Multidimensional trait space outlines the effects of changes in abiotic filtering on aquatic plant community from sub-Antarctic ponds

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ARTICLE INFO

ABSTRACT

In the current context of climate changes, which causes strong habitat variation, an understanding of the mechanisms underlying plant community dynamics is crucial to predict species fates. The taking of inter- and intraspecific trait variability into account would aid the identification of these mechanisms. Recently, a method involving the calculation of hypervolumes (*n*-dimensional spaces of trait values) was developed for the study of plant responses to their environments. Through hypervolume comparison, we examined the effects of interannual variations in abiotic conditions on aquatic plant communities in ponds of the sub-Antarctic Iles Kerguelen. This model system is particularly relevant for the examination of the consequences of climate changes–related habitat variation, as aquatic plant communities are adapted to cold and overall stable habitat conditions and the sub-Antarctic climate is changing rapidly. We conducted field sampling over four years at three sites. For all aquatic species, we measured five foliar, shoot, and clonal traits characterizing individual growth strategies that are likely to respond to variations in abiotic conditions on 1565 ramets over the four years. We measured 10 abiotic variables to characterize the plants' habitats every three months during the survey period. Hypervolumes were calculated for each site and year to assess variation in aquatic plant strategies at the community level. We demonstrated (i) the importance of spatiotemporal gradients of trophic status, temperature, and pH and dissolved oxygen concentration for the functional structure of aquatic plant communities; (ii) that the shape of the mean response was trait dependent, with traits related to plant metabolism (specific leaf area and specific internode mass) and three-dimensional space exploration (height and internode length) responding to the three spatiotemporal abiotic gradients; (iii) that selection pressures were especially high on aerial traits relative to clonal traits; and (iv) that given the community response to interannual variations of abiotic conditions, environmental changes should impact macrophyte community productivity. *Synthesis.* We conclude that the examination of interannual abiotic variation over four years is sufficient to detect rapid responses of macrophyte communities, with likely reliance on phenotypic plasticity. Our findings may inform the characterization of future functional changes in aquatic plant communities of the sub-Antarctic region, where similar species are found.

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1. Introduction

In the current context of climate changes, with the increasing number and extent of extreme weather events [*e.g.*, more frequent episodes of high temperatures, low precipitation, and high nutrient availability (Chaudhry and Sidhu, 2022; Franklin et al., 2016)], an improved understanding of the mechanisms shaping plant community dynamics is critically needed for the accurate prediction of the fates of plant species. Abiotic filters are often key drivers controlling community structure, as they operate on individual traits and contribute to the selection of trait combinations that fit habitat constraints (Chase, 2003; Keddy, 1992; Violle et al., 2007). As they are under selection and are driving forces of community dynamics, functional traits have been foci of study, and trait-based approaches have been suggested to be valuable for the rebuilding of community ecology and establishment of general principles for assembly mechanisms (Mcgill et al., 2006). Plant functional traits are morphological, physiological, and phenological characteristics that impact individual performance directly or through growth, reproduction, or survival (Violle et al., 2007).

Historically, comparative studies focused on interspecific trait variations in plants exposed to changing environments. More recently, the importance of considering intraspecific trait variability, resulting from plasticity or local adaptation (Choler, 2005; Garnier et al., 2004; Mcgill et al., 2006; Quétier et al., 2007), has been emphasized. This variability plays a major role in the maintenance of plant biodiversity by enabling species to express varying phenotypes and thus to resist a large range of environmental filters (Albert et al., 2010; Jung et al., 2010; Messier et al., 2010; Nicotra et al., 2010; Violle et al., 2012). The combined examination of inter- and intraspecific trait variability in analyses of the effects of changes in habitat conditions would greatly improve our ability to obtain a refined understanding of the mechanisms underlying plant community assembly over time.

