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-function relationships are generally investigated at the interspecific level, although intraspecific diversity is increasingly perceived as an important ecological facet of biodiversity. Here, we provide a quantitative synthesis testing –across diverse plant and animal species- whether intraspecific diversity (measured either as the *richness* or *variation* of genotypes/phenotypes in a population) is a major driver of community dynamics and ecosystem functioning. We found a significant relationship between intraspecific *richness* and community and ecosystem dynamics that followed a saturating shape, as observed for biodiversity-function relationships measured at the interspecific level. The strength of the ecological effects of intraspecific *richness* were similar to those reported for interspecific richness. We further found that intraspecific *variation* has substantial effects on ecological dynamics that are twice higher than expected by chance, and that these effects might have been previously underestimated. We finally found that the ecological effects of intraspecific *variation* were not homogeneous and were actually stronger in primary producer than in consumer species, and when measured at the ecosystem than at the community level. Overall, we demonstrated that intraspecific diversity can have strong consequences on community and ecosystem dynamics, which unfolds the pivotal role of this biodiversity facet for understanding ecological dynamics.

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76 **I. Introduction**

77 Understanding the relationships between biodiversity and ecosystem functioning is a
78 field of intense investigations informing on the services provided by biodiversity
79 (Chapin *et al.*, 2000; Loreau, 2000; Hooper *et al.*, 2005; Cardinale *et al.*, 2012).
80 Biodiversity is generally quantified as the taxonomic, functional and/or phylogenetic
81 diversity of a species assemblage, and most studies on biodiversity-ecosystem
82 functioning relationships have to date focused on the *interspecific* facet of biodiversity
83 (Naeem *et al.*, 1994; Downing & Leibold, 2002; Hillebrand & Matthiessen, 2009).
84 However, biodiversity also includes an *intraspecific* facet that is defined as the
85 phenotypic, functional and genetic diversity measured within a single species (Odling-
86 Smee, Laland, & Feldman, 2003; Bolnick *et al.*, 2003). During the last two decades,
87 intraspecific diversity has been demonstrated to account for a non-negligible part of the
88 total biodiversity measured in plants and animals (Fridley & Grime, 2010; de Bello *et*
89 *al.*, 2011), representing in some cases up to a quarter of the total variability measured in
90 communities (Fridley & Grime, 2010; de Bello *et al.*, 2011; Siefert *et al.*, 2015).
91 Furthermore, there is now mounting evidence that intraspecific diversity can strongly
92 affect ecological dynamics at levels higher than the population, i.e. at the community
93 and ecosystem levels (Bolnick *et al.*, 2003, 2011; Hughes *et al.*, 2008; Bailey *et al.*,
94 2009; Violle *et al.*, 2012).

95 Investigations on the relationships between intraspecific diversity and
96 community and ecosystem dynamics (hereafter "ecological dynamics") have attracted
97 many scientists, since this facet of biodiversity is at the thin frontier between evolution
98 and ecology (Schoener, 2011; Hendry, 2016). Consequently, many conceptual insights
99 on the relationships between intraspecific diversity and ecological dynamics arose from
100 studies on eco-evolutionary dynamics. These dynamics aimed at understanding how

evolutionary processes can affect ecological dynamics, and how, in turn, these ecological changes can lead to rapid evolutionary responses (Thompson, 1998; Odling-Smee *et al.*, 2003; Whitham *et al.*, 2003; Schoener, 2011; Matthews *et al.*, 2011; Hendry, 2016). These key concepts have been substantiated by major experimental studies demonstrating how stress-induced phenotypic changes (e.g. through predation) (Werner & Peacor, 2003; Schmitz *et al.*, 2008; Hawlena *et al.*, 2012), individual genotypes (Whitham *et al.*, 2003; Madritch, Greene, & Lindroth, 2009), and rapid adaptation (Harmon *et al.*, 2009; Matthews *et al.*, 2016; Rudman & Schluter, 2016) can alter community and ecosystem dynamics.

Intraspecific diversity can be quantified based on the *richness* of populations, which corresponds to the differences in the number of genotypes/phenotypes composing populations. For instance, populations are often characterized according to their “allelic richness”, which is a population parallel of species richness, a common metric measured at the community level and used to investigate biodiversity-functions relationships (BEF, Crutsinger, 2006). Intraspecific richness can also affect ecological dynamics (hence generating "intraspecific BEF", Whitham *et al.*, 2006; Crutsinger, 2006), and the ecological consequences of intraspecific richness should follow a saturating curve as often described for BEF observed at the interspecific level (Hughes *et al.*, 2008). Although rarely tested empirically, the saturating shape could be due to the combined effects of several mechanisms. Populations with different richness could have different ecological consequences because of ecological complementarity among genotypes/phenotypes (i.e. niche partitioning, facilitation occurring when genotypes use different resources), inhibition among genotypes/phenotypes (when multiple genotypes are in competition for resources), or functional redundancy among genotypes/phenotypes that can make populations ecologically equivalent (Johnson,

126 Lajeunesse, & Agrawal, 2006; Hughes *et al.*, 2008). Yet, the shape of the relationship
127 between intraspecific richness and ecological dynamics has rarely been investigated
128 empirically and –up to our knowledge- never been quantified across species.

129 The ecological consequences of intraspecific diversity can also been investigated
130 through the lens of *variation* in genotypic or phenotypic attributes. Adaptive and non-
131 adaptive evolutionary processes such as natural selection, plasticity or genetic drift can
132 generate unique phenotypic differences among populations. These differences can be
133 associated to key functional processes such as food acquisition or nutrient cycling (e.g.
134 Grant & Grant, 2006; Rudgers & Whitney, 2006; Lowe, Kovach, & Allendorf, 2017),
135 resulting in both trophic and non-trophic effects of intraspecific variation on ecological
136 dynamics (Odling-Smee *et al.*, 2003; Whitham *et al.*, 2003; Matthews *et al.*, 2011). For
137 instance, plant genotypes differing in their susceptibility to herbivores have diverging
138 influences on herbivore communities (Barbour *et al.*, 2009). Similarly, differences in
139 diet within predator populations can modify prey community structure (Post *et al.*,
140 2008; Howeth *et al.*, 2013). Non-trophic interactions can also have an important role.
141 For instance, differences in the chemical composition of individuals can result in
142 differences in excretion rate or in leaf chemistry that can then affect ecosystem
143 functions such as primary production or nutrient recycling (Lecerf & Chauvet, 2008; El-
144 Sabaawi *et al.*, 2015). Recently Des Roches *et al.* (2018) demonstrated that intraspecific
145 variation can affect ecological dynamics as much as the removal or replacement of a
146 species in the environment. Although based on a restricted number of pioneer studies
147 (25 studies and 15 species), this study confirms the hypothesis that intraspecific
148 variation might be a non-negligible driver of ecological dynamics.

