

1 **Distinguishing the signatures of local environmental filtering and**
2 **regional trait range limits in the study of trait-environment**
3 **relationships.**

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17 **Abstract**

18 Understanding the imprint of environmental filtering on community assembly along
19 environmental gradients is a key objective of trait-gradient analyses. Depending on local
20 constraints, this filtering generally entails that species departing from an optimum trait value have
21 lower abundances in the community. The Community-Weighted Mean (CWM) and Variance
22 (CWV) of trait values are then expected to depict the optimum and intensity of filtering,
23 respectively. However, the trait distribution within the regional species pool and its limits can
24 also affect local CWM and CWV values apart from the effect of environmental filtering. The
25 regional trait range limits are more likely to be reached in communities at the extremes of
26 environmental gradients. Analogous to the mid-domain effect in biogeography, decreasing CWV
27 values in extreme environments can then represent the influence of regional trait range limits
28 rather than stronger filtering in the local environment. We name this effect the “Trait-Gradient
29 Boundary Effect” (TGBE). First, we use a community assembly framework to build simulated
30 communities along a gradient from a species pool and environmental filtering with either
31 constant or varying intensity while accounting for immigration processes. We demonstrate the
32 significant influence of TGBE, in parallel to environmental filtering, on CWM and CWV at the
33 extremes of the environmental gradient. We provide a statistical tool based on Approximate
34 Bayesian Computation to decipher the respective influence of local environmental filtering and
35 regional trait range limits. Second, as a case study, we reanalyze the functional composition of
36 alpine plant communities distributed along a gradient of snow cover duration. We show that leaf
37 trait convergence found in communities at the extremes of the gradient reflect an influence of
38 trait range limits rather than stronger environmental filtering. These findings challenge

39 correlative trait-environment relationships and call for more explicitly identifying the
40 mechanisms responsible of trait convergence/divergence along environmental gradients.

41 **Introduction**

42 Quantifying the physiological responses of organisms and communities along
43 environmental gradients is pivotal in ecology and biogeography (Lomolino et al. 2006, Violle et
44 al. 2014). However, we know little about the sensitivity of such responses to environmental or
45 physiological limits, i.e. to boundary effects. Boundary effects have been broadly addressed in
46 biogeography, in terms of taxonomic diversity at the limits of environmental gradients.
47 Specifically, the mid-domain effect represents an artefactual peak of species richness at the center
48 of latitudinal gradient (Colwell and Lees 2000, Colwell et al. 2004) or of species range at the
49 center of an environmental gradient (Letten et al. 2013) due to sampling issues. Here we recast
50 this hypothesis through the lens of trait-based ecology. More specifically, we argue that the
51 parameters of the local trait distribution at the edge of environmental and/or trait gradients can be
52 misinterpreted because the regional trait distribution is not properly quantified. While the
53 influence of the taxonomic composition and richness of a source species pool on local
54 community assembly have received much interest, the influence of the functional composition of
55 the pool has only recently come to focus (Patrick and Brown 2018, Spasojevic et al. 2018). This
56 influence, that we coined ‘trait-gradient boundary effect’ (TGBE), can combine with the effect of
57 environmental filtering, as both constrain the moments of the local trait distribution at community
58 scale (Kraft et al. 2015). We here provide a method to separate the influence of environmental
59 filtering on local community assembly from the imprint of regional trait distribution, in order to
60 avoid misinterpretations on the strength of environmental filtering.

61 Functional traits are attributes reflecting the ability of individuals to survive and
62 reproduce in a local environment (Violle et al. 2007). Assembly processes shape the distribution
63 of functional trait values within communities (McGill et al. 2006), and in particular

64 environmental filtering represents the control of the local trait distribution by abiotic factors
65 (Kraft et al. 2015). Environmental filtering generally includes two components (Shipley 2010):
66 (i) an optimal trait value or combination allowing maximal performance and greater abundance in
67 the community, and (ii) an intensity value quantifying how sharp the decrease of species
68 performance around the optimal trait value is (Fig. 1). Varying the functional composition of
69 communities along environmental gradients is then expected to reflect changing optimal values
70 and/or filtering intensity (Ackerly and Cornwell 2007). Because the variation of performance
71 around the optimal value translates into a variation of species abundances related to trait values,
72 the mean value of trait in communities (Community-Weighted Mean, CWM) and their variance
73 (CWV) (Garnier et al. 2016) are expected to reflect local optimal trait value and filtering
74 intensity, respectively (Cingolani et al. 2007, Violle et al. 2007, Enquist et al. 2015, Borgy et al.
75 2017a). However, a clear relationship between trait-based statistics and the parameters of
76 environmental filtering (“CWM-optimality” hypothesis, Muscarella and Uriarte 2016) may not
77 always hold.

78 In extreme environments, more intense environmental filtering due to local constraints is
79 commonly hypothesized (Weiher et al. 1998, Callaway et al. 2002, Cornwell et al. 2006), but the
80 filtered trait values can also be closer to regional trait range limits. A reduction of variance in
81 extreme environments can thus be allotted to either local environmental filtering or to larger-scale
82 and longer-term constraints leading to a restricted trait variation among immigrants. Regional
83 trait range limits should yield a decrease in local trait variance at the extremes of an
84 environmental gradient and therefore entail a hump-shaped variation of CWV across the
85 environmental gradient, even when the intensity of environmental filtering is constant throughout
86 the gradient (Fig. 1). TGBE can also originate phenomenological relationships between CWM

87 and CWV because of the local convergence induced by the species pool limited trait range. Such
88 hump-shaped patterns between CWM and CWV have been reported previously (Dias et al. 2013),
89 and can reflect the influence of TGBE in real data. A major issue is then to determine whether
90 lower trait variance in extreme environments reflects more intense filtering or the influence of
91 trait limits at a regional scale. To solve the issue, we propose an inference approach that
92 explicitly estimates the influences of regional trait range limits and local environmental filtering.

93 We investigated TGBEs in the context of a spatially-implicit model of community
94 assembly representing how immigration from a species pool and local environmental filtering
95 jointly shape local community composition (*ecolottery* package, Munoz et al. 2018) (Fig. 1).
96 Environmental filtering is modeled as a Gaussian function determining the successful
97 establishment of immigrants and thus defines a decrease of the performance of species around an
98 optimum trait value, the intensity of the filtering being the standard deviation of the function
99 (Webb et al. 2010, Shipley 2010, Enquist et al. 2015). An environmental gradient can then be
100 viewed as a gradient of distinct optima imposed by distinct local environmental filters. When trait
101 range limits among immigrants constrain the functional range in community composition, we
102 expect reduced variance and a skewed local distribution with CWM deviating from optimal trait
103 value (Fig. 1). We used the model to simulate community composition with explicit
104 environmental filtering along an environmental gradient, with and without variation of filtering
105 intensity. It illustrates how TGBEs can arise. In addition, we propose an Approximate Bayesian
106 Computation approach based on intensive simulations of community composition to get an
107 unbiased estimate of the optimum and intensity of environmental filtering, while controlling for
108 the influence of TGBE. This powerful and mechanistic approach allows comparing the outputs of
109 our community assembly model, with different sets of parameters related to distinct processes, to

110 the local trait patterns observed in a given community dataset, so as to unravel the causes
111 originating them (Csilléry et al. 2010, Munoz et al. 2018). We applied the approach to examine
112 TGBE and environmental filtering in alpine plant communities along a gradient of snow cover
113 duration in the French Alps (Choler, 2005).

114

115 **Material and Methods**

116 *Framework of community assembly*

117 Immigrants drawn from a species pool establish and persist in a community depending on
118 environmental filtering (Fig. 1). Each individual displays a synthetic fitness-related trait value, t ,
119 and the probability of successful immigration decreases as t departs from an optimal trait value
120 t_{opt} depending on local environmental conditions (Shipley 2010). We used a Gaussian function of
121 t with mean t_{opt} and standard deviation σ_{opt} to represent this filtering. σ_{opt} depicts the intensity of
122 environmental filtering: the smaller σ_{opt} , the narrower the extent of trait values allowing
123 immigration in the local community (Munoz et al. 2018). Each community is then assigned t_{opt}
124 and σ_{opt} values characterizing local environmental filtering.

125 Our main objective is to disentangle the influence of (i) trait range limits in the species
126 pool, denoted as a for the lower and b for the upper limit, and (ii) the parameters of
127 environmental filtering denoted as t_{opt} and σ_{opt} , on the distribution of trait values in local
128 communities. When t_{opt} is close to a , we expected that the distribution of trait values in the local
129 community is limited below a (Fig. 1), and conversely when t_{opt} is close to b . In the following, we
130 present the consequences of the regional trait limits on (i) the calculation of the first four

131 moments (Enquist et al. 2015) of the local trait distribution, and (ii) how these moments vary
132 across communities along an environmental gradient.

133

134 *Community-level trait based statistics*

135 Synthetic trait-based statistics are commonly used to characterize the functional response
136 of communities. The two first moments of the distribution of trait values in a community,
137 namely, the community weighted mean (CWM) and community weighted variance (CWV), are
138 commonly used to analyze the functional structure of communities while the two following
139 moments, community weighted skewness (CWS) and community weighted kurtosis (CWK) are
140 more rarely considered (Enquist et al. 2015, Gross et al. 2017). The first four moments are
141 expected to be influenced, among other processes, by environmental filtering and are often used
142 for the inference of filtering (Shipley 2010, Enquist et al. 2015, Loranger et al. 2018). With a
143 Gaussian environmental filtering (Fig. 1), we expect CWM and CWV to equal t_{opt} and σ_{opt} ,
144 respectively. As a measure of 'peakedness', CWK should also increase with decreasing σ_{opt}
145 (Enquist et al. 2015, Gross et al. 2017). If the environmental filter is symmetrical, as considered
146 here (Fig. 1), local CWS is not expected to deviate from 0.

147 When the trait range in the species pool is bounded and when the environment selects for
148 trait values close to these boundaries, the local distribution of trait values is bounded beyond the
149 limits of the pool, and is asymmetrical (Fig. 1). This asymmetry should entail a shift in CWM to
150 larger values if the closer trait limit in the species pool is the lower boundary and to lower values
151 if the closer limit is the upper boundary (Fig. 1). In addition, the trait limits should further reduce
152 the range of values in local communities and thus reduce CWV (Fig. 1), increase CWK and

153 increase CWS in absolute value when t_{opt} is closer to the limits. In Appendix S1, we provide the
154 mathematical formulas of the four moments, as a function of t_{opt} , σ_{opt} , and of trait range limits a
155 and b , in a simple case where regional trait abundances are uniformly distributed between a and
156 b .

157

158 *Simulation of communities with environmental filtering and trait range limits*

159 We used a coalescent-based algorithm (package *ecolottery* in R language, Munoz et al.
160 2018) to simulate community assembly with migrants drawn from a species pool and subject to a
161 Gaussian environmental filtering. The coalescent-based approach reconstructs the shared ancestry
162 of coexisting individuals (i.e., their genealogy) at present without simulating complete
163 community dynamics from an initial state through time. The topology of the genealogy depends
164 on immigration, environmental filtering, and demographic stochasticity (Munoz et al. 2018). We
165 considered two types of species pools with either a uniform or a log-series distribution of
166 abundances. Results were comparable with both distributions, and subsequent analyses will
167 concern the case of uniform abundances only. A uniform pool includes 100 species with 1,000
168 individuals per species, hence a total of 100,000 candidate immigrants. Species trait values t_i
169 were drawn from a uniform distribution between either $a = 0$ and $b = 1$ (trait range = 1), or $a = 0$
170 and $b = 2$ (trait range = 2). We varied the range of trait values to assess the relative influence of
171 filtering intensity and trait range. We also simulated a set of communities with intraspecific
172 variation, i.e., with a standard deviation of trait values per species set to $\sigma_i = 0.1$ in the species
173 pool. The environmental filtering function determined the probability p of establishment of an
174 individual with a trait value t according the following function: $p = e^{-\left(\frac{t-t_{opt}}{\sigma_{opt}}\right)^2}$ (Fig. 1). We set

175 the intensity of environmental filtering, ruled by the parameter σ_{opt} , to either 0.25 or 0.05, to
176 represent weak and intense environmental filtering, respectively, compared to the regional range
177 of trait values varying between 0 and 1. For a given species pool, we simulated $n = 100$
178 communities, each including $J = 500$ individuals, with varying t_{opt} values randomly drawn
179 between a and b . The variation of t_{opt} represents a variation of optimal values along the
180 environmental gradient.

181 We also considered another set of simulations where σ_{opt} varied along the gradient, with
182 minimum values of $\sigma_{opt} = 0.05$ at the extremes a and b towards a maximum of $\sigma_{opt} = 0.25$ in the
183 middle of the gradient. In this case, environmental filtering was more intense at the extremes of
184 the gradient. We therefore designed two sets of simulated communities undergoing a fixed and
185 varying environmental filtering, respectively. From these simulated data, local weighted
186 moments were calculated and the environmental filtering parameters \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$ were
187 estimated (see below). A repeatable example of community simulation is provided in Appendix
188 S2.

189

190 ***ABC estimation of parameters of environmental filtering***

191 We performed an Approximate Bayesian Computation (ABC) analysis (Csilléry et al.
192 2010, *coalesc_abc* function in *ecolottery* R package) to estimate the parameters \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$ of
193 environmental filtering from a given community composition. ABC provides posterior
194 distributions of parameter estimates by comparing some summary statistics in communities
195 simulated over a broad range of t_{opt} and σ_{opt} values, to the same summary statistic values in the
196 given community (Csilléry et al. 2010). In our case, the summary statistics were metrics of

197 taxonomic (richness and Shannon diversity) and functional (CWM, CWV, CWS and CWK)
198 composition of a community. Many communities were simulated in ABC analysis using the same
199 coalescent-based algorithm presented above (package *ecolottery* in R language, Munoz et al.
200 2018). In any case, simulated communities received immigrants from the same species pool. We
201 also considered an alternative analysis where the summary statistics included functional
202 dispersion (Laliberté and Legendre 2010) and Rao's quadratic entropy (Botta-Dukát 2005)
203 instead of CWV, CWS and CWK (Appendix S10). Insofar as species pool composition was
204 known, its trait range limits a and b were fixed based on the upper and lower trait range limits in
205 the complete species pool. However, we also devised a case where the trait range limits and the
206 species pool composition were based on the sum of observed communities (Appendix S11). The
207 median values of \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$ in posterior distributions were compared to observed CWM and
208 CWV values, respectively.