Aquatic plant species are generally clonal, *i.e.*, able to produce genetically identical and potentially independent ramets (erect shoots with leaves and roots) connected by plagiotropic stems (van Groenendael et al., 1996). They can cope with environmental variation through vertical (shoot and foliar) and horizontal [clonal (Klimeš et al., 1997; van Groenendael et al., 1996; Ye et al., 2014)] trait modification. Aquatic habitats are among the most abiotically constrained ecosystems in the world (Santamaría, 2002). Indeed, aquatic plants have to deal with limiting habitat conditions related to variations in water physical parameters (e.g., temperature, pH), resource availability (gas, light, nutrients, water), and trophic status (Lacoul and Freedman, 2006). Ongoing climate changes is predicted to further strengthen the intensity of weather constraints (Lee et al., 2021), with cascading consequences on the amplitude of the variations in these habitats' conditions. In cold and humid climates, subtle temperature changes have been found to stimulate plant photosynthesis and growth (Barko et al., 1986; Silveira and Thiébaut, 2017), increasing the individual specific leaf area (SLA), height (Riis et al., 2012), and root length (Kaspar and Bland, 1992; Pregitzer et al., 2000), and to reduce species' risk of exposure to their lower thermal tolerance limits *i.e.*, to weaken the abiotic filter. In upcoming years, milder temperatures should reduce the need for resource storage in connections (Suzuki and Stuefer, 1999), and ramets should aggregate in the resulting favorable habitats through the reduction of internode length (Halassy et al., 2005; van Groenendael et al., 1996). Considerable temperature increases, however, could expose plant species to their upper thermal limits, strengthening the selection pressure of abiotic filters. Thermal stress usually leads to the reduction of plant height, leaf area (Chalanika De Silva and Asaeda, 2017; Shah and Paulsen, 2003), and root length (Pregitzer et al., 2000). Moreover, less abundant precipitation can reduce the water depth, ultimately altering plant morphology to withstand hydric stress [*i.e.*, *via* the reduction of the SLA and increase of the leaf dry matter content (LDMC) and specific root length (Gao et al., 2021; Han et al., 2021; Luo and Xie, 2009)]. The reduction of the water column would entail increases in dissolved nutrient concentrations, causing turbidity (reduced light penetration) and variations in water pH, and thus stress for macrophytes and affecting plants' resource-acquiring organs [*i.e.*, aerial and root traits (Barker et al., 2008; James et al., 2005)]. Under unfavorable conditions, clonal plants invest more in connection length [escape behavior (Slade and Hutchings, 1987)] and resource storage for future growth (Cheplick and Gutierrez, 2000). Thus, the stringency of abiotic filtering determines average aerial and clonal trait values; less-stringent filtering results in higher and lower values, respectively, and filter strengthening has the opposite effects. Since traits interact and are involved in trade-offs (Díaz et al., 2016; Donovan et al., 2011; Freschet et al., 2010), the response of a single trait changes in abiotic parameters would imply multiple changes in other traits. It appears therefore essential to consider traits simultaneously to understand the functional response of communities to climate changes.

Trait variations ultimately influence individual performance [*i.e.*, vegetative biomass production and reproduction rates (Geber and Griffen, 2003)], and thus species' fates in plant communities (Ghalambor et al., 2007). Changes in abiotic filtering should impact their nature and extent, with consequences for community performance. Consistently, Wildova et al. (2007) showed that the magnitude of performance impacts differed among traits within plant species; it was largest for growth traits and smallest for architectural traits. In plant individuals, aerial traits (*e.g.*, height and SLA) determine the efficiency of resource-acquiring organs (Garnier et al., 2004) and thus have stronger positive effects on community performance than do clonal traits, which drive mainly spatial positioning and resource storage (Klimešová et al., 2021).

In this work, we examined aquatic plant communities in the ponds of the sub-Antarctic Iles Kerguelen archipelago. This model system is particularly relevant for the addressing of questions about the consequences of habitat variation, as (i) climate changes effects are especially severe in aquatic ecosystems (Lacoul and Freedman, 2006), (ii) sub-Antarctic aquatic plant communities are highly adapted to cold and overall stable habitat conditions (Lebouvier et al., 2011a; Walther et al., 2002), and (iii) they remain free of human and introduced species influence (both fauna and flora). We conducted field sampling over four consecutive years at three sites. We examined variations of five functional traits (three aerial and two clonal) characterizing individual growth strategies which were likely to respond to temporal variation in abiotic filter strength. In addition, we measured 10 abiotic variables that are known to affect plant growth and survival. To determine variations in the whole plant strategy, we calculated hypervolumes for each site and year based on the functional traits (Blonder, 2018; Blonder et al., 2014). The approach allowed us to take relationships between traits into account and to consider integrated phenotypes, which would drive community assembly (Bonser, 2006; Blonder et al., 2014). We tested the following hypotheses:

