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► To cite this version:

Hugo Saiz, D Renault, Sara Puijalon, Miguel Barrio, Mathilde Bertrand, et al.. Huff and puff and blow down: invasive plants traits response to strong winds at the Southern Oceanic Islands. *Oikos*, 2021, 130 (11), pp.1919-1929. 10.1111/oik.08249 . hal-03366501

HAL Id: hal-03366501

<https://hal.science/hal-03366501>

Submitted on 26 Oct 2021

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Huff and puff and blow down: invasive plants traits response to strong winds at the Southern Oceanic Islands

Hugo Saiz, David Renault, Sara Puijalon, Miguel Barrio, Mathilde Bertrand, Matteo Tolosano, Aurélien Pierre, Charly Ferreira, Clémentine Prouteau and Anne-Kristel Bittebiere

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Abstract:

Invasions constitute a major driver of biodiversity changes. Insular plant communities are particularly vulnerable to invasions, and are then relevant models for investigating mechanisms supporting the establishment and spread of introduced plants. Terrestrial flora of sub-Antarctic islands, must often thrive in highly windy habitats, thus imposing strong mechanical constraints to individuals. Many alien plants at the sub-Antarctic islands are of tropical or temperate origins, where they were exposed to less stringent wind conditions. As wind likely represents a strong environmental filter for the successful establishment and further geographic spread of plants, they should have developed responses to resist and successfully colonize the Iles Kerguelen. We studied responses to wind of three herbaceous species that are invasive at Iles Kerguelen. We sampled plant individuals at different locations, under windy and sheltered conditions. Traits related to wind avoidance, and tolerance, and to resource acquisition were measured. We additionally assessed individual performance (biomass) to determine the consequences of trait variations. We focused on trait mean and variance, in particular through on the calculation of hypervolumes. This study emphasized that wind has important effects on plant economics spectrum, including traits involved in mechanical avoidance and in light acquisition, with varying strategies which seem to depend on the biological type of the species (grass vs. non-grass). Wind generally reduces individual performance and this negative effect is not direct, but operates through the modification of plant trait values. Furthermore, analyses performed at the hypervolume scale indicate that not only functional trait mean but also its variability account for plant performance. The existence of contrasting growth strategies to cope with local environmental conditions suggests that invaders will be able to occupy different niches which may ultimately impact local communities. Our results highlight the importance of considering multi-traits responses to meaningfully capture plant adjustments to stress.

1 **Huff and puff and blow down: invasive plants traits response to strong winds at the**

2 **Southern Oceanic Islands**

3

4 **Introduction**

5 Determining the factors that drive plant community assembly has long remained a challenge
6 for theoretical ecologists (Schimper 1898, Mc Gill et al. 2006, Violle et al. 2012; Cadotte and
7 Tucker 2017), in particular in the context of biological invasions (see *e.g.* Godoy 2019, Helsen
8 et al. 2020). When reaching a new region, non-native plants face a series of environmental
9 filters (*sensu* Kraft et al., 2015a) which determines those that will establish and reproduce
10 (Keddy, 1992). The type and strength of environmental filters depend on the abiotic factors of
11 the newly colonized habitat such as wind (Murren and Pigliucci, 2005), ultimately shaping the
12 phenotypes of the establishing individuals (*i.e.* their traits, Keddy 1992, Diaz et al. 1998). In
13 open habitats such as grasslands, wind exerts drag forces entailing plant mechanical stress (De
14 Langre 2008, Anten et al. 2010), driving the evolution of terrestrial plants (Niklas 1998) and
15 strongly regulating their demography (Ennos 1997). Yet, little is known about the ecological
16 strategies developed by plants living under windy conditions, especially when invading habitats
17 subjected to regular episodes of high winds.

18 Under stressful conditions, plants usually develop resistance strategies that minimize
19 the negative impacts of stress, based on avoidance or tolerance responses (Fitter and Hay 2002).
20 Tolerance and avoidance respectively allow the plant to endure or to prevent the deleterious
21 effects of adverse conditions. In the case of plants exposed to mechanical stress caused by wind,
22 avoidance would actually encompass all of the strategies lowering the intensity of the
23 mechanical constraint (Puijalón et al. 2008, 2011). For instance, reduction of individuals' height
24 (Murren and Pigliucci 2005, Bossdorf and Pigliucci 2009, Paul-Victor and Rowe 2011), or
25 increase in stem flexibility (Henry and Thomas 2002) have been frequently reported.

26 Conversely, tolerance responses would rather rely on enhanced mechanical resistance of the
27 plant organs such as stems (Puijalon et al. 2008, 2011) *e.g.* through higher tissue density.
28 Environmental filtering usually selects for a reduced number of strategies resulting in successful
29 plant growth (Keddy 1992, Weiher et al. 1998, Pausas and Verdú 2008, de Bello et al. 2013).
30 We thus expect plant phenotypes to converge towards the most efficient growth strategies under
31 windy conditions, with traits involved in plant resistance being concomitantly filtered, as
32 revealed by the decrease of their variability.

33 Linkages across organs and coupling among resources result in an integrated whole-
34 plant economics spectrum (PES) (Reich 2014). PES is characterized through traits capturing
35 the essence of plant form and function such as plant height, stem density, and specific leaf area
36 (SLA) (Diaz et al. 2016) reflecting a trade-off between carbon gain (photosynthetic efficiency)
37 and longevity. Strong selection along these trade-off axes, ultimately results in plant
38 convergence on fast, medium, or slow growth strategies *i.e.* rates of resource acquisition. As
39 adjustments in the morphology (avoidance) and tissues (tolerance) of leaves have also been
40 observed in response to wind stress (Anten et al. 2010, Gardiner et al. 2016), we expect wind
41 to affect the whole PES. In addition, traits influence plant performance and fitness consistent
42 with trait-based theory about underlying adaptive mechanisms (Reich 2014). As the functional
43 significance of traits can be highly dependent on local conditions (Blonder et al. 2018), we
44 expect that, while light acquisition traits (*e.g.* SLA) influence plant performance in general,
45 traits enhancing species resistance to wind should play a major role in windy microhabitats
46 only.

47 Recent advances emphasize the importance of trait intraspecific variability in the
48 resistance to filtering processes (Jung et al. 2010, Violle et al. 2012). Among various
49 mechanisms generating trait intraspecific variability (*e.g.* neutral processes, mutation, local
50 adaptation), phenotypic plasticity plays a significant role, in particular at the early stages of

51 species invasion process (Richards et al. 2006, Godoy et al. 2011). It allows the rapid expression
52 of novel advantageous phenotypes (Bradshaw 1965, Pigliucci 2001), and then supports the
53 colonization of a wider range of microhabitats (Moreira et al. 2012). Our current knowledge
54 thus suggests that invasive plant species not only display the most advantageous trait values
55 (*i.e.* trait mean) for a given environmental condition, but would also be the most plastic (*i.e.*
56 high trait variance) (Richards et al. 2006). Nevertheless, this assertion was never tested for
57 plants invading a new habitat with high winds.

58 Due to their geographic isolation and often simplified native communities, insular
59 ecosystems are particularly vulnerable to biological invasions (Herben 2005). Moreover,
60 oceanic islands are considered as sentinel habitats to investigate the mechanisms supporting the
61 establishment and spread of introduced plants (Bergstrom and Chown 1999). In particular, the
62 Southern Oceanic Islands, characterized by windy (Féral et al. 2016) and cool thermal
63 conditions (Lebouvier et al. 2011, Leihy et al. 2018), host a terrestrial flora that handle strong
64 mechanical constraints. While native sub-Antarctic plants have evolved in these harsh abiotic
65 conditions, many alien plants are of tropical or temperate origin (Frenot et al. 2001), where they
66 were exposed to less stringent wind. As wind likely represents a strong environmental filter for
67 the successful establishment and further geographic spread of alien plants at the Southern
68 Oceanic Islands, we expect that they have developed phenotypic responses to improve their
69 capacity to survive in windy habitats. To address this assumption, we assessed the responses to
70 wind of three introduced herbaceous plant species, which are invasive at Iles Kerguelen (French
71 sub-Antarctic archipelago): the common dandelion *Taraxacum officinale*, the Kentucky
72 bluegrass *Poa pratensis*, and the orchard grass *Dactylis glomerata* (Frenot et al. 2001).
73 Individuals of these three plant species were field-sampled from windy and sheltered
74 microhabitats in the archipelago. We then measured four traits characterizing individual
75 abilities to avoid or tolerate windy conditions, as well as their ability to acquire resource *i.e.*