149 Here, we tested –across various species and ecosystems- to which extent
150 intraspecific *richness* and intraspecific *variation* affect the structure of communities and

151 the functioning of ecosystems, and hence whether intraspecific diversity is a major
152 driver of ecological dynamics. We ran two meta-analyses synthesizing published data
153 across taxa and ecosystems for intraspecific richness and variation respectively to fulfil
154 three specific objectives. First, we tested for the significance and the shape of the
155 relationship between intraspecific richness and ecological dynamics. We expect to find
156 a significant saturating relationship between intraspecific richness and ecological
157 dynamics, mainly because of potential facilitation and functional redundancy among
158 genotypes and phenotypes (Hughes *et al.*, 2008). Second, we compared the ecological
159 effects of intraspecific richness to those of interspecific richness obtained from
160 experimental studies manipulating species richness (Duffy, Godwin, & Cardinale,
161 2017). Finally, we provided a novel and extensive quantitative synthesis testing for the
162 effects of intraspecific variation on ecological dynamics. Des Roches *et al.* (2018)
163 previously focused on studies removing or replacing the target species (this for which
164 intraspecific variation is manipulated) to investigate the ecological consequences of
165 intraspecific variation. This strongly restricted the number of available studies on which
166 effects sizes were calculated, and potentially upwardly biased these estimates (Des
167 Roches *et al.*, 2018). We here relaxed this restriction by considering all studies
168 manipulating intraspecific variation, and we used a null model approach to provide a
169 more accurate effect size of intraspecific variation on ecological dynamics. We also
170 built on this extended dataset to thoroughly decompose variance in the ecological
171 consequences of intraspecific variation according to the type of organism that was
172 manipulated and the type of response variable being measured. Amongst other, we
173 tested whether the magnitude of the effects of intraspecific variation on ecological
174 dynamics vary among organism types (primary producers *vs*. consumers) and levels of
175 biological organisation (community *vs*. 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. Material & 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 was naturally observed in populations and 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 instance (see Werner & Peacor, 2003 for a review on this topic). 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 done using the ISI Web of Knowledge® platform (last accessed January 2016). We also scrutinized the reference list of each article to obtain additional articles. When conducted the literature search, the following keywords were used under various combinations: “community genetics”, “intraspecific variation”, “ecosystem functions”, “eco-evolutionary dynamics”, and “intraspecific genetic variation” (see Appendix S1 for details). We selected articles describing the effects of genotypic and/or phenotypic richness (*intraspecific richness*) and/or different genotypes phenotypes (*intraspecific variation*) in a single species (i.e. the target species) on

201 community and/or ecosystem dynamics. A total of 77 articles with available statistics
202 were selected (see Appendix S2). Among them, 18 focused on intraspecific richness and
203 65 focused on intraspecific variation.

204 For each study, we recorded the Latin name of the target species and we
205 classified them as primary producers or consumers (including here primary and
206 secondary consumers as well as predators) and according to the major taxonomic
207 categories that were represented in our dataset, namely arthropods (7 species), fishes (6
208 species), herbaceous (8 species) and trees (26 species). We also recorded the duration
209 (in days, mean duration of survey ± SD: 662 ± 1310, range: from 1 to 6205 days) of the
210 study as a co-variable because we can expect that the ecological divergence among
211 treatments could increase with time. We finally recorded seven main response variables
212 related to community structure and ecosystem functioning. A community was here
213 defined as a group of at least two species, and we focused on three types of response
214 variables describing the structure of communities:

215 - *Species abundance*: total number of individuals of all species;
216 - *Biomass*: total mass of individuals of all species;
217 - *Community structure*: number of species such as Simpson or Shannon indices,
218 species evenness and/or species richness.

219 Regarding response variables at the ecosystem level, we considered four main
220 ecosystem functions:

221 - *Decomposition rate*: rate at which organic matter is recycled;
222 - *Elemental cycling*: quantity of organic or inorganic materials;
223 - *Primary productivity*: measured as several proxies of primary producers: biomass
224 of primary producers excluding the productivity of the target species, chlorophyll *a*
225 concentration, daily oxygen production, and photosynthetically active radiation;

- *Ecosystem respiration*: rate of oxygen consumption.

(2) Meta-analysis

(a) The ecological consequences of intraspecific richness

To test for the consequences of intraspecific richness on ecological dynamics, we focused only on studies investigating the consequences of *genotypic* richness since it was the intraspecific diversity facet most commonly manipulated to test for the effects of intraspecific richness on ecological dynamics. Since measures of variance associated to the effects of intraspecific richness on ecological dynamics were not available for all response variables, we used the log-transformed response ratio (ln*RR*) as an effect size. ln*RR* was computed using the following formula: $\ln\left(\frac{XG}{1G}\right)$, in which $1G$ is the average of the response variable measured for the treatment with a single genotype (i.e. monoculture), and XG is the average of the response variable measured for each treatment independently including more than one genotype. For each response variable, ln*RR* increases as the difference in the mean response variable measured in the treatment with a single genotype and treatments including more than one genotype increases. We also recorded the difference in the number of genotypes between the single genotype treatment (monoculture) and all other treatments separately (i.e. treatment including more than one genotype, from two to twelve genotypes) that was termed "difference in intraspecific richness". In our dataset, difference in intraspecific richness varied between one and eleven genotypes. This approach allowed quantifying the ecological consequences of increasing the number of genotypes for each target species. Since each study generally assessed the effects of intraspecific richness on more than one response variable, our dataset included a total of 101 assays.

We aimed at testing the shape and the significance of the relationship between ln*RR* and the difference in intraspecific richness across all case studies. The general

251 expectation is that ecological differences between treatments increase as the differences
252 in intraspecific richness increase, although this increase could be non-linear (Hughes *et*
253 *al.*, 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* and differences in
255 intraspecific richness. More precisely, we modelled this relationship according to four
256 different models to determine the most likely shape of the relationship between ln*RR*
257 and difference in intraspecific richness:

258 - A null model (1 parameter) was computed for the null effect hypothesis (i.e. no
259 significant relationship between ln*RR* and difference in intraspecific richness);
260 - A linear model (2 parameters) suggesting a positive and linear relationship between
261 ln*RR* and difference in intraspecific richness;
262 - A Michaelis-Menten model (2 parameters) suggesting that ln*RR* increases with the
263 differences in intraspecific richness, until a plateau is reached (saturating shape);
264 - An asymptotic exponential model (2 parameters) suggesting a shape similar to the
265 Michaelis-Menten model, except that the plateau is reached sooner.

