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The community and ecosystem consequences of intraspecific diversity: a meta-analysis

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ABSTRACT

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

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

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

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71 **I. INTRODUCTION**

72 Understanding the relationships between biodiversity and ecosystem functioning is an

73 intensely active field of research informing on the services provided by biodiversity

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

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

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

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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.

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

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

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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

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

II. MATERIALS AND METHODS

(1) Data collection

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

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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

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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.

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

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

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

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

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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*-squared, 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

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

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

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

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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

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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 α and the slope β 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, $P = 0.914$; $\beta < 0.001$, $P = 0.961$).

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

III. RESULTS

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

(1) The intraspecific richness–ecological dynamics relationship

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

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

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

(2) The ecological consequences of intraspecific variation

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

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

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

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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

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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 & Mirotchnick, 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.*,

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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,

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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

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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

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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).

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

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

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

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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

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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

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VIII. SUPPORTING INFORMATION

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

Appendix S1. Papers used in the meta-analysis.

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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.

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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.

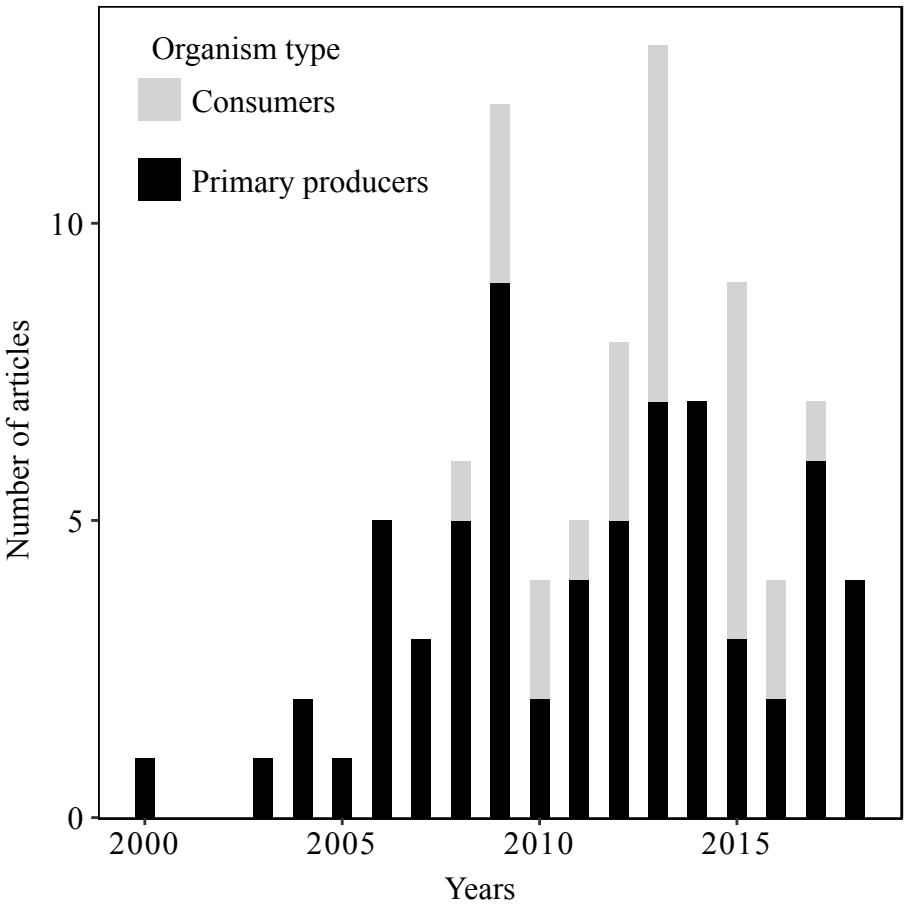
1166

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).

1171

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 ± 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 ± 1 SE.

