., LAROCHE, F., DAVID, P., MASSOL, F. & JARNE, P. (2017). The contribution of  
908 species-genetic diversity correlations to the understanding of community  
909 assembly rules. *Oikos* **126**, 759–771.
- 910 LECERF, A. & CHAUVET, E. (2008). Intraspecific variability in leaf traits strongly affects  
911 alder leaf decomposition in a stream. *Basic and Applied Ecology* **9**, 598–605.
- 912 LEROY, C.J., WHITHAM, T.G., WOOLEY, S.C. & MARKS, J.C. (2007). Within-species  
913 variation in foliar chemistry influences leaf-litter decomposition in a Utah river.  
914 *Journal of the North American Benthological Society* **26**, 426–438.

- 915 LOREAU, M. (2000). Biodiversity and ecosystem functioning: recent theoretical  
916 advances. *Oikos* **91**, 3–17.
- 917 LOREAU, M., MOUQUET, N. & HOLT, R.D. (2003). Meta-ecosystems: a theoretical  
918 framework for a spatial ecosystem ecology. *Ecology Letters* **6**, 673–679.
- 919 LOWE, W.H., KOVACH, R.P. & ALLENDORF, F.W. (2017). Population genetics and  
920 demography unite ecology and evolution. *Trends in Ecology & Evolution* **32**,  
921 141–152.
- 922 MADRITCH, M., DONALDSON, J.R. & LINDROTH, R.L. (2006). Genetic identity of  
923 *Populus tremuloides* litter influences decomposition and nutrient release in a  
924 mixed forest stand. *Ecosystems* **9**, 528–537.
- 925 MADRITCH, M.D., GREENE, S.L. & LINDROTH, R.L. (2009). Genetic mosaics of  
926 ecosystem functioning across aspen-dominated landscapes. *Oecologia* **160**, 119–  
927 127.
- 928 MADRITCH, M.D. & HUNTER, M.D. (2003). Intraspecific litter diversity and nitrogen  
929 deposition affect nutrient dynamics and soil respiration. *Oecologia* **136**, 124–  
930 128.
- 931 MADRITCH, M.D. & HUNTER, M.D. (2004). Phenotypic diversity and litter chemistry  
932 affect nutrient dynamics during litter decomposition in a two species mix. *Oikos*  
933 **105**, 125–131.
- 934 MADRITCH, M.D. & HUNTER, M.D. (2005). Phenotypic variation in oak litter influences  
935 short- and long-term nutrient cycling through litter chemistry. *Soil Biology &*  
936 *Biochemistry* **37**, 319–327.
- 937 MADRITCH, M.D. & LINDROTH, R.L. (2011). Soil microbial communities adapt to  
938 genetic variation in leaf litter inputs. *Oikos* **120**, 1696–1704.
- 939 MANLY, B.F. (1997). *Randomization, bootstrap and Monte Carlo methods in biology*.  
940 Chapman and Hall, London.
- 941 MATTHEWS, B., AEBISCHER, T., SULLAM, K.E., LUNDSGAARD-HANSEN, B. &  
942 SEEHAUSEN, O. (2016). Experimental evidence of an eco-evolutionary feedback  
943 during adaptive divergence. *Current Biology* **26**, 483–489.
- 944 MATTHEWS, B., DE MEESTER, L., JONES, C.G., IBELINGS, B.W., BOUMA, T.J.,  
945 NUUTINEN, V., DE KOPPEL, J. VAN & ODLING-SMEE, J. (2014). Under niche  
946 construction: an operational bridge between ecology, evolution, and ecosystem  
947 science. *Ecological Monographs* **84**, 245–263.
- 948 MATTHEWS, B., NARWANI, A., HAUSCH, S., NONAKA, E., PETER, H., YAMAMICHI, M.,  
949 SULLAM, K.E., BIRD, K.C., THOMAS, M.K., HANLEY, T.C. & TURNER, C.B.  
950 (2011). Toward an integration of evolutionary biology and ecosystem science.  
951 *Ecology Letters* **14**, 690–701.

