

1 **Full paper**

2 **Running head: Within ecosystem filtering**

3 **Title: From plant populations to communities: using hierarchical trait environment**  
4 **relationships to reveal within ecosystem filtering**

5 **Authors:** Lucas Deschamps<sup>1\*</sup>, Raphaël Proulx<sup>1</sup>, Nicolas Gross<sup>2</sup>, Guillaume Rheault<sup>1</sup>,  
6 Vincent Maire<sup>1</sup>

7 **Address:**

8 1 Département des sciences de l'environnement, Université du Québec à Trois-Rivières,  
9 Trois Rivières, Canada

10 2 INRA, USC1339 Chizé (CEBC) 79360, Villiers-en-Bois, France;

11 \* **Corresponding author:** [lucas.deschamps2@gmail.com](mailto:lucas.deschamps2@gmail.com)

12

13 **Webmail:** [vmair24@gmail.com](mailto:vmair24@gmail.com), [raphael.proulx@uqtr.ca](mailto:raphael.proulx@uqtr.ca), [nicolas.gross@cebc.cnrs.fr](mailto:nicolas.gross@cebc.cnrs.fr),  
14 [y.b-pinguet@orange.fr](mailto:y.b-pinguet@orange.fr), [guillaume.rheault@uqtr.ca](mailto:guillaume.rheault@uqtr.ca)

15

16 **Word count:**

17 • Abstract: 270/350                      Main body: 5100/6500

18 • References: 61/50                      Figures+Tables: 5/8

19

20 **Keywords:** Alpha diversity, Environmental filtering, Functional traits, Intra-specific  
21 variation, Demography, Density-dependent mechanisms, Community ecology,  
22 Hierarchical models

23 **Abstract**

24 Explaining the existence of highly diverse plant communities under strong abiotic filtering  
25 is a long-standing challenge in ecology. Hierarchical aspects of abiotic and biotic filters  
26 are rarely taken into account and studies focus mainly on community-level aggregated  
27 patterns. Because variations in biotic conditions might take place in short abiotic gradient  
28 and within the tolerance of species in regional pool, it is likely that biotic filtering will  
29 select individuals within species and adjust population characteristics. To challenge this  
30 idea, we replicated a diversity gradient in four highly contrasted wetlands with an almost  
31 complete species turn-over, sampling individuals in communities irrespective of their  
32 taxonomic identities or status. Using hierarchical distributional modelling, we analyzed the  
33 variation of the mean and dispersion of functional trait space at the ecosystem, community  
34 and species level. We found that the abiotic differences between ecosystems filtered  
35 species contrasted in their growth/nutrient conservation trade-off, while within ecosystems  
36 community variation were mainly due to the partitioning of canopy and leaf adaptations to  
37 light conditions. We found strong species-specific functional and demographic responses  
38 of dominant species along the diversity gradient, especially for traits linked to biomass and  
39 space occupation. Two contrasted strategies emerged, with species using plasticity to  
40 maintain equally dense populations, while others used plasticity to become  
41 overwhelmingly abundant when in favorable conditions. Our results demonstrate that  
42 within ecosystems, variation in biotic conditions selects individuals within populations,  
43 revealing the importance of phenotypic variation for a species to be maintained in more or  
44 less diverse communities. Because phenotypic variations are related to demographic  
45 responses, it offers a way to link the study of species diversity and eco-evolutionary  
46 dynamics.

## 47 **Introduction**

48 Environmental selection of individuals growing in plant communities is described as a  
49 hierarchical succession of abiotic and biotic filters (Lortie *et al.*, 2004; HilleRisLambers *et*  
50 *al.*, 2012). Consequences of these filters have been greatly unraveled using functional  
51 traits, which are measurable characteristics of individuals linked to their fitness (Violle *et*  
52 *al.*, 2007). When aggregated at the community level, the response of trait values to  
53 environmental gradients is the most widely used tool to reveal how different environments  
54 filter individuals for their ability to exhibit traits allowing them to grow under a given set  
55 of conditions and resources (thereafter summarized as “ecological constraints”). The  
56 *directionality* of the filtering describes the displacement of the mean value of the trait to  
57 cope with the set of ecological constraints occurring along an environmental gradient. The  
58 filtering *intensity* occurs when constraints at a given position along the environmental  
59 gradient reduce or enlarge the envelope of trait values allowing individuals to grow and  
60 reproduce (Laughlin & Joshi, 2015). The former process is tackled with the community-  
61 aggregated average, while the latter is studied with the statistical dispersion (thereafter  
62 called “dispersion”). Variation in community mean and dispersion might be due to species  
63 sorting, change in species relative abundances or even intra-specific responses (De Bello  
64 *et al.*, 2012; Bjorkman *et al.*, 2018). This trait-environment approach successfully allowed  
65 understanding the main abiotic drivers of functional traits (Maire *et al.*, 2015), predicting  
66 species turn-over across ecosystems (Shipley, 2010; Maire *et al.*, 2012), and revealing the  
67 variation of principal biotic mechanisms in play in different ecosystems characterized by  
68 contrasted abiotic conditions (Hulshof *et al.*, 2013; Berdugo *et al.*, 2018). Because filtering  
69 acts on individuals, it remains unclear if the information carried by community level traits  
70 is sufficient to understand the constraints driving trait assembly, especially within  
71 ecosystems where abiotic gradients might not be sufficient to exceed species tolerance.

72       Within ecosystem, local biotic constraints (e.g., intra- and inter-specific competition,  
73 facilitation, enemy-release) also shape the direction and intensity of filtering. At this scale,  
74 the relative importance of abiotic filtering likely decreases in comparison with biotic  
75 filtering (Chalmandrier *et al.*, 2017). Directionality may occur when relative fitness  
76 advantage of species vary, displacing the community trait mean toward the most

77 competitive strategy in case of competitive hierarchy (Kunstler *et al.*, 2012), or toward the  
78 center of a multimodal distribution when different equivalent strategies coexist (Le  
79 Bagousse-Pinguet *et al.*, 2016). Filtering intensity will decrease when the dispersion of trait  
80 values is increased by competitive exclusion (Mayfield & Levine, 2010), or by limit-to-  
81 similarity process forcing plants to exploit different strategies to balance intra- and inter-  
82 specific competition (Grime, 2006; Gross *et al.*, 2013). To study the response of  
83 directionality and intensity to the strength of biotic filtering, one would require an  
84 environmental gradient that is methodologically feasible, biologically sound and  
85 independent from other environmental gradients. Rarely these considerations have  
86 however been applied to study environmental selection in natural ecosystems.

87 For a given community trait distribution, filtering may still operate at the species  
88 level. Both directionality and intensity of filtering may be used to describe the niche of  
89 species (Austin & Smith, 1989). Individuals of different populations may tend to exhibit  
90 different mean trait values depending upon the competitive advantage it provides (Weiner  
91 & Thomas, 1986). The dispersion of species traits may be contracted, when individuals  
92 tend to exploit the same specialized resources and limit overlap with neighbors (Violle *et al.*  
93 *et al.*, 2012; Hulshof *et al.*, 2013; Meilhac *et al.*, 2019), or dilated when neighbors vary in  
94 strategies, potentially avoiding competition between very similar conspecific or to limit  
95 between species differences in fitness (Le Bagousse-Pinguet *et al.*, 2014).

96 Such changes in species trait distribution may have two demographic consequences,  
97 as described by Richards *et al.* 2006. *Jack-of-all-trade* strategists described species that  
98 exploit their intra-specific variations to maintain their demography through contrasted  
99 environmental constraints. Such species will be as dense when dominating a community  
100 as when coexisting in diverse ones. *Master-of-some* strategists would instead take  
101 advantage of more favorable environment to dominate and maintain higher demographic  
102 rates, and will be denser in dominated communities than in more diverse ones. While it has  
103 already been demonstrated that accounting for intraspecific trait variation allowed to detect  
104 community level patterns potentially linked to biotic interactions (Siefert *et al.*, 2015;  
105 Chalmandrier *et al.*, 2017), few studies explored the way intra-specific variation might  
106 shape community functional structure.

107 Directionality and intensity needs to be studied on multiple traits that describe ability  
108 of individual to cope with changes to environmental (biotic and abiotic) constraints. It has  
109 been shown that variation of distinct traits takes place at different levels of biological  
110 organization (de Bello *et al.*, 2013; Siefert *et al.*, 2014), and that uncorrelated sets of  
111 functional traits rely to different resources and filtering processes (Maire *et al.* 2012, Maire  
112 *et al.* 2009, Pontes *et al.* 2015). Indeed, the multidimensionality of their ecological niches  
113 allows individuals to be adapted to multiple environmental constraints (Cornwell *et al.*,  
114 2006). To better understand species selection within communities, we need therefore to  
115 select a set of traits representing the different functional niche dimensions of individuals.