76 involved in the PES. These traits were further analyzed through univariate, and multi-traits
77 approaches based on hypervolume calculation (Blonder et al. 2014; Blonder et al. 2018). The
78 n-dimensional hypervolume was originally proposed by Hutchinson (1957) to delineate the
79 shape and volume of the hyperspace describing fundamental niche of species (Blonder 2018;
80 Mammola 2019). More recently, hypervolumes have been extensively used in trait-based
81 studies to explore functional diversity of populations (see e.g. Bittebiere et al. 2019). This
82 method is especially appreciated as it provides a simple mean to determine variations in the
83 species entire strategy (instead of considering a single trait) in response to environmental
84 factors. Based on this methodological framework, we tested the following hypotheses:

- 85 1) Plants sampled from windy microhabitats should converge toward avoidance (lower
86 height and higher stem flexibility) or tolerance strategies (higher stem density) as
87 compared with their relatives sampled from sheltered microhabitats. Wind filtering for
88 multiple traits should also decrease resistance traits variability.
- 89 2) Trait adjustments in plants from windy microhabitats ultimately affect individual
90 performance, either directly or through the alteration of resource acquisition rates (*i.e.*
91 PES).
- 92 3) Individual performance under windy conditions will depend not only on trait values, but
93 also on their plasticity (*i.e.* on trait mean and variability).

94

95 **Materials and methods**

96 *Studied models: three alien plant species from the sub-Antarctic Kerguelen archipelago*

97 Plants were field-sampled at the French sub-Antarctic Iles Kerguelen (southern Indian Ocean,
98 in the 40-50° latitudinal belt), in early December 2018. At these islands, mean annual
99 temperature is 4.6 °C, and precipitations vary from >3200 mm in the western part of the
100 archipelago to < 800 mm in the eastern part (Frenot et al. 2001). Several habitats of Iles

101 Kerguelen exhibit strong and regular winds (annual mean velocity of wind = 35 km.h⁻¹),
102 occasionally reaching 200 km.h⁻¹ (Féral et al. 2016).

103 The ecological responses to wind of three alien plant species amongst the most invasive
104 in this archipelago (Frenot et al. 2001, Chapuis et al. 2004) were studied. We considered two
105 Poaceae species (*i.e.* closely phylogenetically related): *Poa pratensis* L. and *Dactylis glomerata*
106 L., and one Asteraceae species: *Taraxacum officinale* Weber ex. F.H.Wigg. We expected that
107 closely related species would display more similar trait responses than the phylogenetically
108 distant one (Pigliucci et al. 1999, Pavoine et al. 2011). The presence of *P. pratensis* was first
109 recorded at Iles Kerguelen in 1874, while *T. officinale* and *D. glomerata* and were first observed
110 in 1958 and 1977, respectively (Frenot et al. 2001).

111

112 *Individual sampling design*

113 To strengthen the genericity of the pattern we would obtain, the study was repeated at three
114 different sampling sites of Iles Kerguelen for each plant species. The sampling sites differed
115 between plant species as they have distinct geographic occurrences over the archipelago.
116 Individuals were sampled at: Ile Mayes, Port-aux-Français, and Ile Haute for *D. glomerata*, and
117 at Ile Mayes, Port-aux-Français and Ile Guillou for *P. pratensis* and *T. officinale* (see
118 Supplementary materials for additional details on sampling localities – Fig. S1 – and wind
119 mean velocity of the sampled microhabitats – Table S1). Within each sampling site, individuals
120 were collected from one windy and one sheltered microhabitat (*i.e.* three sampling sites × two
121 microhabitats for each plant species). In this study, sheltered microhabitats were protected from
122 high winds by physical obstacles (embankments, fence, buildings) compared to windy
123 microhabitats. The sheltered vs. windy dichotomy within a given sampling site was confirmed
124 by measurements of wind velocity (Table S1). Importantly, the two sampled microhabitats
125 (‘windy’, ‘sheltered’) of a given sampling site were separated by a maximum distance of 150

126 m. All of these precautions allowed us to limit differences in light, soil, temperature and rainfall
127 characteristics among the two microhabitats from the same site, and to assume that abiotic
128 differences between them were mostly driven by wind velocity.

129 For each studied microhabitat, 20 individuals (*i.e.* clonal fragments) of similar
130 phenology were randomly collected from a restricted area of 10×10 m². We considered one
131 tussock of aggregated ramets, or a rosette, as one individual, respectively in Poaceae species
132 and *T. officinale*. Plant individuals were collected at a distance of at least one meter from each
133 other within the sampled microhabitats, so that their relatedness was avoided while genetic
134 variability was maximized. For each individual, a flowering stem having a mature and healthy
135 leaf was sampled. The sampled individuals (n = 120 individuals in total per studied plant
136 species) were then stored for a maximum of 12h at 5 °C before trait measurements.

137

138 *Trait measurements and analyses*

139 Four traits were measured on each sampled plant individual. The selected traits are related to
140 the plant response to wind, either directly (avoidance or tolerance strategies), or through the
141 optimization of resource acquisition under stressful conditions. More specifically, to
142 characterize the plant avoidance strategy, the individual height and second moment of area I (in
143 m⁴, contribution to stem flexibility) were measured. I quantifies the distribution of material
144 around the axis of bending, describing the contribution of cross-sectional geometry of the stem
145 to its ability to resist bending (Niklas 1992). I is negatively related to flexibility (the lower are
146 the values of I , the higher is stem flexibility). The individual stem section was assessed by
147 photographing a cross-section of the stem basis (within the first centimeter) and I was calculated
148 using the formula for full or hollow ellipse cross-section (Fig. S2, Niklas 1992). The plant
149 resistance strategy was assessed through the stem density, calculated as the ratio between dry
150 and fresh masses of 1cm of the stem basis, as the maximum mechanical stress occur at the stem

151 basis (Niklas and Speck 2001). In parallel, we measured the Specific Leaf Area (SLA)
152 following the method of Cornelissen et al. (2003); SLA characterizes plant photosynthetic
153 efficiency (*i.e.* light acquisition). Leaf and stem dry masses, obtained after drying the samples
154 at 65 °C for 48 h with a Sartorius® balance (0.1 mg precision), were used to calculate SLA and
155 stem density.

156 We tested the effect of wind on individual traits of the three plant species by ANOVA
157 using linear mixed-effects model procedures, including the interaction between species (*D.*
158 *glomerata*, *P. pratensis*, and *T. officinalis*) and wind (windy vs. sheltered microhabitats) as
159 explanatory variables (fixed effects), and traits (height, stem second moment of area *I* and
160 density, and SLA) as response variables. In these models, site was included as random effect to
161 take our block sampling design into account (one windy and one sheltered microhabitats per
162 sampling site). When significant species effect was found, we applied a Tukey post-hoc test
163 with Bonferroni correction to assess pairwise differences between species.

164

165 *Constructing the hypervolumes*

166 For each plant species, we built the hypervolume using a procedure of multidimensional kernel
167 density estimation (Blonder et al. 2014). This method allows the construction of species
168 hypervolumes with an arbitrary number of dimensions (*sensu*, number of traits). We did not
169 include individual height because it was significantly correlated to other traits (Table S2).
170 Hypervolumes were thus built with *I*, stem density, and SLA, using a kernel based on the
171 Silverman estimator (Silverman 1992). Before analysis, all trait data were centered and scaled
172 (*sensu*, data were standardized using the mean and standard deviation of the data from all wind
173 conditions and species simultaneously, Blonder et al. 2014). All hypervolumes were
174 constructed in R 3.4.1. (R Core Team 2014) using the “hypervolume” package (Blonder et al.
175 2014).