266 All models cited above included article ID as a random term, and the reverse of the
267 sample size as a weighting parameter so as to give more weight to articles including
268 more replicates. Models were compared according to AIC and we retained (as "best
269 models") all models that fell within a ΔAIC < 4 (Burnham & Anderson, 2002). We also
270 calculated for each model the Akaike weight that provides a conditional probability for
271 each model to be best supported by the data (Burnham & Anderson, 2002).

272 We then compared the ecological effects of intraspecific and interspecific
273 richness by extracting from each study and for each response variable the |ln*RR*|
274 corresponding to the most extreme levels of genotypic richness (x_{max}) manipulated in
275 each study (N = 48). These values were subsequently compared to published ln*RR*

276 calculated following a similar method for experiments manipulating interspecific
277 richness (Duffy *et al.*, 2017) (N = 35) using a Kruskal-Wallis rank sum test.
278 Finally, to compare the ecological consequences of intraspecific richness
279 between levels of biological organisation, we performed meta-regression as a linear
280 mixed effect model. The absolute value of ln*RR* was used as the dependent variable, the
281 articles ID was used as a random factor, whereas the level of biological organisation
282 (community *vs*. ecosystem response variables) was fixed effects. The type of organisms
283 was not included in the analysis given that studies on intraspecific richness focused
284 almost exclusively on primary producers (excepted one on fungus).

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

286 Given that most studies (81 %) did not include a control (i.e. a treatment without the
287 target species), we compared the strength of effects among all unique genotypes and/or
288 phenotypes that were considered in each study. Studies generally compared the
289 consequences of 2 to 10 different unique genotypes and/or phenotypes (i.e. 2 to 10
290 treatments, with each treatment corresponding to a unique genotype/phenotype) on
291 community and/or ecosystem dynamics; we gathered from each study the statistic (*t*, *F*,
292 *Chi*-squared, Pearson's *r*, Spearman's *r*, R^2 or Hedge's *g*) associated with the between-
293 treatments comparison (i.e. the variation of the phenotypes/genotypes). The higher the
294 absolute value of the statistic, the higher the community and ecosystem consequences
295 due to the variation of genotypes and/or phenotypes. The absolute value of each statistic
296 was converted into a correlation coefficient (*r*) ranging from 0 to 1 (see Table S1 for the
297 formulas used to convert each statistic into a *r*). We did not use the direction of the
298 statistic (i.e. positive or negative) because it depended upon the ecological response
299 variable that was considered, which makes inconvenient comparisons on the direction
300 of effects. Then, the *Z*-Fisher transformation was used to obtain a standardized effect

size using the following formulae: $Zr = 0.5\ln\frac{(1+r)}{(1-r)}$. For each *Zr* value, we calculated the corresponding standard error using the following formulae: $se_{Zr} = \frac{1}{\sqrt{n-3}}$ (Nakagawa & Cuthill, 2007). Since each study generally focused on more than one response variable, we obtained a total of 430 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* (MES_{obs} for mean effect size observed) 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, the article ID as random effect and se_{Zr} was included as a weighting parameter to give more weight to studies with 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 difficult the assessment of 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 what was 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 (Student, Fisher…) with the adequate degree of freedom. This resampled set of statistics (N = 430) was transformed into *Zr* as explained above to build 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} corresponds to the range of possible MES values expected if the null hypothesis was true. Finally, we calculated the probability of

325 MES_{obs} to be larger than expected under this null hypothesis using a one-tailed test
326 (Manly, 1997).

327 We then compared the median of effect sizes (MES_{common}) of studies that were
328 common between our extended dataset and the dataset used by Des Roches *and*
329 *colleagues* (Des Roches *et al.*, 2018) (i.e. 15 studies) to a selection of 15 studies
330 randomly sampled from our extended dataset. We calculated the median effect size for
331 the subset of random studies (MES_{ran}) and repeated this resampling procedure 1000
332 times to obtain 1000 values of $MES_{ran.}$ We then compared MES_{common} to each MES_{ran}
333 value to calculate the probability that MES_{common} was higher than a random subset of 15
334 studies taken from the whole dataset (Manly, 1997).

335 We finally tested whether effect sizes (*Zr*) differed among organism types, for
336 which intraspecific variation was manipulated, and among the ecological response
337 variables considered. We hence computed meta-regressions based on linear mixed
338 effect models with *Zr* values (for all 65 articles and 430 measures) as the dependent
339 variable, and the organism type or the ecological response variable as fixed effects. The
340 article ID was included as a random effect, and se_{Zr} was included as a weighting
341 parameter. Four models were run to assess the differences of effect sizes (i) between
342 organism types classified as consumers or primary producers, and (ii) between detailed
343 taxonomic categories (arthropods, fishes, herbaceous and trees). We then tested whether
344 the effect sizes of intraspecific variation differed among ecological response variables
345 (iii) classified as community or ecosystem variables, and (iv) classified according to
346 more detailed categories (abundance, biomass, community structure, decomposition,
347 nutrient cycling, primary productivity and respiration of the ecosystem).

348

349 *(3) Publications biases*

350 For both intraspecific variation and intraspecific richness, we assessed potential
351 publication biases by combining Egger's regressions and funnel plots (Egger *et al.*,
352 1997). Egger's regressions and funnel plots were computed using the residuals of meta-
353 regressions related effect sizes to the main modifiers (i.e. the explicative variables) and
354 a measure of the study size (the inverse of se_{Zr} and the sample size for intraspecific
355 variation and intraspecific richness, respectively, (Horvathova, Nakagawa, & Uller,
356 2012; Nakagawa & Santos, 2012). Typically, for intraspecific variation we ran an
357 Egger's regression model including the residuals of the meta-regression linking
358 intraspecific variation to the modifiers as a response variable and the inverse of $\mathrm{se}_{\mathrm{Zr}}$ as
359 the explicative variable. A similar approach was used for intraspecific richness. The
360 intercept α and the slope β of the Egger's regressions are expected not to be
361 significantly different from zero if the data sets are unbiased towards significant results.
362 Finally, funnel plots were produced as a scatterplot linking the residuals described
363 above to the respective measure of the study size. An unbiased data set is expected to
364 generate a funnel plot in which articles with larger sample sizes will be close to the
365 mean effect size, whereas articles with small sample sizes will show more variance
366 around the mean effect size (Horvathova *et al.*, 2012; Nakagawa & Santos, 2012).