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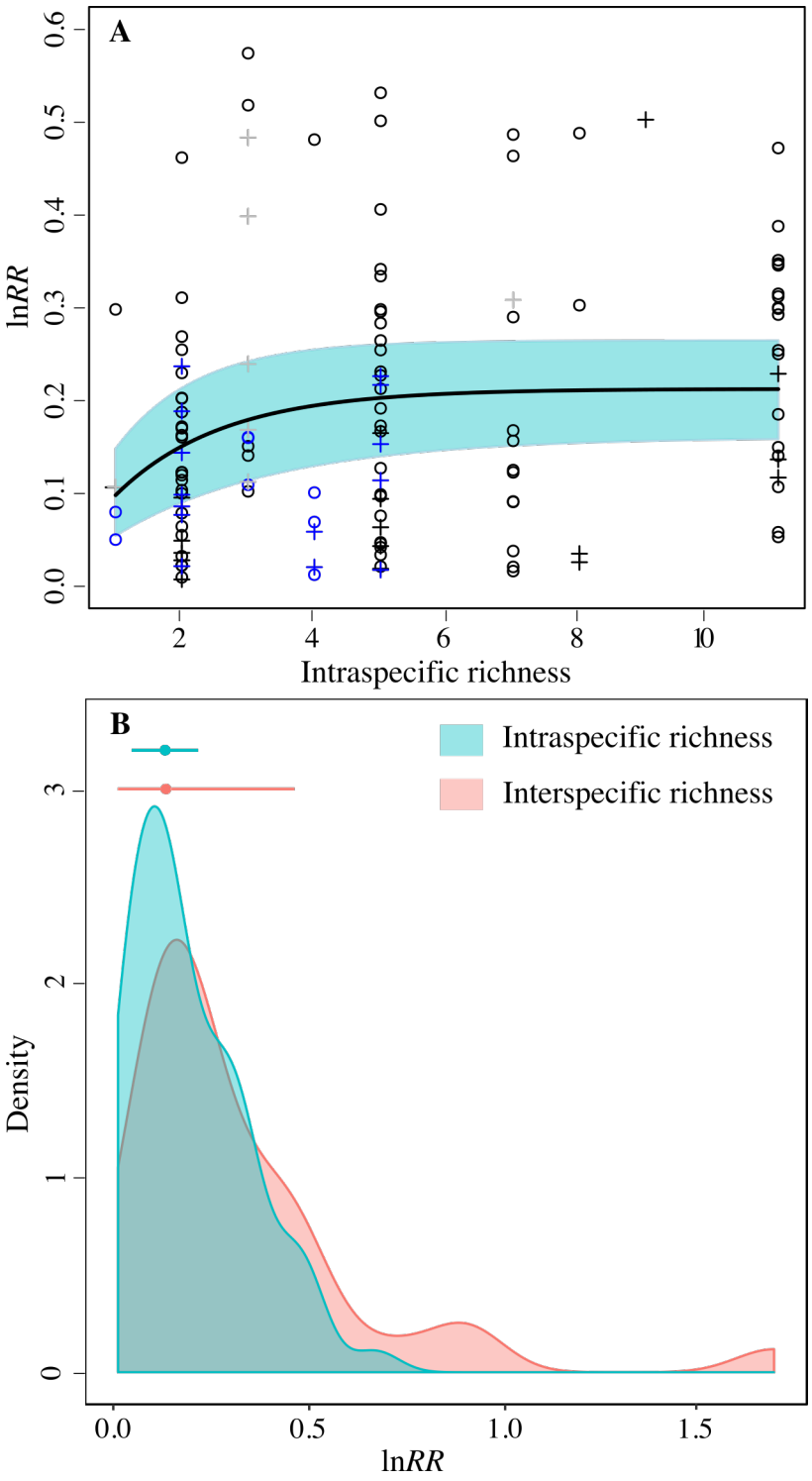


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1179 Fig. 1

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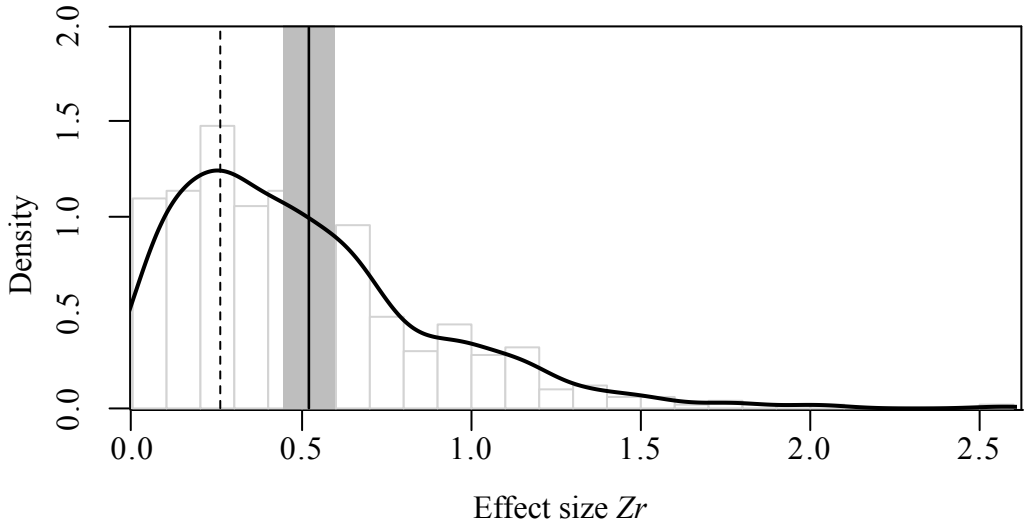