176 Two sets of hypervolumes were computed to determine the effects of (i) wind, and (ii)
177 species. Specifically, we built one hypervolume including the three species (*D. glomerata*, *P.*
178 *pratensis*, and *T. officinale* together) for each wind condition (n = 180 individuals), and one
179 hypervolume (n = 120 individuals) for each plant species including both wind conditions
180 (windy and sheltered). For each hypervolume, we calculated its volume and the contribution of
181 each trait to the hypervolume shaping. Volume informs about the variability of all traits shaping
182 the hypervolume simultaneously *i.e.* the variability of the whole growth strategy, while trait
183 contribution informs about each individual trait variability relative to other traits. Specifically,
184 the contribution of a given trait to the definition of the hypervolume is calculated as the ratio
185 between the volume of the hypervolume built using all traits, and the hypervolume built using
186 all traits but the trait of interest. The more variable one trait is, the higher will be its contribution
187 to hypervolume shaping.

188 To evaluate the effect of wind and species on hypervolumes, we used a null model
189 approach based on simulating random hypervolumes (Benavides et al. 2019). Specifically, we
190 compared each of the observed hypervolumes against 100 simulated hypervolumes built by
191 randomly selecting individuals (as many individuals as those used to create the observed
192 hypervolumes) from the whole dataset, which represent the expected hypervolumes for our
193 study area. To assess for significant differences between observed and expected volumes and
194 trait contributions, we compared the observed hypervolume indices against the 95% confidence
195 interval of the expected hypervolume indices built considering the percentile 2.5 and 97.5 of
196 the simulations.

197

198 *Effect of traits on plant performance*

199 We evaluated the effect of individual traits and hypervolume on plant individual performance.
200 To that aim, individual performance was assessed by measuring its biomass (including

201 vegetative and flowering parts), after having oven-dried plant material at 65 °C for 48 h. To
202 assess the effect of individual traits on plant performance, we used Confirmatory Path Analysis
203 (CPA; [Shipley 2009](#), package ‘piecewiseSEM’ in R - [Lefcheck 2016](#)). This analysis allows
204 including relationships among variables that serve as predictors in one single model. In our
205 case, CPA included the effect of the four traits (stem density and second moment of area, height,
206 and SLA) in the performance (individual biomass), together with the effect of wind in all
207 variables. In addition, we also included the effect of SLA and stem density on the other two
208 traits, as resource acquisition and tissue resistance could influence plant architecture ([Puijalón
209 et al. 2011](#); [Lienin and Kleyer 2012](#)). To take into account a potential relationship between
210 height and stem second moment of area, we also included the correlation between both traits in
211 the model. Finally, the site was included as a random effect for all the paths in the model. We
212 ran one CPA for each species for a total of three models, and we calculated both the direct and
213 indirect effects of all variables on plant performance.

214 To evaluate the effect of species hypervolume on their performance, we first built one
215 hypervolume using three traits (stem density and second moment of area, SLA) for each
216 combination of wind condition, species and site (two wind conditions × three species × three
217 sites = 18 hypervolumes). For each hypervolume, we then calculated the contribution and the
218 centroid of each trait. Centroid is the arithmetic mean position of all the values of a given trait
219 within the hypervolume, and is related to the trait mean value ([Benavides et al. 2019](#)). Then,
220 we ran a linear mixed model using the lme4 package in R ([Bates et al. 2015](#)) where we included
221 the interaction between wind and species, together with the centroid and contribution for each
222 trait as explanatory variables; biomass (calculated as the individual mean biomass on each
223 combination of wind conditions, species, and site) was included as a response variable. Centroid
224 informs about the effect of trait values on plant performance, while contribution will inform
225 about the effect of trait variability. Site was included as a random effect in all models. We

226 applied a model selection procedure where we first fitted the complete model, and fitted the
227 same model after removing the variable with least explanatory power. If the reduced model
228 showed lower AIC than the complete one, we selected the reduced model as the candidate for
229 the best model and repeated the same procedure. We selected the final model as the one
230 presenting the lowest AIC during the whole selection process. Finally, we used a variance
231 partitioning method using the hier.part package in R (Nally and Walsh 2004) on the final model
232 to evaluate the explained variance associated with wind, species, trait values (centroid) and
233 variability (contribution).

234

235 **Results**

236 *Wind induces changes in plant stature and flexibility*

237 We found significant effects of wind on plant height and second moment of area (I , Table 1).
238 Plants exposed to wind were significantly smaller and characterized by changes in stem cross-
239 sections contributing to higher flexibility (lower I , Fig. 1). Effects of wind on plant traits were
240 species-specific (significant interaction between species and wind for all traits, Table 1): in
241 general, differential responses were measured in grass (*D. glomerata* and *P. pratensis*) as
242 compared with non-grass (*T. officinalis*) species (see Table S3 for the detailed results of post-
243 hoc tests), depicting wind-induced morphological responses dependent on species phylogeny.
244 Grasses were overall taller, and showed higher stem density, and lower second moment of area
245 (resulting in higher flexibility) and SLA than non-grasses (Table 1, Fig. 1). SLA showed
246 contrasting responses to wind between species: grasses had decreased SLA when growing in
247 windy microhabitats, while SLA was increased in non-grasses (Fig. 1).

248

249 *Wind filters for multiple traits*

250 Wind had significant effects on species hypervolumes (Figs. 2a, 3a). On the one hand,
251 hypervolumes of plants from windy microhabitats had significantly lower volume (Fig. 2a), *i.e.*
252 their growth strategy is less variable. Moreover, a lower contribution of SLA than expected
253 were reported for these plants (Fig. 3a). On the other hand, plants from sheltered microhabitats
254 were characterized by significantly higher contributions of SLA and stem density to
255 hypervolume, while the contribution of *I* was significantly lower (Fig. 3a); in these plants, the
256 volume ranged within the range of expected values.

257 Hypervolumes differed however among species (Figs. 2b, 3b). For example, *P.*
258 *pratensis* had the highest volume (Fig. 2b), together with high stem density and *I* contributions,
259 indicating that these two traits were more variable than expected (Fig. 3b). On the contrary, *D.*
260 *glomerata* had no trait that was more variable than expected, while in *T. officinale*, only the
261 stem density contributed significantly more to the hypervolume shaping.

262

263 *Trait effects on individual plant performance*

264 Wind significantly affects plant performance through modifications of individual trait values
265 (Fig. 4). Wind and individual traits (*i.e.* all variables included in the model) explained 77% to
266 96% of biomass variance, depending on the species (Fig. 4). For all plant species, wind had no
267 strong direct effects on plant biomass. However, when accounting for the indirect paths through
268 traits, wind had cumulative effects similar, or even stronger, than those of individual plant traits
269 (Fig. 4). Additionally, increase in height and *I* (lower stem flexibility) positively influenced
270 individual performance, regardless of species. Cumulative effects of height and *I* on plant
271 performance were the highest compared to the two other traits. SLA and stem density however,
272 had contrasting roles (positive or negative influence) and importance in plant performance
273 depending on the considered species. For example, in *D. glomerata*, SLA had positive indirect
274 effects on plant performance through its fostering on height. Conversely, in *T. officinale*, SLA

275 showed direct negative effects on plant performance, and in *P. pratensis*, it displayed an
276 intermediate influence on individual performance.

277 Considering the relationship between hypervolumes (*i.e.* growth strategies) and
278 individual performances, while for SLA only the centroid (*i.e.* trait mean) had significant
279 effects, for stem traits (stem density and *I*), we rather observed a significant influence of
280 contributions (*i.e.* trait variance) (Table 2). Specifically, SLA centroid and *I* contribution had
281 negative effects on performance while stem density had a positive effect. Looking at the
282 variance explained by different variables, trait variability (*i.e.* contributions) showed higher
283 cumulative effects on plant performance than trait mean values (*i.e.* centroids), wind and species
284 (Fig. 5).

285

286 **Discussion**

287 Here, we report the systemic effect of mechanical stress exerted by wind on multiple traits of
288 three invasive plant species from Iles Kerguelen. In this model system, wind acted as a strong
289 environmental filter, resulting in smaller plants with higher stem flexibility (avoidance
290 strategy), and reducing the overall variability of the individual growth strategy. Contrasting
291 responses were also reported among the studied plant species regarding light acquisition.
292 Importantly, wind had an indirect negative effect on plant performance, mediated by changes
293 of the measured functional traits. In addition, plant performance was not only determined by
294 SLA value, but was also governed by the plastic responses of stem density and *I*.