- 952 MCART, S.H., COOK-PATTON, S.C. & THALER, J.S. (2012). Relationships between  
953 arthropod richness, evenness, and diversity are altered by complementarity  
954 among plant genotypes. *Oecologia* **168**, 1013–1021.
- 955 MIMURA, M., YAHARA, T., FAITH, D.P., VÁZQUEZ-DOMÍNGUEZ, E., COLAUTTI, R.I.,  
956 ARAKI, H., JAVADI, F., NÚÑEZ-FARFÁN, J., MORI, A.S., ZHOU, S.,  
957 HOLLINGSWORTH, P.M., NEAVES, L.E., FUKANO, Y., SMITH, G.F., SATO, Y.-I., ET  
958 AL. (2016). Understanding and monitoring the consequences of human impacts  
959 on intraspecific variation. *Evolutionary Applications* **10**, 121–139.
- 960 MORRISSEY, M.B. (2016a). Meta-analysis of magnitudes, differences and variation in  
961 evolutionary parameters. *Journal of Evolutionary Biology* **29**, 1882–1904.
- 962 MORRISSEY, M.B. (2016b). Rejoinder: Further considerations for meta-analysis of  
963 transformed quantities such as absolute values. *Journal of Evolutionary Biology*  
964 **29**, 1922–1931.
- 965 NAEEM, S., THOMPSON, LINDSEY J, LAWLER, SHARON P, LAWTON, JOHN H & WOODFIN,  
966 RICHARD M (1994). Declining biodiversity can alter the performance of  
967 ecosystems. *Nature* **368**, 734–737.
- 968 NAKAGAWA, S. & CUTHILL, I.C. (2007). Effect size, confidence interval and statistical  
969 significance: a practical guide for biologists. *Biological Reviews* **82**, 591–605.
- 970 NAKAGAWA, S. & SANTOS, E.S.A. (2012). Methodological issues and advances in  
971 biological meta-analysis. *Evolutionary Ecology* **26**, 1253–1274.
- 972 NELL, C.S., MEZA-LOPEZ, M.M., CROY, J.R., NELSON, A.S., MOREIRA, X., PRATT, J.D.  
973 & MOONEY, K.A. (2018). Relative effects of genetic variation sensu lato and  
974 sexual dimorphism on plant traits and associated arthropod communities.  
975 *Oecologia* **187**, 389–400.
- 976 NOBLE, D.W.A., LAGISZ, M., O’DEA, R.E. & NAKAGAWA, S. (2017). Nonindependence  
977 and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular*  
978 *Ecology* **26**, 2410–2425.
- 979 ODLING-SMEE, J., LALAND, K.N. & FELDMAN, M.W. (2003). *Niche construction the*  
980 *neglected process in evolution*. Princeton University Press.
- 981 PAINE, R.T. (1969). A note on trophic complexity and community stability. *The*  
982 *American Naturalist* **103**, 91–93.
- 983 PALKOVACS, E.P., FRYXELL, D.C., TURLEY, N.E. & POST, D.M. (2015). Ecological  
984 effects of intraspecific consumer biodiversity for aquatic communities and  
985 ecosystems. In *Aquatic Functional Biodiversity* pp. 37–51. Elsevier.
- 986 PALKOVACS, E.P., MARSHALL, M.C., LAMPHERE, B.A., LYNCH, B.R., WEESE, D.J.,  
987 FRASER, D.F., REZNICK, D.N., PRINGLE, C.M. & KINNISON, M.T. (2009).  
988 Experimental evaluation of evolution and coevolution as agents of ecosystem  
989 change in Trinidadian streams. *Philosophical Transactions of the Royal Society*  
990 *B-Biological Sciences* **364**, 1617–1628.

- 991 PALKOVACS, E.P. & POST, D.M. (2009). Experimental evidence that phenotypic  
992 divergence in predators drives community divergence in prey. *Ecology* **90**, 300–  
993 305.
- 994 PINHEIRO, J., BATES, D., DEBROY, S., SARKAR, D. & R CORE TEAM (2014). nlme: linear  
995 and nonlinear mixed effects models. R package version 3.1-117.
- 996 POST, D.M., PALKOVACS, E.P., SCHIELKE, E.G. & DODSON, S.I. (2008). Intraspecific  
997 variation in a predator affects community structure and cascading trophic  
998 interactions. *Ecology* **89**, 2019–2032.
- 999 PRATT, J.D., DATU, A., TRAN, T., SHENG, D.C. & MOONEY, K.A. (2017). Genetically  
1000 based latitudinal clines in *Artemisia californica* drive parallel clines in arthropod  
1001 communities. *Ecology* **98**, 79–91.
- 1002 PREGITZER, C.C., BAILEY, J.K. & SCHWEITZER, J.A. (2013). Genetic by environment  
1003 interactions affect plant-soil linkages. *Ecology and Evolution* **3**, 2322–2333.
- 1004 REISS, J., BRIDLE, J.R., MONTOYA, J.M. & WOODWARD, G. (2009). Emerging horizons  
1005 in biodiversity and ecosystem functioning research. *Trends in Ecology &*  
1006 *Evolution* **24**, 505–514.
- 1007 RENNEVILLE, C., ROUZIC, A.L., BAYLAC, M., MILLOT, A., LOISEL, S. & EDELINE, E.  
1008 (2016). Morphological drivers of trophic cascades. *Oikos* **125**, 1193–1202.
- 1009 ROBINSON, K.M., INGVARSSON, P.K., JANSSON, S. & ALBRECHTSEN, B.R. (2012). Genetic  
1010 variation in functional traits influences arthropod community composition in  
1011 aspen (*Populus tremula* L.). *PLoS ONE* **7**, e37679.
- 1012 RODRIGUEZ-CABAL, M.A., BARRIOS-GARCIA, M.N., RUDMAN, S.M., MCKOWN, A.D.,  
1013 SATO, T. & CRUTSINGER, G.M. (2017). It is about time: genetic variation in the  
1014 timing of leaf-litter inputs influences aquatic ecosystems. *Freshwater Biology*  
1015 **62**, 356–365.
- 1016 ROYAUTÉ, R. & PRUITT, J.N. (2015). Varying predator personalities generates  
1017 contrasting prey communities in an agroecosystem. *Ecology* **96**, 2902–2911.
- 1018 RUDGERS, J.A. & WHITNEY, K.D. (2006). Interactions between insect herbivores and a  
1019 plant architectural dimorphism. *Journal of Ecology* **94**, 1249–1260.
- 1020 RUDMAN, S.M., RODRIGUEZ-CABAL, M.A., STIER, A., SATO, T., HEAVYSIDE, J., EL-  
1021 SABA AWI, R.W. & CRUTSINGER, G.M. (2015). Adaptive genetic variation  
1022 mediates bottom-up and top-down control in an aquatic ecosystem. *Proceedings*  
1023 *of the Royal Society B: Biological Sciences* **282**, 125–132.
- 1024 RUDMAN, S.M. & SCHLUTER, D. (2016). Ecological impacts of reverse speciation in  
1025 threespine stickleback. *Current Biology* **26**, 490–495.
- 1026 RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013a). Ontogenetic functional diversity: Size  
1027 structure of a keystone predator drives functioning of a complex ecosystem.  
1028 *Ecology* **94**, 1046–1056.