367 Overall -and after accounting for important modifiers- we found that there was
368 no strong visual signs of publication biases, neither for intraspecific variation nor for
369 intraspecific richness (Fig S1). This visual inspection of funnel plots was confirmed by
370 the Egger's regressions since parameter values were not significant, neither for
371 intraspecific variation ($\alpha = 0.014$, $p = 0.485$; $\beta = -0.0014$, $p = 0.562$) nor for
372 intraspecific richness ($\alpha = -0.007$, $p = 0.654$; $\beta = 0.0001$, $p = 0.736$).

373 All statistical analyses were performed using the R environment (R core team,
374 2013). The nlme package (Pinheiro *et al.*, 2014) was used to compute linear and non-
375 linear mixed effect models.

376 ## *III.* Results

377 All articles (n = 77) selected for investigating the effects of intraspecific richness and
378 intraspecific variation were published between 2000 and 2016, and 70 % used primary
379 producers as target species, which were also the first model organisms used (Fig. 1).
380 The first studies focusing on consumers were published only recently (in 2008), using
381 fish (70 %) and arthropods (30 %) as model species.
382

383 ### *(1) The intraspecific richness-ecological dynamics relationship*

384 As expected, we found a significant, positive and non-linear relationship between
385 intraspecific richness and ecological dynamics that likely followed a saturating shape
386 (Fig. 2A). Indeed, the AIC selection procedure revealed that two out of the four tested
387 models were likely to be supported by the data (ΔAICs < 4, Table 1). Interestingly these
388 two models were both non-linear models varying slightly in the specification of the non-
389 linear term, and both the linear and null models were strongly rejected (ΔAICs > 12,
390 Table 1). Among these two supported models, the model that best supported the data
391 was the exponential asymptotic model (86% of chances of being the best fitting model
392 according to the Akaike weight and ΔAIC = 3.694 for the other model, Table 1),
393 suggesting that the relationship between intraspecific richness and changes in
394 community structure and ecosystem functioning (effect size: ln*RR*) likely followed a
395 saturating shape (Fig. 2A).
396

397 We further found that the ecological effects of intraspecific richness represented
398 66% of the ecological effects induced by interspecific richness (Fig. 2B). Although
399 effect sizes measured for interspecific and intraspecific richness respectively were
400 significantly different (χ^2 = 5.704, d.f = 1, p = 0.016), they largely overlapped (Fig. 2B).
401 Interestingly, this difference was mainly driven by few studies on interspecific richness
402 with strong ecological effects (Fig. 2B). The ecological effects of intraspecific richness
403 did not significantly vary between the community (lnRR = 0.18, SE = 0.02) and
404 ecosystem (lnRR = 0.12, SE = 0.02) response variables (F = 0.504, d.f = 1, 16, p =
405 0.488).

406 *(2) The ecological consequences of intraspecific variation*

407 We extended the meta-analysis performed by Des Roches *and colleagues* to 44 species
408 (*vs*. 15 species in Des Roches *et al.*, 2018). We found that that the observed effect size
409 of intraspecific variation on community structure and ecosystem dynamics was
410 significant, and actually twice higher than the resampled effect size expected under a
411 null expectation (MES_{obs} = 0.52, 95% confident interval (CI) = 0.44-0.59, and MES_{null} =
412 0.26, CI = 0.26-0.27, resampled test, p < 0.001, Fig. 3, see also Appendix S3 and Fig
413 S2).

414 We tested to which extent the restricted dataset analysed by Des Roches *et al.*
415 (2018) was representative of our extended dataset, or on the contrary biased upward as
416 expected by Des Roches *et al.* (2018). We found that that effect sizes measured from
417 Des Roches et al's dataset (MES_{common} = 0.29, 95% percentile interval (PI) = 0.03-1.05)
418 was not significantly different from the distribution of effect sizes measured in our
419 extended dataset (MES_{ran} = 0.41, PI = 0.02-1.43, resampling test, p = 0.091, Fig S3),
420 and actually tended to be downwardly biased.

421 Finally, the ecological effects induced by intraspecific variation were stronger
422 when primary producers rather than consumers were manipulated (F = 4.082 d.f. = 1,
423 364, p = 0.044, Fig. 4A). Nonetheless, the strongest ecological effects of intraspecific
424 variation were observed in arthropods and herbaceous species, whereas the smallest
425 effects were observed in fish and tree species (F = 2.445 d.f. = 3, 362, p = 0.063, Fig.
426 4A). Irrespectively of organism type, the effects of intraspecific variation were
427 significantly stronger when the response variables were measured at the ecosystem level
428 rather than at the community level (F = 5.226, d.f = 1, 364, p = 0.023, Fig. 4B). The
429 strongest effects were detected when response variables concerned nutrient cycling and
430 the assembly of community, whereas the lowest effects were found for general
431 measures of abundance and density of species (F = 3.068, d.f = 6, 358, p = 0.006, Fig.
432 4B).

433 **IV. Discussion**

434 Intraspecific diversity is increasingly recognized as an important facet of biodiversity
435 that can affect all biological levels (Bailey *et al.*, 2009). We here provide quantitative
436 estimates of the consequences of intraspecific richness and variation on community
437 structure and ecosystem functioning. We demonstrated for the first time that the
438 intraspecific BEF followed –as theoretically expected- a non-linear saturating shape.
439 We confirmed that genotypic and/or phenotypic variation observed between populations
440 can have non-negligible effects on community structure and ecosystem functions, and
441 we demonstrated that previous estimates (Des Roches *et al.*, 2018) of these ecological
442 effects of intraspecific variation actually tended to be underestimated. Finally, our
443 exhaustive quantitative survey pointed out that the ecological consequences of
444 intraspecific variation differed among biological level of organisation, and among

445 organism types. These findings provide novel and integrative insights into the
446 ecological role of intraspecific diversity.
447

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

449 Although the form of the relationship between intraspecific richness and
450 ecological consequences has already been discussed conceptually (Hughes *et al.*, 2008),
451 our meta-analysis provides for the first time a qualitative and quantitative assessment of
452 intraspecific BEF. Specifically -and although considering almost only primary
453 producers-, our results demonstrated that an increase in intraspecific richness resulted in
454 a non-linear (saturating) increase in the magnitude of its effects on ecological dynamics.
455 Our finding supports the idea that ecological divergences between an environment
456 hosting populations composed of a single genotype and an environment hosting
457 populations composed of multiple genotypes increase until a plateau is reached as the
458 number of genotypes composing the later increases. This result echoes BEF defined at
459 the interspecific level (Reiss *et al.*, 2009; Cadotte, Carscadden, & Mirotchnick, 2011)
460 and suggests that the saturating shape might arise from similar mechanisms occurring at
461 the intraspecific and interspecific levels (Johnson *et al.*, 2006; Hughes *et al.*, 2008).
462 More specifically, the initial linear increase is assumed to be due to complementarity
463 and facilitation among genotypes, whereas the plateau is likely due to functional
464 redundancy among genotypes (Johnson *et al.*, 2006). Redundant genotypes probably
465 display functionally similar traits since two genotypes do not necessarily generate two
466 functionally different traits (e.g. through synonymous mutations or trait convergences).
467 Thus manipulating traits richness -rather than genotypic richness only-, and more
468 precisely functional effect traits (i.e. traits having ecological effects, Violle *et al.*, 2007),

469 in future experiments should confirm mechanisms underlying intraspecific biodiversity-
470 ecological dynamics relationship.