295

296 *Switch of species strategies toward the avoidance of wind stress*

297 In accordance with our first hypothesis, wind strongly affected plant height and stem second
298 moment of area *I*. Plants thriving in windy microhabitats were smaller, with stem cross section
299 resulting in higher flexibility, regardless of the plant species. However, no intraspecific

300 differences in stem density between plants from windy vs. sheltered microhabitats were
301 recorded. These findings highlight changes in plants' growth strategies toward stress avoidance
302 rather than tolerance, in line with previous works testing plant responses to wind (e.g. [Jaffe and](#)
303 [Forbes 1993](#), [Zhang et al. 2021](#), see [Gardiner et al. 2016](#) for review). Working with plants from
304 other sub-Antarctic Islands (Iles Crozet), [Bazichetto et al. \(2020\)](#) also found that low-stature
305 discriminated invasive from non-invasive alien plant species, and this morphological feature
306 may strongly contribute to explain the greater geographic expansion capacities of non-native
307 plants at this archipelago. Moreover, long-established alien plants from Iles Kerguelen may
308 have evolved adaptation to cope with the strong winds of this region, which would explain the
309 fixity of stem density we are reporting. Genetic assimilation, which turns the plastic response
310 into a genetically invariant one, is one possible mechanism leading to a stable expression of the
311 trait regardless of wind conditions ([West-Eberhard 2003](#); [Ghalambor et al. 2007](#); [Lande 2009](#)).

312 Our investigations also suggest that *P. pratensis* exhibits a higher degree of trait
313 plasticity, more precisely of stem density and *I*, than the two other species. This observation is
314 consistent with previous work demonstrating that grasses are usually more plastic than non-
315 grass plants when they are coping with environmental variability ([Siebenkäs et al. 2015](#)). In
316 their grassland open habitat, tall grasses suffering from mechanical stress due to wind such as
317 *P. pratensis*, may have been selected for greater responsiveness. From this result, it can be
318 assumed that grasses should be more suited for successful colonization of a wide range of
319 habitats of the windswept Iles Kerguelen. This assumption is supported by our long-term
320 monitoring of the geographic expansion of *P. pratensis* at Iles Kerguelen (long-term
321 observations of the sub-Antarctic biota, database 'Habitats-Flora-Invertebrates' managed by
322 'RN TAF' and 'IPEV 136 SUBANTECO').

323

324 *Influence of wind on plant economics spectrum*

325 As expected, we observed a decrease in the variability of the whole growth strategy under windy
326 conditions. However, and contrary to our hypotheses, this decrease was not due to traits related
327 to wind resistance (stem density or I), but to a strong filtering of SLA values. This result
328 suggests that wind is a strong environmental filter for plant communities at Iles Kerguelen,
329 selecting distinctive trait values, particularly for light acquisition. We found however
330 contrasting SLA responses to wind among species, with *T. officinale* having increased SLA
331 when sampled from windy microhabitats, while grasses had decreased SLA values (although it
332 is only a trend in *P. pratensis*). As SLA strongly governs plant responses to competition (e.g.
333 [Bittebiere et al. 2012](#); [Kraft et al. 2015b](#)), its decrease in grass species may indicate a reduction
334 of their competitive ability. This finding reveals two contrasting growth strategies in our studied
335 invasive plants species and underlines that the whole PES is affected in windy microhabitats.
336 The two grasses *P. pratensis* and *D. glomerata* likely invest into mechanical responses
337 facilitating wind stress avoidance, subsequently adopting a slow growth strategy. By contrast,
338 *T. officinale* gathers more light resources but with reduced height, which corresponds to a
339 medium growth strategy. As also demonstrated by [Zhang et al. \(2021\)](#) on steppe plants, I and
340 height displayed common response patterns across our three species, while SLA response varies
341 among species. Wind generates these differences in leaf morphology either through mechanical
342 stress, or through enhanced water stress by reducing boundary layers at leaf surface ([Onoda and](#)
343 [Anten 2011](#)).

344 Conversely, plants from sheltered microhabitats displayed increased variability of their
345 SLA, while stem traits were more (stem density) or less (I) variable than expected. Increased
346 variability can be associated with higher niche differences in the community, reducing
347 competitive interactions between native and alien species, ultimately supporting their
348 persistence in the ecosystem. This likely depicts the involvement of PES in mechanisms (fitness
349 equalizing or niche stabilizing) supporting species coexistence under competitive interactions

350 (Chesson 2000, Herben and Goldberg 2014; Kraft et al. 2015b), especially in invasion contexts
351 (Helsen et al. 2020).

352

353 *The role of traits in plant performance*

354 Wind strongly affects plant performance but mostly indirectly, through modifications of
355 functional trait values. We would not have been able to detect this indirect effect of wind on
356 individual performance without including traits in our analyses. Importantly, traits involved in
357 species tolerance to wind (*i.e.* height and *I*) had significant effects on plant individual
358 performance. Height and *I* are involved in PES and also participate to individual ability to
359 efficiently capture light resource (Niinemets 2010; Diaz et al. 2016) through their influence on
360 individual architecture, ultimately affecting its performance. Increasing height and *I* fostered
361 plant biomass, whereas reduced height and *I* (higher stem flexibility) promoted individual
362 avoidance of wind mechanical stress. These findings demonstrate that the avoidance response
363 comes with a cost for the plant, which is consistent with previous works on terrestrial and
364 aquatic plants recording reduced flowering or seed production (Niklas 1998; Cipolini 1999;
365 Puijalon et al. 2008). On the other hand, while light acquisition influences plant performance,
366 its actual effects also greatly depend on species identity. Indeed, SLA effects on plant
367 performance were either direct (*T. officinale*), indirect (*D. glomerata*), or both (*P. pratensis*).
368 Moreover, these direct and indirect effects were respectively negative and positive. Knowing
369 that grasses showed lower SLA when exposed to wind (only a tendency in *P. pratensis*),
370 whereas *T. officinale* displayed higher SLA, these two responses both resulted in lower plant
371 biomass. SLA plasticity thus incurred direct performance costs that would favor populations
372 with higher fixity of this trait under windy conditions. Moreover, this provides new evidence
373 that models on the evolution of phenotypic plasticity have to incorporate plasticity costs that
374 vary in magnitude depending on the microhabitat conditions (Steinger et al. 2003).

375

376 *Importance of trait mean and variability*

377 Analyses performed at the hypervolume scale indicate that not only functional trait values, but
378 also their variability (resulting from plasticity or local adaptation), accounted for plant biomass.
379 Indeed, while for SLA only the mean influenced plant performance, for stem traits (*i.e.* density
380 and second moment of area), their variability was a more important determinant of the
381 performance. Plant populations with higher degree of phenotypic plasticity of stem traits should
382 better perform when subjected to mechanical stress caused by wind. However, our results also
383 suggest that wind is a filter so strong that it prevents plants to express any intraspecific
384 variability through plasticity in our study area. Variability in stem density only occurs within
385 sheltered microhabitats likely in response to competition. This result is in line with the
386 assumption that phenotypic plasticity (and to a larger extent intraspecific variability) assists
387 species colonization (Richards et al. 2006, Godoy et al. 2011) in two non-exclusive ways: (i)
388 high plasticity allows the rapid expression of advantageous phenotypes (Bradshaw 1965,
389 Pigliucci 2001) resistant to local environmental filters (here related to wind mechanical stress);
390 (ii) high plasticity supports higher niche differentiation promoting coexistence between native
391 and alien species (as illustrated by stem density in our study). These results were based on a
392 multi-trait approach accounting for trade-offs between traits. As described in the PES, traits are
393 involved in multiple processes (competition, wind stress resistance), explaining why we
394 observe these complex patterns of responses to environmental filtering.