116 To explore consequences of successive abiotic and biotic filters on species  
117 assemblages, we designed an original hierarchical approach that disentangles  
118 consequences of filtering at the species, community and ecosystem levels. We first selected  
119 wetland ecosystems characterized by highly contrasted site pH, but within the same  
120 climatic envelope. Within each ecosystem, we selected natural communities along a  
121 species diversity gradient, from mono-dominated to highly diverse communities, which  
122 minimized for differences in abiotic conditions (Rheault *et al.*, 2015). Because diversity  
123 gradient is known as the result of different modalities of species interactions (Chesson,  
124 2000; Levine & HilleRisLambers, 2009) and resource partitioning (Tilman *et al.*, 1997b),  
125 and is consequently thought as an important driver of ecosystem functioning (Tilman *et al.*  
126 *et al.*, 1997a), we choose it to describe potential variations in biotic filtering. Plant ramets  
127 were sampled irrespective of their taxonomic identity to both study the community  
128 distribution and capture the role of phenotypic variation in the local selection processes.  
129 We formulated models with explicit parameters for mean and dispersion of community and  
130 species distribution of key functional traits known to be related to nutrient immobilization  
131 and light acquisition and processing. Accounting for differences between ecosystems, we  
132 tested through modeling of community trait distribution (1) where biotic filtering could be  
133 more accurately detected: community or species level, or said differently, what is the role  
134 of intra-specific variation in fine-scale community assembly; (2) if the response is trait-  
135 dependent; and (3) if species exhibited contrasted growth strategies in response to biotic  
136 filtering, linking functional trait responses to population fitness variation. Along the pH  
137 gradient, we assumed that traits linked with nutritive stress response (e.g. LDMC, SLA)

138 would follow a directional filtering at community level, displacing community mean and  
139 dispersion. In contrast, along the diversity gradient at species level, we expect traits linked  
140 with competitive ability for light capture and space occupation strategy (e.g. LA, EL) to  
141 respond stronger than other traits.

## 142 **Material and Methods**

### 143 *Study sites*

144 In the lowland of the Fleuve St-Laurent in Eastern Canada, a diversity gradient of eight  
145 communities were replicated in four highly contrasted wetland ecosystems (total number  
146 of communities = 31, with only seven plots sampled in the wet meadow). Every ecosystem  
147 was situated in the same climatic envelope (mean annual temperature = 5.4°C, mean annual  
148 precipitation = 1030.5mm, mean length growing season = 112 days) and within an acidic  
149 regional context due to the proximity to the granitic Canadian shield. These ecosystems are  
150 ranked along a fertility gradient (soil pH as proxy, Fig. S1a), and characterized as bog (Lac-  
151 à-la-Tortue, 46°33'15"N 72°39'46"W), fen (Red-Mill, 46°25'38.9"N 72°29'46.6"W), wet  
152 meadow (SCIRBI, conservation society, 46°04'12.9"N 73°10'11.1"W) and fluvial marsh  
153 (Maskinonge, 46°11'39.1"N 72°59'58.7"W). Within each site, we selected communities of  
154 similar area to build a species richness gradient. The gradient ranged from two species to  
155 highly diverse community (up to 16 species, Fig. S1b) and were of comparable range  
156 between sites (Fig. S1b). Importantly, there was no relationship between soil pH nor ramets  
157 density and species diversity of communities within and among ecosystems (Fig. S1c and  
158 d), and the design has been thought to minimize abiotic differences within ecosystems  
159 (Rheault et al. 2015).

### 160 *Vegetation sampling*

161 Within each community, we sampled 80 individuals, irrespective of their taxonomic  
162 characteristics, with at least two mature leaves and during two sampling campaigns (from  
163 the 14<sup>th</sup> of June to the 5<sup>th</sup> of July and from the 22<sup>th</sup> of August to the 3<sup>rd</sup> of September  
164 2016). The method of point-plant distance sampling was used and simultaneously realized  
165 by two independent harvesters, each one directed by successive random bearings and  
166 distances. When approaching from the edge of the community, the harvester bounced with  
167 an angle of 45° toward the plot. At the point determined by those indications, the closest  
168 mature plant was harvested, and its distance to the point measured. Plant density within  
169 communities were computed using the following equation, where  $dens_p$  is the density in

170 individuals/m<sup>2</sup> of plot  $p$ ,  $n$  the number of individuals harvested in the plot, and  $d_{pi}$  the  
171 distance, in cm, between the point and the individual  $i$  of plot  $p$ :

$$172 \quad dens_p = \frac{1}{10000} \frac{\sum_{i=1}^n d_{pi}^2}{n}$$

### 173 *Trait measurements*

174 We selected a set of plant functional traits that are linked to different biological functions  
175 and covary along different dimensions of the species niche (Fig. S2). Leaf Area (LA) and  
176 Extended Length (EL) and leaf angle are linked to the space occupation strategies that are  
177 used to compete for light interception (Hikosaka & Hirose 1997, Weiner & Thomas 1986),  
178 while superficial chlorophyll content represents the fine scale adaptation to optimize light  
179 utilization by the leaf (Kull & Niinemets 1998). All these traits are also components of the  
180 leaf energy balance that regulates leaf temperature and biochemical processes. Leaf dry  
181 matter content (LDMC) and flavonoid content are related to nutrient conservation,  
182 involved in response to stress and/or herbivory (Hodgson *et al.* 2011, Izaguirre *et al.* 2007).  
183 Specific Leaf Area (SLA) directly scales with the relative growth rate of individuals in  
184 herbaceous ecosystems (Garnier *et al.*, 2004; Poorter *et al.*, 2012). LA, LDMC and SLA  
185 were measured following the protocols described in (Pérez-Harguindeguy *et al.*, 2013), on  
186 the last mature leaf of plants. EL is the length of individuals from the ground to the edge  
187 of their deployed leaves, in cm. Superficial chlorophyll content is the concentration of  
188 chlorophyll in the leaf epidermis ( $\mu\text{g cm}^{-2}$ ), and flavonoid content is an index of flavonoids  
189 concentration in this superficial layer, which is related to phenol accumulation and UV  
190 protection. Both were measured using a portable Dualex device (Force-A, Orsay, France),  
191 which uses a combination of fluorescence signals at various excitation band to quantify  
192 pigments and chemical compounds. This method have been successfully used to follow the  
193 phenology of leaf and individuals (Mattila *et al.*, 2018), as the response of leaf metabolism  
194 to nutrients (Scogings, 2018) or light manipulation (Agati *et al.*, 2011). The relationships  
195 between superficial chlorophyll content and total chlorophyll extracted with methanol are  
196 presented by Fig. S3.

197 *Data analysis*

198 Our aim is to explain how plant trait varies along environmental gradients and test if the  
199 variation of the mean and dispersion of trait values observed at community and species  
200 levels is related to differences in the number of species present in the community. We  
201 explored this principle across a series of traits to evaluate if the filtering has differently  
202 acted on traits.

203 The bayesian distributional modeling framework has been used to model the  
204 community and species trait distribution (Rigby & Stasinopoulos, 2005). This framework  
205 allows modeling each parameter of a given probability trait distribution by an independent  
206 equation, thus relaxing the fixed dispersion assumption classically stated in the GLM  
207 framework (Smyth, 1989; Cepeda-Cuervo, 2015). We modeled the distribution of traits at  
208 the community and the species level with two parameters distributions. *Gamma*  
209 distribution parameterized in terms of mean ( $\mu$ ) and dispersion ( $\phi$ ) have been used to model  
210 traits with strictly positive distribution (all but LDMC). As being distributed on [0,1]  
211 interval, LDMC has been modeled as a *beta* distribution parameterized by the mean ( $\mu$ )  
212 and precision ( $\phi$ ) (detailed equations in appendix A). Importantly, the statistical dispersion  
213 defined in this statistical framework is not spuriously linked to the number of species in  
214 community, as explained in Appendix A.

215 Posterior distributions of parameters have been sampled by four independent chains  
216 using the *No-U-Turn Sampler* implemented in *stan* through the *R* package *brms* (Bürkner,  
217 2017). Careful attention has been paid to built-in diagnostics to avoid divergent iterations  
218 and ensure chains convergence. Then, every chain and every posterior distribution have  
219 been checked visually, and visual posterior-predictive checks have been performed to  
220 ensure that models captured features of the data (Appendix A).

221 Models have been compared by the mean of weights based on the stacking of  
222 predictive distribution. With this method related to Bayesian model averaging, model  
223 weights were estimated to maximize leave-one-out predictive density of a complete model  
224 containing all sub-models (Yao *et al.*, 2017). The higher the weight of a model was, better  
225 were the predictions of future data. It represents one of the less biased and less sensible to

226 overfitting method in Bayesian model selection, and includes uncertainty about every  
227 model during weights computation (Yao *et al.*, 2017).