209 We performed ABC analysis on each of the simulated community presented above, to get
210 a cross-validation of estimated \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$ values for simulated data with known t_{opt} and σ_{opt}^2
211 values. We also compared CWM and CWV in communities to t_{opt} and σ_{opt}^2 . Figures 2b and 2d
212 represent the variation in ABC estimates along a gradient of t_{opt} values. For simulations with
213 fixed σ_{opt}^2 , any variation in CWV at the extremes was expected to reveal an influence of regional
214 trait limits only (TGBE). Conversely, we expected decreasing $\hat{\sigma}_{opt}^2$ at the extremes of the
215 gradient of t_{opt} , for the set of simulations where σ_{opt}^2 was indeed smaller at the extremes. The \hat{t}_{opt}
216 $\sim \hat{\sigma}_{opt}^2$ relationship was also compared to the CWM \sim CWV relationship, to check the
217 consistency of the variation in estimated environmental filtering parameters with
218 phenomenological patterns of functional convergence measured with CWV (Appendix S3).

219

220 *Application to alpine plant communities*

221 We analyzed the variation in functional composition of plant communities along a
222 gradient of snow cover duration in alpine grassland vegetation (Choler 2005). This gradient
223 ranged from 140 to 210 days of snow cover in 1998. The alpine vegetation dataset (*aravo* in `ade4`
224 R package) includes 75 communities for a total of 82 species, located between 2700 and 2750
225 meters in French Alps. This vegetation undergoes harsh high-elevation conditions but also covers
226 a broad environmental gradient of duration of snow cover, due to topographical and
227 microclimatic heterogeneity (Choler 2005). The gradient determines varying abiotic stress and
228 length of growing season, and thus largely influences functional trait variation among
229 communities, such as leaf nitrogen concentration on a mass basis (N_{mass}) and specific leaf area
230 (SLA) (Choler 2005), which are two foliar traits characterizing the resource acquisition-
231 conservation tradeoff in plants (Garnier et al. 2016). Long snow cover protects from freezing
232 stress but reduces the length of growing season, which should favor resource-acquisitive plants,
233 relatively to the local species pool, with higher N_{mass} and SLA. On the contrary, short snow cover
234 increases exposure to wind and frost while increasing length of growing season, which should, in
235 this specific context, favor resource-conservative plants with lower N_{mass} and SLA (Choler 2005).

236 We estimated parameters of environmental filtering t_{opt} and σ_{opt} for foliar traits in this
237 dataset, and examined their variation along the gradient of snow cover duration. The species pool
238 used in ABC analysis was built from the species present in all the observed communities.

239

240 **Results**

241 *TGBE in simulated communities*

242 We simulated communities along an environmental gradient with different t_{opt} values but
243 constant filtering intensity σ_{opt}^2 (Fig. 2). The variations in CWM and CWV illustrate the influence
244 of TGBE. First, CWM went below t_{opt} when closer to the upper limit of trait range, and above t_{opt}
245 when closer to the lower limit (Fig. 2a). The observed range of CWM values was thereby smaller
246 than the range of t_{opt} . Second, we found a hump-shaped variation in CWV, with lower values at
247 the extremes of the t_{opt} gradient (Fig. 2c). CWS and CWK also varied along the t_{opt} gradient with
248 a decrease in CWS and an increase in CWK towards the extremes (Appendix S5). Because
249 filtering intensity was set constant, the reduction of CWV at the extremes, and the respective
250 variations of CWS and CWK, was attributable to the influence of trait range limits in the species
251 pool (Fig. 1). We obtained consistent results under more intense but constant environmental
252 filtering ($\sigma_{opt} = 0.05$, Appendix S4, more contrasted), with intraspecific variability (Appendix S6,
253 $\sigma = 0.1$), with log-series distribution of regional abundances (Appendix S7) and when using the
254 sum of observed communities as a species pool (Appendix S11).

255 We expected the influence of TGBE to extend farther from the extremes when σ_{opt}^2 was
256 larger for a fixed range $[a; b]$. The extent of the influence of regional trait limits was thereby
257 expected to depend on the intensity of local filtering relatively to trait range $[a; b]$. Appendix S8
258 shows how the ratio of σ_{opt}^2 and trait range influences the deviation of CWM from t_{opt} . It shows
259 that the ratio of trait range $(b - a)$ and filtering intensity (σ_{opt}^2) determines the influence of TGBE
260 along the gradient. For instance, $\sigma_{opt} = 0.5$ and $[0; 1]$ trait range gives the same deviation than σ_{opt}
261 $= 1$ and $[0; 2]$ trait range.

262

263 ***Deciphering environmental filtering and TGBE in extreme environments***

264 In communities where filtering intensity was set constant, we obtained unbiased
265 estimation of t_{opt} (Fig. 2b, slope coefficient of the regression between \hat{t}_{opt} and $t_{opt} = 0.97$), and
266 unbiased and constant estimation of σ_{opt} , while there was variation in CWV due to TGBE (Fig.
267 2d). Indeed, the square distance between σ_{opt}^2 and $\hat{\sigma}_{opt}^2$ was, in average, twice low over the t_{opt}
268 gradient (Fig. 2d) than the square distance between σ_{opt}^2 and CWV (Fig. 2c) ($8.91e-3$ and $2.23e-2$
269 respectively). When using other metrics than CWV to evaluate local functional convergence and
270 to estimate t_{opt} and σ_{opt}^2 , namely functional dispersion and Rao's quadratic entropy, we obtained
271 similar results with significant quadratic relationships between these metrics and t_{opt} along t_{opt}
272 gradient while the environmental filtering intensity remained constant (Appendix S10). In
273 addition, we simulated an environmental gradient where filtering was more intense at the
274 extremes (i.e., smaller σ_{opt} value, black line on Fig. 3a and 3b). Figure 3d shows that the
275 estimated value of σ_{opt} followed the expected variation of filtering intensity. In this case, CWV
276 also displayed a hump-shaped pattern along the gradient, similar to Figure 2c, but here this was
277 due to both regional trait limits and actual variation in filtering intensity.

278 Therefore, the variation in CWV could not inform on the respective influences of
279 environmental filtering and trait range limits in the pool (Fig. 1c, Fig. 3c), while the ABC-based
280 estimation of σ_{opt}^2 allowed grasping the specific influence of environmental filtering.

281

282 ***TGBE and environmental filtering in alpine plant communities***

283 We estimated t_{opt} and σ_{opt}^2 , and the variations in CWV and CWM values of foliar traits in
284 alpine plant communities (Figs. 4 & 5). As expected with TGBE, CWM departed from estimated
285 \hat{t}_{opt} in extreme environmental conditions, and the range of t_{opt} values was larger than the range of

286 CWM values (Fig. 4ab & 5ab). CWV decreased at lowest duration (great exposure to cold) for
287 both SLA and N_{mass} and at highest duration (short vegetative period) of snow cover for N_{mass} only
288 (Fig. 4). On the contrary, ABC-based estimations showed that $\widehat{\sigma}_{opt}^2$ did not vary along the snow
289 cover gradient (Fig. 4cd & 5cd). Except for SLA at long snow cover duration (Fig. 5cd), $\widehat{\sigma}_{opt}^2$
290 was larger than the corresponding CWV.

291 In addition, departure of community weighted skewness (CWS) from 0 reflected the
292 influence of regional trait limits and asymmetry in local trait distribution, as observed in
293 simulated communities with constant σ_{opt} (Appendix S5). In alpine plant communities,
294 increasingly negative community weighted skewness (CWS) with increasing snow cover duration
295 in alpine vegetation was consistent with an influence of an upper trait limit on the local
296 distribution of N_{mass} and SLA at longest snow cover duration (Appendix S9).

297

298

299 **Discussion**

300 In ecology and biogeography, trait-gradient analyses examine the functional trait
301 distributions in communities to characterize community responses along environmental gradients
302 (Ackerly and Cornwell 2007, Lepš et al. 2011, Garnier et al. 2016, Borgy et al. 2017a). Here we
303 showed that a reduced variance of the local trait distribution, i.e., trait convergence, can reflect a
304 combined influence of local environmental constraints within the community and of a bounded
305 trait distribution in the regional species pool. These two influences need to be disentangled in
306 order to identify the specific role of local environmental filtering. However, while much
307 emphasis has been put on the idea that environmental filtering can be more intense at the

308 extremes of environmental gradients (Weiher et al. 2011), far less attention has been devoted to
309 how the functional composition of species pools influences local community composition
310 (Spasojevic et al. 2018). To address the issue, we used a simulation-based, Approximate
311 Bayesian Computation (ABC) approach (*ecolottery* package, Munoz et al. 2018). By explicitly
312 modelling immigration and environmental filtering, the approach allows separating out the
313 influence of constraints on trait distributions at species pool and local community levels. With
314 this approach, we can obtain unbiased estimation of t_{opt} and σ_{opt} in simulated communities along
315 gradients. The mid-domain effect is a better-known example of the influence of regional limits
316 (of species niches and distributions) influencing local taxonomic diversity at the extremes of
317 gradients (in geographical, Colwell and Lees 2000, or environmental space, Letten et al. 2013).
318 The TGBE issue presented here extends this perspective to examine how trait range limits in
319 species pools influence functional composition in local communities. We discuss the
320 consequences of TGBE for trait-based approaches in functional ecology, community ecology and
321 (functional) biogeography.

322 Environmental filtering is often viewed as a humped filtering function along a niche axis,
323 similar to a Gaussian function with optimal value t_{opt} and filtering intensity σ_{opt} . Although
324 environmental filtering generally concerns the influence of abiotic constraints (Kraft et al. 2015),
325 the framework proposed here can apply to any filtering around an optimal trait value t_{opt}
326 conferring, e.g., greater competitive ability (Mayfield and Levine 2010), better colonization or
327 chances of establishment (Ehrlén and Eriksson 2000, Bernard-Verdier et al. 2012). The current
328 paradigm in functional ecology is that community weighed mean (CWM) is a proxy for t_{opt} , the
329 “CWM-optimality” hypothesis (Muscarella and Uriarte 2016), and that community weighed
330 variance (CWV) is a proxy for σ_{opt}^2 under environmental filtering. The “CWM-optimality”

331 hypothesis found some support in recent studies linking the distance between species' traits and
332 CWM to species' abundances for single traits (Umaña et al. 2015) or multivariate measures
333 (Muscarella and Uriarte 2016), but was challenged in other contexts (Mitchell et al. 2017,
334 Laughlin et al. 2018). CWM can be disconnected from t_{opt} when stabilizing mechanisms such as
335 competitive interactions and limiting similarity break the linkage of trait values with fitness
336 differences (Chesson 2000, Adler et al. 2013), or when neutral stochastic dynamics affect species
337 abundance independently from trait values (Hubbell 2001). Here we challenge the CWM-
338 optimality hypothesis by demonstrating that CWM and CWV can depart from t_{opt} and σ_{opt}^2 ,
339 respectively, when the local distribution is bounded due to trait range limits in the pool of
340 immigrants. The distribution of trait values in the regional species pool therefore influences local
341 community assembly (Patrick and Brown 2018, Spasojevic et al. 2018) and can challenge the
342 CWM-optimality hypothesis by preventing CWM to reach the optimum for certain environments.
343 It is likely that trait range limits of the species pool are reached in extreme environments, i.e. trait
344 values required for persistence are not possible, due to physiological limits or evolutionary
345 history (Koch et al. 2004, Alpert 2005). It is essential to distinguish the respective signatures of
346 local environmental filtering and of processes driving the functional composition of species pools
347 at a larger scale and over a long term (Jiménez-Alfaro et al. 2018). Consequently, identifying
348 TGBEs means determining the specific influence of local community assembly amidst the
349 influence of large-scale and long-term evolutionary legacy (Lessard et al. 2016).

350 We found that TGBE can be responsible of a hump-shaped variation in CWV along
351 environmental gradients even when the intensity of environmental filtering is constant (Fig. 2c).
352 TGBE also generated a hump-shaped relationship between CWV and CWM (Appendix S3),
353 similar to patterns reported in a previous study (Dias et al. 2013). Although a link between CWM

354 and CWV (or similar functional diversity metrics) can represent a statistical artifact (Ricotta and
355 Moretti 2011, Dias et al. 2013), our study also shows that TGBE can yield this relationship. The
356 analysis of alpine plant communities illustrated trait variance reduction in extreme environmental
357 conditions (Fig. 4 & 5), while the estimated $\widehat{\sigma}_{opt}^2$ did not show reduction. Variance reduction
358 could thus be due to TGBE and not to more intense environmental filtering in these alpine plant
359 communities (Fig. 4). Similarly, the \widehat{t}_{opt} -environment relationships had a steeper slope than the
360 CWM-environment relationship (Fig. 2, Fig. 4ab & Fig. 5ab), suggesting that CWM did not
361 represent optimal trait values all along the environmental gradient.

