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

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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.

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## Southern Oceanic Islands

## Introduction

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

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

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

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

Recent advances emphasize the importance of trait intraspecific variability in the resistance to filtering processes (Jung et al. 2010, Violle et al. 2012). Among various mechanisms generating trait intraspecific variability (e.g. neutral processes, mutation, local adaptation), phenotypic plasticity plays a significant role, in particular at the early stages of
species invasion process (Richards et al. 2006, Godoy et al. 2011). It allows the rapid expression of novel advantageous phenotypes (Bradshaw 1965, Pigliucci 2001), and then supports the colonization of a wider range of microhabitats (Moreira et al. 2012). Our current knowledge thus suggests that invasive plant species not only display the most advantageous trait values (i.e. trait mean) for a given environmental condition, but would also be the most plastic (i.e. high trait variance) (Richards et al. 2006). Nevertheless, this assertion was never tested for plants invading a new habitat with high winds.

Due to their geographic isolation and often simplified native communities, insular ecosystems are particularly vulnerable to biological invasions (Herben 2005). Moreover, oceanic islands are considered as sentinel habitats to investigate the mechanisms supporting the establishment and spread of introduced plants (Bergstrom and Chown 1999). In particular, the Southern Oceanic Islands, characterized by windy (Féral et al. 2016) and cool thermal conditions (Lebouvier et al. 2011, Leihy et al. 2018), host a terrestrial flora that handle strong mechanical constraints. While native sub-Antarctic plants have evolved in these harsh abiotic conditions, many alien plants are of tropical or temperate origin (Frenot et al. 2001), where they were exposed to less stringent wind. As wind likely represents a strong environmental filter for the successful establishment and further geographic spread of alien plants at the Southern Oceanic Islands, we expect that they have developed phenotypic responses to improve their capacity to survive in windy habitats. To address this assumption, we assessed the responses to wind of three introduced herbaceous plant species, which are invasive at Iles Kerguelen (French sub-Antarctic archipelago): the common dandelion Taraxacum officinale, the Kentucky bluegrass Poa pratensis, and the orchard grass Dactylis glomerata (Frenot et al. 2001). Individuals of these three plant species were field-sampled from windy and sheltered microhabitats in the archipelago. We then measured four traits characterizing individual abilities to avoid or tolerate windy conditions, as well as their ability to acquire resource i.e.
involved in the PES. These traits were further analyzed through univariate, and multi-traits approaches based on hypervolume calculation (Blonder et al. 2014; Blonder et al. 2018). The n-dimensional hypervolume was originally proposed by Hutchinson (1957) to delineate the shape and volume of the hyperspace describing fundamental niche of species (Blonder 2018; Mammola 2019). More recently, hypervolumes have been extensively used in trait-based studies to explore functional diversity of populations (see e.g. Bittebiere et al. 2019). This method is especially appreciated as it provides a simple mean to determine variations in the species entire strategy (instead of considering a single trait) in response to environmental factors. Based on this methodological framework, we tested the following hypotheses:

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

## Materials and methods

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

 Plants were field-sampled at the French sub-Antarctic Iles Kerguelen (southern Indian Ocean, in the $40-50^{\circ}$ latitudinal belt), in early December 2018. At these islands, mean annual temperature is $4.6{ }^{\circ} \mathrm{C}$, and precipitations vary from $>3200 \mathrm{~mm}$ in the western part of the archipelago to $<800 \mathrm{~mm}$ in the eastern part (Frenot et al. 2001). Several habitats of IlesKerguelen exhibit strong and regular winds (annual mean velocity of wind $=35 \mathrm{~km} \cdot \mathrm{~h}^{-1}$ ), occasionally reaching $200 \mathrm{~km} . \mathrm{h}^{-1}$ (Féral et al. 2016).