228 To explore the directionality and intensity of filtering at the community level along  
229 the diversity gradient, we used all available data ( $n = 2480$ ). The most complex model  
230 (M3d) describing the distribution from which the trait value of the  $i$ th individual,  $y_i$ , is  
231 drawn, was written as follows:

$$232 \quad y_i \sim f(\mu_i, \phi_i)$$
$$233 \quad g_1(\mu_i) = \beta_0 + \beta_{C2} + \beta_{Ee} + \beta_{Pp} + \beta_{1Ee}D_p$$
$$234 \quad g_2(\phi_i) = \gamma_0 + \gamma_{C2} + \gamma_{Ee} + \gamma_{Pp} + \gamma_{1Ee}D_p$$

235  $f()$  is a probability distribution parameterized in term of  $\mu$  and  $\phi$ , while  $g1()$  and  $g2()$   
236 are link functions.  $\beta_0$  and  $\gamma_0$  are intercepts for the first sampling campaign, while  $\beta_{C2}$  and  
237  $\gamma_{C2}$  are the deviations for the second sampling campaign for the mean and the dispersion of  
238 the distribution, respectively.  $\beta_{Ee}$  and  $\beta_{Pp}$  are deviation parameters describing how the mean  
239 of each ecosystem  $e$  and plot  $p$  differ from the overall mean of each campaign.  $\gamma_{Ee}$  and  $\gamma_{Pp}$   
240 are intercepts describing the differences of dispersion.  $\beta_{Pp}$  and  $\gamma_{Pp}$  are treated as hierarchical  
241 parameters, normally distributed with estimated variances.  $\beta_{1Ee}$  and  $\gamma_{1Ee}$  are the ecosystem-  
242 specific slopes describing the effect of an increase of one species (D standing for species  
243 richness) on the mean and dispersion of community trait distribution, respectively.

244 To describe the consequences of a variation in species diversity on community trait  
245 distribution, we put four models in competition. The reference model, Mcom0, described  
246 trait distributions of each plot as a series of intercepts. Mcom1 included a slope per  
247 ecosystem describing the link between species diversity and the mean of the community  
248 trait distribution, while Mcom2 included a slope linking species diversity to trait  
249 dispersion. Mcom3 included both slopes, assuming that biotic filtering exhibited both  
250 directionality and varying intensity.

251 To explore the importance of within species filtering to cope with within ecosystem  
252 diversity gradient, we refitted Mcom3 by replacing observed values by mean species value  
253 (Mcom3'), estimated from a model containing an intercept for each campaign and a

254 hierarchical intercept per species, distributed normally with estimated standard deviation.  
255 By removing intra-specific variation, we aim to create a model with parameters estimated  
256 as if the response of community trait distributions were only due to abundance variation.  
257 We then evaluate the predictive ability of these model by using observed data. That way,  
258 if the predictive ability of this model is lower than models containing ITV, it would mean  
259 that abundance variation is not able to capture the process underlying within ecosystems  
260 variation in trait distributions.

261 To analyze consequences of the number of species in community on species trait  
262 distribution, we used a subset of data, containing only the individuals of 11 species ( $n =$   
263  $1045$ ). To be selected, these species had to be dominant when they occurred in poorly  
264 diverse plots and growing in communities along the entire diversity gradient of their  
265 ecosystem. The most complex model determined both niche mean and dispersion as a  
266 function of intercepts and diversity, with equations for  $\mu$  and  $\phi$ :

$$267 \quad y_i \sim f(\mu_i, \phi_i)$$
$$268 \quad g_1(\mu_i) = \beta_0 + \beta_{C2} + \beta_{Ee} + \beta_{Pp} + \beta_{Ss} + \beta_{1Ss}diversity_p$$
$$269 \quad g_2(\phi_i) = \gamma_0 + \gamma_{C2} + \gamma_{Ee} + \gamma_{Pp} + \gamma_{Ss} + \gamma_{1Ss}diversity_p$$

270 With  $\beta_{Ss}$  and  $\gamma_{Ss}$  being species-specific deviation parameters for mean and dispersion,  
271 and  $\beta_{1Ss}$  and  $\gamma_{1Ss}$  species-specific slopes between species richness and mean and dispersion,  
272 respectively. They are all hierarchical parameters distributed multinormally with estimated  
273 covariance matrix.

274 The reference model, Msp0, contained only the series of intercepts, while Msp1  
275 contained a slope per ecosystem linking both species mean and dispersion to species  
276 richness. Msp2 included a slope per ecosystem for dispersion, but a slope per species  
277 linking diversity to species mean trait value. The more complex model, Msp3, allowed  
278 mean and dispersion of each species to move idiosyncratically with the number of species  
279 with which they grow.

280 To explore the strategies of species to cope with variation in biotic conditions, and  
281 their potential impact on fitness, we summarized for each species the traits and the density  
282 responses. Given the importance of vegetative reproduction in wetlands, we considered  
283 density as a good proxy of species demographic performance (7.9% of our individuals were  
284 harvested with flower or fruits). To explore responses of species relative density along the  
285 diversity gradient, we estimated a hierarchical model including a series of intercepts for  
286 campaigns, ecosystems and species identity, and a slope per species linking taxonomic  
287 diversity of each plot to the relative density of the species of interest. Species intercepts  
288 and slopes were distributed multinormally with estimated covariance matrix. Adapting the  
289 framework presented by (Richards *et al.*, 2006), we considered a dominant species with  
290 high density in poor communities and low density in rich communities as exhibiting a  
291 “master of some” strategy, with plasticity used to take overwhelming advantage when in  
292 favorable conditions. A plastic species maintaining its density equal all along the diversity  
293 gradient was considered as a “jack-of-all-trades” strategist, potentially using plasticity to  
294 cope accurately with multiple conditions.

## 295 **Results**

### 296 *Importance of ITV in community responses*

297 *While filtering among ecosystems sorted species to produce an almost complete turnover,*  
298 *filtering of individuals within species were the principal mechanism along the diversity*  
299 *gradient. Both mean and dispersion of traits distribution varied among ecosystems for*  
300 *every trait but LDMC, with the best models being the one containing intercept for each*  
301 *ecosystem for both aspects of trait distribution (Figs. 1a, 1b, Tab. S1). Within ecosystems,*  
302 *estimating the response of community distributions while using species mean instead of*  
303 *observed values always produced worst predictions than estimating community responses*

304 *including ITV (Table 1, max weight of  $Mcom3' = 0.04$ ). Community level response to the*  
305 *environmental gradient among ecosystems*

306 While mean and dispersion of traits related to space filling and light acquisition (EL, LA  
307 and SLA) increased monotonically along the pH gradient, the mean of traits related to  
308 nutrient conservation (LDMC and flavonoids) decreased in ecosystems with higher pH  
309 (Fig. 1, Fig. S4). Dispersion of flavonoid values increased along the pH gradient, while  
310 model including a varying dispersion of LDMC distributions among ecosystems was not  
311 better than the one with varying means only. Leaf angle and chlorophyll content both varied  
312 in mean and dispersion between ecosystems, but without ordered pattern along the pH  
313 gradient (Fig. S4).

314 *Community level response to the plant diversity gradient within ecosystems*

315 We detected community level responses to diversity for both mean and dispersion for  
316 functional traits in every aspect of plant strategies (Fig. 2). Light interception traits (EL  
317 and LA), SLA, leaf angle and nutrient conservation traits (LDMC and flavonoids content)  
318 were all best predicted by modelling mean and dispersion (Tab. 1). Chlorophyll was best  
319 predicted by modelling only the mean parameter (Tab. 1).

320 Community functional distributions followed both general and system specific  
321 responses. Mean of traits related to space and fine scale light utilization responded in every  
322 ecosystem but the wet meadow, suggesting that the number of species in communities  
323 imply a directional filtering toward particular values. Both mean and diversity of SLA  
324 increased with species richness in every ecosystem, suggesting a great importance of fine  
325 scale light conditions and growth trade-offs (Tab. 2, Figs. 2b, S6). In the harshest  
326 ecosystems, the bog and the fen, plants were taller in more diverse communities, but with  
327 lower LA, while having more dispersed trait values on both traits (Figs. 2a, S4, S5).  
328 Interestingly, their leaves presented less chlorophyll per surface, while being also more  
329 variable (Fig. S7). LDMC and flavonoids distributions were more variable in more diverse  
330 communities only in these ecosystems, suggesting that assemblage of more diverse  
331 communities filtered for different strategies of nutrient conservation (Figs. 2c, S9). In the  
332 wet meadow, only SLA responded to the diversity gradient, suggesting a lower importance

333 of space, light and nutrient acquisition (Fig. S6). In the fluvial marsh, plants were both  
334 smaller and with smaller leaves in more diverse communities, but also more variable (Figs.  
335 2b, S4, S5). Richer communities presented also more variable chlorophyll content and leaf  
336 angle distribution, suggesting canopy partitioning and adjustment to fine scale light  
337 conditions.