395

396 *Concluding remarks and prospects*

397 This study emphasized that wind, which is an overlooked cause of stress in vegetation, has
398 important effects on plant functional traits, including not only traits involved in mechanical
399 resistance but also in resource acquisition, and generally reduces species performance. More

400 importantly, the effects of wind operate through the modification of plant trait values. The
401 contrasting responses to wind that we evidenced in the three studied species, warn about their
402 negative impact on local community. Most often, the successful colonization of new geographic
403 regions by invasive plants highly depends on their capacity to occupy vacant niches, or by out-
404 competing established species in the communities (Moles et al. 2008; Drenovski et al. 2012; Te
405 Beest et al. 2015). At Iles Kerguelen, the presence of multiple invaders having diverse growth
406 strategies for handling stressful environmental conditions, would represent major threats for
407 local plant communities, as these have the potential to occupy a wide diversity of ecological
408 niches and habitats. This hypothesis is supported by Momberg et al. (2021) demonstrating the
409 importance of wind as driver of plant community composition. Our study thus contributes to
410 the understanding of wind role in plant community assembly, and underlines that this ubiquitous
411 environmental stress should be more thoroughly taken into account in assembly theories,
412 especially in the context of invading windy habitats.

413

414 **Data availability**

415 Data were archived in FigShare: <https://doi.org/10.6084/m9.figshare.15054165.v1>.

416

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615

616 **Tables**

617 **Table 1.** Wind influence on species traits. Trait means were compared using ANOVAs,
 618 performed with a mixed model procedure (see Materials and Methods for details).

		Species (df = 2)		Wind (df = 1)		Species × Wind (df = 2)	
		F	P	F	P	F	P
Avoidance traits	Height	30.03	***	303.88	***	8.98	***
	<i>I</i>	316.74	***	78.65	***	11.73	***
Tolerance trait	Stem density	330.28	***	0.01	ns	4.69	**
Light acquisition trait	SLA	37.68	***	1.93	ns	14.73	***

619 *Note:* Asterisks indicate significant difference, *i.e.*, ns = not significant; * $P < 0.05$; ** $P < 0.01$;

620 *** $P < 0.001$.

621

622 **Table 2.** Effects of trait mean (centroid) and variance (contribution), species, and wind on
 623 individual performance. (-) indicates that after model optimization, these variables were
 624 removed from the best model (*i.e.* the most parsimonious with the lowest AIC). Species
 625 estimates represent the difference between *D. glomerata* and others. Microhabitat estimate
 626 represents the difference between windy and shelter microhabitats.

		Estimate	Std error	t-value	P
SLA	Centroid	-0.339	0.336	-3.767	0.006**
	Contribution	-	-	-	-
Stem density	Centroid	-	-	-	-
	Contribution	0.181	0.059	3.073	0.015*
<i>I</i>	Centroid	-	-	-	-
	Contribution	-0.188	0.082	-2.306	0.05.
Species	<i>P. pratensis</i>	-0.664	0.136	-4.864	0.001**
	<i>T. officinalis</i>	-0.543	0.157	-3.467	0.009**
Microhabitat	Shelter	0.45	0.11	4.101	0.003**

627 *Note:* Symbols next to P indicate significant difference, *i.e.*, . < 0.1; * $P < 0.05$; ** $P < 0.01$;

628 *** $P < 0.001$.

629

630 **Figures**

631 **Figure 1.** Mean traits (\pm SD) of the three species under windy or sheltered conditions (white
632 bars: windy microhabitats; grey bars: sheltered microhabitats). *I* (second moment of area) is
633 negatively related to stem flexibility. Asterisks above the bars indicate significant differences
634 between microhabitats for a given species: ns = not significant; . $P < 0.1$; * $P < 0.05$; ** $P <$
635 0.01 ; *** $P < 0.001$. D.glo: *Dactylis glomerata*, P.pra: *Poa pratensis*, T.off: *Taraxacum*
636 *officinale*.

637

638 **Figure 2.** Hypervolume size (volume) of a) plants from windy vs. sheltered microhabitats, and
639 of b) the three species regardless of wind conditions. Red lines represent the confidence
640 intervals showing differences between observed and expected values of volume (bars below or
641 above the confidence intervals are significantly different from expected values, and highlighted
642 by the star). D.glo: *Dactylis glomerata*, P.pra: *Poa pratensis*, T.off: *Taraxacum officinale*.

643

644 **Figure 3.** Contributions of traits to hypervolume shaping, in plants thriving in a) windy vs.
645 sheltered microhabitats, and in b) the three species regardless of wind. Trait contribution is
646 related to its variability relatively to the two other traits. Red lines represent the confidence
647 intervals showing differences between observed and expected values of volume (bars below or
648 above the confidence intervals are significantly different from expected values, and highlighted
649 by the star). *I*: second moment of area. D.glo: *Dactylis glomerata*, P.pra: *Poa pratensis*, T.off:
650 *Taraxacum officinale*.

651

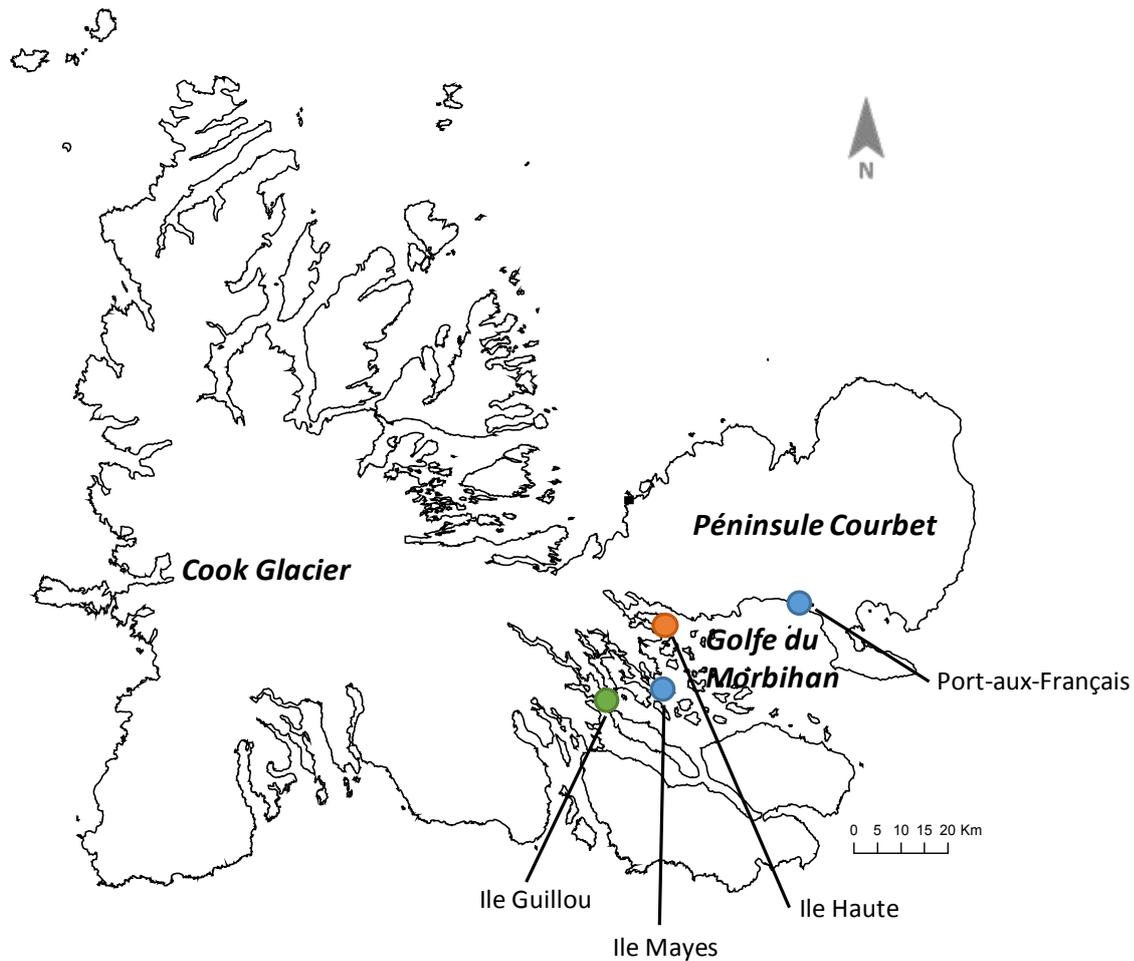
652 **Figure 4. (Left)** Confirmatory Path Analysis of the effects of wind and traits on individual
653 performance in a) *Dactylis glomerata*, b) *Poa pratensis*, and c) *Taraxacum officinale*. Numbers
654 adjacent to arrows are standardized path coefficients (analogous to relative regression weights)

655 and indicative of the effect of the relationship. Continuous arrows show positive and dashed
656 arrows negative relationships, with arrow thickness being proportional to relationship strength.
657 The proportion of variance explained (R^2) is shown besides each response variable in the model.
658 Goodness-of-fit statistics are shown below the plot as the Fischer's C value, the P-value, and
659 the degrees of freedom (DF) for each model. *P < 0.05; **P < 0.01; ***P < 0.001. Non-
660 significant arrows are removed to simplify model interpretation, marginally significant arrows
661 (P<0.1) do not show any symbol. Models only show effects for sheltered habitats; models
662 showing effects for windy habitats are shown in Fig. S3. (*Right*), absolute standardized direct,
663 indirect, and total sum effects of wind and traits on individual performance. *I*: second moment
664 of area; S. density: stem density.