- that the average values of aerial (growth and light-acquiring) and clonal (space exploration and resource storage) traits would increase and decrease, respectively, with less-stringent abiotic filtering and decrease and increase, respectively, with filter strengthening;
- that strong abiotic filters, particularly thermal and nutrient stresses, would lead to (i) similar adaptive strategies (*i.e.*, stabilizing selection) at the community level, (ii) the overall reduction of individual strategy variability, and (iii) aerial and clonal trait convergence toward values that allow individuals to better cope with environmental changes;
- that aerial traits would have stronger influences on individual performance than would clonal traits.

2. Materials and methods

2.1. Study area

This study was conducted within the National Natural Reserve of the Terres australes françaises, on the main island of the Iles Kerguelen, in the eastern part of the archipelago (South Indian Ocean; 48°30'–50°00'S, 68°27'–70°35'E). The climate on the island is characterized by cold temperatures [annual mean of 4.6°C with little variation (2.1–7.7°C) over the year (Frenot et al., 2001, 2006; Lebouvier, 2007)] and low to abundant precipitation (500–3200 mm/year) along an east–west gradient (Frenot et al., 1998). We conducted sampling in shallow freshwater ponds near the shoreline. Such ponds are filled by precipitation and enriched with nutrients from marine animal dejections (mostly elephant seal and bird) (Smith, 2008). They are the main habitats of the sub-Antarctic aquatic plant communities that we studied (Douce et al., 2023). These communities display a low richness and are only composed of native species: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), *Ranunculus biternatus* Smith, *Ranunculus pseudotrullifolius* Skottsb., and *Ranunculus moseleyi* Hook.f (Ranunculaceae). *Callitriche antarctica* has a floating canopy, and the other species have rosette architectures or erect shoots (*J. scheuchzerioides*) and are rooted in the sediment. These species propagate horizontally through clonal growth (van Groenendael et al., 1996). Aquatic plant communities can be disturbed by passing elephant seals (mostly from January to March) but they are not affected by introduced herbivorous species (rabbit, reindeers).

2.2. Field survey

Sampling was conducted at three sites (from west to east, Molloy, Isthme Bas, and Cap Ratmanoff, Fig. 1) in November (*i.e.*, at the beginning of the growing season) of 2018–2021. These sites are located at distance from historic human settlements (Fig. 1). At each site, 15 ponds were selected randomly to represent a gradient of pond sizes. Each year, we randomly positioned 1-m² quadrats (five for ponds with surface areas > 5 m² and three or four for ponds with surface areas ≤ 5 m²) per pond. In each quadrat, we collected one ramet (one node with leaves and roots and one connection internode) of each of the target species (when present) for the measurement of functional traits. This resulted in 1565 ramets collected over the four years (Fig. S1 shows the proportions of individuals of each species available). After sampling, ramets were stored at 6 °C and transferred to the laboratory for measurements within 24 h.

To characterize the community composition, we estimated the surface covered by each species in the quadrat. In addition, physical and chemical parameters were measured every three months during the survey period. Mean water depth (based on three measurements), pH, specific conductance, mean dissolved oxygen concentration (calculated from measurements taken near the surface, in the middle of the water column, and at the pond bottom; HQ20; HACH™, Dusseldorf, Germany), and temperature [recorded every 30 min in the middle of water column from September 2020 to October 2021 (HOBO Pendant MX2202; ONSET™, Cape Cod, MA, USA)], were measured in the field. From each pond, one 30-mL water sample and one 50-mL sediment sample were collected for laboratory nutrient analyses. The water and sediments were each collected from three points in the pond to account for the possible heterogeneity of nutrient distribution. They were stored at 6 °C and brought to the laboratory within 24 h.