### 338 *Species level response to the plant diversity gradient within ecosystems*

339 We detected in every ecosystem two contrasted species responses to the diversity gradient.  
340 The first, “Jack-of-all-trade” strategy consisted in species with fixed or slightly increasing  
341 median relative density all along the diversity gradient, but with deformed trait  
342 distributions (Fig. 3, left part of the panel). This deformation occurred both on mean and  
343 dispersion of light and space acquisition related traits, with the best out-of-sample  
344 predictions of EL, LA and SLA provided by the model with species-specific slopes within  
345 each ecosystem (Tab. 1). For example, *Typha latifolia* exhibited lower and less variable  
346 LA in richer fluvial marsh communities, with a median leaf measuring 73.9 ( $\pm 45.4$ ) cm<sup>2</sup>  
347 when growing with 2 species and 56.8 ( $\pm 30.1$ ) cm<sup>2</sup> when growing with 14 species (Fig. 3).  
348 However, in the wet meadow, *Lythrum salicaria* trait mean and dispersion and density  
349 remained unchanged along the diversity gradient. Conversely, “Master of some” strategies  
350 were detected when dominant species were highly dense in taxonomically poor  
351 communities, but were less dense in richer communities. Species showing density response  
352 may or may not have been plastic responses depending on the trait but tended to present  
353 more dispersed trait distribution. For example, in the fen, there was in average 640 ( $\pm 70$ )  
354 *Carex oligosperma* individuals per m<sup>2</sup> in 5 species communities, and 66 ( $\pm 4.4$ ) individuals  
355 in 14 species communities. Interestingly, *C. oligosperma* LA, SLA, LDMC and leaf angles  
356 were more variables in richer communities, while chlorophyll was less variable. It is worth  
357 noting LDMC and chlorophyll species dispersion were best predicted by a common slope  
358 shared by species within each ecosystem (tab. 1).

### 359 **Discussion**

360 We detected change to the distribution of functional traits, in both direction and intensity,  
361 along a gradient of plant diversity replicated in four highly contrasted ecosystems filtering

362 for different trait distributions. Such biotic filtering structured trait variation at the  
363 community and species levels on respective dimensions of plant strategy. Our study reveals  
364 that multiple mechanisms detectable at different levels of biological organization are  
365 concomitantly at play to shape the distribution of traits along environmental gradients. This  
366 echoes recent studies showing that the drivers of trait variations may not be the same while  
367 looking within and between species(e.g. Anderegg et al. 2018), or while sampling at  
368 different spatial scales (Messier *et al.* 2016). However, our study is the first one to structure  
369 the different levels of trait variation within a common statistical framework and to show  
370 *in-natura* that the within-species variation can be strongly structured by biotic interactions.

371 Our results revealed two sets of traits each responding at a specific level of biological  
372 organisation: across ecosystems, every trait was better predicted by including ecosystems  
373 identity for mean and dispersion, some of them showing directional and intense filtering in  
374 line along the soil fertility gradient. Mean traits related to space occupation (EL, LA) and  
375 to nutrient acquisition (LDMC and flavonoids content) increased and decrease from less to  
376 more fertile ecosystems, respectively. Selection intensity showed an opposite pattern, trait  
377 dispersion of EL, LA and flavonoid increasing. Dispersion of LDMC tended to decrease in  
378 more fertile ecosystems (Fig S4), but this was not supported by model selection. These  
379 results are coherent with known functional trade-off between nutrient conservation and  
380 growth along fertility gradients (Jager *et al.*, 2015), along which plants selected in the more  
381 fertile ecosystems are the ones with the lowest investment in leaf longevity but with the  
382 greatest ability to compete for space (Grime, 1977; Wright *et al.*, 2004). On the contrary,  
383 while an almost complete turnover of species drove differences between ecosystems, SLA  
384 and fine-scale light acquisition traits (chlorophyll content, leaf angle) did not show clear  
385 patterns across ecosystems. Within ecosystem, filtering along the species diversity gradient  
386 selected individuals from a common species pool particular to each ecosystem. Filtering  
387 intensity was observed with an increase of the dispersion of trait values for traits related to  
388 every functional axis. Within species, filtering intensity was particularly associated with  
389 EL, LA and SLA, only. This suggests that biotic interactions have particularly constrained  
390 species to deform their niches within their phenotypic plasticity to adapt to changes in  
391 space and/or light resources.

392 Communities' trait distribution revealed both filtering directionality and intensity  
393 along the diversity gradient (Table 2). Both in nutrient-poor and in nutrient-rich  
394 ecosystems, less diverse communities exhibited mean leaves with less area per gram than  
395 in less diverse ones. This reveals that individuals exhibited more long-life, robust and  
396 uniform leaves when neighbors were conspecific. Most of the time, these individuals were  
397 graminoid-like species with self-supported great leaves (e.g. *Typha* in nutrient rich  
398 ecosystem, *Eriophorum* and *Carex* in nutrient-poor ecosystem). With increasing species  
399 diversity, individuals were, on average, longer and exhibited, smaller and lower  
400 chlorophyll-investment leaves, and were especially characterized by more heterogeneous  
401 leaves when neighbors are heterospecific. Such trait response likely resulted from trade-  
402 offs in resource allocation to adapt to light conditions: light capture (high SLA, low  
403 chlorophyll) vs light use (opposite syndrome). This is well-known that competition for  
404 light structures plant communities in nutrient-rich environments but this has rarely been  
405 highlighted in resource-poor environments (but see Wiktor and Diggelen 2004). While  
406 responding mainly to the abiotic gradient across ecosystems, LDMC showed also a biotic  
407 filtering which was more intense in less diverse communities, particularly in acidic  
408 ecosystems. While the statistical dispersion of LDMC values increased with diversity in  
409 more acidic ecosystems, the mean remained stable. This suggest that a limit-to-similarity  
410 process takes place in these ecosystems relatively to the way nutrients are conserved,  
411 coexistence in diverse communities being based upon a long-term partitioning of soil  
412 resources (McKane *et al.*, 2002; Gubsch *et al.*, 2011), with a non-detectable selection for a  
413 value conferring disproportional fitness advantage.

414 At species level, functional responses to diversity went through the adjustment of  
415 both the mean and the dispersion of their trait values. Importantly, we show that  
416 idiosyncratic behaviors characterised the species level compared with the community level.  
417 These strong responses allow stating that intra-specific variation was a major specific  
418 characteristic to deal with biotic constraints. We showed that more important than the  
419 extent of this variation in a community, the ability of species to exploit different regions of  
420 the functional space is fundamental to allow coexistence. Species particularly adjusted their  
421 space and light related trait distributions, suggesting that their position in the canopy or  
422 their light interception are strongly related to the number of species with which they grow.

423 In our study, we showed that dominant species might simultaneously present two strategies  
424 when growing with a different number of species. The first one is exemplified by *Acorus*  
425 *calamus* individuals which had far more similar LA and EL when dominant than when  
426 coexisting with 16 species, and this in two different ecosystems. At the contrary, *Typha*  
427 *latifolia*, which can also form almost monospecific stands and coexists with *A. calamus* in  
428 the more diverse communities, is both smaller and less diverse when growing with a higher  
429 number of species.

430 To understand the co-occurrence of both increasing and decreasing dispersion of  
431 dominant species trait distribution along the diversity gradient, we turn our attention on  
432 coexistence theories considering demography of coexisting species. Commonly, an  
433 adjustment of species distributions is expected to limit a species similarity with potential  
434 competitors (decreasing dispersion and overlap, Grime 2006, Violle et al. 2012), or to  
435 equalize fitness differences by presenting an especially adapted phenotype, with each  
436 species exploiting equally the same resources (increasing dispersion and overlap, Le  
437 Bagousse-Pinguet et al. 2014). On the other side, phenotypic plasticity globally decreases  
438 the likelihood of long term coexistence by decreasing species-level differentiation and  
439 favoring abundant competitors (Hart *et al.*, 2016). Based on our results, we argue that  
440 instead of being a signature of a given environment, these two processes act simultaneously  
441 in communities, but with different consequences depending upon the demographic strategy  
442 of coexisting species. This is coherent with population level frameworks concerning the  
443 role of phenotypic plasticity. Richards et al. (2006) described a framework opposing  
444 “Master of some” species vs. “Jack-of-all-trades” ones. The formers are able to maintain  
445 demographic rates across various environmental conditions, while the later used their intra-  
446 specific variation to take a disproportional advantage when in a favorable environment.  
447 Aggregating the signature of these two strategies in community-level indices, for example  
448 by using averaged trait overlap, might avoid detecting the underlying mechanisms of  
449 community assemblage. The averaging of contrasted patterns might lead to unclear or even  
450 flat patterns of trait variations, and would decrease our ability to understand how  
451 individuals are selected in communities, especially if one does not take demography into  
452 account. Our multi-level approach was able to detect both Master-of-Some and Jack-of-

453 all-trades demographic strategies and that these strategies co-occurred within a given  
454 community and in all ecosystems.