665

666 **Figure 5.** Proportion of individual biomass variance explained by trait centroid, trait
667 contribution in the hypervolume, species, and wind. Centroid and contribution include the sum
668 of explained variances due to each individual trait.

669

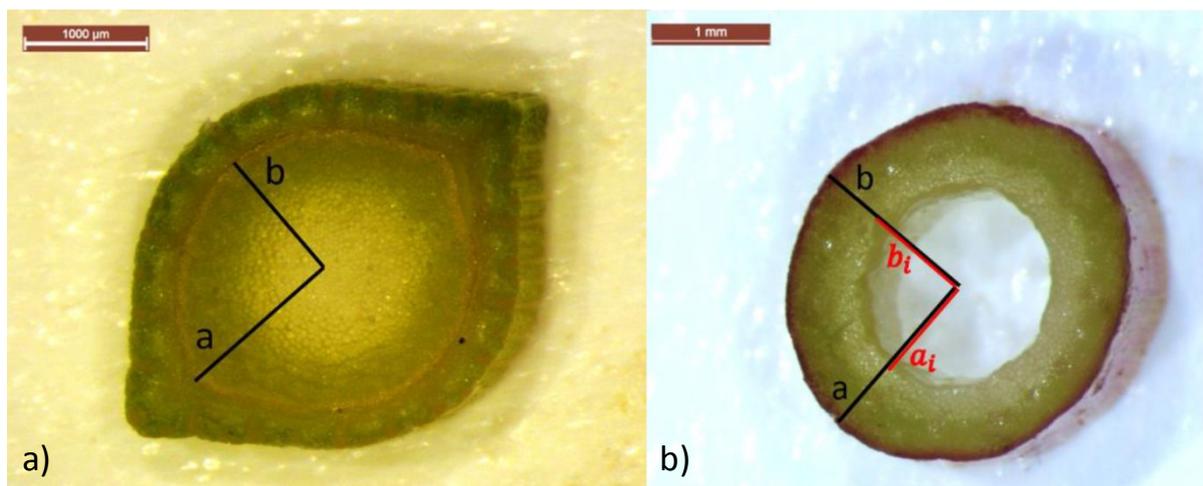
1 **Supplementary materials**

2

3 **Figure S1.** Sampling sites localizations on the Kerguelen archipelago. For each site, individuals
4 were sampled from windy and sheltered microhabitats. Blue dots indicate sites where the three
5 species were sampled. Orange and green dots respectively indicate where one (*D. glomerata*)
6 or two (*P. pratensis*, *T. officinale*) species were sampled.

7

8



$$I = \frac{\pi}{4} * (b^2 * a)$$

$$I = \frac{\pi}{4} * (b^2 * a - b_i^2 * a_i)$$

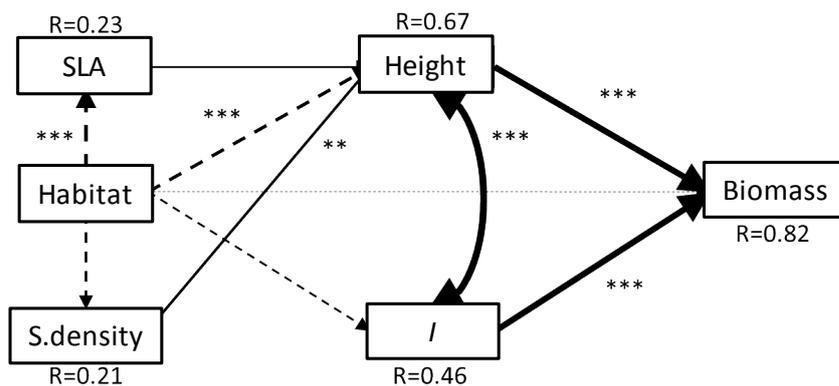
9

10 **Figure S2.** Calculation of the second moment of area I depending on the stem section11 morphology: a) full section in *Dactylis glomerata*, b) hollow section in *Taraxacum officinale*.

12

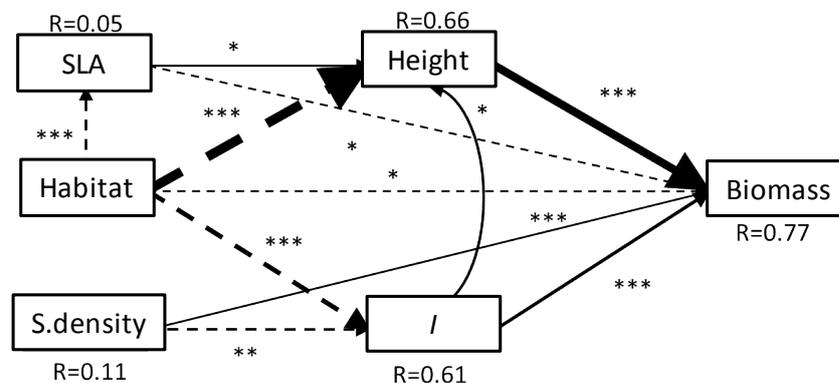
13

a) *Dactylis glomerata*, Windy



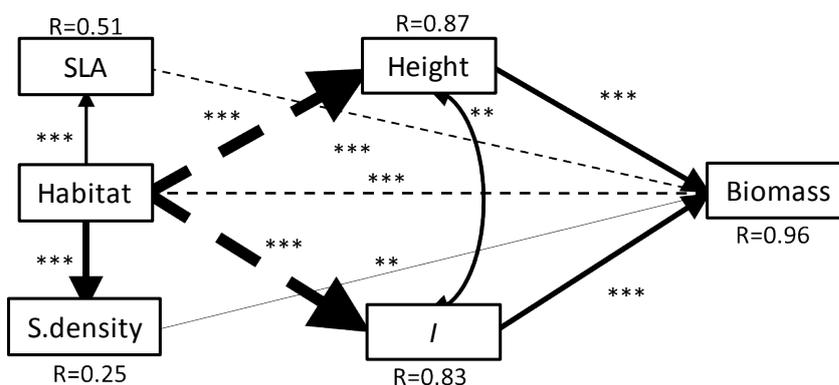
C-score=2.419, P-value=0.298, Df=2

b) *Poa pratensis*, Windy



C-score=0.932, P-value=0.628, Df=2

c) *Taraxacum officinale*, Windy



C-score=4.636, P-value=0.098, Df=2

14

15 **Figure S3.** Confirmatory Path Analysis for the effect of wind and traits on individual
 16 performances in a) *Dactylis glomerata*, b) *Poa pratensis* and c) *Taraxacum officinale*. Numbers

3

17 adjacent to arrows are standardized path coefficients (analogous to relative regression weights)
18 and indicative of the effect of the relationship. Continuous arrows show positive and dashed
19 arrows negative relationships, with arrow thicknesses proportional to the strength of the
20 relationship. The proportion of variance explained (R^2) is shown besides each response variable
21 in the model. Goodness-of-fit statistics are shown in below the plot as the Fischer's C value,
22 the P-value, and the degrees of freedom (DF) for each model. *P < 0.05; **P < 0.01; ***P <
23 0.001. Non-significant arrows are removed to simplify model interpretation. Marginally
24 significant arrows do not show any symbol. Absolute standardized effects are the same as in
25 Figure 4. *I*: second moment of area; S.density: stem density.