362 We have proposed a spatially-implicit framework of community assembly acknowledging
363 immigration from a species pool and local environmental filtering (Munoz et al. 2018). The
364 definition of the pool is flexible and several options have been proposed, either based on a
365 regional list of species (Zobel 1997), on the complete composition of a metacommunity (Leibold
366 et al. 2004), or on a spatially restricted source of dispersers (Lessard et al. 2016). The pool can
367 represent an external forcing based on long-term and large-scale regional dynamics (top-down
368 perspective as in Hubbell 2001) or reflect the emergent composition of available immigrants in a
369 metacommunity (bottom-up perspective, Leibold et al. 2004, Mittelbach and Schemske 2015). In
370 both cases, its composition illustrates the influence of long-term assembly dynamics across
371 communities in a specific area, and its boundaries represent the limits imposed by these
372 processes. In the present analyses, while we simulated and used the composition of complete
373 species pools in ABC analyses of simulated communities, the species pool of alpine communities
374 was based on the sum of sampled communities (see in Appendix S11 the results for simulations
375 with a species pool based on the sum of sampled communities). The composition and the relative
376 abundances considered in the reference species pool can greatly influence analyses of community

377 assembly dynamics (Lessard et al. 2011). Dark diversity, representing the species that are absent
378 from the pool but could contribute to immigration and community assembly (Pärtel et al. 2011),
379 can extend trait range limits in the reference species pool. Further investigation of the influence
380 of trait range limits with different definitions of the species pool should help address under which
381 conditions TGBE can be reliably detected. Furthermore, the influence of the shape of the trait
382 distribution in the pool should be addressed in more details in the future (Spasojevic et al. 2018)
383 and appears essential since it can vary from a biogeographical context to another even though
384 local environmental filtering can operate in a similar way. For sake of simplicity, we considered a
385 uniform distribution of trait values among species at regional scale, and two types of distribution
386 of regional abundances, uniform and log-series. Even though the results were robust to some
387 variation in these parameters, further investigation of the sensitivity of the model will be needed.
388 Lastly, we defined environmental filtering in our study as a Gaussian function around a single
389 optimum (Shipley 2010). However, other filtering functions, such as disruptive filtering with two
390 modes yielding trait divergence (Loranger et al. 2018), could be considered to study trait patterns
391 at the community level, and are already implemented in *ecolottery* R package (Munoz et al.
392 2018).

393 Independently from the assumptions mentioned above, the way CWM and CWV deviate
394 from t_{opt} and σ_{opt}^2 due to TGBE depends on the ratio between the trait range limits and the
395 strength of local environmental filtering along a gradient (Appendix S8). In a biogeographical
396 perspective, a physiological trait ~ environment relationship could yield different patterns of
397 CWM and CWV variation across regions where distinct biogeographical histories entailed
398 different range limits (Forrestel et al. 2017). Moreover, for a given regional species pool, the
399 influence of TGBE should change depending on the strength of local environmental filtering.

400 Therefore, when the filtering acting on a specific trait is strong, the deviation should concern only
401 communities closest to the extremes. The influence of TGBE on trait ~ environment relationship
402 can also differ across functional traits, depending on the nature of underlying filters acting on
403 different traits (Borgy et al. 2017b). The detection and influence of TGBE will therefore be
404 dependent upon the interplay of biogeographical history and the local mechanisms filtering, with
405 certain intensity, trait values.

406 ABC-based estimation of environmental filtering relies on simulating and comparing
407 basic statistics that summarize the observed and simulated trait distributions. The moments of
408 local trait distributions can be used as summary statistics to infer the trait-based assembly
409 processes, as advocated by the Trait Driver Theory (TDT) (Enquist et al. 2015). While much
410 emphasis has been put on analyzing the two first moments CWM and CWV, TDT underlines that
411 the next moments, skewness (CWS) and kurtosis (CWK), also convey insights on assembly
412 dynamics. Gross et al. (2017) emphasized that CWS and CWK allow better characterizing the
413 coexistence of multiple functional strategies beyond the influence of a single optimum. We
414 showed that TGBE strongly impacts CWV variations (Figs. 1, 2c and 2d) but also other moments
415 (Appendices S5 and S9). As a consequence, applying TDT along gradients also probably implies
416 addressing TGBE issues. Community-level metrics are more and more used to characterize the
417 functional composition of communities of plants (Violle et al. 2007), but also other organisms
418 (e.g., Newbold et al. 2012, Fierer et al. 2014, Pey et al. 2014). We stress here that these metrics
419 should not be viewed as direct proxies of underlying assembly processes, especially in harsh
420 environmental conditions that are the focus of much research and where TGBE more likely
421 occurs. Furthermore, acknowledging intraspecific variation in trait-based community analyses
422 has gained much momentum in recent years (Lepš et al. 2011, Violle et al. 2012, Siefert et al.

423 2015). Having intraspecific trait variation could extend beyond the trait limits of a pool defined
424 based on trait values averaged at species level (Violle et al. 2012), which should affect associated
425 trait range limits and therefore TGBE. Our individual-based modelling framework can
426 acknowledge the influence of intraspecific trait variation in community dynamics (Appendix S6),
427 but these data are mostly unavailable at large spatial scales of functional biogeography, so that
428 trait values averaged at species level are still mainly used in practice (Borgy et al. 2017b).

429 Community-level trait metrics are common currencies for functional biogeography
430 (Violle et al. 2014). They can be used to elucidate the drivers of taxonomic diversity patterns
431 (Lamanna et al. 2014) as well as to target conservation areas (Violle et al. 2017) or to map and
432 predict ecosystem properties from landscape to regional and global scales (Violle et al. 2015).
433 The approach is primarily based on the “CWM-optimality” hypothesis (Muscarella and Uriarte
434 2016), and the idea that CWV reflects the intensity of the local environmental filtering. Other
435 processes can affect local community assembly and functional composition (Hubbell 2001,
436 Levine and Murrell 2003, Mayfield and Levine 2010, Muscarella and Uriarte 2016), and our
437 work further underlines that the functional composition of the species pool providing immigrants
438 is influential. Taking into account the functional diversity of the species pool, and acknowledging
439 the underlying biogeographical and evolutionary dynamics, is an important issue that has only
440 recently come to focus (Patrick and Brown 2018, Spasojevic et al. 2018). TGBE shows the need
441 to better integrate local and regional dynamics when examining the functional composition of
442 local communities. Therefore, ecologists need to be aware of TGBE when interpreting patterns of
443 functional composition and their causes, notably at the extremes of environmental gradients.

444

445 **Declarations**

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450 (FRB; www.fondationbiodiversite.fr) in the context of the CESAB project ‘Causes and
451 consequences of functional rarity from local to global scales’ (FREE).

452 *Data Accessibility*

453 R code to generate the simulated data is provided in Appendix S2 and is archived on a Zenodo
454 URL link: <https://zenodo.org/record/1165400>.

455 The *aravo* dataset describing alpine plant communities is available in the *ade4* R package and is
456 described in Choler (2005).

457

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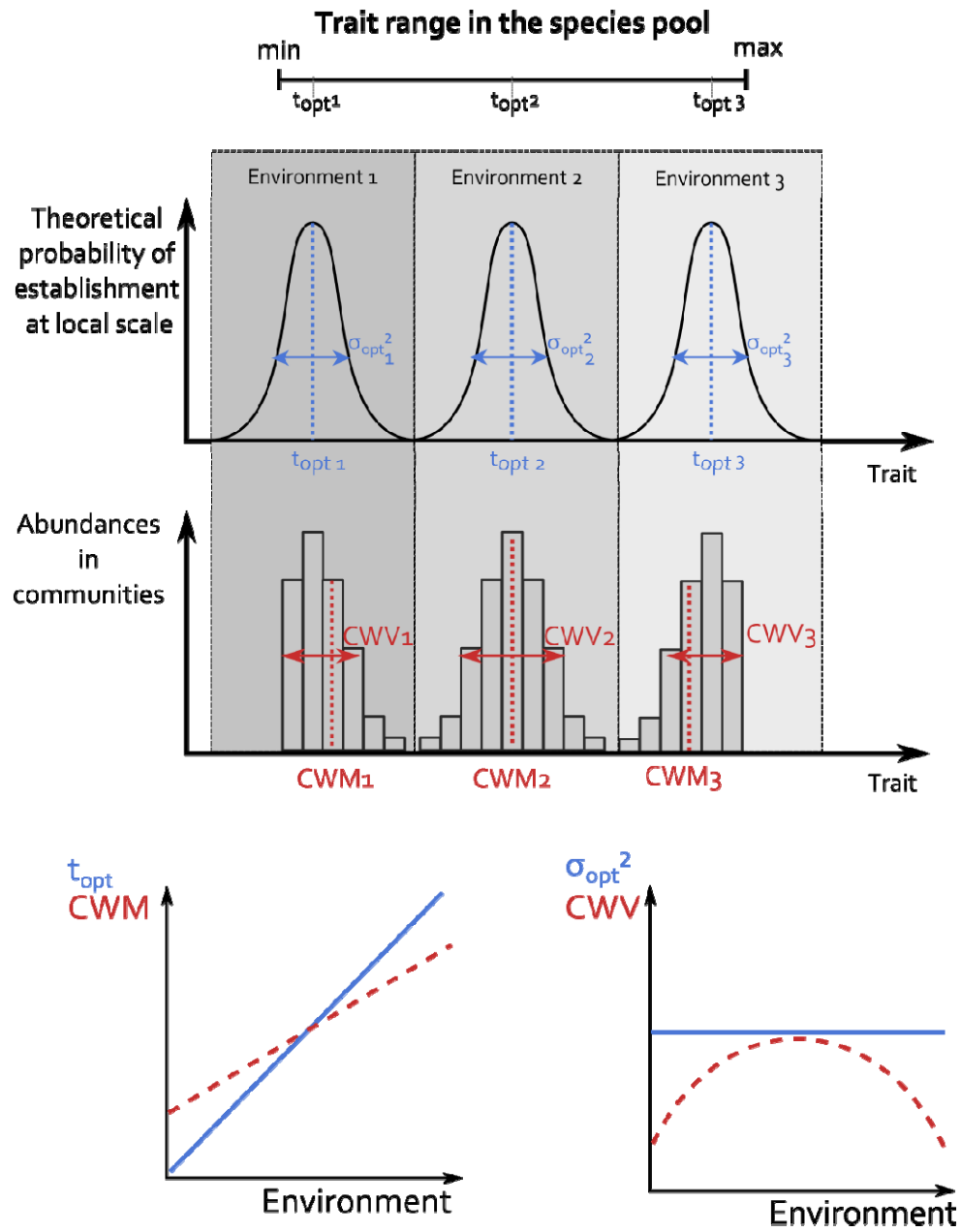
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- 574

575 **Figures**

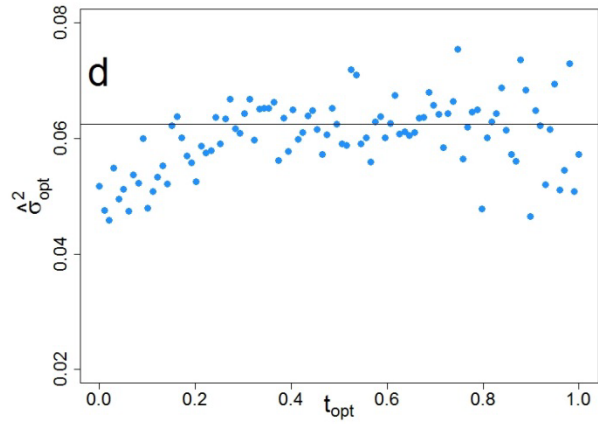
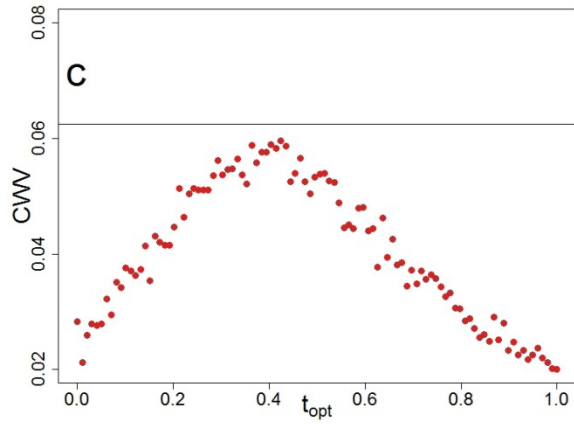
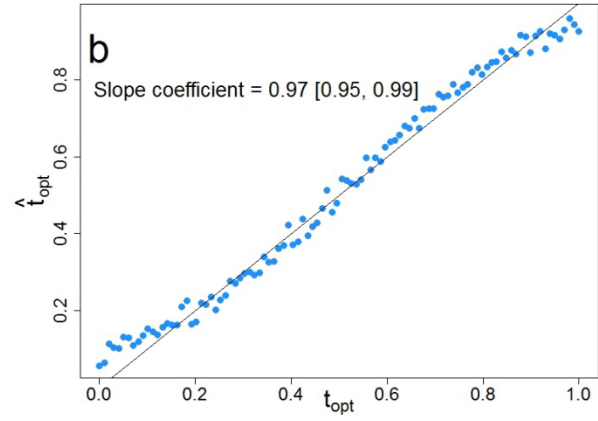
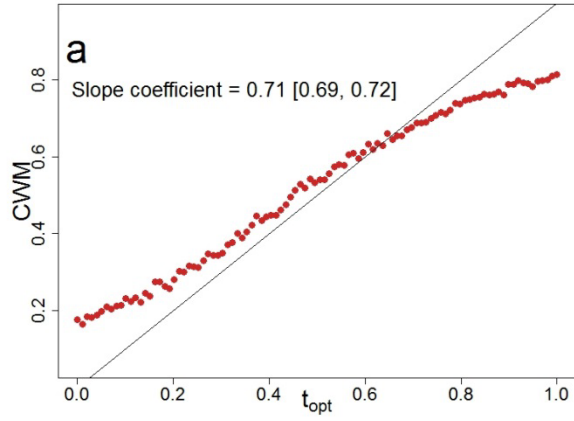
576 **Figure 1.** Departure of CWM and CWV from the parameters of environmental filtering, t_{opt} and
577 σ_{opt}^2 , respectively, due to trait limits in the species pool.

578 The trait distribution in communities (histograms) reflects the joint influence of trait range limits among
579 immigrants from the species pool (top horizontal black line), and of a Gaussian environmental filter
580 determining immigrant establishment success with mean t_{opt} (dashed blue lines) and standard deviation
581 σ_{opt}^2 (blue horizontal arrows) in specific environments (grey rectangles). The dashed red lines
582 represent the observed Community Weighted Mean (CWM) values in each community. CWM deviates
583 from t_{opt} when closer to the limits of the trait range in the species pool because of the bounded species
584 pool's trait range. The range of observed CWM values (red segment) is then smaller than the one of t_{opt}
585 values as shown in the CWM ~ Environment plot. Similarly, while σ_{opt}^2 , which represents the
586 environmental filtering intensity, remains constant over the environment gradient, CWV, depicted by the
587 horizontal red arrows, decreases when approaching environment selecting for trait values closed to the
588 species pool boundaries. The hump-shaped relationship between realized CWV and the environment thus
589 represents the influence of the trait range limits and not a more intense filtering at the extremes of the
590 gradient.