455         Showing the importance of intraspecific variation to cope with biotic environment  
456 and its relation to demographic strategies, we highlight the potential evolutionary  
457 perspective of individual filtering during community assembly, and the need to bring  
458 concepts of community and population ecology closer. Hennion et al. (2016) showed that  
459 biotic filtering, represented as species diversity, was able to persistently alter the amine  
460 metabolic profile of a grassland species. Waterway et al. (2016) demonstrated that  
461 competitive interactions have driven the historical diversification of coexisting sedge  
462 species in fens. While it is regularly argued that the filtering of individuals within  
463 community is of evolutionary importance (Post & Palkovacs, 2009), the joint study of  
464 population and community levels are rarely crossbred in community and functional  
465 ecology (Salguero-Gómez *et al.*, 2018). Here, we show that using a hierarchical approach  
466 along an abiotic and an independent biotic gradient, we were able to better understand how  
467 traits varied across scales. Filtering directionality and intensity occurred at each level of  
468 biological organization but on different dimensions of plant functional strategy: nutrient-  
469 acquisition / conservation trade-off across ecosystems, light-acquisition / utilization trade-  
470 off across communities, space positioning across species. Filtering intensity was a strong  
471 structuring factor across all levels and should be better considered separately at each of  
472 these levels rather than considered as a ratio (Violle *et al.*, 2012). It is worth noting that  
473 statistical dispersion used to detect filtering intensity is preserved from spurious sampling  
474 effect related to the number of species in communities. Appendix C demonstrates that the  
475 mean deviation around the mean does not increase systematically with the number of  
476 species but becomes more accurately estimated. In summary, disentangling biological  
477 organisation levels and considering a rich set of traits representing different niche  
478 dimensions, allowed revealing the simultaneous selection pressures acting on individuals.  
479 By focusing on individuals, we were able to link within ecosystem population trait  
480 dynamics to two contrasted demographic strategies, highlighting the particular importance  
481 of intra specific trait variation for community assembly, and the potential evolutionary  
482 consequences of fine scale biotic gradients.

483 **Acknowledgements**

484 We thank Caroline Beaulieu, Ariane Bisson, Antoine Filion, Hugo Germain, Benjamin  
485 Gosselin, Annie Picard, Mélodie Plourde, Alexandre Proulx, Joannie Vertefeuille for their  
486 technical help during site sampling and laboratory analyses. We thank Marco Rodriguez  
487 for his help on statistical analyses and Fernando Maestre for his input. This study was  
488 supported by the Natural Sciences and Engineering Research Council of Canada (NSERC-  
489 Discovery-2016-05716 and NSERC-Discovery-2016).

490 **Authors contribution**

491

492

493 **References**

- 494 **Agati G, Cerovic ZG, Pinelli P, Tattini M. 2011.** Light-induced accumulation of ortho-  
495 dihydroxylated flavonoids as non-destructively monitored by chlorophyll fluorescence  
496 excitation techniques. *Environmental and Experimental Botany* **73**: 3–9.
- 497 **Anderegg LDL, Berner LT, Badgley G, Sethi ML, Law BE, HilleRisLambers J.**  
498 **2018.** Within-species patterns challenge our understanding of the leaf economics  
499 spectrum. *Ecology Letters* **21**: 734–744.
- 500 **Austin MP, Smith TM. 1989.** A new model for the continuum concept. *Vegetatio* **83**:  
501 35–47.
- 502 **Le Bagousse-Pinguet Y, De Bello F, Vandewalle M, Leps J, Sykes MT. 2014.** Species  
503 richness of limestone grasslands increases with trait overlap: Evidence from within- and  
504 between-species functional diversity partitioning. *Journal of Ecology* **102**: 466–474.
- 505 **Le Bagousse-Pinguet Y, Gross N, Maestre FT, Maire V, Bello F de, Fonseca CR,**  
506 **Kattge J, Valencia E, Leps J, Liancourt P. 2016.** Testing the environmental filtering  
507 concept in global drylands. *Journal of Ecology*.
- 508 **de Bello F, Lavorel S, Lavergne S, Albert CH, Boulangeat I, Mazel F, Thuiller W.**  
509 **2013.** Hierarchical effects of environmental filters on the functional structure of plant  
510 communities: A case study in the French Alps. *Ecography* **36**: 393–402.
- 511 **De Bello F, Price JN, Münkemuüller T, Liira J, Zobel M, Thuiller W, Gerhold P,**  
512 **Götzenberger L, Lavergne S, Leps J, et al. 2012.** Functional species pool framework to  
513 test for biotic effects on community assembly Functional species pool framework to test  
514 for biotic effects on community assembly. *Ecology* **93**: 2263–2273.
- 515 **Berdugo M, Maestre FT, Kéfi S, Gross N, Le Bagousse-Pinguet Y, Soliveres S. 2018.**  
516 Aridity preferences alter the relative importance of abiotic and biotic drivers on plant  
517 species abundance in global drylands. *Journal of Ecology*: 1–13.
- 518 **Bjorkman A, H. Myers-Smith I, C. Elmendorf S, Normand S, Rüger N, Beck P,**  
519 **Blach-Overgaard A, Blok D, Hans C. Cornelissen J, C. Forbes B, et al. 2018.** Plant  
520 functional trait change across a warming tundra biome. *Nature* **562**.

- 521 **Bürkner P-C. 2017.** brms: An R Package for Bayesian Multilevel Models Using Stan.  
522 *Journal of Statistical Software* **80**: 1–28.
- 523 **Cepeda-Cuervo E. 2015.** Beta regression models: Joint mean and variance modeling.  
524 *Journal of Statistical Theory and Practice* **9**: 134–145.
- 525 **Chalmandrier L, Münkemüller T, Colace MP, Renaud J, Aubert S, Carlson BZ,**  
526 **Clément JC, Legay N, Pellet G, Saillard A, et al. 2017.** Spatial scale and intraspecific  
527 trait variability mediate assembly rules in alpine grasslands. *Journal of Ecology* **105**:  
528 277–287.
- 529 **Chesson P. 2000.** Mechanisms of Maintenance of Species Diversity. *Annual Review of*  
530 *Ecology and Systematics* **31**: 343–66.
- 531 **Cornwell WK, Schwilk DW, Ackerly DD. 2006.** A trait-based test for habitat filtering:  
532 Convex hull volume. *Ecology* **87**: 1465–1471.
- 533 **Garnier E, Cortez J, Billès G, Navas M-L, Roumet C, Debussche M, Laurent G,**  
534 **Blanchard A, Aubry D, Bellmann A, et al. 2004.** Plant functional markers capture  
535 ecosystem properties during secondary succession. *Ecology* **85**: 2630–2637.
- 536 **Grime JP. 1977.** Evidence for the Existence of Three Primary Strategies in Plants and Its  
537 Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169–  
538 1194.
- 539 **Grime JP. 2006.** Trait convergence and trait divergence in herbaceous plant  
540 communities: Mechanisms and consequences. *Journal of Vegetation Science* **17**: 255–  
541 260.
- 542 **Gross N, Börger L, Duncan RP, Hulme PE. 2013.** Functional differences between alien  
543 and native species: Do biotic interactions determine the functional structure of highly  
544 invaded grasslands? *Functional Ecology* **27**: 1262–1272.
- 545 **Gubsch M, Roscher C, Gleixner G, Habekost M, Lipowsky A, Schmid B, Schulze**  
546 **ED, Steinbeiss S, Buchmann N. 2011.** Foliar and soil  $\delta^{15}\text{N}$  values reveal increased  
547 nitrogen partitioning among species in diverse grassland communities. *Plant, Cell and*  
548 *Environment* **34**: 895–908.

- 549 **Hart SP, Schreiber SJ, Levine JM, Coulson T. 2016.** How variation between  
550 individuals affects species coexistence. *Ecology Letters* **19**: 825–838.
- 551 **HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012.**  
552 Rethinking Community Assembly through the Lens of Coexistence Theory. *Annu. Rev.*  
553 *Ecol. Evol. Syst* **43**: 227–48.
- 554 **Hulshof CM, Violle C, Spasojevic MJ, McGill B, Damschen E, Harrison S, Enquist**  
555 **BJ. 2013.** Intra-specific and inter-specific variation in specific leaf area reveal the  
556 importance of abiotic and biotic drivers of species diversity across elevation and latitude.  
557 *Journal of Vegetation Science* **24**: 921–931.
- 558 **Jager MM, Richardson SJ, Bellingham PJ, Clearwater MJ, Laughlin DC. 2015.** Soil  
559 fertility induces coordinated responses of multiple independent functional traits. *Journal*  
560 *of Ecology* **103**: 374–385.
- 561 **Kunstler G, Lavergne S, Courbaud B, Thuiller W, Vieilledent G, Zimmermann NE,**  
562 **Kattge J, Coomes DA. 2012.** Competitive interactions between forest trees are driven by  
563 species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest  
564 community assembly. *Ecology Letters* **15**: 831–840.
- 565 **Laughlin DC, Joshi C. 2015.** Theoretical consequences of trait-based environmental  
566 filtering for the breadth and shape of the niche: New testable hypotheses generated by the  
567 TraitSpace model. *Ecological Modelling* **307**: 10–21.
- 568 **Levine JM, HilleRisLambers J. 2009.** The importance of niches for the maintenance of  
569 species diversity. *Nature* **461**: 254–7.
- 570 **Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI. 2004.**  
571 Rethinking plant community theory Edited by Foxit Reader. *Oikos* **107**: 433–438.
- 572 **Maire V, Gross N, Börger L, Proulx R, Wirth C, Pontes LDS, Soussana JF, Louault**  
573 **F. 2012.** Habitat filtering and niche differentiation jointly explain species relative  
574 abundance within grassland communities along fertility and disturbance gradients. *New*  
575 *Phytologist* **196**: 497–509.
- 576 **Maire V, Wright IJ, Prentice IC, Batjes NH, Bhaskar R, van Bodegom PM,**  
577 **Cornwell WK, Ellsworth D, Niinemets Ü, Ordóñez A, et al. 2015.** Global effects of