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

## Individual sampling design

To strengthen the genericity of the pattern we would obtain, the study was repeated at three different sampling sites of Iles Kerguelen for each plant species. The sampling sites differed between plant species as they have distinct geographic occurrences over the archipelago. Individuals were sampled at: Ile Mayes, Port-aux-Français, and Ile Haute for D. glomerata, and at Ile Mayes, Port-aux-Français and Ile Guillou for P. pratensis and T. officinale (see Supplementary materials for additional details on sampling localities - Fig. S1 - and wind mean velocity of the sampled microhabitats - Table S1). Within each sampling site, individuals were collected from one windy and one sheltered microhabitat (i.e. three sampling sites $\times$ two microhabitats for each plant species). In this study, sheltered microhabitats were protected from high winds by physical obstacles (embankments, fence, buildings) compared to windy microhabitats. The sheltered vs. windy dichotomy within a given sampling site was confirmed by measurements of wind velocity (Table S1). Importantly, the two sampled microhabitats ('windy', 'sheltered') of a given sampling site were separated by a maximum distance of 150
m . All of these precautions allowed us to limit differences in light, soil, temperature and rainfall characteristics among the two microhabitats from the same site, and to assume that abiotic differences between them were mostly driven by wind velocity.

For each studied microhabitat, 20 individuals (i.e. clonal fragments) of similar phenology were randomly collected from a restricted area of $10 \times 10 \mathrm{~m}^{2}$. We considered one tussock of aggregated ramets, or a rosette, as one individual, respectively in Poaceae species and $T$. officinale. Plant individuals were collected at a distance of at least one meter from each other within the sampled microhabitats, so that their relatedness was avoided while genetic variability was maximized. For each individual, a flowering stem having a mature and healthy leaf was sampled. The sampled individuals $(\mathrm{n}=120$ individuals in total per studied plant species) were then stored for a maximum of 12 h at $5^{\circ} \mathrm{C}$ before trait measurements.

## Trait measurements and analyses

Four traits were measured on each sampled plant individual. The selected traits are related to the plant response to wind, either directly (avoidance or tolerance strategies), or through the optimization of resource acquisition under stressful conditions. More specifically, to characterize the plant avoidance strategy, the individual height and second moment of area $I$ (in $\mathrm{m}^{4}$, contribution to stem flexibility) were measured. $I$ quantifies the distribution of material around the axis of bending, describing the contribution of cross-sectional geometry of the stem to its ability to resist bending (Niklas 1992). I is negatively related to flexibility (the lower are the values of $I$, the higher is stem flexibility). The individual stem section was assessed by photographing a cross-section of the stem basis (within the first centimeter) and $I$ was calculated using the formula for full or hollow ellipse cross-section (Fig. S2, Niklas 1992). The plant resistance strategy was assessed through the stem density, calculated as the ratio between dry and fresh masses of 1 cm of the stem basis, as the maximum mechanical stress occur at the stem
basis (Niklas and Speck 2001). In parallel, we measured the Specific Leaf Area (SLA) following the method of Cornelissen et al. (2003); SLA characterizes plant photosynthetic efficiency (i.e. light acquisition). Leaf and stem dry masses, obtained after drying the samples at $65^{\circ} \mathrm{C}$ for 48 h with a Sartorius ${ }^{\circledR}$ balance ( 0.1 mg precision), were used to calculate SLA and stem density.

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

## Constructing the hypervolumes

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

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

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

## Effect of traits on plant performance

We evaluated the effect of individual traits and hypervolume on plant individual performance. To that aim, individual performance was assessed by measuring its biomass (including
vegetative and flowering parts), after having oven-dried plant material at $65^{\circ} \mathrm{C}$ for 48 h . To assess the effect of individual traits on plant performance, we used Confirmatory Path Analysis (CPA; Shipley 2009, package 'piecewiseSEM' in R - Lefcheck 2016). This analysis allows including relationships among variables that serve as predictors in one single model. In our case, CPA included the effect of the four traits (stem density and second moment of area, height, and SLA) in the performance (individual biomass), together with the effect of wind in all variables. In addition, we also included the effect of SLA and stem density on the other two traits, as resource acquisition and tissue resistance could influence plant architecture (Puijalon et al. 2011; Lienin and Kleyer 2012). To take into account a potential relationship between height and stem second moment of area, we also included the correlation between both traits in the model. Finally, the site was included as a random effect for all the paths in the model. We ran one CPA for each species for a total of three models, and we calculated both the direct and indirect effects of all variables on plant performance.