2.3. Nutrient analyses

The water samples were passed through Whatman GF/F filters (pore size, 0.7 μm; Cytiva, Amersham, United Kingdom). The water and sediment samples were then stored at –20°C for several weeks before chemical analyses. The $N–NH_4^+$ $N–NO_3^-$ and $P–PO_4^{3-}$ concentrations were determined using standard colorimetric methods (Grasshoff et al., 1999) and a sequential analyzer (SmartChem200; AMS Alliance, Barsanti, Italy).
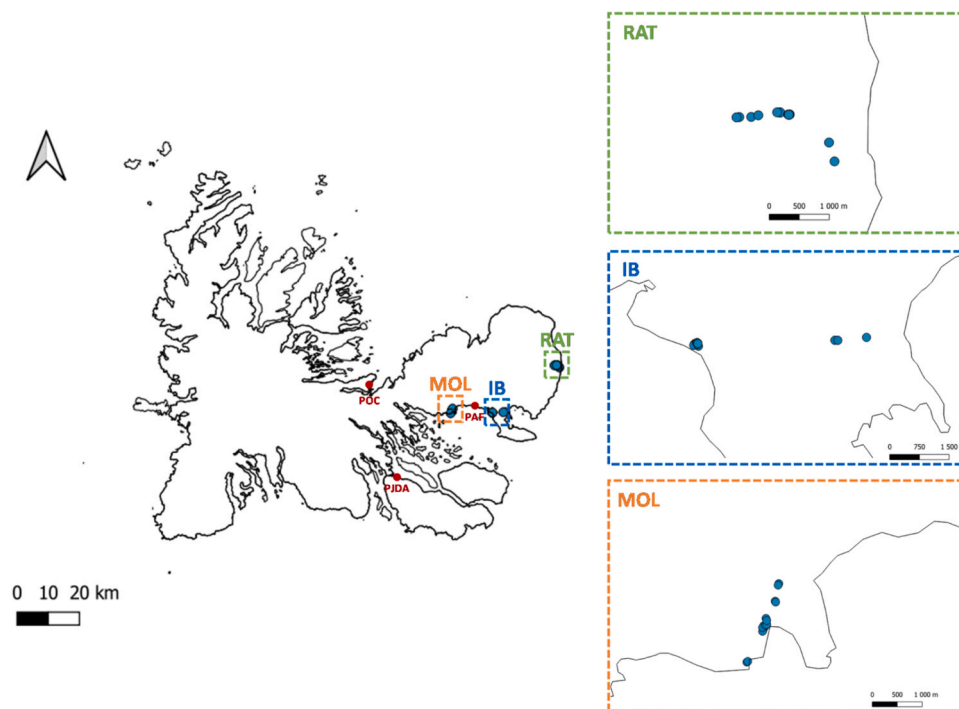
Fig. 1. On the left: Locations of the three sampled sites and their associated ponds on the French sub-Antarctic Iles Kerguelen (48°30–50°S, 68°27–70°35E). The red points indicate the positions of historic locations of human influence (PAF Port-aux-Français - French station -, POC Port Couvreux, PJDA Port Jeanne D'Arc). The blue points indicate the pond positions. On the right: Detailed positions of the ponds on the three sampled sites. MOL Molloy, RAT Cap Ratmanoff, IB Isthme Bas.

The sediment nitrogen and carbon concentrations were measured using the capsule method (Brodie et al., 2011). Specifically, 5 mg ($\pm$ 10 %) homogeneous sediment was acidified with HCl in silver capsules to eliminate carbonates. The liquid was then evaporated on a 65°C hot plate for 12 h, followed by capsule drying at 80°C for a few days. Carbon and nitrogen nutrient analyses were then performed using an elementary analyzer (FlashEA 1112 NC®; Thermo Fisher Scientific, Waltham, MA, USA). Following Ni, Wang, and Wang (2016), the available organic phosphorus was extracted from 50-mg dry sediment samples with 5 mL NaOH (1 M) and 16 h rotatory shaking at room temperature. The supernatant was collected and its pH was stabilized at 7 with the addition of HCl (4 M). The extracted phosphorous, which had been converted to orthophosphate, was quantified using the molybdate/ascorbic acid blue method (Murphy and Riley, 1962), with the results reported as milligrams of available phosphorous per gram of dry sediment.