591

1 **Figure 2.** Variation in CWM and CWV values (left, red color), and of estimated \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$
2 (right, blue color), for simulated communities along t_{opt} gradient.
3 Communities were simulated with constant environmental filtering ($\sigma_{opt} = 0.25$), uniform distribution of
4 trait values and uniform abundances in the species pool. Top figures (a) and (b) represent CWM and \hat{t}_{opt} ,
5 and figures (c) and (d) represent CWV and $\hat{\sigma}_{opt}^2$. The \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$ values were obtained with the
6 ABC approach and correctly estimated the t_{opt} and σ_{opt}^2 values (b and d). Conversely, CWM departed from
7 t_{opt} and CWV was below σ_{opt}^2 when the influence of trait range limits increased at the extremes. The black
8 solid line represents equality of CWM and CWV to the parameters of environmental filtering (t_{opt} and
9 σ_{opt}^2 , respectively). Slope coefficients and the associated confidence intervals of the linear regression
10 equations between CWM and t_{opt} are displayed in panel (a) and (b). The mean of the difference between
11 σ_{opt}^2 and CWV (c) is twice higher than for the difference between σ_{opt}^2 and $\hat{\sigma}_{opt}^2$ (d) (respectively 2.23e-2
12 and 8.91e-3).

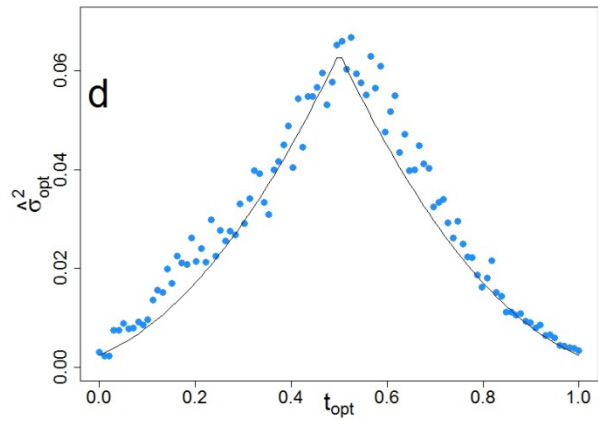
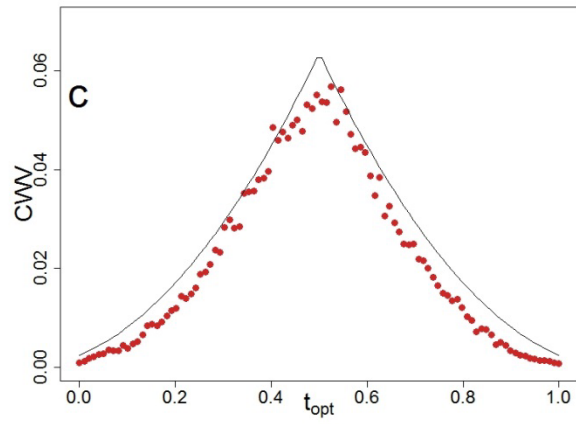
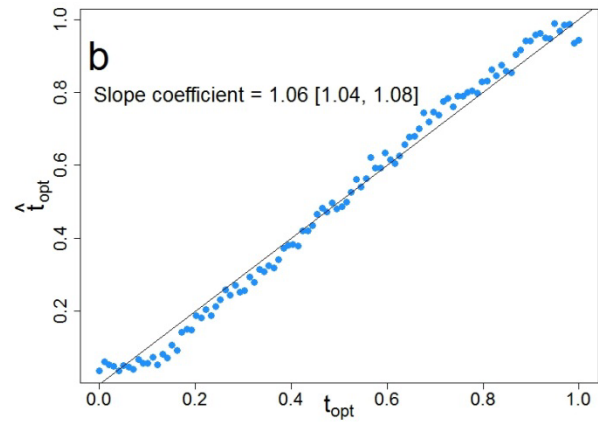
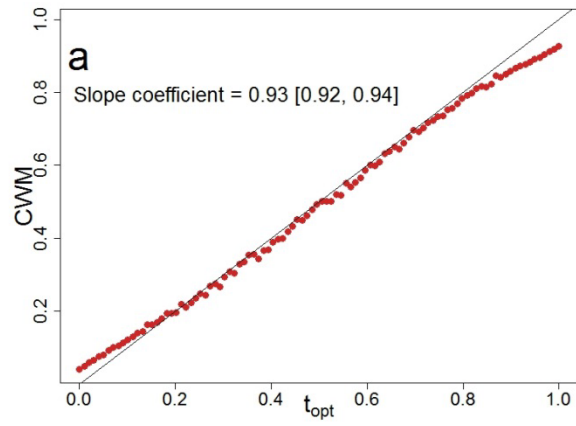


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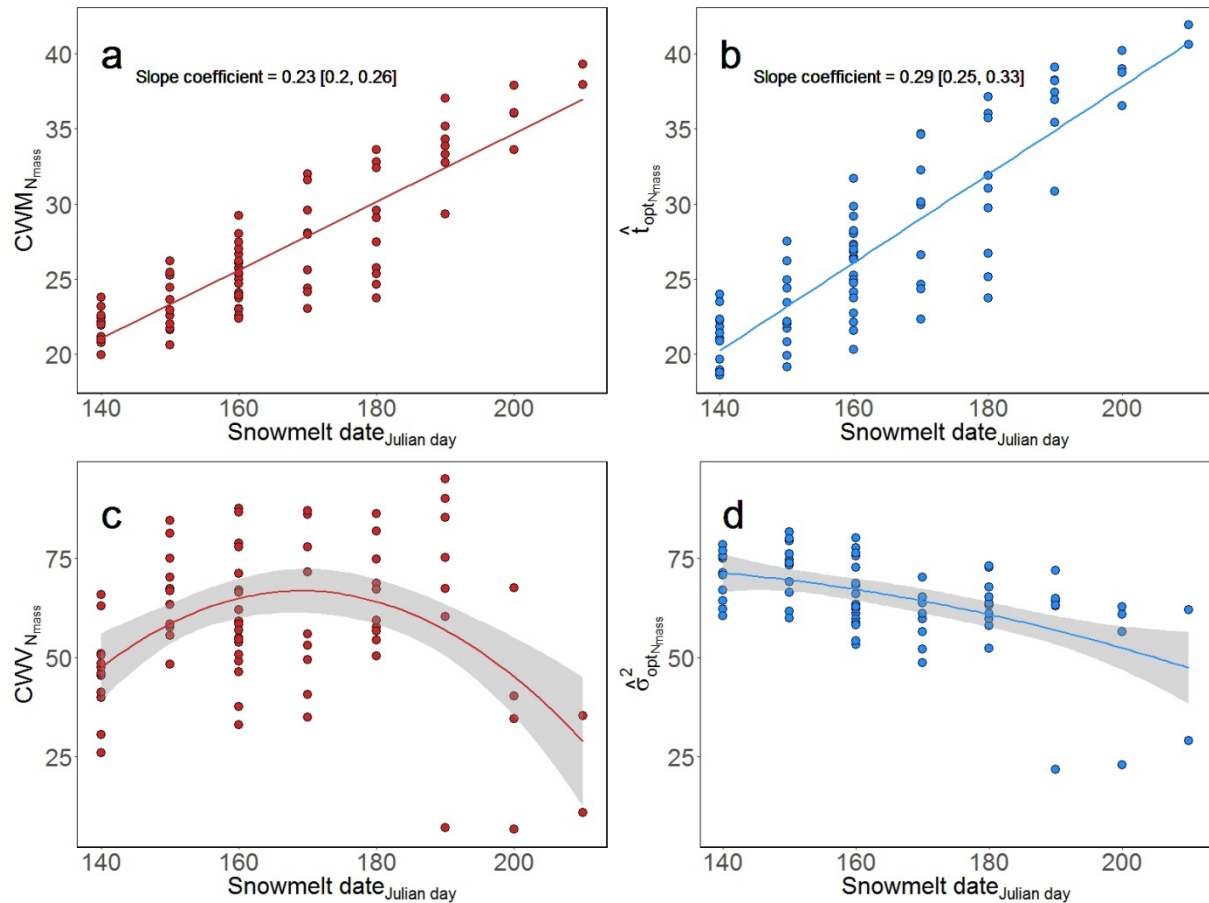
2

1 **Figure 3.** Variation in CWM and CWV (left, red color), and in estimated \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$ (right,
2 blue color) along the t_{opt} gradient, with increasing intensity of environmental filtering at the
3 extremes of the gradient.

4 Top figures (a) and (b) represent CWM and \hat{t}_{opt} , and figures (c) and (d) represent CWV and $\hat{\sigma}_{opt}^2$. The
5 estimation of parameters \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$, obtained with the ABC approach, acknowledges the effect of
6 trait range limits, and departs from CWM and CWV, respectively when the influence of the trait range
7 limits increases at the extremes. The black solid line represents equality of CWM and CWV to the
8 parameters of environmental filtering (t_{opt} and σ_{opt} , respectively). Slope coefficients and the associated
9 confidence intervals of the linear regression equations between CWM and t_{opt} are displayed in panel (a)
10 and (b). The mean of the difference between σ_{opt}^2 and CWV (c) and between σ_{opt}^2 and $\hat{\sigma}_{opt}^2$ (d) is
11 comparable but lower for the latter case (respectively 4.08 e-2 and 3.37e-2).



1
2
3



1

2 **Figure 4.** Relationships of CWV (red color) and estimated σ_{opt}^2 (blue color) for the leaf nitrogen
3 content on a mass basis (N_{mass} , panel a) and the specific leaf area (SLA, panel b),
4 according to the gradient of snow cover melting date (in Julian days, abscissa).

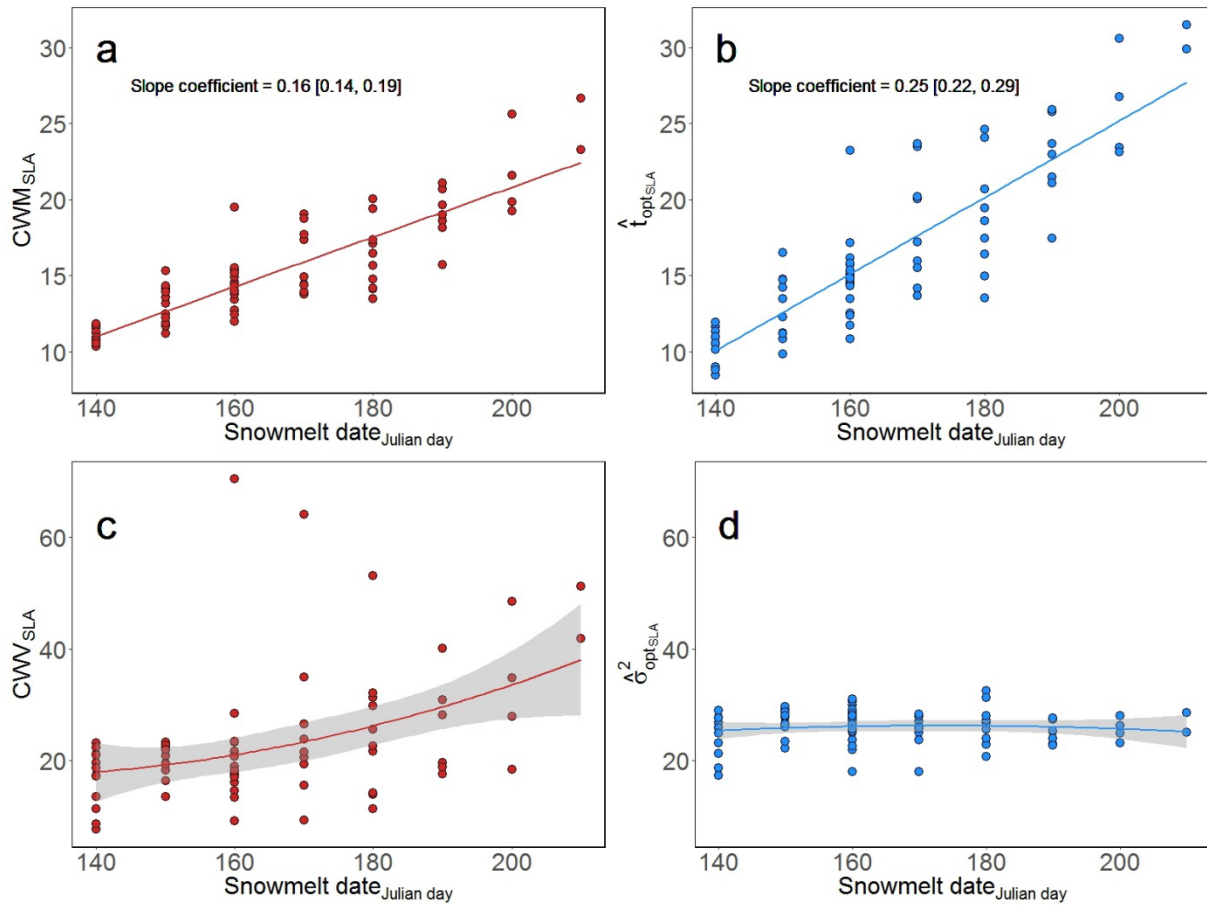
5 Linear regressions were fitted for each variable against the snowmelt date in panels a and c. While both

6 highly significant, the slope term was higher for with the estimated \hat{t}_{opt} (slope = 0.29) than with the

7 CWV (slope = 0.23). For the panels c and d, a quadratic regression between CWV and snowmelt date was

8 significant while the quadratic term became non-significant with $\hat{\sigma}_{opt}^2$. N_{mass} is measured in mg[N]/mg.

9



1

2 **Figure 5.** Relationships of CWV (red color) and estimated σ_{opt}^2 (blue color) for the specific leaf
3 area (SLA), according to the gradient of snow cover melting date (in Julian days,
4 abscissa).