26

27 **Table S1.** Mean (\pm SD) wind speeds under the sampling conditions (in $\text{m}\cdot\text{s}^{-1}$). These mean
 28 values were obtained by calculating the mean of five mean values of wind speed, each measured
 29 during 30s at 30cm from the soil surface (corresponding to the vegetation height), on different
 30 days. For each species, we performed an ANOVA test, based on a linear model procedure (with
 31 wind speed as response variable, and Site \times Microhabitat as explanatory variables), to
 32 demonstrate that the microhabitat ('windy', 'sheltered') significantly influenced wind speeds
 33 (and thus the magnitude of the mechanical stress on plants). Additional Tukey post-hoc tests
 34 indicated that for all species in all sites, there was a significant difference in wind speed between
 35 sheltered and windy microhabitats.

		<i>T. officinale</i>	<i>P. pratensis</i>	<i>D. glomerata</i>
Port-aux-Français	Sheltered	0.72 (\pm 0.29)	0.72 (\pm 0.29)	0.68 (\pm 0.22)
	Windy	1.86 (\pm 0.66)	1.86 (\pm 0.66)	1.86 (\pm 0.66)
Ile Mayes	Sheltered	0.63 (\pm 0.30)	0.63 (\pm 0.30)	0.63 (\pm 0.30)
	Windy	1.98 (\pm 0.70)	1.98 (\pm 0.70)	1.98 (\pm 0.70)
Ile Guillou	Sheltered	0.54 (\pm 0.58)	0.54 (\pm 0.58)	-
	Windy	1.76 (\pm 0.44)	1.76 (\pm 0.44)	-
Ile Haute	Sheltered	-	-	0.12 (\pm 0.12)
	Windy	-	-	1.20 (\pm 0.66)

36

37

38 **Table S2.** Pair correlations between the four traits measured in the three plant species. *I*: second
 39 moment of area. Tables show Pearson coefficient of correlation (*r*). Results are showed for each
 40 species individually and for all species together.

		Height	SLA	<i>I</i>	Stem density
<i>Dactylis glomerata</i>	Height	1	0.02	0.71	0.46
	SLA	0.02	1	-0.18	-0.08
	<i>I</i>	0.71	-0.18	1	0.26
	Stem density	0.46	-0.08	0.26	1
<i>Poa pratensis</i>	Height	1	0.26	0.53	0.04
	SLA	0.26	1	0.08	-0.01
	<i>I</i>	0.53	0.08	1	0.26
	Stem density	0.04	-0.01	0.26	1
<i>Taraxacum officinale</i>	Height	1	-0.43	0.79	-0.46
	SLA	-0.43	1	-0.4	0.26
	<i>I</i>	0.79	-0.4	1	-0.49
	Stem density	-0.46	0.26	-0.49	1
All species	Height	1	0.05	0.32	0.34
	SLA	0.05	1	-0.36	0.26
	<i>I</i>	0.32	-0.36	1	-0.5
	Stem density	0.34	0.26	-0.5	1

41

42

43 **Table S3.** Tukey tests for multiple comparisons for the differences in traits between species. *I*:
 44 second moment of area. Dglo: *Dactylis glomerata*; Pprat: *Poa pratensis*; Toff: *Taraxacum*
 45 *officinale*. All p-values have been corrected using Bonferroni method.

		Estimate	Standard error	z-value	p-value
Height	Dglo – Pprat	-0.1852	0.1174	-1.577	0.344 ns
	Dglo – Toff	0.5188	0.1172	4.427	<0.001***
	Pprat – Toff	0.704	0.1073	6.563	<0.001***
SLA	Dglo – Pprat	-0.1171	0.1637	-0.716	1 ns
	Dglo – Toff	0.2869	0.1633	1.757	0.237
	Pprat – Toff	0.4041	0.1507	2.682	0.022*
<i>I</i>	Dglo – Pprat	0.4065	0.1059	3.838	<0.001***
	Dglo – Toff	-0.9949	0.1057	9.41	<0.001***
	Pprat – Toff	-1.4041	0.0968	-14.477	<0.001***
Stem density	Dglo – Pprat	-1.1776	0.1149	-10.254	<0.001***
	Dglo – Toff	0.7233	0.1146	6.311	<0.001***
	Pprat – Toff	1.9009	0.1065	17.842	<0.001***

46 *Note:* Asterisks indicate significant difference, *i.e.*, ns = not significant; * $P < 0.05$; ** $P < 0.01$;

47 *** $P < 0.001$.

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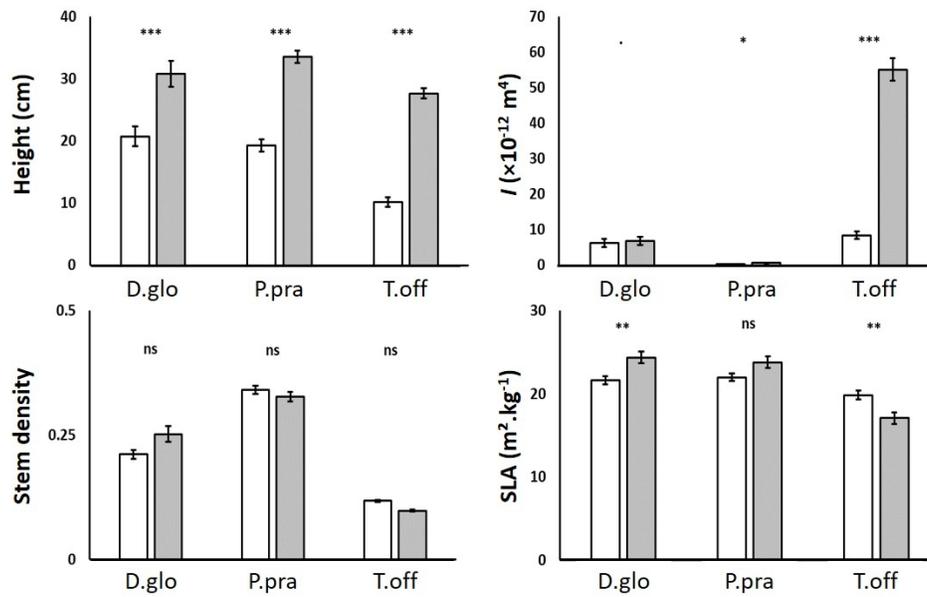


Figure 1. Mean traits (\pm SD) of the three species under windy or sheltered conditions (white bars: windy microhabitats; grey bars: sheltered microhabitats). I (second moment of area) is negatively related to stem flexibility. Asterisks above the bars indicate significant differences between microhabitats for a given species: ns = not significant; . $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. D.glo: *Dactylis glomerata*, P.pra: *Poa pratensis*, T.off: *Taraxacum officinale*.

194x122mm (150 x 150 DPI)

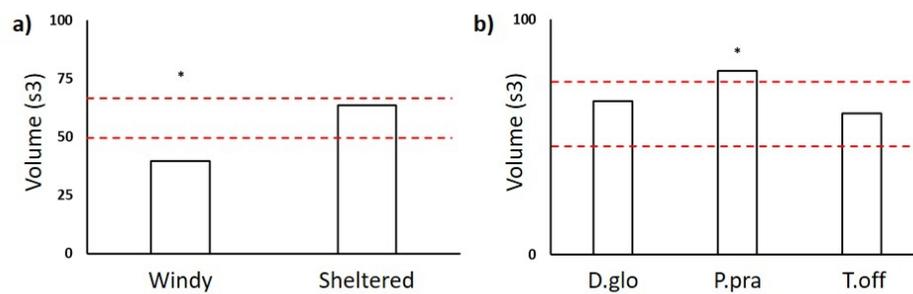


Figure 2. Hypervolume size (volume) of a) plants from windy vs. sheltered microhabitats, and of b) the three species regardless of wind conditions. Red lines represent the confidence intervals showing differences between observed and expected values of volume (bars below or above the confidence intervals are significantly different from expected values, and highlighted by the star). D.glo: *Dactylis glomerata*, P.pra: *Poa pratensis*, T.off: *Taraxacum officinale*.