471 We found that effect sizes found for intraspecific richness were within the range
472 of the values recently reported for experimental interspecific BEF, indicating that the
473 ecological effects of varying phenotypic/genotypic richness within populations are in
474 some cases similar to those induced by varying species richness within communities.
475 This later finding posits several questions regarding the general relationships between
476 intraspecific diversity, community structure, ecosystem functioning and common
477 abiotic constraints. A large body of literature has demonstrated that intraspecific genetic
478 diversity and species diversity (a measure of community structure) might co-vary over
479 space because of common environmental drivers and/or reciprocal causal relationships
480 between intraspecific genetic diversity and species diversity (i.e. the species-genetic
481 diversity correlation framework, SGDC, Vellend & Geber, 2005; Vellend, 2005).
482 Because most studies considered in our meta-analysis are experimental, our findings
483 confirm that intraspecific diversity can directly influence the structure of communities -
484 irrespective of the abiotic environments-, hence adding weight to the SGDC framework.
485 Additionally, we suggest expanding the SGDC framework since intraspecific diversity
486 can also affect ecosystem functioning. This suggests that intraspecific diversity,
487 community structure and ecosystem functioning may actually be tightly linked into a
488 tripartite relationship. A major future challenge will be to tease apart the causal
489 relationships linking these three components within a common abiotic environment.
490 These relationships might indeed be direct (e.g. intraspecific diversity directly affects
491 community structure), indirect (e.g. intraspecific diversity indirectly affects ecosystem
492 functions through its direct effect on community structure such as the trophic cascade),
493 and/or due to the parallel effects of common abiotic drivers (e.g. temperature affects

494 directly intraspecific diversity, community structure and ecosystem functions). As it has
495 been done recently for the BEF (Grace *et al.*, 2016; Duffy *et al.*, 2016) and the SGDC
496 (Fourtune *et al.*, 2016; Lamy *et al.*, 2017) frameworks, we argue that a future important
497 step will be to combine appropriate statistical methods (e.g. path analysis, Shipley,
498 2000; Grace, 2006) and powerful experimental designs to disentangle causal
499 relationships between intraspecific diversity, community structure, ecosystem functions
500 and their common environment.

501 We further demonstrated that intraspecific variation has significant ecological
502 effects across a large set of species, hence confirming and refining a previous estimate
503 based on a restricted set of species (Des Roches *et al.*, 2018). By tripling the number of
504 species being investigated in this meta-analysis, we taxonomically broaden the
505 conclusion that intraspecific variation matters for shaping ecological dynamics, and that
506 the ecological effects of intraspecific variation in nature might be more common than
507 expected. Moreover, we demonstrated that previous estimates provided by (Des Roches
508 *et al.*, 2018) were not upwardly biased (which was expected due to the focus on a non-
509 random pool of species), but were well within the range of estimates we report here and
510 actually tended to be slightly underestimated. Our finding hence strongly supports the
511 idea that adaptive and non-adaptive processes can lead to unique populations
512 differentially and significantly affecting ecological systems.

513 Although our conclusions held true for many species, the ecological effects of
514 intraspecific variation were not homogeneous across species, and this is partly
515 explained by the trophic level of species. Indeed –and according to our expectations-,
516 the ecological effects of intraspecific variation were stronger when the target species
517 was a primary producer than when it was a consumer. Several non-exclusive
518 mechanisms might explain this result. For instance, many primary producers considered

here provide a habitat for many invertebrates species (Southwood, Brown, & Reader, 1979) (this is not the case for considered consumer species), and this habitat can be modulated by changes in plant structures. Non-exclusively, the relative biomass of primary producers is higher than that of consumers; as such primary producers could generate stronger effects on communities and ecosystems than consumers because of a pure biomass effect. However, when decomposing variance in the ecological effects of intraspecific variation into a greater detail, we found that these effects were stronger for arthropod and herbaceous species than for fish (and to a lesser extent tree) species. This suggests that the trophic level of species cannot be seen as the only predictor of the ecological effects of intraspecific diversity, and we argue that future works should aim at testing specifically why intraspecific variation ecologically matters for some species and not for others.

Finally, the effects of intraspecific variation were globally higher on ecosystems than on communities, hence generalizing across organism and ecosystem types a similar observation on freshwater consumer species (Palkovacs *et al.*, 2015). We can speculate that this difference of effects holds because intraspecific variation acts on community dynamics through trophic mechanisms, whereas ecosystem functions can be modulated through both trophic *and* non-trophic interactions (e.g. excretion rate or leaf chemistry, Vanni, 2002; Schmitz *et al.*, 2014). For instance, a consumer species varying intraspecifically in resource selectivity and/or consumption rate can affect both the community structure and productivity of its resource (Harmon *et al.*, 2009). Non-trophic mechanisms such as variability in organisms stoichiometry can reinforce the effect of the consumer species on several ecosystem functions (e.g. primary production or soil mineralization, (Schmitz, Hawlena, & Trussell, 2010; Hawlena *et al.*, 2012). Alternatively -yet non-exclusively-, changes in ecosystem functions might be due to

544 both direct effects of intraspecific diversity and indirect effects of intraspecific diversity
545 mediated through changes in community structure, which may overall strengthened the
546 effects of intraspecific diversity at the ecosystem level. However, as observed for the
547 taxonomic predictors, an analysis accounting for a greater detail revealed that a lot of
548 variation exists between sub-categories of response variables (Fig. 4B), and that the
549 dichotomy between variables measured at the community and ecosystem levels is not a
550 straightforward. Although providing the first attempts to decompose variance in the
551 ecological effects of intraspecific variation, our findings call for further studies on
552 various taxa and in different ecosystems to fully appreciate the intensity of ecological
553 effects of intraspecific diversity (Box 1).

554 **V. Conclusions**

555 (1) We provided empirical evidence that the ecological effects of intraspecific
556 richness increase asymptotically, paralleling well-known patterns observed at the
557 interspecific level (Loreau, 2000; Hooper *et al.*, 2005) and confirming conceptual ideas
558 (Hughes *et al.*, 2008).