5 Linear regressions were fitted for each variable against the snowmelt date in panels a and c. While both
6 highly significant, the slope term was higher for with the estimated \hat{t}_{opt} (slope = 0.25) than with the
7 CWV (slope = 0.16). For both panels c and d, both quadratic regressions between CWV and $\hat{\sigma}_{opt}^2$ with
8 snowmelt date were non-significant. SLA is measured in m²/kg.

9

1 Supporting information

2 Appendix S1. Moments of the located trait distribution.

3 With a uniform distribution of species trait values in the species pool ranging between a and
 4 b , and a local Gaussian environmental filter with parameters t_{opt} and σ_{opt} , the local trait
 5 distribution should follow a truncated Gaussian distribution, such as:

$$Eqn\ 1 \rightarrow CWM = t_{opt} + \frac{\varphi(\alpha) - \varphi(\beta)}{Z} \sigma_{opt}$$

$$Eqn\ 2 \rightarrow CWV = \sigma_{opt}^2 \left[1 + \frac{\alpha\varphi(\alpha) - \beta\varphi(\beta)}{Z} - \left(\frac{\varphi(\alpha) - \varphi(\beta)}{Z} \right)^2 \right]$$

$$Eqn\ 3 \rightarrow CWS = t_{opt}^3 + 3t_{opt}\sigma_{opt}^2 - \sigma \frac{(t_{opt}^2 + 2\sigma_{opt}^2 + bt_{opt} + b^2)\varphi(\beta) - (t_{opt}^2 + 2\sigma_{opt}^2 + at_{opt} + a^2)\varphi(\alpha)}{Z}$$

$$Eqn\ 4 \rightarrow CWK$$

$$= t_{opt}^4 + 6t_{opt}^2\sigma_{opt}^2 + 3\sigma^4$$

$$- \sigma \frac{(t_{opt}^3 + \sigma_{opt}^2(3b + 5t_{opt}) + bt_{opt}^2 + b^2t_{opt} + b^3)\varphi(\beta) - (t_{opt}^3 + \sigma_{opt}^2(3a + 5t_{opt}) + at_{opt}^2 + a^2t_{opt} + a^3)\varphi(\alpha)}{Z}$$

6

$$Eqn\ 5 \rightarrow m_k = (k-1)\sigma_{opt}^2 m_{k-2} + \mu m_{k-1} - \sigma_{opt} \frac{b^{k-1}\varphi\left(\frac{b-t_{opt}}{\sigma_{opt}}\right) - a^{k-1}\varphi\left(\frac{a-t_{opt}}{\sigma_{opt}}\right)}{\phi\left(\frac{b-t_{opt}}{\sigma_{opt}}\right) - \phi\left(\frac{a-t_{opt}}{\sigma_{opt}}\right)}, k = 1, 2, \dots$$

7 Where $\alpha = \frac{a-t_{opt}}{\sigma_{opt}}$, $\beta = \frac{b-t_{opt}}{\sigma_{opt}}$, $Z = \phi(\beta) - \phi(\alpha)$, φ is the probability density function of the
 8 standard normal distribution and Φ is its cumulative density function (Barr & Sherrill, 1999), m_k
 9 is the k^{th} moment of the truncated normal distribution (based on $m_{-1} = 0$ and $m_0 = 1$), a and b are
 10 the trait range limits (with $a < b$), t_{opt} the mean and σ_{opt} the standard deviation of the Gaussian

1 filtering function, $\alpha = \frac{a-t_{opt}}{\sigma_{opt}}$, $\beta = \frac{b-t_{opt}}{\sigma_{opt}}$, $Z = \phi(\beta) - \phi(\alpha)$, ϕ is the probability density function

2 of the standard normal distribution and Φ is its cumulative density function (Barr and Sherrill

3 1999).

4

5 **Reference**

6 Barr, D. R. and Sherrill, E. T. 1999. Mean and variance of truncated normal distributions. - Am. Stat. 53:
7 357–361.

8

1 **Appendix S2.** R code to simulate and analyze communities.

2 This example is divided into two parts. The first part simulates communities using the R package
3 *ecolottery* (Munoz et al. 2018), <https://cran.r-project.org/web/packages/ecolottery/index.html>). In
4 the example of the paper, the parameters used to build communities are the following: species
5 pool with 100.000 individuals belonging to 100 species with equal abundances (i.e., 1000
6 individuals each), and species trait values drawn from a uniform distribution between $a=0$ and
7 $b=1$. Each community includes 500 individuals and the immigrants establishing in communities
8 are drawn from the species pool. Stabilizing environmental filtering determines establishment
9 probability of immigrants depending on the departure of their trait value t from a local optimum
10 t_{opt} . We thus choose a Gaussian filtering function of mean t_{opt} , which varies among communities,
11 and standard deviation σ_{opt} equal to 0.25. The data frame of simulated communities is called *sim*.
12 The community-weighted mean (CWM) and variance (CWV) are calculated for each community,
13 as well as functional dispersion (Laliberté and Legendre 2010) and Rao's entropy (Botta-Dukát
14 2005).

15 The second section estimates the two parameters t_{opt} and σ_{opt} in each community, by comparing
16 observed summary statistics of the community to summary statistics simulated over a broad
17 range of t_{opt} and σ_{opt} values, with approximate Bayesian computation (ABC) analysis
18 (*coalesc_abc* function, Munoz et al. 2018).

19 Finally, the third just presents the code to generate the plot equivalent to the Figure 2 of the
20 manuscript.

```
21 rm(list = ls())
22 #-----
23 # PART I/ Generate simulations: uniform species abundances and trait values in
24 # regional pool, trait values bounded between 0 and 1
25 #-----
26 # Installing package from CRAN and loading
27 install.packages("ecolottery")
28 library(ecolottery)
29 J <- 500
30 m <- 1
31 sim <- c()
32 # Trait range
33 a <- 0
34 b <- 1
35 # Generate a regional pool/metacommunity with equal species abundances and
36 # uniform trait distribution
37 # 100000 individuals, 100 species, trait values bounded between 0 and 1
38 pool <- cbind(1:100000, rep(sample(1:100), 1000), rep(NA, 100000))
39 colnames(pool) <- c("ind", "sp", "tra")
40 t.sp <- runif(1000, min = a, max = b)
41 pool[, "tra"] <- t.sp[pool[, "sp"]]
42 # Intraspecific variability
43 pool[, "tra"] <- rnorm(pool[, "tra"], pool[, "tra"], 0.001)
```

```
44 pool[, "tra"] <- ifelse(pool[, "tra"] > 1, 0.99, pool[, "tra"])
45 pool[, "tra"] <- ifelse(pool[, "tra"] < 0, 0.01, pool[, "tra"])
46 # Generate communities with habitat filtering, in 100 communities with
47 # distinct topt
48 # sigmaopt is fixed at 0.25
49 topt <- seq(from = a, to = b, by = (b-a) / 99)
50 sigmaopt <- 0.25
51 for(j in 1:length(topt)) {
52   comm <- coalesc(J, m, pool=pool, traits=NULL,
53                 filt = function(x) exp(-(x-topt[j])^2/(2*sigmaopt^2)))
54   sim <- rbind(sim, cbind(rep(j, nrow(comm$com)),
55                           rep(topt[j], nrow(comm$com)), comm$com))
56 }
57 # Column names of the metacommunity dataset
58 colnames(sim) <- c("com", "topt", "ind", "sp", "tra")
59 # Conversion to data.frame
60 sim <- as.data.frame(sim)
61 # Table of species abundances per community
62 temp <- as.data.frame(table(sim$sp, sim$com))
63 colnames(temp) <- c("sp", "com", "ab")
64 # Relative abundances
65 temp$abrel <- temp$ab / J
66 # Merging abundances with simulation
```

```
67 library(dplyr)
68 sim$sp_com <- paste(sim$sp, sim$com, sep="_")
69 temp$sp_com <- paste(temp$sp, temp$com, sep="_")
70 sim <- inner_join(sim, temp[, c("sp_com", "ab", "abrel")],
71                 by="sp_com")
72 # Computing CWM => not weighted by abundances because of intraspecific variability
73 cwm <- tapply(sim$tra, sim$com, mean)
74 cwm <- data.frame("com" = names(cwm), "cwm" = as.numeric(cwm))
75 sim$com <- as.character(sim$com)
76 sim <- inner_join(sim, cwm, by = "com")
77
78 # Computing CWV => not weighted by abundances because of intraspecific variability
79 cwv <- tapply(sim$tra, sim$com, var)
80 cwv <- data.frame("com" = names(cwv), "cwv" = as.numeric(cwv))
81 sim <- inner_join(sim, cwv, by = "com")
82
83 # Computing Fdis and Rao
84 library(FD)
85 FD_com <- c()
86 for(i in 1:length(unique(sim$com))){
87   com <- sim[which(sim$com == unique(sim$com)[i]), c("ind", "tra", "abrel")]
88   com <- com[!duplicated(com), ]
89   tra_ind <- com[, c("ind", "tra")]
```



```
90   rownames(tra_ind) <- tra_ind$ind
91   tra_ind <- tra_ind[, "tra", drop = FALSE]
92   ab_ind <- rep(1, nrow(com))
93   names(ab_ind) <- com$ind
94   tmp <- dbFD(tra_ind, a = ab_ind, w.abun = FALSE)
95   FD_com <- rbind(FD_com, c(unique(sim$com)[i], as.numeric(tmp$FDis),
96 as.numeric(tmp$RaoQ)))
97 }
98 FD_com <- data.frame(FD_com)
99 colnames(FD_com) <- c("com", "fdis", "rao")
100 sim <- inner_join(sim, FD_com, by = "com")
101 sim$fdis <- as.numeric(as.character(sim$fdis))
102 sim$rao <- as.numeric(as.character(sim$rao))
103 # Plot showing correlations between CWV and functional diversity metrics
104 library(GGally)
105 ggpairs(sim[!duplicated(sim$com), c("cwv", "fdis", "rao")]) +
106   theme_classic()
107 #-----
108 # PART II/ ABC-based parameter estimation
109 #-----
110 require(vegan)
111 # Function to compute 6 summary statistics: the four first orders of community
112 # weighted moments (mean, variance, skewness and kurtosis) and two taxonomic
```

```
113 # statistics (specific richness and Shannon diversity index)
114 f.sumstats <- function(com){
115     array(dimnames = list(c("cwm", "cwv", "cws", "cwk", "S", "Es")),
116           c(mean(com[, 3]), var(com[, 3]), e1071::skewness(com[, 3]),
117             e1071::kurtosis(com[, 3]), vegan::specnumber(table(com[, 2])),
118             vegan::diversity(table(com[, 2]))))
119 }
120
121 # Observed summary statistics
122 ss.obs <- c()
123 for(i in 1:length(unique(sim$com))) {
124     comm <- sim[which(sim$com == unique(sim$com)[i]), c("ind", "sp", "tra")]
125     ss.obs[[i]] <- f.sumstats(comm)
126 }
127 comm.sd <- unlist(lapply(ss.obs, function(x) sqrt(x["cwv"])))
128 comm.cwm <- unlist(lapply(ss.obs, function(x) x["cwm"]))
129 # Possibility to reconstruct the pool of species from communities composition
130 # true_pool <- pool
131 # pool <- sim[, c("ind", "sp", "tra")]
132
133 # Filtering function
134 filt_gaussian <- function(t, params) exp(-(t-params[1])^2/(2*params[2]^2))
135 # Parameters values
```

```
136  params <- data.frame(rbind(c(min(pool[, "tra"]), max(pool[, "tra"])),
137                          c(min(comm.sd), sd(pool[, "tra"]))))
138  row.names(params) <- c("topt", "sigmaopt")
139  # Number of values to sample in prior distributions
140  nb.samp <- 10^6
141  # ABC estimation of the parameters based on summary statistics of the observed
142  # community
143  # The function makes vary the migration rate, m, and the parameters of
144  # environmental filtering defined in params
145  res <- c()
146  for(i in 1:length(unique(sim$com))) {
147    comm <- sim[which(sim$com == unique(sim$com)[i]), c("ind", "sp", "tra")]
148    res[[i]] <- coalesc_abc(comm, pool, f.sumstats = f.sumstats,
149                          filt.abc = filt_gaussian,
150                          params=params, nb.samp = 1000, parallel = TRUE,
151                          tol = 1, pkg = c("e1071", "vegan"),
152                          method = "neuralnet")
153  }
154  # Mean estimated values of the parameters
155  topt.abc <- unlist(lapply(res, function(x) weighted.mean(x$abc$adj.value[, "topt"], w =
156  x$abc$weights)))
157  sigmaopt.abc <- unlist(lapply(res, function(x) weighted.mean(x$abc$adj.value[,
158  "sigmaopt"], w = x$abc$weights)))
```

```
159 m.abc <- unlist(lapply(res, function(x) weighted.mean(x$abc$adj.value[, "m"], w =
160 x$abc$weights)))
161 # Adding topt and sigmaopt to original dataset
162 library(dplyr)
163 topt_sim <- data.frame("com" = unique(sim$com), "topt_abc" = topt.abc)
164 sim <- inner_join(sim, topt_sim, by = "com")
165 sigmaopt_sim <- data.frame("com" = unique(sim$com), "sigmaopt_abc" = sigmaopt.abc)
166 sim <- inner_join(sim, sigmaopt_sim, by = "com")
167 m_sim <- data.frame("com" = unique(sim$com), "m_abc" = m.abc)
168 sim <- inner_join(sim, m_sim, by = "com")
169
170 ##-----
171 # PART III/ Plots
172 ##-----
173
174 simplot <- sim[!duplicated(sim$com), ]
175 # Slope tests
176 mobs <- lm(cwm ~ topt, data = simplot)
177 mabc <- lm(topt_abc ~ topt, data = simplot)
178 # Quadratic regression for CWV
179 mvobs <- lm(cwv ~ topt + I(topt^2), data = simplot)
180 mvabc <- lm(sigmaopt_abc ~ topt + I(topt^2), data = simplot)
181 obs_slope <- paste0("Slope coefficient = ", round(summary(mobs)$coefficients[2, 1], 2),
182 " [", round(confint(mobs)[2, 1], 2), ", ", round(confint(mobs)[2, 2], 2), " ]")
```

```
183 abc_slope <- paste0("Slope coefficient = ",round(summary(mabc)$coefficients[2, 1], 2),
184 " [" , round(confint(mabc)[2, 1], 2), " , ",round(confint(mabc)[2, 2], 2), " ]")
185 # Four panels
186 par(mfrow = c(2, 2), mai = c(1, 0.9, 0.1, 0.3))
187 y_lim <- c(round((min(simpplot$cwm, simpplot$topt_abc)*2/2), 2),
188           round((max(simpplot$cwm, simpplot$topt_abc)*2/2), 2))
189 # CWM ~ topt
190 plot(simpplot$topt, simpplot$cwm, xlab = "", ylab = "", xaxt = "n", yaxt = "n",
191       xlim = c(0, 1), ylim = c(y_lim[1], y_lim[2]),
192       col = "firebrick3", pch = 16, cex = 1.5)
193 axis(1, cex.axis = 1.4)
194 mtext(expression("t"["opt"]), side = 1, line = 2.2, cex = 2)
195 axis(2, cex.axis = 1.4)
196 mtext("CWM", side = 2, line = 2.2, cex = 2)
197 abline(0, 1, lwd = 1)
198 legend(x = -0.1, y = 11/10 * y_lim[2],
199       bty = "n", legend = "a", cex = 2, col = "black")
200 legend(-0.2, 10/10 * y_lim[2], obs_slope, bty = "n", cex = 2)
201
202 # topt_ABC ~ topt
203 plot(simpplot$topt, simpplot$topt_abc, xlab = "", ylab = "", xaxt = "n",
204       yaxt = "n", xlim = c(0, 1), ylim = c(y_lim[1], y_lim[2]),
205       col = "dodgerblue", pch = 16, cex = 1.5)
```

```
206 axis(1, cex.axis = 1.4)
207 mtext(expression("t"["opt"]), side = 1, line = 2.2, cex = 2)
208 axis(2, cex.axis = 1.4)
209 mtext(expression(hat("t")["opt"]), side = 2, line = 2.2, cex = 2)
210 abline(0, 1, lwd = 1)
211 legend(x = -0.1, y = 11/10 * y_lim[2],
212        bty = "n", legend = "b", cex = 2, col = "black")
213 legend(-0.2, 10/10 * y_lim[2], abc_slope, bty = "n", cex = 2)
214
215 # CWV ~ topt
216 y_lim <- c(round((min(simplot$cwv, simplot$sigmaopt_abc^2) * 9/10), 2),
217           round((max(simplot$cwv, simplot$sigmaopt_abc^2) * 11/10), 2))
218
219 cwv_diff <- mean(abs(simplot$cwv - 0.25^2))
220 cwv_diff <- scales::scientific_format()(cwv_diff)
221 plot(simplot$topt, simplot$cwv, xlab = "", ylab = "", xaxt = "n", yaxt = "n",
222      xlim = c(0, 1), ylim = c(y_lim[1], y_lim[2]),
223      col = "firebrick3", pch = 16, cex = 1.5)
224 legend(x = -0.1, y = y_lim[2] * 11/10, bty = "n", legend = "c", cex = 2, col = "black")
225 axis(1, cex.axis = 1.4)
226 mtext(expression("t"["opt"]), side = 1, line = 2.2, cex = 2)
227 axis(2, cex.axis = 1.4)
228 mtext("CWV", side = 2, line = 2.2, cex = 2)
```

```
229  abline(0.25^2, 0, cex = 2)

230

231  # sigmaopt_ABC^2 ~ topt

232  sigmaopt_abc_diff <- mean(abs(simplot$sigmaopt_abc^2 - 0.25^2))

233  sigmaopt_abc_diff <- scales::scientific_format()(sigmaopt_abc_diff)

234  plot(simplot$topt, simplot$sigmaopt_abc^2, xlab = "", ylab = "", xaxt = "n",

235       yaxt = "n", xlim = c(0, 1), ylim = c(y_lim[1], y_lim[2]),

236       col = "dodgerblue", pch = 16, cex = 1.5)

237  legend(x = -0.1, y = y_lim[2] * 11/10,

238        bty = "n", legend = "d", cex = 2, col = "black")

239  axis(1, cex.axis = 1.4)

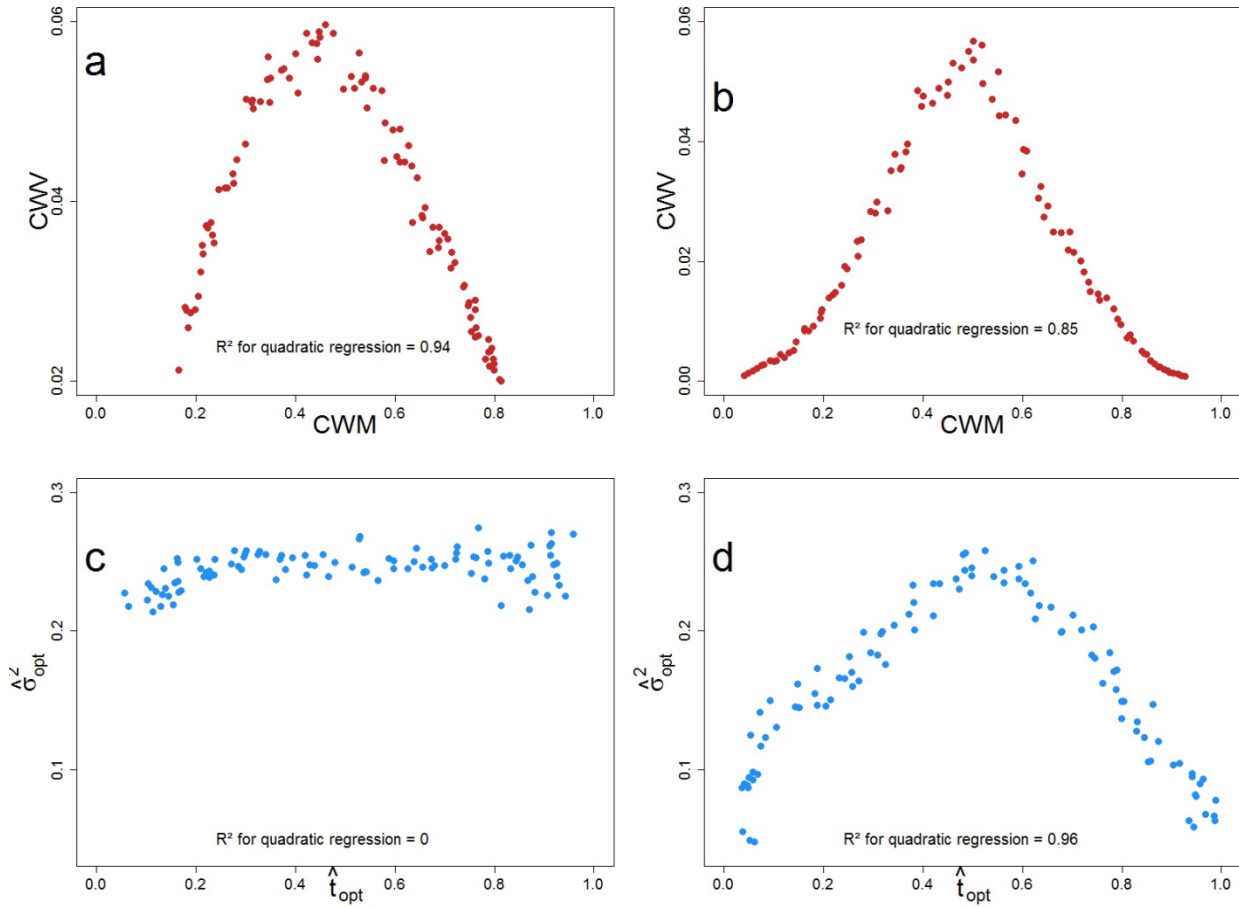
240  mtext(expression("t"["opt"]), side = 1, line = 2.2, cex = 2)

241  axis(2, cex.axis = 1.4)

242  mtext(expression(hat(sigma) ["opt"] ^"2"), side = 2, line = 2.2, cex = 2)

243  abline(0.25^2, 0, cex = 2)
```