To evaluate the effect of species hypervolume on their performance, we first built one hypervolume using three traits (stem density and second moment of area, SLA) for each combination of wind condition, species and site (two wind conditions $\times$ three species $\times$ three sites $=18$ hypervolumes). For each hypervolume, we then calculated the contribution and the centroid of each trait. Centroid is the arithmetic mean position of all the values of a given trait within the hypervolume, and is related to the trait mean value (Benavides et al. 2019). Then, we ran a linear mixed model using the lme4 package in $R$ (Bates et al. 2015) where we included the interaction between wind and species, together with the centroid and contribution for each trait as explanatory variables; biomass (calculated as the individual mean biomass on each combination of wind conditions, species, and site) was included as a response variable. Centroid informs about the effect of trait values on plant performance, while contribution will inform about the effect of trait variability. Site was included as a random effect in all models. We
applied a model selection procedure where we first fitted the complete model, and fitted the same model after removing the variable with least explanatory power. If the reduced model showed lower AIC than the complete one, we selected the reduced model as the candidate for the best model and repeated the same procedure. We selected the final model as the one presenting the lowest AIC during the whole selection process. Finally, we used a variance partitioning method using the hier.part package in R (Nally and Walsh 2004) on the final model to evaluate the explained variance associated with wind, species, trait values (centroid) and variability (contribution).

## Results

## Wind induces changes in plant stature and flexibility

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

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

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

## Trait effects on individual plant performance

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

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

## Discussion

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

## Switch of species strategies toward the avoidance of wind stress

In accordance with our first hypothesis, wind strongly affected plant height and stem second moment of area $I$. Plants thriving in windy microhabitats were smaller, with stem cross section resulting in higher flexibility, regardless of the plant species. However, no intraspecific
differences in stem density between plants from windy $v$ s. sheltered microhabitats were recorded. These findings highlight changes in plants' growth strategies toward stress avoidance rather than tolerance, in line with previous works testing plant responses to wind (e.g. Jaffe and Forbes 1993, Zhang et al. 2021, see Gardiner et al. 2016 for review). Working with plants from other sub-Antarctic Islands (Iles Crozet), Bazichetto et al. (2020) also found that low-stature discriminated invasive from non-invasive alien plant species, and this morphological feature may strongly contribute to explain the greater geographic expansion capacities of non-native plants at this archipelago. Moreover, long-established alien plants from Iles Kerguelen may have evolved adaptation to cope with the strong winds of this region, which would explain the fixity of stem density we are reporting. Genetic assimilation, which turns the plastic response into a genetically invariant one, is one possible mechanism leading to a stable expression of the trait regardless of wind conditions (West-Eberhard 2003; Ghalambor et al. 2007; Lande 2009).

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

## Influence of wind on plant economics spectrum

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

Conversely, plants from sheltered microhabitats displayed increased variability of their SLA, while stem traits were more (stem density) or less (I) variable than expected. Increased variability can be associated with higher niche differences in the community, reducing competitive interactions between native and alien species, ultimately supporting their persistence in the ecosystem. This likely depicts the involvement of PES in mechanisms (fitness equalizing or niche stabilizing) supporting species coexistence under competitive interactions
(Chesson 2000, Herben and Goldberg 2014; Kraft et al. 2015b), especially in invasion contexts (Helsen et al. 2020).