- 1029 RUDOLF, V.H.W. & RASMUSSEN, N.L. (2013b). Population structure determines  
1030 functional differences among species and ecosystem processes. *Nature*  
1031 *Communications* **4**.
- 1032 SCHMITZ, O.J., HAWLENA, D. & TRUSSELL, G.C. (2010). Predator control of ecosystem  
1033 nutrient dynamics. *Ecology Letters* **13**, 1199–1209.
- 1034 SCHMITZ, O.J., RAYMOND, P.A., ESTES, J.A., KURZ, W.A., HOLTGRIEVE, G.W., RITCHIE,  
1035 M.E., SCHINDLER, D.E., SPIVAK, A.C., WILSON, R.W., BRADFORD, M.A.,  
1036 CHRISTENSEN, V., DEEGAN, L., SMETACEK, V., VANNI, M.J. & WILMERS, C.C.  
1037 (2014). Animating the carbon cycle. *Ecosystems* **17**, 344–359.
- 1038 SCHWEITZER, J.A., BAILEY, J.K., FISCHER, D.G., LEROY, C.J., LONSDORF, E.V.,  
1039 WHITHAM, T.G. & HART, S.C. (2008). Plant–soil–microorganism interactions:  
1040 heritable relationship between plant genotype and associated soil  
1041 microorganisms. *Ecology* **89**, 773–781.
- 1042 SEMCHENKO, M., SAAR, S. & LEPIK, A. (2017). Intraspecific genetic diversity modulates  
1043 plant-soil feedback and nutrient cycling. *New Phytologist* **216**, 90–98.
- 1044 SENIOR, A.M., GRUEBER, C.E., KAMIYA, T., LAGISZ, M., O'DWYER, K., SANTOS, E.S.A.  
1045 & NAKAGAWA, S. (2016). Heterogeneity in ecological and evolutionary meta-  
1046 analyses: its magnitude and implications. *Ecology* **97**, 3293–3299.
- 1047 SHIPLEY, B. (2000). *Cause and correlation in biology: a user's guide to path analysis,*  
1048 *structural equation and causal inference*. Cambridge University Press.
- 1049 SIEFERT, A., VIOLLE, C., CHALMANDRIER, L., ALBERT, C.H., TAUDIERE, A., FAJARDO,  
1050 A., AARSSSEN, L.W., BARALOTO, C., CARLUCCI, M.B., CIANCIARUSO, M.V., DE L.  
1051 DANTAS, V., DE BELLO, F., DUARTE, L.D.S., FONSECA, C.R., FRESCHET, G.T., ET  
1052 AL. (2015). A global meta-analysis of the relative extent of intraspecific trait  
1053 variation in plant communities. *Ecology Letters* **18**, 1406–1419.
- 1054 SILFVER, T., KONTRO, M., PAASO, U., KARVINEN, H., KESKI-SAARI, S., KEINÄNEN, M.,  
1055 ROUSI, M. & MIKOLA, J. (2018). Intrapopulation genotypic variation in leaf litter  
1056 chemistry does not control microbial abundance and litter mass loss in silver  
1057 birch, *Betula pendula*. *Plant and Soil* **426**, 253–266.
- 1058 SILFVER, T., MIKOLA, J., ROUSI, M., ROININEN, H. & OKSANEN, E. (2007). Leaf litter  
1059 decomposition differs among genotypes in a local *Betula pendula* population.  
1060 *Oecologia* **152**, 707–714.
- 1061 SILFVER, T., PAASO, U., RASEHORN, M., ROUSI, M. & MIKOLA, J. (2015). Genotype x  
1062 herbivore effect on leaf litter decomposition in *Betula Pendula* saplings:  
1063 ecological and evolutionary consequences and the role of secondary metabolites.  
1064 *PLoS One* **10**.
- 1065 SILFVER, T., ROUSI, M., OKSANEN, E. & ROININEN, H. (2014). Genetic and  
1066 environmental determinants of insect herbivore community structure in a *Betula*  
1067 *pendula* population. *F1000Research* **3**, 34–34.