559 (2) We also demonstrated that the variation of phenotypes or genotypes within
560 species is an important driver of community and ecosystem dynamics. These major
561 ecological effects of intraspecific diversity held true for organisms including several
562 species of plants and animals, although much remains to be tested (Box 1).

563 (3) Overall these findings demonstrated that intraspecific diversity -beyond its
564 importance for species to adapt to environmental changes- is an important facet of
565 biodiversity for understanding and predicting the ecological dynamics of communities
566 and ecosystems, which reinforces the needs for better appraising the causes and
567 consequences of intraspecific diversity in natural populations and for improving
568 associated conservation plans.

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796

797 **Figure captions**

798 **Fig. 1.** Publication year of the 77 selected articles used in the present study.

799

800 **Fig. 2. (A)** Relationship between intraspecific richness and effect size (ln*RR*) on
801 ecological dynamics. The line represents the shape of the relationship as predicted by
802 the exponential asymptotic non-linear mixed effect model. Blue shadow represents 95%
803 CI. **(B)** Medians (vertical dotted lines) and density of absolute effect size (ln*RR*) for
804 intraspecific and interspecific richness on ecological dynamics.

805

806 **Fig. 3.** Density probability of *Zr* effect size. The vertical grey straight line represents the
807 resampled *Zr* mean under the null hypothesis (confidence intervals not shown because
808 they were to narrow); the black curve shows the distribution of observed *Zr* and its
809 mean (vertical black straight line), grey shades represent 95% CIs.

810

811 **Fig. 4. (A)** Mean of *Zr* effect size in function of the model species. The sample sizes
812 (N) are given as indication, and represent the number of species and the number of
813 effect sizes respectively. The horizontal dotted line represents the mean effect size; error
814 bars represent ± 1 SE. **(B)** Mean of *Zr* effect size in function of the ecological response
815 variables. The sample sizes (N) of the number of effect sizes are given as indication.
816 The horizontal dotted line represents the mean effect size; error bars represent ± 1 SE.

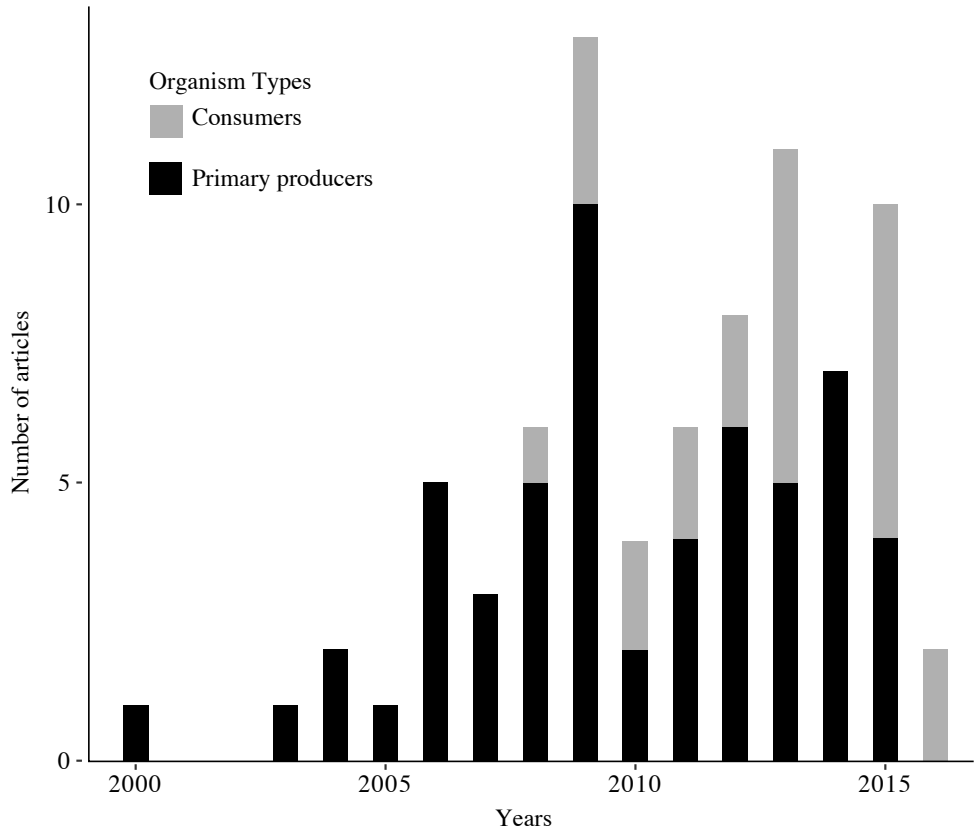
Organism Types
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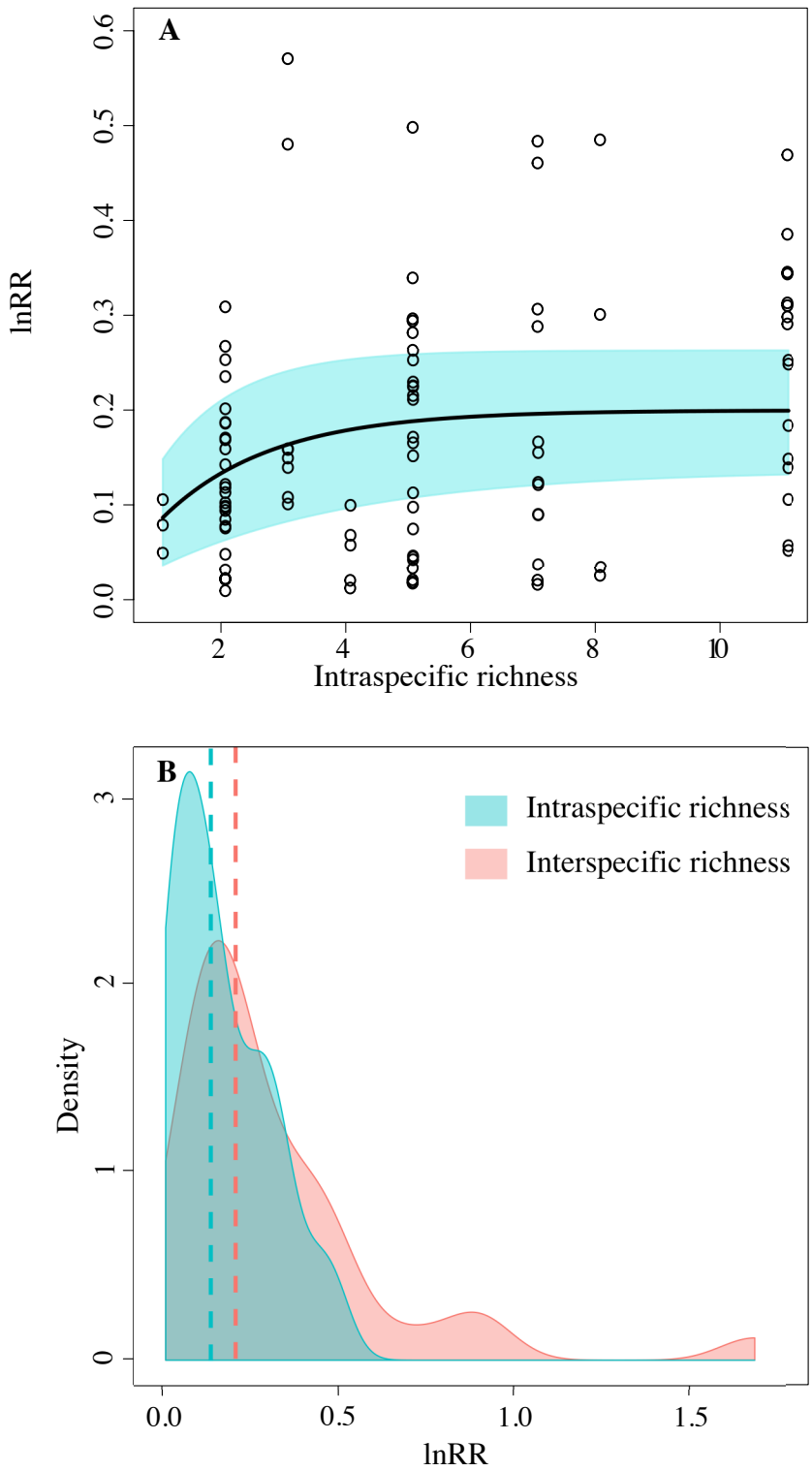
Fig. 1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4
6
8
10
Intraspecific richness
B
Intraspecific richness
Interspecific richness
Density
0
1
2
3
0.0
0.5
1.0
1.5
lnRR