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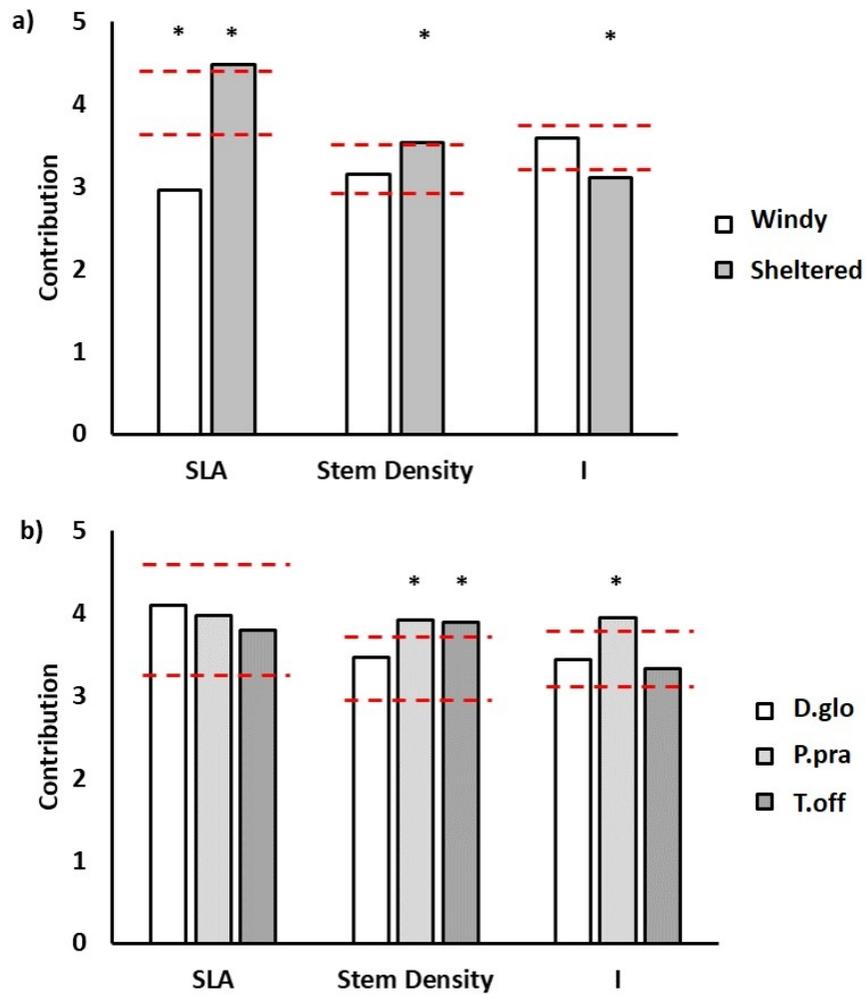


Figure 3. Contributions of traits to hypervolume shaping, in plants thriving in a) windy vs. sheltered microhabitats, and in b) the three species regardless of wind. Trait contribution is related to its variability relatively to the two other traits. Red lines represent the confidence intervals showing differences between observed and expected values of volume (bars below or above the confidence intervals are significantly different from expected values, and highlighted by the star). I: second moment of area. D.glo: *Dactylis glomerata*, P.pra: *Poa pratensis*, T.off: *Taraxacum officinale*.

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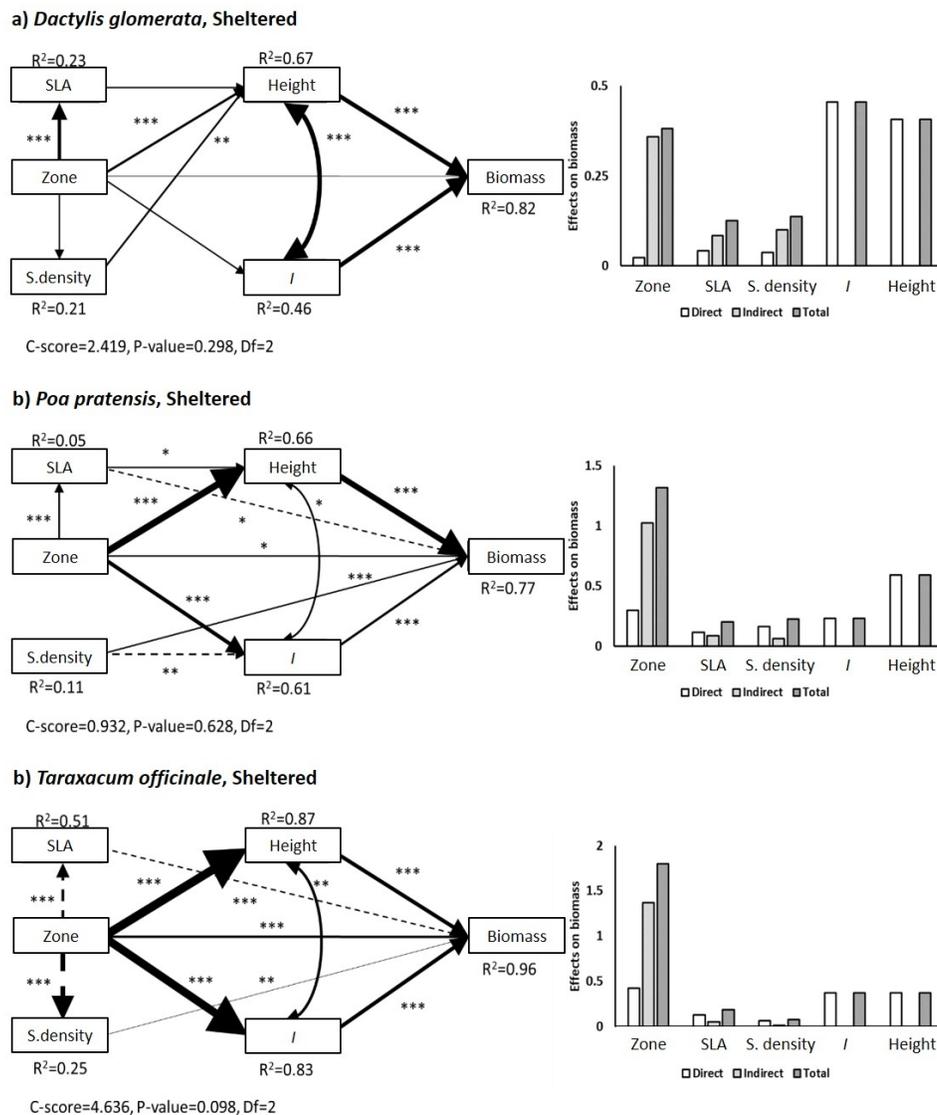


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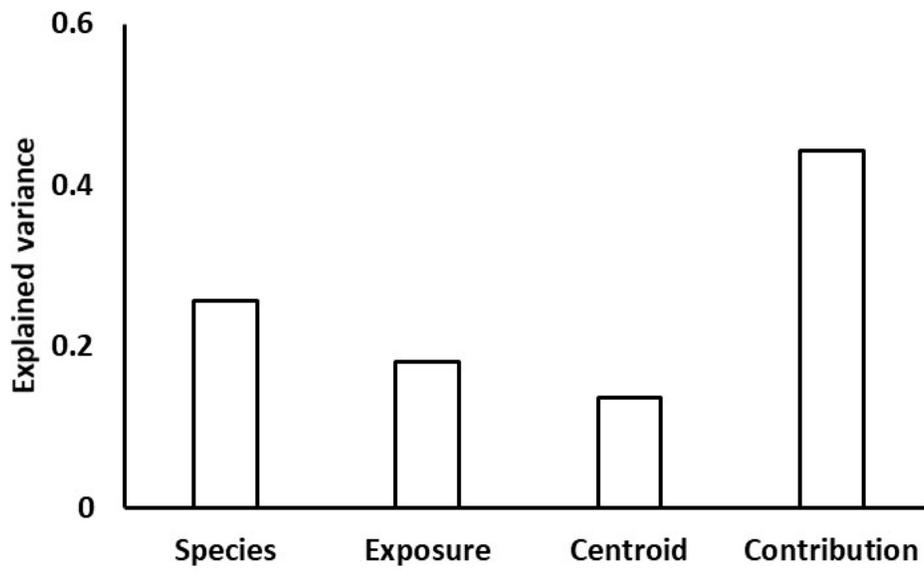


Figure 5. Proportion of individual biomass variance explained by trait centroid, trait contribution in the hypervolume, species, and wind. Centroid and contribution include the sum of explained variances due to each individual trait.

127x76mm (150 x 150 DPI)