- 1068 SOUTHWOOD, T.R., BROWN, V.K. & READER, P.M. (1979). The relationships of plant  
1069 and insect diversities in succession. *Biological Journal of the Linnean Society*  
1070 **12**, 327–348.
- 1071 STHULTZ, C.M., WHITHAM, T.G., KENNEDY, K., DECKERT, R. & GEHRING, C.A. (2009).  
1072 Genetically based susceptibility to herbivory influences the ectomycorrhizal  
1073 fungal communities of a foundation tree species. *New Phytologist* **184**, 657–667.
- 1074 TACK, A.J.M., OVASKAINEN, O., PULKKINEN, P. & ROSLIN, T. (2010). Spatial location  
1075 dominates over host plant genotype in structuring an herbivore community.  
1076 *Ecology* **91**, 2660–2672.
- 1077 TACK, A.J.M. & ROSLIN, T. (2011). The relative importance of host-plant genetic  
1078 diversity in structuring the associated herbivore community. *Ecology* **92**, 1594–  
1079 1604.
- 1080 TOVAR-SANCHEZ, E., VALENCIA-CUEVAS, L., CASTILLO-MENDOZA, E., MUSSALI-  
1081 GALANTE, P., PEREZ-RUIZ, R.V. & MENDOZA, A. (2013). Association between  
1082 individual genetic diversity of two oak host species and canopy arthropod  
1083 community structure. *European Journal of Forest Research* **132**, 165–179.
- 1084 TRAP, J., HÄTTENSCHWILER, S., GATTIN, I. & AUBERT, M. (2013). Forest ageing: An  
1085 unexpected driver of beech leaf litter quality variability in European forests with  
1086 strong consequences on soil processes. *Forest Ecology and Management* **302**,  
1087 338–345.
- 1088 UTSUMI, S. (2015). Feeding evolution of a herbivore influences an arthropod  
1089 community through plants: implications for plant-mediated eco-evolutionary  
1090 feedback loop. *Journal of Ecology* **103**, 829–839.
- 1091 VANNI, M.J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual*  
1092 *Review of Ecology and Systematics* **33**, 341–370.
- 1093 VELLEND, M. (2005). Species diversity and genetic diversity: parallel processes and  
1094 correlated patterns. *The American Naturalist* **166**, 199–215.
- 1095 VELLEND, M. & GEBER, M.A. (2005). Connections between species diversity and  
1096 genetic diversity. *Ecology Letters* **8**, 767–781.
- 1097 VIOLLE, C., ENQUIST, B.J., MCGILL, B.J., JIANG, L., ALBERT, C.H., HULSHOF, C., JUNG,  
1098 V. & MESSIER, J. (2012). The return of the variance: intraspecific variability in  
1099 community ecology. *Trends in Ecology & Evolution* **27**, 244–252.
- 1100 VIOLLE, C., NAVAS, M.-L., VILE, D., KAZAKOU, E., FORTUNEL, C., HUMMEL, I. &  
1101 GARNIER, E. (2007). Let the concept of trait be functional! *Oikos* **116**, 882–892.
- 1102 WAGG, C., BOLLER, B., SCHNEIDER, S., WIDMER, F. & VAN DER HEIJDEN, M.G.A.  
1103 (2015). Intraspecific and intergenerational differences in plant-soil feedbacks.  
1104 *Oikos* **124**, 994–1004.
- 1105 WALSH, M.R., DELONG, J.P., HANLEY, T.C. & POST, D.M. (2012). A cascade of  
1106 evolutionary change alters consumer-resource dynamics and ecosystem