Fig. 2

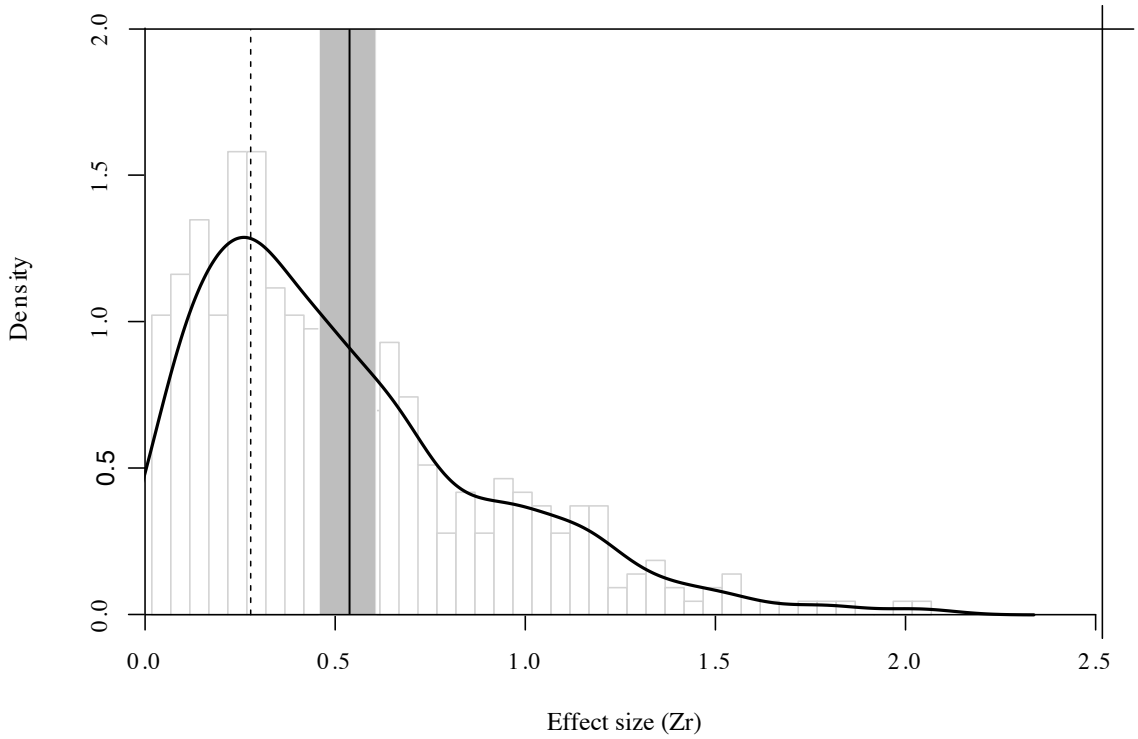

Fig. 3

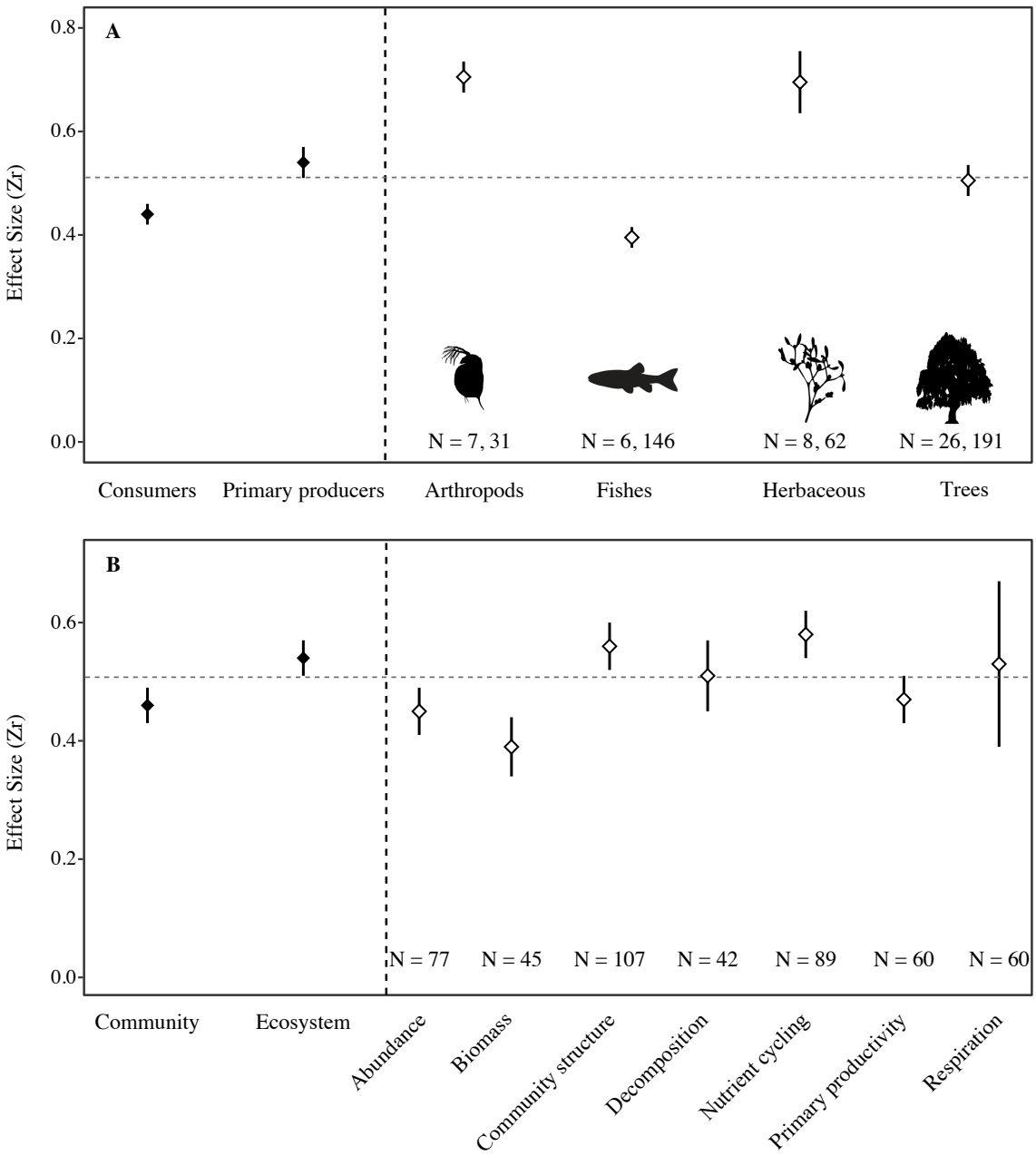
A
Effect Size (Zr)
0.8
0.6
0.4
0.2
0.0
N = 7, 31
N = 6, 146
N = 8, 62
N = 26, 191
Consumers
Primary producers
Arthropods
Fishes
Herbaceous
Trees
B
Effect Size (Zr)
0.6
0.4
0.2
0.0
N = 77
N = 45
N = 107
N = 42
N = 89
N = 60
N = 60
Community
Ecosystem
Abundance
Biomass
Community structure
Decomposition
Nutrient cycling
Primary productivity
Respiration

Fig. 4

Table 1. Summary table of the model selection by 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 articles ID as random factor, equations and parameters estimates are given as indication. IR = intraspecific richness, ln*RR* = effect size of intraspecific richness of ecological dynamics.

Model	AIC	ΔAIC	AIC Weight	Equation	Parameter estimates
Asymptotic exponential model	-141.726	0	0.862	$lnRR = a * (1 - e^{-b*IR})$	a = 0.201 b = 0.572
Michaelis-Mentens model	-138.032	3.694	0.136	$lnRR = V * \frac{IR}{k + IR}$	V = 0.225 k = 1.001
Linear model	-129.038	12.689	0.001	$lnRR = b0 + b1 * IR$	$b1$ = 0.011 $b0$ = 0.118
Null model	-120.455	-21.2714	< 0.001	$lnRR = b0$	$b0$ = 0.172

Box 1. **Research perspectives on the relationships between intraspecific diversity and the dynamics of communities and ecosystems.**

We hereafter highlight several research avenues that may greatly favour the understanding of the relationships between intraspecific diversity and the dynamics of communities and ecosystems.

(i) Our review demonstrated that the ecological effect size of intraspecific diversity strongly varies from one species to another. We demonstrated that this inter-species variance in effect size is partly explained by the type of organism (i.e. primary producer or consumer). However, species composing a community also vary according to its commonness, its role in the ecosystem (e.g. keystone species or not, (Paine, 1969)), its body length (or height for plants), its life-history strategy (e.g. r-K strategy), its recent history (e.g. whether or not the species is non-native), functional characteristics (e.g. stoichiometry, metabolism), etc... A next challenge will be to better partition this inter-species variance in effect size by determining the species characteristics that best predict the strength of effect sizes, which is a pre-requisite to set coherent conservation plans at the intraspecific level (Mimura *et al.*, 2016);