- 578 soil and climate on leaf photosynthetic traits and rates. *Global Ecology and*  
579 *Biogeography* **24**: 706–717.
- 580 **Mattila H, Valev D, Havurinne V, Khorobrykh S, Virtanen O, Antinluoma M,**  
581 **Mishra KB, Tyystjärvi E. 2018.** Degradation of chlorophyll and synthesis of flavonols  
582 during autumn senescence—the story told by individual leaves. *AoB PLANTS* **10**: 1–13.
- 583 **Mayfield MM, Levine JM. 2010.** Opposing effects of competitive exclusion on the  
584 phylogenetic structure of communities. *Ecology Letters* **13**: 1085–1093.
- 585 **McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin**  
586 **AE, Kielland K, Kwiatkowski BL, Laundre JA, et al. 2002.** Resource-based niches  
587 provide a basis for plant species diversity and dominance in arctic tundra. *Nature* **415**:  
588 68–71.
- 589 **Meilhac J, L. D, V. M, S. F, I. L. 2019.** Both selection and plasticity drive temporal  
590 niche differentiation in experimental grasslands. *Nature Plants* **Accepted A**.
- 591 **Pérez-Harguindeguy N, Diaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P,**  
592 **Bret-Harte MSS, Cornwell WKK, Craine JMM, Gurvich DEE, et al. 2013.** New  
593 Handbook for standardized measurement of plant functional traits worldwide. *Australian*  
594 *Journal of Botany* **61**: 167–234.
- 595 **Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012.** Biomass  
596 allocation to leaves, stems and roots: Meta-analyses of interspecific variation and  
597 environmental control. *New Phytologist* **193**: 30–50.
- 598 **Post DM, Palkovacs EP. 2009.** Eco-evolutionary feedbacks in community and  
599 ecosystem ecology: Interactions between the ecological theatre and the evolutionary play.  
600 *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**: 1629–1640.
- 601 **Rheault G, Proulx R, Bonin L. 2015.** Plant species richness prolongs the growing  
602 season of freely assembled riparian herbaceous communities under dry climatic  
603 conditions. *Agriculture, Ecosystems & Environment* **200**: 71–78.
- 604 **Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M. 2006.** Jack of all  
605 trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology*  
606 *Letters* **9**: 981–993.

- 607 **Rigby RA, Stasinopoulos DM. 2005.** Generalized additive models for location, scale  
608 and shape. *Applied statistics* **54**: 507–554.
- 609 **Salguero-Gómez R, Violle C, Gimenez O, Childs D. 2018.** Delivering the promises of  
610 trait-based approaches to the needs of demographic approaches, and vice versa.  
611 *Functional Ecology* **32**: 1424–1435.
- 612 **Scogings PF. 2018.** Foliar flavonol concentration in *Sclerocarya birrea* saplings responds  
613 to nutrient fertilisation according to growth-differentiation balance hypothesis.  
614 *Phytochemistry Letters* **23**: 180–184.
- 615 **Shipley B. 2010.** *From Plant Traits to Vegetation Structure*. Cambridge University Press.
- 616 **Siefert A, Fridley JD, Ritchie ME. 2014.** Community functional responses to soil and  
617 climate at multiple spatial scales: When does intraspecific variation matter? *PLoS ONE* **9**.
- 618 **Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen  
619 LW, Baraloto C, Carlucci MB, Cianciaruso M V, et al. 2015.** A global meta-analysis  
620 of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*  
621 **18**: 1406–1419.
- 622 **Smyth GK. 1989.** Generalized Linear Models with Varying Dispersion. *Journal of the  
623 Royal Statistical Society. Series B (Methodological)* **51**: 47–60.
- 624 **Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E. 1997a.** *The Influence  
625 of Functional Diversity and Composition on Ecosystem Processes*.
- 626 **Tilman D, Tilman D, Lehman CL, Lehman CL, Thomson KT, Thomson KT. 1997b.**  
627 Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the  
628 National Academy of Sciences of the United States of America* **94**: 1857–61.
- 629 **Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J.  
630 2012.** The return of the variance: Intraspecific variability in community ecology. *Trends  
631 in Ecology and Evolution* **27**: 244–252.
- 632 **Violle C, Navas M-LL, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007.**  
633 Let the concept of trait be functional! *Oikos* **116**: 882–892.
- 634 **Waterway MJ, Martins KT, Dabros A, Prado A, Lechowicz MJ. 2016.** Ecological

- 635 and Evolutionary Diversification Within the Genus *Carex* (Cyperaceae): Consequences  
636 for Community Assembly in Subarctic Fens. *Systematic Botany* **41**: 558–579.
- 637 **Weiner J, Thomas SC. 1986.** Size Variability and Competition in Plant Monocultures.  
638 *Oikos* **47**: 211–222.
- 639 **Wiktor K, Diggelen R van. 2004.** Light as an environmental filter in fen vegetation.  
640 *Journal of Vegetation Science* **15**: 583–594.
- 641 **Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-**  
642 **bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004.** The worldwide leaf  
643 economics spectrum. *Nature* **428**.
- 644 **Yao Y, Vehtari A, Simpson D, Gelman A. 2017.** Using stacking to average Bayesian  
645 predictive distributions. *Bayesian Analysis*.
- 646

647 **Table 1:** Stacking weights of competing models describing trait variation across biological  
 648 organization levels. *Community level (Mcom):* *Mcom0* contained only intercepts for  
 649 campaign, ecosystems and plots identity (the last two considered as a hierarchical  
 650 parameter with estimated variance). *Mcom1* and *Mcom2* estimated a slope per ecosystem  
 651 between species richness and mean and dispersion of trait distribution, respectively.  
 652 *Mcom3* estimated the ecosystem specific slopes for both mean and dispersion considering  
 653 estimated species mean during each campaign, only, i.e. without considering species  
 654 plasticity. *Mcom3'* is based on *Mcom3* but considering species phenotypic and ontogenic  
 655 plasticity plasticity between individuals and campaign. *Species level (Msp):* *Msp0* contains  
 656 only categorical effects of campaigns, ecosystem, plot and species identity (the last two  
 657 considered as a hierarchical parameter with estimated variance). *Msp1* is a model  
 658 containing categorical effects and a slope per ecosystem linking species diversity to traits  
 659 mean and diversity of each dominant species within this ecosystem. In *Msp2* trait mean is  
 660 modeled with a slope per species and dispersion per ecosystem, while *Msp3* contained a  
 661 slope per species for both mean and dispersion. Parameters  $\beta$  and  $\gamma$  represent slopes  
 662 between species richness and mean and dispersion of trait distribution, respectively. Indices  
 663 *E* and *S* mean that the slopes were estimated for each ecosystems or for each species,  
 664 respectively. LA = Leaf Area (cm<sup>2</sup>), SLA = Specific Leaf Area (cm<sup>2</sup> g<sup>-1</sup>), Chl. = superficial  
 665 chlorophyll content, Angle = Leaf angle (°), LDMC = Leaf Dry Matter Content (g<sub>dry</sub> g<sub>fresh</sub><sup>-1</sup>),  
 666 Flav. = flavonoids.