- 1107 function. *Proceedings of the Royal Society B-Biological Sciences* **279**, 3184–  
1108 3192.
- 1109 WANG, X.-Y., MIAO, Y., YU, S., CHEN, X.-Y. & SCHMID, B. (2014). Genotypic diversity  
1110 of an invasive plant species promotes litter decomposition and associated  
1111 processes. *Oecologia* **174**, 993–1005.
- 1112 WEIS, J.J. & POST, D.M. (2013). Intraspecific variation in a predator drives cascading  
1113 variation in primary producer community composition. *Oikos* **122**, 1343–1349.
- 1114 WERNER, E.E. & PEACOR, S.D. (2003). A review of trait-mediated indirect interactions  
1115 in ecological communities. *Ecology* **84**, 1083–1100.
- 1116 WHITHAM, T.G., BAILEY, J.K., SCHWEITZER, J.A., SHUSTER, S.M., BANGERT, R.K.,  
1117 LEROY, C.J., LONSDORF, E.V., ALLAN, G.J., DIFAZIO, S.P., POTTS, B.M.,  
1118 FISCHER, D.G., GEHRING, C.A., LINDROTH, R.L., MARKS, J.C., HART, S.C., ET AL.  
1119 (2006). A framework for community and ecosystem genetics: from genes to  
1120 ecosystems. *Nature Reviews Genetics* **7**, 510–523.
- 1121 WHITHAM, T.G., YOUNG, W.P., MARTINSEN, G.D., GEHRING, C.A., SCHWEITZER, J.A.,  
1122 SHUSTER, S.M., WIMP, G.M., FISCHER, D.G., BAILEY, J.K., LINDROTH, R.L.,  
1123 WOOLBRIGHT, S. & KUSKE, C.R. (2003). Community and ecosystem genetics: A  
1124 consequence of the extended phenotype. *Ecology* **84**, 559–573.
- 1125 WILKINSON, A., ALEXANDER, I. & JOHNSON, D. (2012). Genotype identity determines  
1126 productivity and CO<sub>2</sub> efflux across a genotype-species gradient of  
1127 ectomycorrhizal fungi. *Fungal Ecology* **5**, 571–580.
- 1128 WILKINSON, A., SOLAN, M., TAYLOR, A.F.S., ALEXANDER, I.J. & JOHNSON, D. (2010).  
1129 Intraspecific diversity regulates fungal productivity and respiration. *Plos One* **5**,  
1130 e12604.
- 1131 ZYTYNSKA, S.E., FAY, M.F., PENNEY, D. & PREZIOSI, R.F. (2011). Genetic variation in a  
1132 tropical tree species influences the associated epiphytic plant and invertebrate  
1133 communities in a complex forest ecosystem. *Philosophical Transactions of the  
1134 Royal Society B: Biological Sciences* **366**, 1329–1336.
- 1135 ZYTYNSKA, S.E., KHUADR, M.S., HARRIS, E. & PREZIOSI, R.F. (2012). Genetic effects of  
1136 tank-forming bromeliads on the associated invertebrate community in a tropical  
1137 forest ecosystem. *Oecologia* **170**, 467–475.

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## 1139 **VIII. SUPPORTING INFORMATION**

1140

1141 Additional supporting information may be found in the online version of this article.

1142 **Appendix S1.** Papers used in the meta-analysis.

- 1143 **Fig. S1.** Flow diagram of manuscript screening and eligibility for this meta-analysis.
- 1144 **Table S1.** Formulae used to convert different statistical values into an  $r$  correlation  
1145 coefficient.
- 1146 **Fig. S2.** Funnel plots describing the residuals effect size distribution against an estimate  
1147 of the study size for (A) intraspecific variation and (B) intraspecific richness.
- 1148 **Appendix S2.** R script of the principal functions used in analyses.
- 1149 **Fig. S3.** Distribution of effect sizes ( $\ln RR$ ) across ecological metrics.
- 1150 **Fig. S4.** Distribution of resampled mean effect size (MES) expected under the null  
1151 hypothesis, i.e. the effect of intraspecific identity in all studies is zero.
- 1152 **Fig. S5.** Distribution of median effect sizes calculated for each of the 1000 sets of 15  
1153 studies randomly selected within our extended data set of 75 studies.

1154 Figure legends

1155 **Fig. 1.** Publication year of the 90 selected articles used in the meta-analysis.