(ii) Intraspecific diversity has often been manipulated for a single target species at a time. However, in nature, species are interacting and we argue that next studies should manipulate intraspecific diversity within multiple interacting species to better reflect reality, and to partition the relative importance of intraspecific diversity between interacting (potentially co-evolving) species;

(iii) Ecosystems are connected one each others through cross-ecosystem fluxes of matter (Loreau, Mouquet, & Holt, 2003). For instance, freshwater ecosystems such as rivers receive a large amount of material from the surrounding terrestrial ecosystem (e.g. dead leaves falling from trees, (Bartels *et al.*, 2012). A major -yet fascinating- challenge would be to assess the relative consequence of intraspecific diversity on allochtonous ecosystems *vs* autochtonous ecosystems; for instance testing whether or not the consequences of intraspecific diversity manipulated in a fish species is higher on aquatic ecosystems than on terrestrial ecosystems (Jackrel & Wootton, 2014; Crutsinger *et al.*, 2014; Rudman *et al.*, 2015), for the first 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;

(iv) Previous studies mainly assessed the consequences on 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 of *functional effect traits* that are defined as the traits having an ecological impact (e.g. excretion rate or leaf nutrient content, (Violle *et al.*, 2007; Díaz *et al.*, 2013). We suggest that directly manipulating functional traits diversity of individuals within species, rather than genotypic or phenotypic diversity as a whole would be a powerful mean to understand the mechanisms by which intraspecific diversity act on ecological dynamics;

(v) Although we contributed to generalise the idea that intraspecific diversity is essential to the community and ecosystem facets of ecological dynamics, comparisons to other major and indisputable ecological constraints (e.g. temperature, interspecific

biodiversity, human disturbances) have rarely been conducted (but see (Burkle *et al.*, 2013; El-Sabaawi *et al.*, 2015). To better evaluate and quantify the importance of intraspecific diversity in natural system, it is urgent to assess the relative contribution of intraspecific diversity compare to indisputable determinants of ecosystem functioning. This is a key step to confirm that intraspecific is actually part of these indisputable determinants, and not a random signal in complex systems.