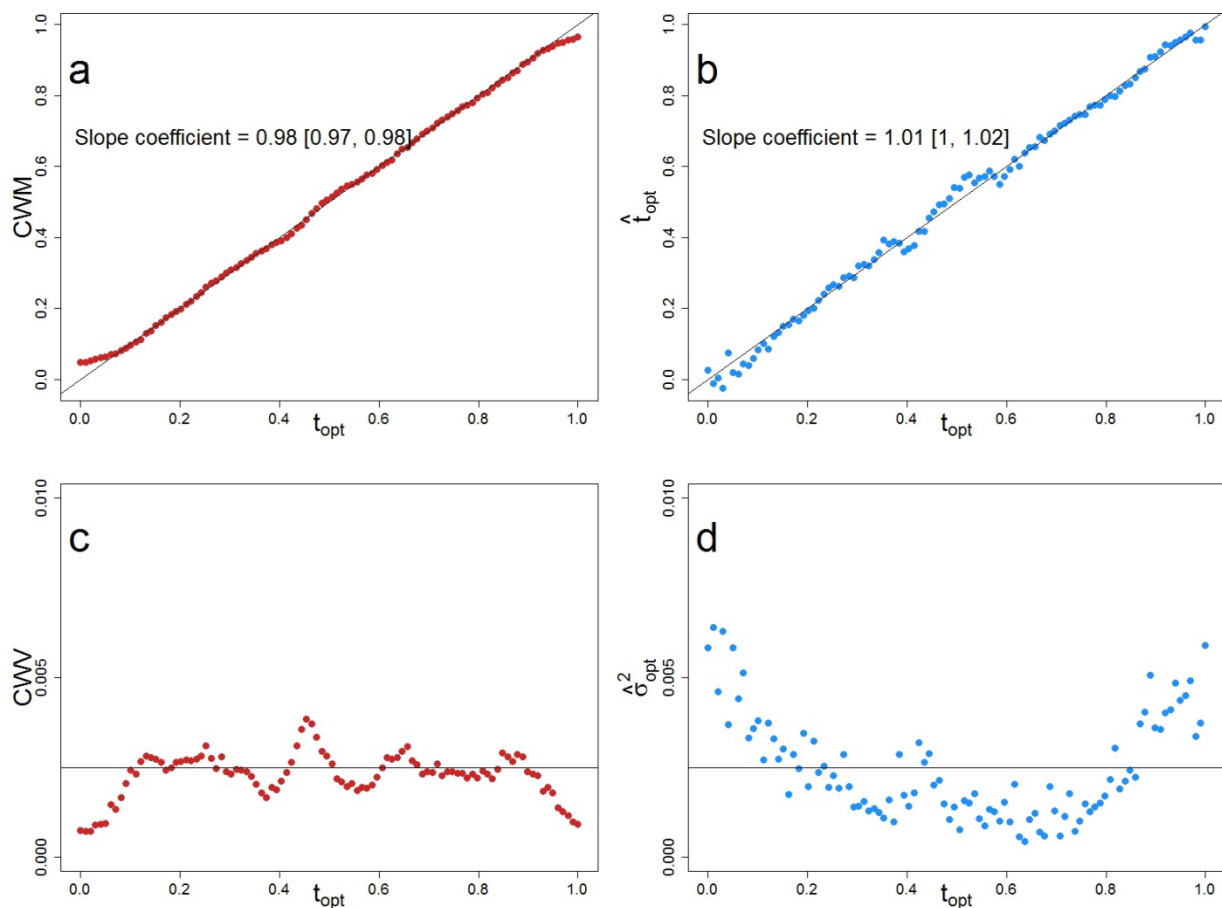
244 **Appendix S3.** Variation of CWW values with CWM (top, red color), and of $\hat{\sigma}_{opt}^2$ with t_{opt} and
245 (bottom, blue color), for two sets of simulated communities with constant (left, $\sigma_{opt} = 0.25$) or
246 varying (σ_{opt} from 0.25 to 0.05, peaking at $t_{opt} = 0.5$) intensity of environmental filtering.



247

248 **Appendix S4.** Analysis of simulated communities with constant and strong environmental filtering ($\sigma_{opt} =$
249 0.05), low intraspecific variability ($\sigma = 0.001$ for each species trait value) and uniform distribution of
250 species pool abundances.

251 The left red curves show the variation of CWM (top) and CWV (bottom) according to t_{opt} . The right blue
252 curves show the estimated \hat{t}_{opt} (top) and $\hat{\sigma}_{opt}^2$ (bottom) values according to t_{opt} . The black solid line
253 represents equality of CWM and CWV to the parameters of environmental filtering (t_{opt} and σ_{opt} ,
254 respectively). Slope coefficients and the associated confidence intervals of the linear regression equations
255 between CWM / \hat{t}_{opt} and t_{opt} are displayed in panel (a) and (b). The mean of the difference between σ_{opt}^2
256 and CWV (c) is comparable to the difference between σ_{opt}^2 and $\hat{\sigma}_{opt}^2$ (d) (respectively 6.02e-2 and 6e-2).



257

258

259 **Appendix S5.** Community-weighted skewness (CWS) and kurtosis (CWK) of simulated communities.