667

	Models	Parameters	Length	LA	SLA	Chl.	Angle	LDMC	Flav.
Community level	Mcom0	Int	0.01	0.09	0.03	0.05	0.45	0	0.03
	Mcom1	$\beta_{1E}$	0	0.2	0	0.84	0	0	0
	Mcom2	$\gamma_{1E}$	0.01	0	0.13	0	0.09	0.17	0.07
	Mcom3'	$\beta_{1E}, \gamma_{1E}$ , no ITV	0	0	0	0	0	0.04	0.04
	Mcom3	$\beta_{1E}, \gamma_{1E}$	0.98	0.71	0.83	0.11	0.47	0.79	0.86
Species level	Msp0	Int	0	0.23	0	0.31	0.4	0	0.55
	Msp1	$\beta_{1E}, \gamma_{1E}$	0.32	0	0.38	0	0.24	0.8	0
	Msp2	$\beta_{1S}, \gamma_{1E}$	0	0	0	0.69	0	0	0
	Msp3	$\beta_{1S}, \gamma_{1S}$	0.68	0.77	0.62	0	0.36	0.2	0.45

668  
669

670 **Table 2:** Summary of estimated communities' trait distribution multiplicative slopes with  
 671 species diversity. The overall lines represent the global mean response across the data set.  
 672 We displayed 80% credible intervals of exponentiated slopes. Values before 1  
 673 characterizes negative slopes, while values above one characterizes positive ones.  $\mu$   
 674 represents the mean of the distribution, while  $\varphi$  represents dispersion. Green and blue case  
 675 represents negative and positive substantial variation in mean trait value ( $\mu$ ) or dispersion  
 676 or precision ( $\varphi$ ) in response to variation in community species richness. Predictions are  
 677 available in Fig. S5-S11. LA = Leaf Area (cm<sup>2</sup>), SLA = Specific Leaf Area (cm<sup>2</sup>.g<sup>-1</sup>), Chl.  
 678 = superficial chlorophyll content, Angle = Leaf angle (°), LDMC = Leaf Dry Matter  
 679 Content (g<sub>dry</sub>.g<sub>fresh</sub><sup>-1</sup>), Flav. = flavonoids.  
 680

Ecosystem	Parameter	Length	LA	SLA	Chl.	Angle	LDMC	Flav.
Overall	$\mu$	1.03	0.99	1	0.95	1.02	1	1.01
		1.08	1.03	1.03	0.98	1.08	1.02	1.03
Overall	$\varphi$	0.96	1.07	1.18	1.02	1.02	0.88	1.08
		1.13	1.18	1.35	1.16	1.2	0.93	1.2
Bog	$\mu$	1.06	0.98	1	0.9	1.03	1	1.01
		1.17	1.05	1.06	0.96	1.16	1.03	1.07
Bog	$\varphi$	0.93	1.14	1.38	1.03	1.04	0.78	1.16
		1.29	1.39	1.82	1.34	1.43	0.86	1.44
Fen	$\mu$	0.98	1.05	1.01	0.97	1.01	0.99	0.99
		1	1.15	1.04	1	1.06	1.03	1.01
Fen	$\varphi$	0.94	1.21	1.04	0.94	1	0.76	0.94
		1.03	1.53	1.14	1.02	1.14	0.86	1.02
Wet meadow	$\mu$	1.08	0.99	0.99	0.95	0.98	0.99	0.97
		1.12	1.04	1.02	0.98	1.02	1.02	1
Wet meadow	$\varphi$	1.13	1.01	1.1	0.96	1.01	0.93	1.09
		1.3	1.15	1.24	1.05	1.12	1.01	1.19
Fluvial marsh	$\mu$	1.07	0.9	0.93	0.85	1	0.97	1.05
		1.32	0.98	1.06	0.98	1.29	1.01	1.19
Fluvial marsh	$\varphi$	0.67	0.88	1.33	1.02	0.81	0.89	1.12
		1.33	1.09	2.38	1.75	1.59	0.98	1.78

681  
682

683 **Table 3:** Summary of estimated species slopes along the species diversity gradient.  
 684 Parameters were recovered from the best model for each trait, presented in table 1. We  
 685 removed models predicting LDMC and flavonoids as they had less support for species  
 686 specific variations and presented no substantial estimates. For sake of clarity, we resumed  
 687 slopes by symbols representing their sign. We considered the inclusion of zero in the 85%  
 688 credible interval of parameters. Given the complexity of estimated models, a more  
 689 conservative interval would exclude pertinent inferences. For the density, symbols + and –  
 690 represents substantial variation of species mean relative density with species richness  
 691 within each ecosystem. For each trait they represented substantial variation in mean trait  
 692 value ( $\mu$ ) or dispersion ( $\phi$ ) in response to variation in community species richness.  
 693 Model predictions are available in Fig. S12-18. LA = Leaf Area ( $\text{cm}^2$ ), SLA = Specific  
 694 Leaf Area ( $\text{cm}^2.\text{g}^{-1}$ ), Chl. = superficial chlorophyll content, Angle = Leaf angle ( $^\circ$ ).  
 695

Ecosystem	Species	Density	Parameter	Length	LA	SLA	Chl.	Angle
Bog	<i>Chamaedaphne calyculata</i>	0	$\mu$	0	+	0	0	0
			$\phi$	+	+	0	0	0
	<i>Eriophorum virginicum</i>	-	$\mu$	0	0	0	0	0
			$\phi$	0	0	0	0	0
Fen	<i>Carex lasiocarpa</i>	+	$\mu$	0	0	0	0	0
			$\phi$	-	0	-	0	0
	<i>Carex oligosperma</i>	-	$\mu$	0	0	0	0	0
			$\phi$	0	+	+	-	+
	<i>Carex sect. Phacocystis</i>	-	$\mu$	0	-	0	0	0
$\phi$			0	0	+	-	+	
Wet meadow	<i>Acorus calaḡus</i>	-	$\mu$	0	+	0	0	0
			$\phi$	+	0	0	0	0
	<i>Lythrum salicaria</i>	0	$\mu$	0	0	0	0	0
			$\phi$	0	0	0	0	0
Fluvial marsh	<i>Acorus calaḡus</i>	-	$\mu$	0	0	0	0	0
			$\phi$	+	0	0	0	+
	<i>Comarum palustre</i>	0	$\mu$	0	+	0	0	0
			$\phi$	0	0	0	0	0
	<i>Lythrum salicaria</i>	0	$\mu$	0	-	0	0	0
			$\phi$	+	+	0	0	0
<i>Typha latifolia</i>	0	$\mu$	0	-	0	0	0	
		$\phi$	0	-	0	0	0	

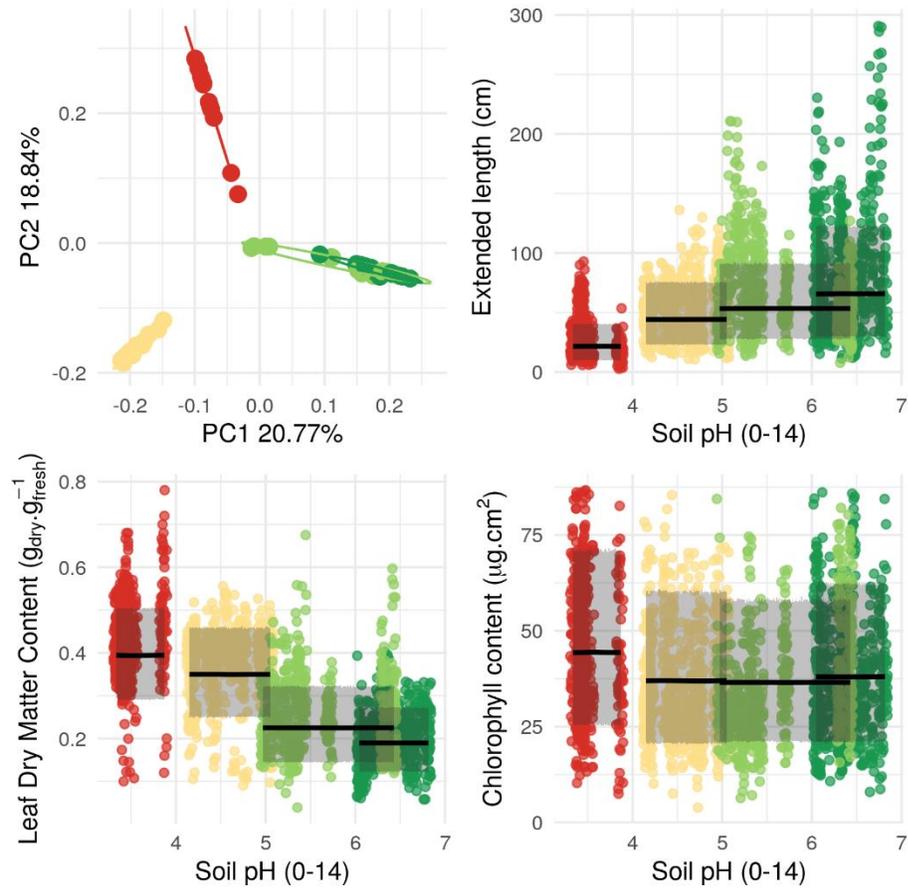
696  
697

698 **Figure 1:** Differences among ecosystems in term of species and functional traits. Panel a  
699 represents a principal component analysis of Hellinger transformed species density. Lines  
700 represents 95% ellipses capturing 95% of the points. Panel b to d represents observed trait  
701 values with predictions of the model containing an intercept per ecosystem for both mean  
702 and dispersion. Lines represent mean predicted value. Shaded area represent 95%  
703 predictive interval of community trait distribution. Panel b and c represent mean Leaf Dry  
704 Matter Content and both Leaf Area mean and dispersion varying monotonically among  
705 ecosystems. Panel d represents an absence of among ecosystem monotonic variation for  
706 chlorophyll content per unit area of leaves. . *Red* = bog, *yellow* = fen, *light green* = wet  
707 meadow, *dark green* = fluvial marsh.