2.4. Trait measurements

The aerial traits measured were the height, SLA, and LDMC, the latter two determined following Cornelissen et al. (2003) for one randomly selected healthy, mature leaf per ramet. The clonal traits measured were the internode length and specific internode mass, calculated as the ratio between the internode dry mass and length (g.cm^{-1}). The total ramet (*i. e.,* aerial and root components and one clonal internode) dry biomass was measured to characterize performance (Adomako et al., 2021; Keser et al., 2014; Younginger et al., 2017). The dry masses were measured after drying for 48 h in an oven at 65°C. All plants were cleaned before measurement.

2.5. Data analyses

Water temperature simulation. We performed linear regression analyses to determine the relationship between the water temperature, recorded from September 2020 to October 2021, in each pond and the air temperature recorded at the Iles Kerguelen meteorological station (2020–2021 records of Météo France, Port-aux-Français), after confirming the normality of the distribution of the model residuals. The relationships between air and water temperatures were significant (with $R^2 \geq 0.55$, $P < 0.05$) for all but two ponds (see Douce et al., 2023 for more details). These two ponds also showed significant relationships between air and water temperatures that were just slightly weaker ($R^2 = 0.40$ and $R^2 = 0.36$, $P < 0.05$). These relationships were then used to infer the water temperature from November 2017–August 2020 based on 2017–2020 Météo France records. From these simulated and observed data, we calculated the mean water temperature for each year before sampling, defined from November to October, at the pond and site scales.

Characterization of plant species habitats. Before statistical analysis, the abiotic parameters and species abundances recorded in the different quadrats of each pond were averaged for each sampling date. To characterize the habitat of each plant species (*i.e.,* the environmental conditions where the species was present), we subjected the pond abiotic parameters (Table S1) to principal component analysis (PCA) using the *FactoMineR* R package (Lê et al., 2008). The pond score for the first three axes was then averaged by site × year.

The Simpson diversity index for each pond was also calculated using the *vegan* R package (Oksanen et al., 2015), and averaged the values by site × year.

Construction of five-dimensional hypervolumes. The five-dimensional trait spaces of the aquatic plant communities were built through space and time using multidimensional kernel density estimation procedure (Blonder, 2018; Blonder et al., 2014). One hypervolume per site and year (total = 12) was built by combining the trait data for all species present in the fifteen ponds (to ensure a minimum of 100 ramets to calculate one hypervolume, following Blonder et al. 2018 recommendations; Fig. S1 shows the proportions of individuals of each species

available) and using a kernel based on the Silverman (2017) estimator. Before analysis, we checked for redundancy between traits; no correlation coefficient was > 0.5 (Dormann et al., 2013). The trait data were standardized using the mean and standard deviation of all data simultaneously (Blonder et al., 2014). For centered-reduced data, hypervolumes are reported in units of SDs to the power of the number of trait dimensions used. All hypervolumes were built using the *hypervolume* R package (Blonder et al., 2014).

Analysis of the influence of habitat on aquatic plant community similarity. To analyze the effect of habitat on aquatic plant community traits, we calculated the overlap (intersection in the trait-defined five-dimensional space) between each pair of hypervolumes over space (i.e., three sites) and time (i.e., 4 years) using the Sorensen similarity index (Mammola, 2019): 2 × volume shared by hypervolumes A and B / volume of hypervolume (A + B). The volume is a measure of hypervolume size, considering the range of values observed along each axis, *i. e.,* the variability of all traits forming the hypervolume simultaneously. Similarities between hypervolume pairs were then compared using Ward's clustering method (Murtagh and Legendre, 2014). The effects of (i) space and time, and of (ii) abiotic parameters and species abundances, on the similarities were assessed using multivariate permutational analysis of variance (PERMANOVA) with the Adonis function of the vegan R package. Significant positive effects indicated that communities with similar hypervolumes had similar habitat conditions.