1156

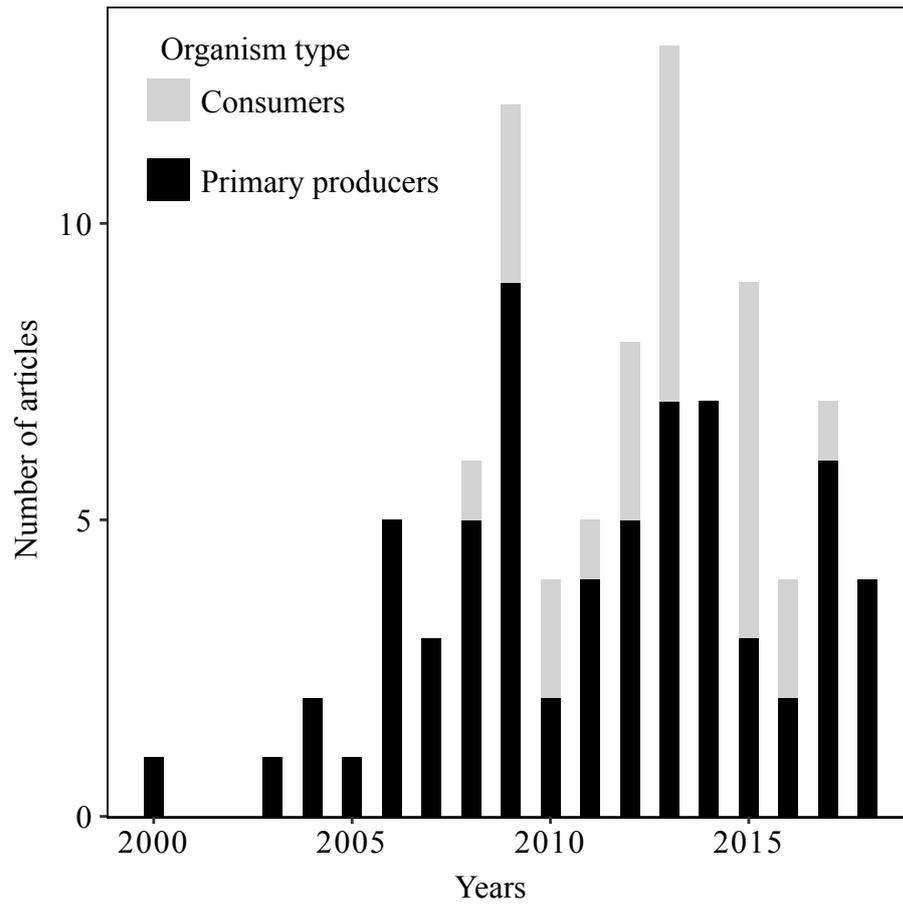
1157 **Fig. 2.** (A) Relationship between intraspecific richness and effect size ( $\ln RR$ ) on  
1158 community (points) and ecosystem (crosses) dynamics. The line represents the shape of  
1159 the relationship as predicted using an exponential asymptotic non-linear mixed effect  
1160 model. The blue shadow represents 95% CI. Symbol colours denote the target species:  
1161 herbaceous plant (black), tree (blue) or fungus (grey). (B) Density of absolute effect size  
1162 ( $\ln RR$ ) for intraspecific and interspecific richness on ecological dynamics. Posterior  
1163 means and 95% percentile intervals (points and horizontal lines, respectively) were  
1164 estimated using a model including article ID as the random effect and the inverse of  
1165 sample size as a weighting parameter.

1166

1167 **Fig. 3.** Density probability of effect size  $Zr$ . The vertical broken line represents the  
1168 resampled  $Zr$  mean under the null hypothesis (confidence intervals not shown because  
1169 they are too narrow); the black curve shows the distribution of observed  $Zr$  and its mean  
1170 (vertical black straight line) and 95% CIs (grey shading).