260 CWS is calculated for community j as

$$\text{Eqn. 5} \rightarrow CWS_j = \frac{\sum_{i=1}^S p_{ij}(t_{ij} - CWM_j)^3}{CWM_j^{3/2}}$$

261 and CWK is calculated for community j as

$$\text{Eqn. 6} \rightarrow CWK_j = \frac{\sum_{i=1}^S p_{ij}(t_{ij} - CWM_j)^4}{CWM_j^2} - 3$$

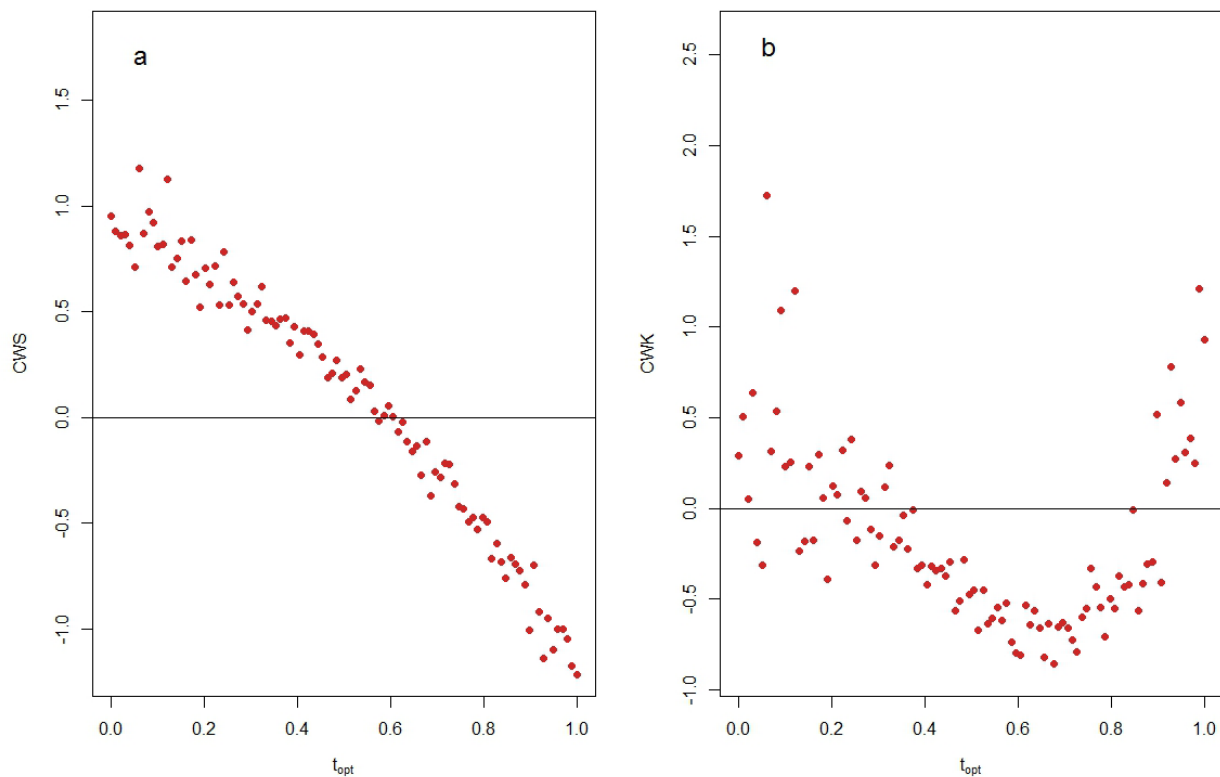
262 Where S is the number of species in community j , p_{ij} is the relative abundance of species i in community j ,

263 t_{ij} is the average trait value of species i in community j .

264 Panel (a) displays the variation of CWS and panel (b) of CWK in simulated communities according to t_{opt} ,

265 with uniform species pool abundances and constant environmental filtering ($\sigma_{opt} = 0.25$; same dataset as in

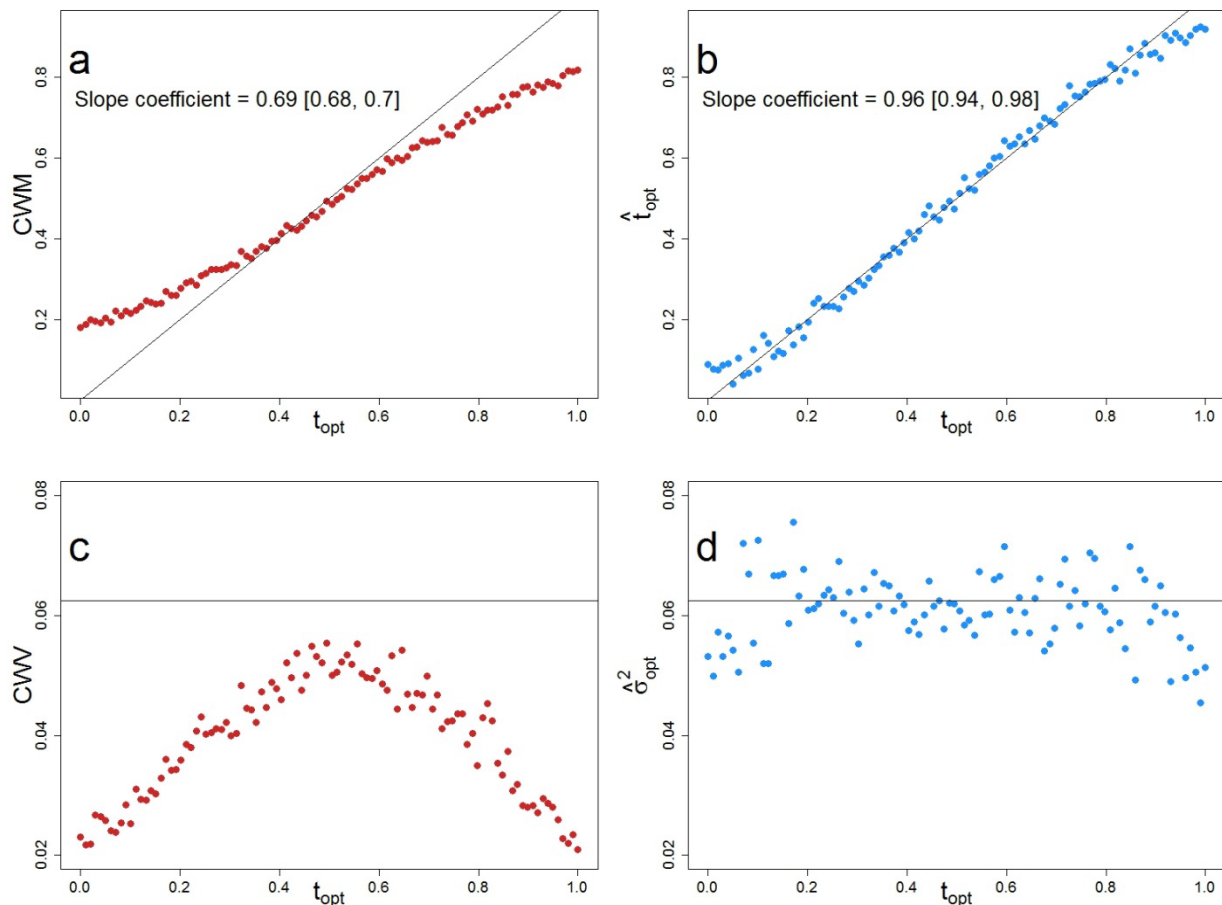
266 Fig. 2).



267

268 **Appendix S6.** Variation of CWM and CWV according to t_{opt} , with constant environmental filtering
269 intensity ($\sigma_{opt} = 0.25$), large intraspecific variability ($\sigma = 0.1$ for each species trait value) and a uniform
270 distribution of species pool abundances.

271 The left part (red curves) shows the variation of CWM (top) and CWV (bottom) according to t_{opt} . The
272 right part (blue curves) shows the estimated \hat{t}_{opt} (top) and $\hat{\sigma}_{opt}^2$ (bottom) values. The black solid line
273 represents equality of CWM and CWV to the parameters of environmental filtering (t_{opt} and σ_{opt} ,
274 respectively). Slope coefficients and the associated confidence intervals of the linear regression equations
275 between CWM / \hat{t}_{opt} and t_{opt} are displayed in panel (a) and (b). The mean of the difference between σ_{opt}^2
276 and CWV (c) is twice higher than the difference between σ_{opt}^2 and $\hat{\sigma}_{opt}^2$ (d) (respectively $2.3e-2$ and
277 $4.78e-3$).

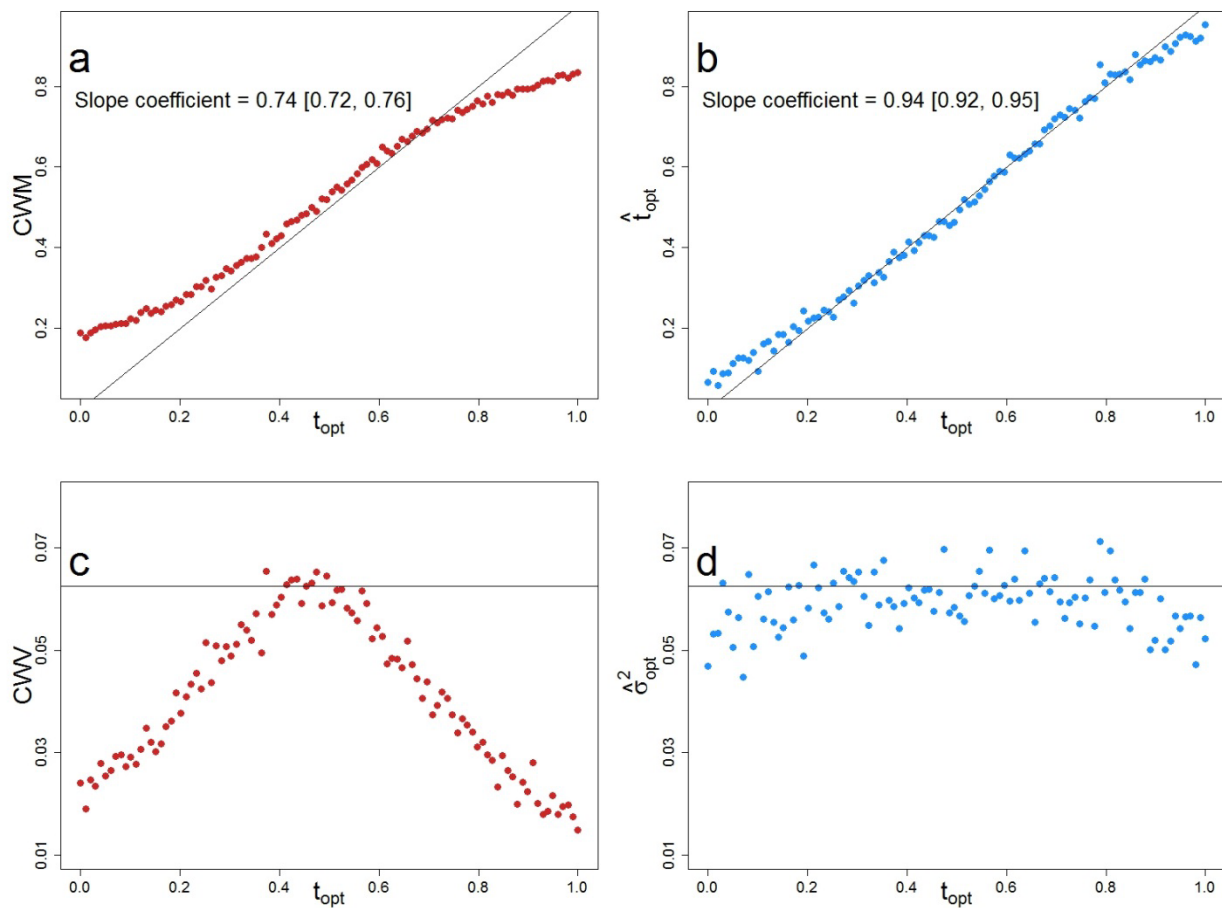


278

279

280 **Appendix S7.** Variation of CWM and CWV according to t_{opt} , with constant environmental filtering
281 intensity ($\sigma_{opt} = 0.25$) and a log-series (biodiversity parameter $\theta = 50$) distribution of species pool
282 abundances.

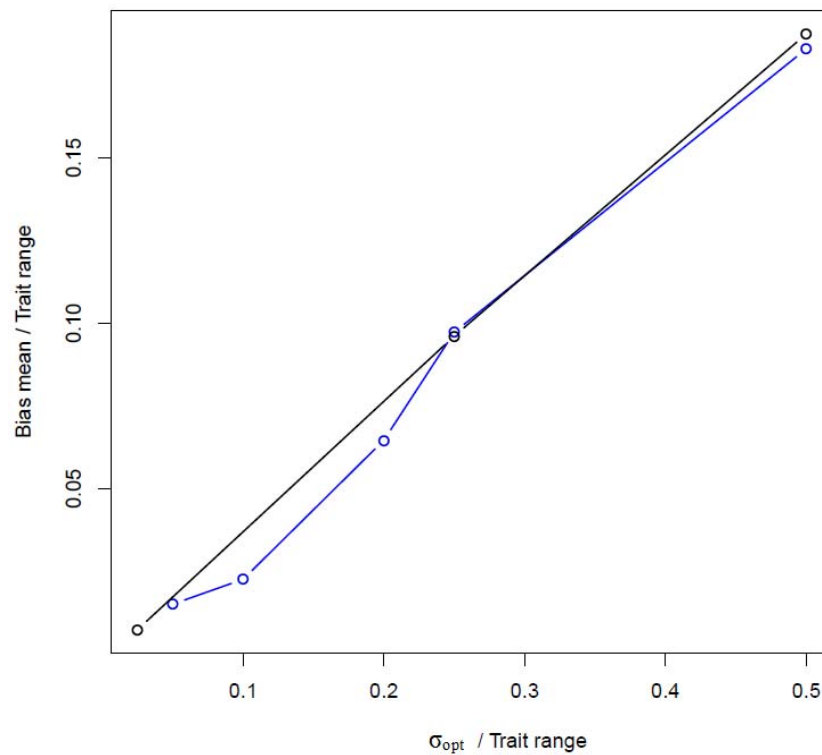
283 The left red curves show the variation of CWM (top) and CWV (bottom) according to t_{opt} . The right blue
284 curves show the estimated \hat{t}_{opt} (top) and $\hat{\sigma}_{opt}^2$ (bottom) values. The black solid line represents equality
285 of CWM and CWV to the parameters of environmental filtering (t_{opt} and σ_{opt}^2 , respectively). Slope
286 coefficients and the associated confidence intervals of the linear regression equations between CWM /
287 \hat{t}_{opt} and t_{opt} are displayed in panel (a) and (b). The mean of the difference between σ_{opt}^2 and CWV (c) is
288 twice higher than the difference between σ_{opt}^2 and $\hat{\sigma}_{opt}^2$ (d) (respectively $2.18e-2$ and $4.79e-3$).