## The role of traits in plant performance

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

## Importance of trait mean and variability

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

## Concluding remarks and prospects

This study emphasized that wind, which is an overlooked cause of stress in vegetation, has important effects on plant functional traits, including not only traits involved in mechanical resistance but also in resource acquisition, and generally reduces species performance. More
importantly, the effects of wind operate through the modification of plant trait values. The contrasting responses to wind that we evidenced in the three studied species, warn about their negative impact on local community. Most often, the successful colonization of new geographic regions by invasive plants highly depends on their capacity to occupy vacant niches, or by outcompeting established species in the communities (Moles et al. 2008; Drenovski et al. 2012; Te Beest et al. 2015). At Iles Kerguelen, the presence of multiple invaders having diverse growth strategies for handling stressful environmental conditions, would represent major threats for local plant communities, as these have the potential to occupy a wide diversity of ecological niches and habitats. This hypothesis is supported by Momberg et al. (2021) demonstrating the importance of wind as driver of plant community composition. Our study thus contributes to the understanding of wind role in plant community assembly, and underlines that this ubiquitous environmental stress should be more thoroughly taken into account in assembly theories, especially in the context of invading windy habitats.

## Data availability

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

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Tables

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

|  |  | Species ( $\mathrm{df}=2$ ) |  | Wind ( $\mathrm{df}=1$ ) |  | Species $\times$ Wind (df=2) |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | F | P | F | P | F | P |
|  | Height | 30.03 | *** | 303.88 | *** | 8.98 | *** |
| Avoidance traits | $I$ | 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

Table 2. Effects of trait mean (centroid) and variance (contribution), species, and wind on individual performance. (-) indicates that after model optimization, these variables were removed from the best model (i.e. the most parsimonious with the lowest AIC). Species estimates represent the difference between D. glomerata and others. Microhabitat estimate 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 | Centroid | - | - | - | - |
|  | Contribution | -0.188 | 0.082 | -2.306 | 0.05. |
| Species | P. pratensis | -0.664 | 0.136 | -4.864 | 0.001** |
|  | T. officinalis | -0.543 | 0.157 | -3.467 | 0.009** |


| Microhabitat | Shelter | 0.45 | 0.11 | 4.101 | $0.003^{* *}$ |
| :--- | :--- | :--- | :--- | :--- | :--- |

Note: Symbols next to P indicate significant difference, i.e., . $<0.1$; * $P<0.05 ; * * P<0.01$; *** $P<0.001$.

## Figures

Figure 1. Mean traits ( $\pm \mathrm{SD}$ ) 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: $\mathrm{ns}=$ 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.

Figure 2. Hypervolume size (volume) of a) plants from windy $v s$. 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.

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.

Figure 4. (Left) Confirmatory Path Analysis of the effects of wind and traits on individual performance in a) Dactylis glomerata, b) Poa pratensis, and c) Taraxacum officinale. Numbers adjacent to arrows are standardized path coefficients (analogous to relative regression weights)
and indicative of the effect of the relationship. Continuous arrows show positive and dashed arrows negative relationships, with arrow thickness being proportional to relationship strength. The proportion of variance explained $\left(\mathrm{R}^{2}\right)$ is shown besides each response variable in the model. Goodness-of-fit statistics are shown below the plot as the Fischer's C value, the P-value, and the degrees of freedom (DF) for each model. ${ }^{*} \mathrm{P}<0.05 ; * * \mathrm{P}<0.01 ; * * * \mathrm{P}<0.001$. Nonsignificant arrows are removed to simplify model interpretation, marginally significant arrows ( $\mathrm{P}<0.1$ ) do not show any symbol. Models only show effects for sheltered habitats; models showing effects for windy habitats are shown in Fig. S3. (Right), absolute standardized direct, indirect, and total sum effects of wind and traits on individual performance. $I$ : second moment of area; S. density: stem density.

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.

Supplementary materials


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

b)

$$
I=\frac{\pi}{4} *\left(b^{\square} * a\right)
$$

$$
I=\frac{\pi}{4} *\left(b^{\square} * a-b_{\square}^{\square} * a_{\square}\right)
$$