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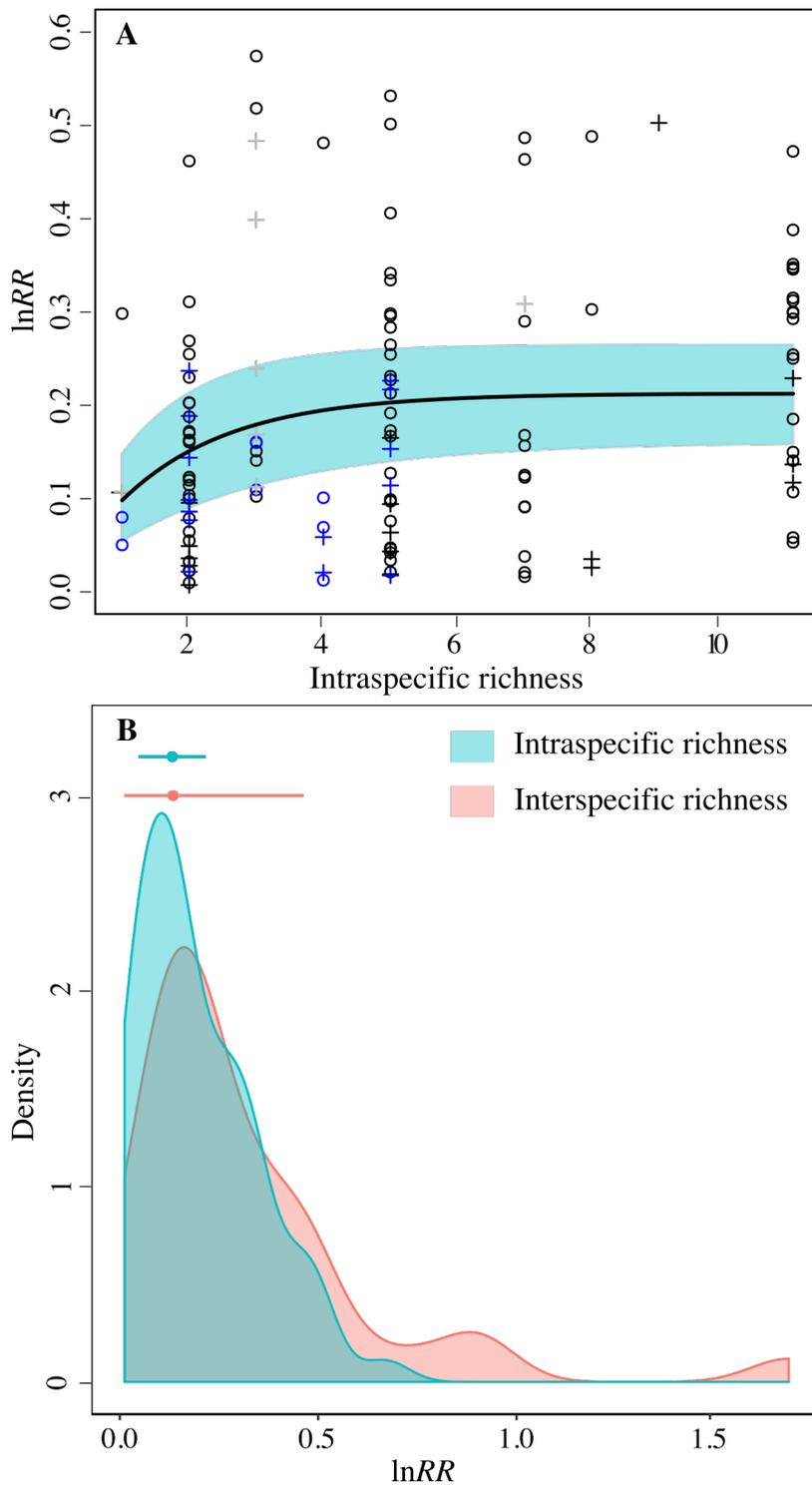
1172 **Fig. 4.** (A) Mean effect size  $Zr$  for different species groups. The sample sizes ( $N$ )  
1173 represent the number of species and the number of effect sizes, respectively. The  
1174 horizontal broken line represents the mean effect size; error bars represent  $\pm 1$  SE. (B)  
1175 Mean  $Zr$  for the ecological response variables. The sample sizes ( $N$ ) of the number of  
1176 effect sizes are given. The horizontal broken line represents the mean effect size; error  
1177 bars represent  $\pm 1$  SE.



1178

1179 Fig. 1

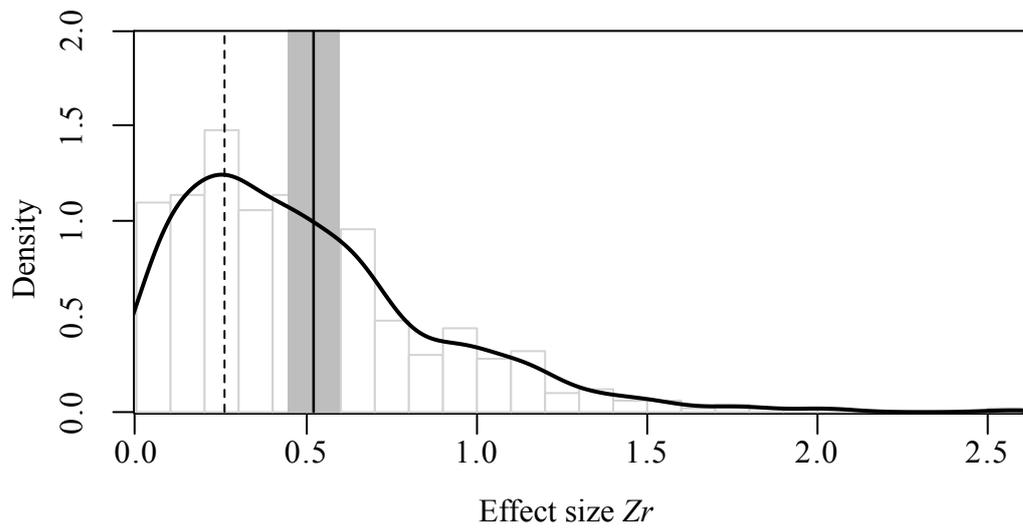
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1182 Fig. 2