289

290

291 **Appendix S8.** Influence of environmental filtering intensity and trait range extent on the
292 departure of CWM from t_{opt} .
293 The global deviation of CWM from t_{opt} over the trait range (average distance between CWM and 1:1 line),
294 summarizes the influence of the trait range limits on CWM over the whole environmental gradient. Blue,
295 resp. black, points represent simulations with a trait range on [0; 1], resp. [0; 2], and varying filtering
296 intensity (σ_{opt} , on abscissa).



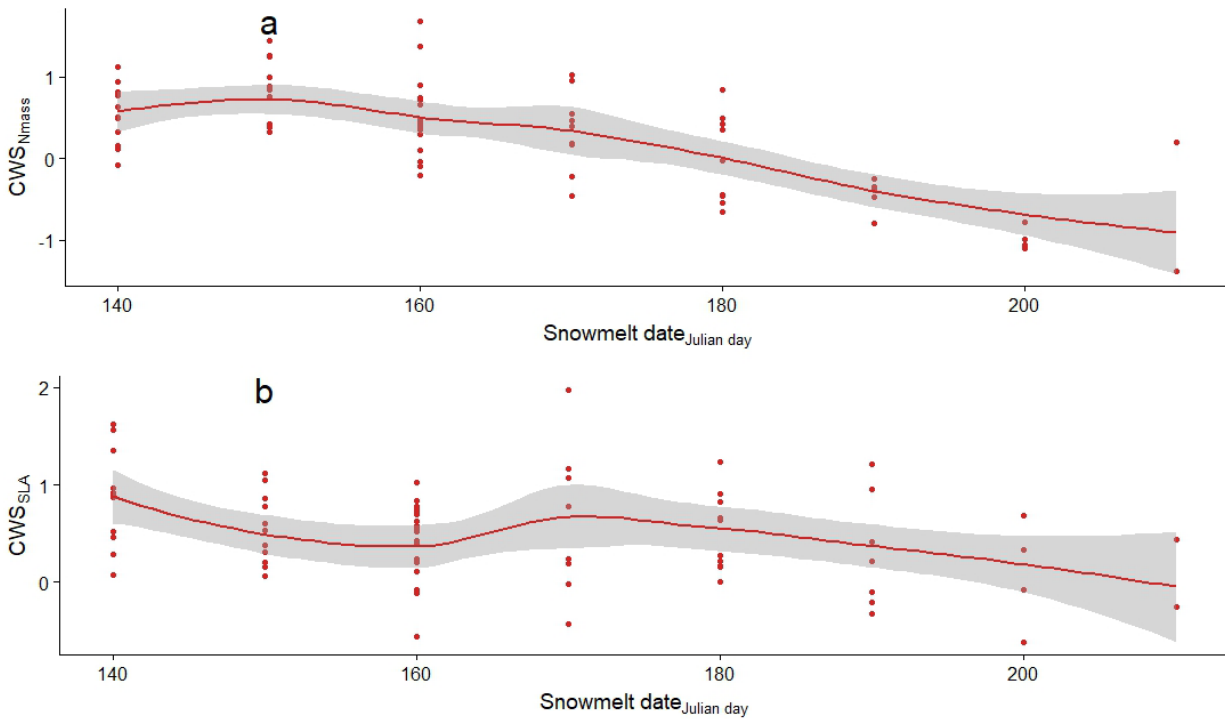
297

298

299 **Appendix S9.** Observed weighted skewness in communities (CWS) for the *aravo* dataset.

300 Panels a & b display the result for the alpine plant communities for N_{mass} (panel a) and SLA (panel b).

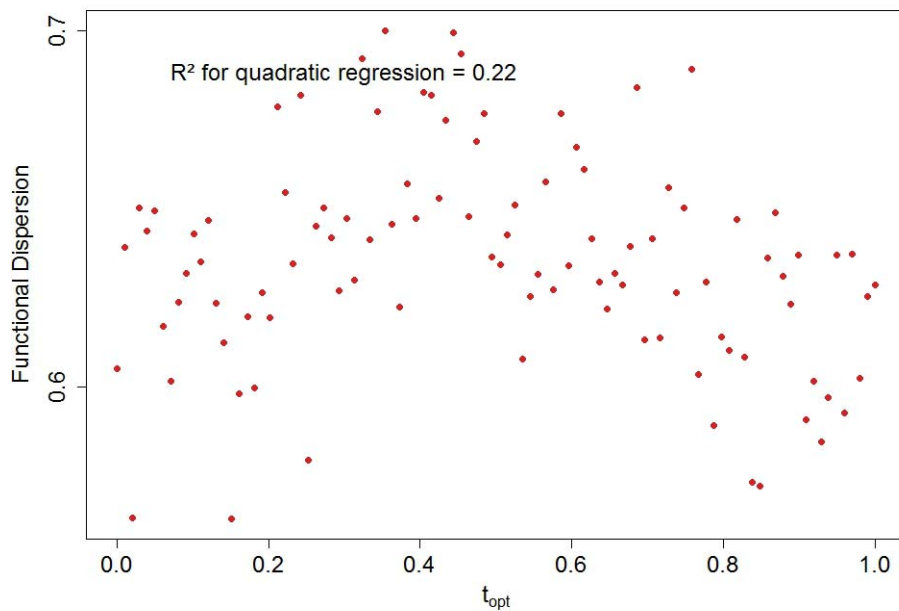
301



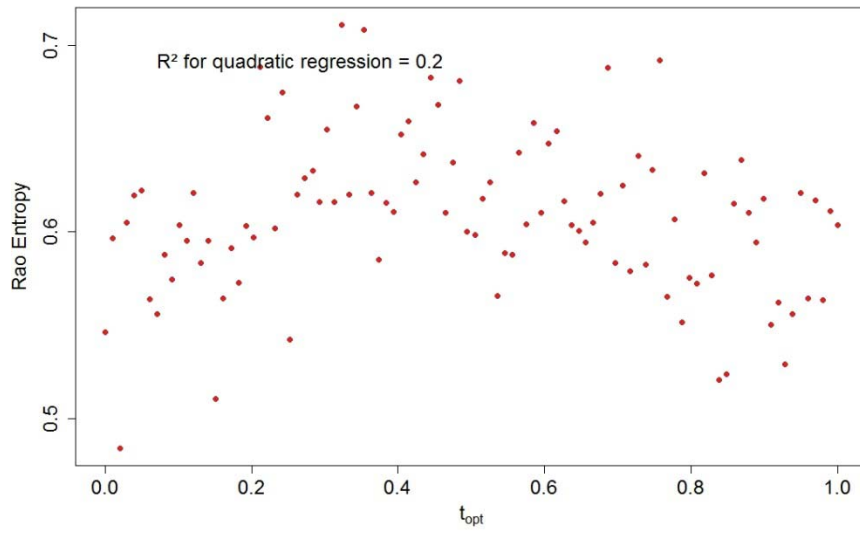
302

303

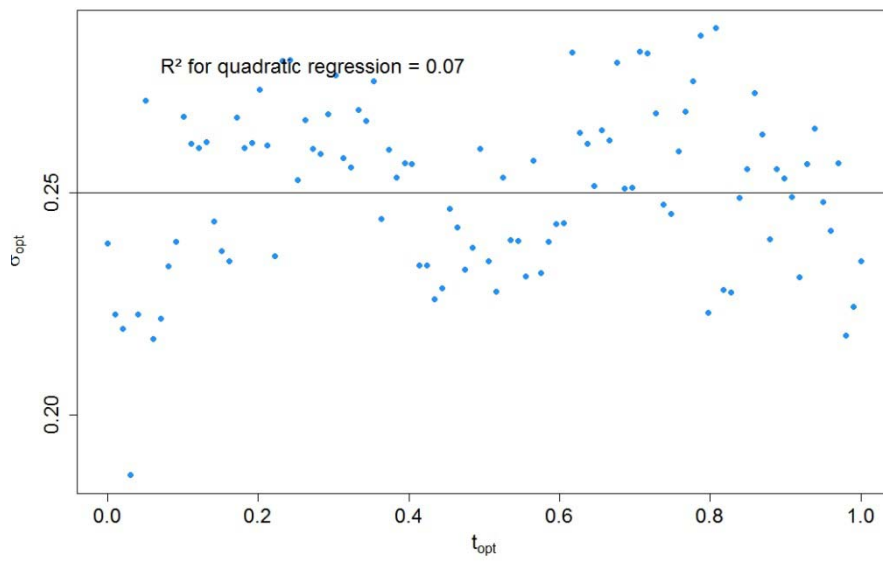
304 **Appendix S10.** Variation of functional dispersion, Rao's quadratic entropy and $\hat{\sigma}_{opt}$ according to t_{opt} ,
305 with constant environmental filtering intensity ($\sigma_{opt} = 0.25$) and uniform distribution of species pool
306 abundances.
307 The first two red curves show the variation of functional dispersion (first panel) and Rao's quadratic
308 entropy (second panel) according to t_{opt} . The third right blue curve shows the estimated $\hat{\sigma}_{opt}$ values. The
309 black solid line represents equality of CWV to the parameter of environmental filtering σ_{opt} . The fraction
310 of variance explained by quadratic regression between the three metrics and σ_{opt} (R^2) are displayed.



311



312

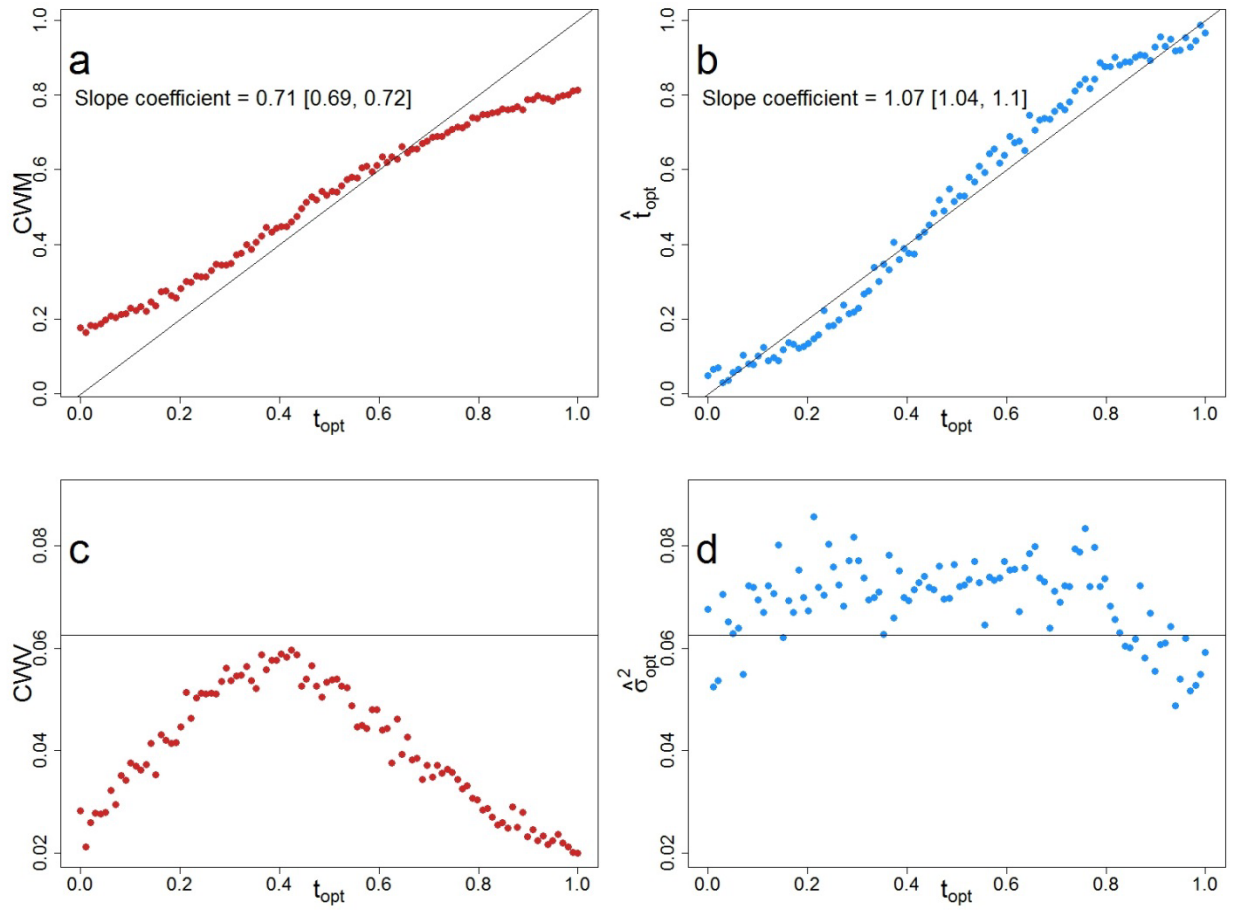


313

314

315 **Appendix S11.** Variation in CWM and CWV values (left, red color), and of estimated \hat{t}_{opt} and
316 $\hat{\sigma}_{opt}^2$ (right, blue color), for simulated communities along t_{opt} gradient with the observed species
317 pool.

318 Communities were simulated with constant environmental filtering ($\sigma_{opt} = 0.25$), uniform distribution of
319 trait values and uniform abundances in the species pool. Top figures (a) and (b) represent CWM and \hat{t}_{opt} ,
320 and figures (c) and (d) represent CWV and $\hat{\sigma}_{opt}^2$. The \hat{t}_{opt} and $\hat{\sigma}_{opt}^2$ values were obtained with the ABC
321 approach and correctly estimated the t_{opt} and σ_{opt}^2 values (b and d). The species pool used for ABC
322 estimation of the parameters corresponds to the actual sum of observed communities. Conversely, CWM
323 departed from t_{opt} and CWV was below σ_{opt}^2 when the influence of the trait range limits increased at the
324 extremes. The black solid line represents equality of CWM and CWV to the parameters of environmental
325 filtering (t_{opt} and σ_{opt}^2 , respectively). Slope coefficients and the associated confidence intervals of the
326 linear regression equations between CWM / \hat{t}_{opt} and t_{opt} are displayed in panel (a) and (b). The mean of
327 the difference between σ_{opt}^2 and CWV (c) is twice higher than the difference between σ_{opt}^2 and $\hat{\sigma}_{opt}^2$ (d)
328 (respectively 2.23e-2 and 8.91e-3).



329

330