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


C-score=2.419, P-value $=0.298, \mathrm{Df}=2$
b) Poa pratensis, Windy


C-score $=0.932$, P-value $=0.628, \mathrm{Df}=2$

## c) Taraxacum officinale, Windy



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

Figure S3. Confirmatory Path Analysis for the effect of wind and traits on individual performances in a) Dactylis glomerata, b) Poa pratensis and c) Taraxacum officinale. Numbers
adjacent to arrows are standardized path coefficients (analogous to relative regression weights) and indicative of the effect of the relationship. Continuous arrows show positive and dashed arrows negative relationships, with arrow thicknesses proportional to the strength of the relationship. The proportion of variance explained $\left(R^{2}\right)$ is shown besides each response variable in the model. Goodness-of-fit statistics are shown in below the plot as the Fischer's C value, the P-value, and the degrees of freedom (DF) for each model. ${ }^{*} \mathrm{P}<0.05 ; * * \mathrm{P}<0.01 ; * * * \mathrm{P}<$ 0.001. Non-significant arrows are removed to simplify model interpretation. Marginally significant arrows do not show any symbol. Absolute standardized effects are the same as in Figure 4. I: second moment of area; S.density: stem density.

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

|  |  | T. officinale | P. pratensis | D. glomerata |
| :--- | :---: | :---: | :---: | :---: |
| 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 | - | - | $1.20( \pm 0.66)$ |


|  |  | Height | SLA | $I$ | Stem density |
| :--- | :--- | :---: | :---: | :---: | :---: |
| Dactylis glomerata | Height | 1 | 0.02 | 0.71 | 0.46 |
|  | SLA | 0.02 | 1 | -0.18 | -0.08 |
|  | $I$ | 0.71 | -0.18 | 1 | 0.26 |
|  | Stem density | 0.46 | -0.08 | 0.26 | 1 |
| Poa pratensis | Height | 1 | 0.26 | 0.53 | 0.04 |
|  | SLA | 0.26 | 1 | 0.08 | -0.01 |
|  | I | 0.53 | 0.08 | 1 | 0.26 |
| Taraxacum officinale | Height | 1 | -0.43 | 0.79 | -0.46 |
|  | SLA | -0.43 | 1 | -0.4 | 0.26 |
|  | $I$ | 0.04 | -0.01 | 0.26 | 1 |
|  | 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 |
|  | Stem density | 0.34 | 0.26 | -0.5 | 1 |

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

|  |  | 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 | 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 | $<0.001^{* * *}$ |

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

Note: Asterisks indicate significant difference, i.e., ns = not significant; * $P<0.05 ; * * P<0.01$; *** $P<0.001$.


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: $\mathrm{ns}=$ not significant; $\mathrm{P}<0.1$; * $\mathrm{P}<0.05$; ** $\mathrm{P}<0.01$; *** $\mathrm{P}<0.001$. D.glo: Dactylis glomerata, P.pra: Poa pratensis, T.off: Taraxacum officinale.


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.


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.
a) Dactylis glomerata, Sheltered


C-score $=2.419$, P-value $=0.298, \mathrm{Df}=2$
b) Poa pratensis, Sheltered


C-score=0.932, P-value $=0.628, \mathrm{Df}=2$
b) Taraxacum officinale, Sheltered


C-score $=4.636, \mathrm{P}$-value $=0.098, \mathrm{Df}=2$

Figure 4. (Left) Confirmatory Path Analysis of the effects of wind and traits on individual performance in a)
Dactylis glomerata, b) Poa pratensis, and c) Taraxacum officinale. Numbers adjacent to arrows are standardized path coefficients (analogous to relative regression weights) and indicative of the effect of the relationship. Continuous arrows show positive and dashed arrows negative relationships, with arrow thickness being proportional to relationship strength. The proportion of variance explained (R2) is shown besides each response variable in the model. Goodness-of-fit statistics are shown below the plot as the Fischer's C value, the P-value, and the degrees of freedom (DF) for each model. *P < 0.05; **P < 0.01 ; ***P < 0.001. Non-significant arrows are removed to simplify model interpretation, marginally significant arrows ( $\mathrm{P}<0.1$ ) do not show any symbol. Models only show effects for sheltered habitats; models showing effects for windy habitats are shown in Fig. S3. (Right), absolute standardized direct, indirect, and total sum effects of wind and traits on individual performance. I: second moment of area; S. density: stem density.


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.

$$
127 \times 76 \mathrm{~mm}(150 \times 150 \mathrm{DPI})
$$