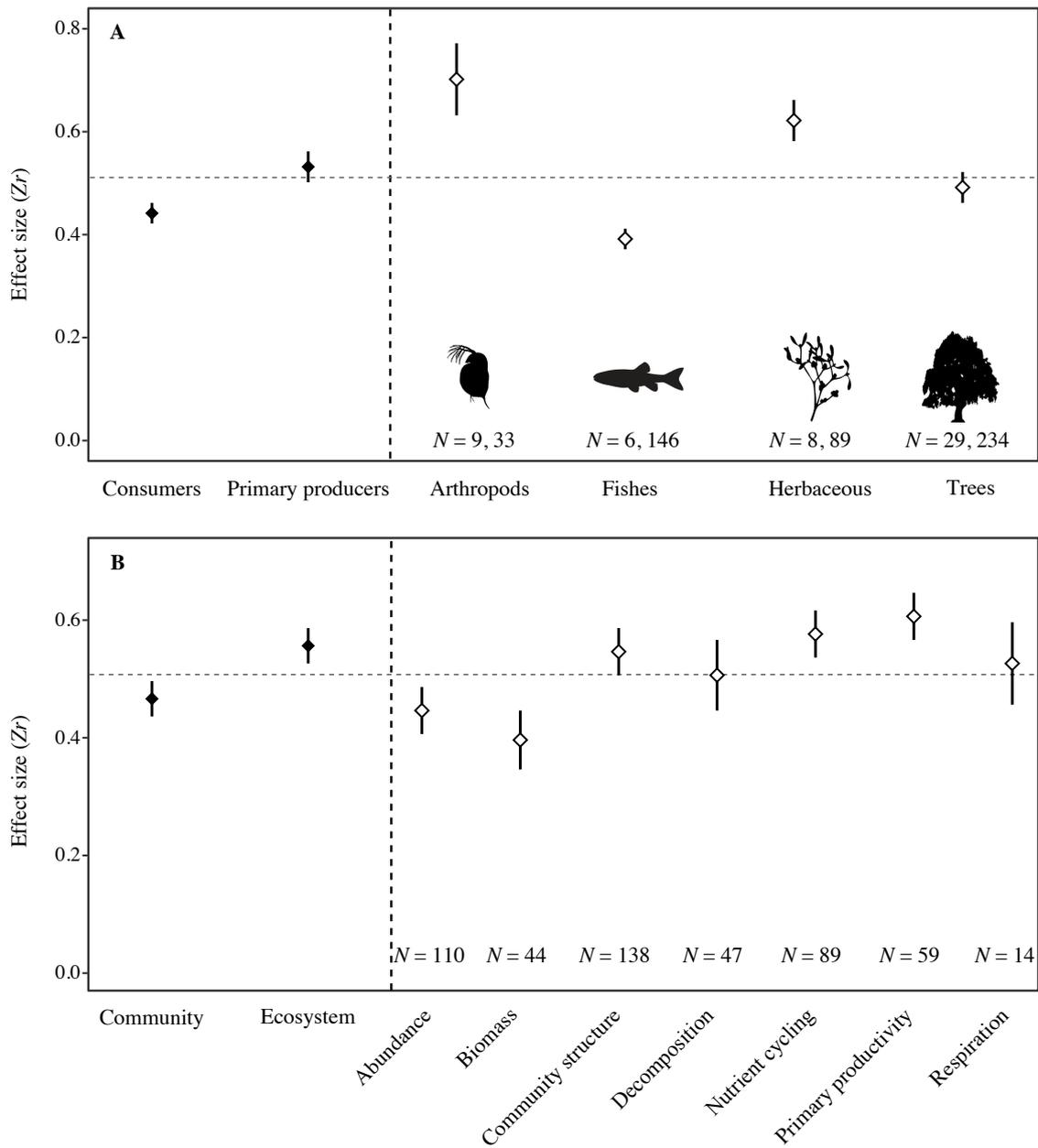
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1185 Fig. 3

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1188 Fig. 4

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1191 Table 1. Summary table of model selection by Akaike information criterion (AIC)  
 1192 comparison to explain the shape of the relationship between the ecological  
 1193 consequences and the intraspecific richness. Models were run as non-linear mixed-  
 1194 effect models with the article ID as a random factor; equations and parameters estimates  
 1195 are also shown. IR, intraspecific richness;  $\ln RR$ , effect size of intraspecific richness on  
 1196 ecological dynamics.  
 1197

Model	AIC	$\Delta AIC$	AIC weight	Equation	Parameter estimates
Asymptotic exponential model	-176.695	0	0.999	$\ln RR = a * (1 - e^{-b*IR})$	$a = 0.221$ $b = 0.617$
Michaelis–Menten model	-11.873	164.821	< 0.001	$\ln RR = V * \frac{IR}{k + IR}$	$V = 0.054$ $k = -2.712$
Linear model	-160.974	15.721	< 0.001	$\ln RR = b0 + b1 * IR$	$b1 = 0.012$ $b0 = 0.122$
Null model	-144.191	32.503	< 0.001	$\ln RR = b0$	$b0 = 0.183$

1198