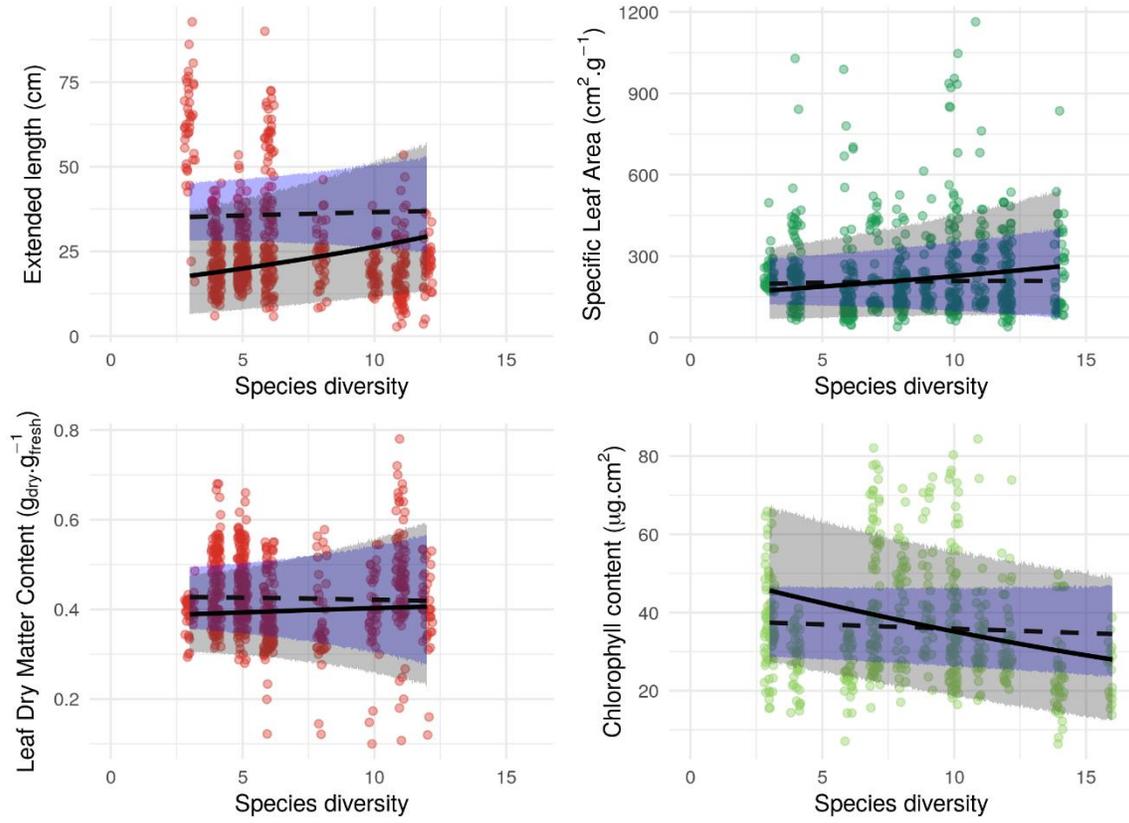
708 **Figure 2:** Example of response of community trait distribution to within-ecosystem species  
709 diversity gradient. Plain lines represents mean predicted values based on observed data  
710 (with ITV), while dashed lines represents mean predicted values of models fitted using  
711 species mean values (without ITV). Gray and blue shaded area represents 90% predictive  
712 interval of community trait distribution with and without ITV, respectively. *Red* = bog,  
713 *yellow* = fen, *light green* = wet meadow, *dark green* = fluvial marsh.

714  
715 **Fig. 3:** Models predictions of species morphological trait distribution and fitness trait  
716 (relative density) in function of the number of species in community, representing the  
717 presence of two contrasted response within each ecosystem. The “Master of some”  
718 response represents species which were substantially more abundant when they were  
719 dominant than when they were growing in rich communities, with or without detected trait  
720 variation. This species were potentially able to dominate in favorable conditions, but  
721 unable to maintain fitness when conditions changes. The “Jack-of-all-trades” response  
722 represents species with stable relative density, but with substantial trait variation,  
723 represented by displacement of the mean and/or increase/decrease of diversity of trait  
724 values. Potentially, these species were able to cope with changing conditions by deforming  
725 their trait distribution. Full line represents the species median trait value, while the grey  
726 area represents the 90% predictive interval of trait distribution. Dashed line represents the  
727 median predicted relative density of each species. LA = Leaf area (cm<sup>2</sup>), EL = Extended  
728 length (cm), Density = Relative density (ind.m<sup>-2</sup>). Species are *Chamaedaphne calyculata*,

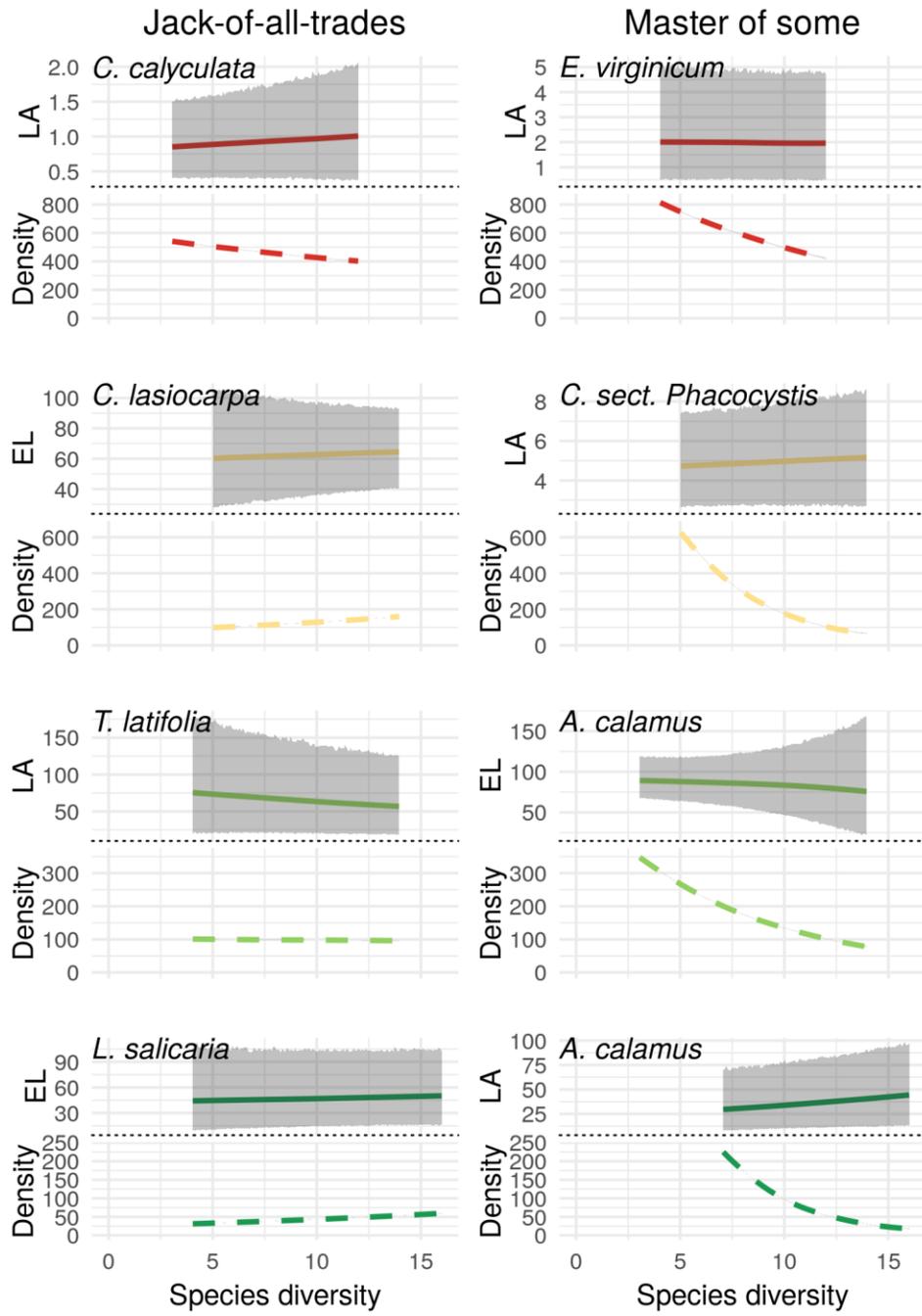
729 *Eriophorum virginicum*, *Carex lasiocarpa*, *Carex sec. phacocystis*, *Typha latifolia*, *Acorus*  
730 *calamus et Lythrum salicaria*.



731



732



733  
734