1181

1182 Fig. 2

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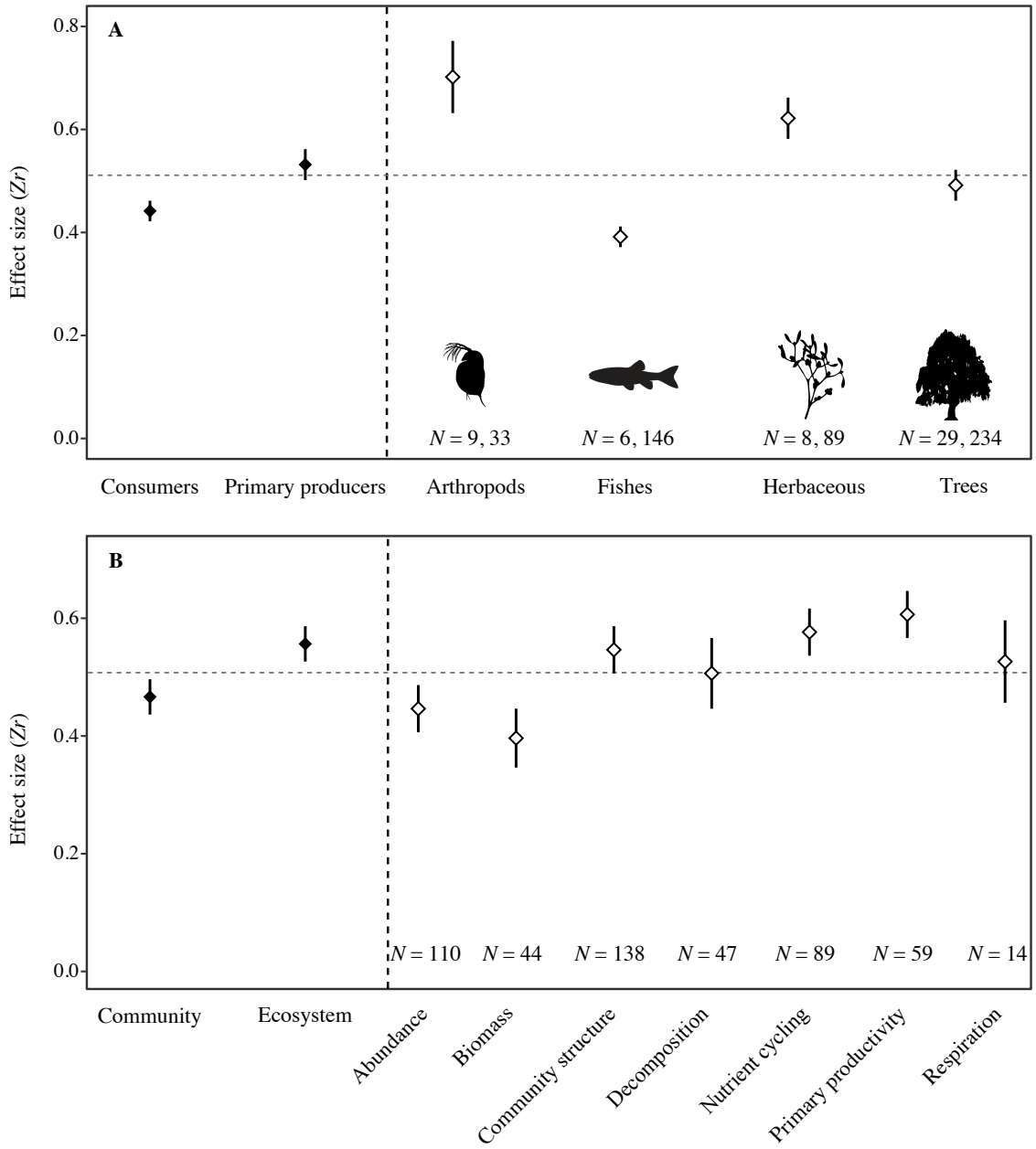


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1185 Fig. 3

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1188 Fig. 4

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

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