Analysis of the influence of habitat on the multidimensional trait space volume. To characterize the effect of habitat on growth strategies at the community level, the hypervolume volume was calculated for each aquatic plant community over space and time. Decrease in hypervolume volume indicates lower variability in growth strategies at the community level. As the volume is related to the number of individuals used to calculate the hypervolume (Blonder, 2018) bootstrapping was used to simulate 100 hypervolumes per community for comparison (Bittebiere et al., 2019). Random selection of individuals with replacement was performed for each aquatic plant community, with the number of individuals used set to the smallest number of sampled individuals among all communities (*i.e.,* 100). Then, the log-transformed hypervolume volumes were entered as response variables in linear mixed-effects models [*nlme* R package (Pinheiro et al., 2013)]. Space and time were used as main effects in a first model, and the first three PCA axes and the Simpson diversity index as main effects in a second model. The aquatic plant community designation (depending on space and time) was included as a random variable to control for non-independence between simulated hypervolumes. Quadratic terms were also included to test for potential non-linear effects in the second model. Every possible subset of this model was tested, and best-fitting variable combinations [Akaike's information criterion (AIC) < 2 (Akaike, 1974)] were compiled by model averaging [*MuMIN* R package (Bartoń, 2013)]. The same analysis was performed for each trait centroid coordinate (mean point on each axis) of the simulated hypervolumes.

Analysis of modifications of trait contributions to hypervolume shape. For each aquatic plant community through space and time, the contributions of the five traits to the multidimensional trait space were calculated as the ratios between volumes of the hypervolumes considering all traits to those of the hypervolumes considering all traits but the trait of interest (Mammola, 2019). The trait contribution was thus related to the trait variability relative to that of other traits. Comparing volumes with and without the trait of interest, necessarily leads to compare volumes of different dimensionality, and therefore trait contribution is bound to be greater than one. Hypervolumes representing the potential multidimensional trait spaces of the communities were simulated by resampling 100 individuals from all sites and years combined (*i.e.,* the 1565 individuals measured), 100 times. These simulated hypervolumes were used to build 95% confidence intervals (*i.e.,* by selecting the 2.5th and 97.5th percentiles). Then, the observed contribution of each trait for each community was compared to the confidence

intervals. Trait contributions falling outside of the confidence interval differed significantly from the expectation.

Analysis of trait effects on community performance. The community weighted mean [CWM, (Zelený, 2018)] biomass was used as a proxy of community performance (Adomako et al., 2021; Keser et al., 2014; Younginger et al., 2017). As species abundances (percentage of cover) and individual biomasses were estimated at the quadrat scale, the CWM biomass was first calculated at this scale and then averaged by pond and by site × year. As only one hypervolume was calculated per aquatic plant community (providing no variability for the assessment of the effect on community performance), bootstrapping was used to simulate 100 hypervolumes for each community through space and time. Each simulation contained data from 40 randomly selected quadrats in a community for each site × year, from which the CWM biomass and corresponding hypervolume were calculated. Then, the log-transformed CWM biomasses were used as response variables in linear mixed-effects models [*nlme* R package (Pinheiro et al., 2013)], with the centroids and contributions of the five traits of the corresponding hypervolume serving as main effects and the aquatic plant community designation (depending on space and time) included as a random variable to control for non-independence between simulated hypervolumes. Every possible subset of this model was tested, and best-fitting variable combinations [AIC < 2 (Akaike, 1974)] were compiled by model averaging [*MuMIN* R package (Bartoń, 2013)]. All analyses were conducted with R 4.1.2 (www.r-project.org).

3. Results

3.1. Characterization of plant species environment

The first three axes of the pond abiotic parameter PCA explained 53.2% of the total variance (Fig. S2a, b). The first axis (PCA1) described the trophic status of the ponds based on water and sediment nutrient concentrations (Fig. S2c); the second axis (PCA2) was related to the temperature (32.8 %), water depth, and nitrogen and carbon sediment concentrations; and the third axis (PCA3) was associated with the pH and dissolved oxygen concentration. The pond score for these axes was then averaged by site × year (Fig. S3). The diversity of pond plant communities was on average high and stable through time and space (Fig. 2). These communities were dominated by *Callitriche antarctica*, *Juncus scheuchzerioides*, and *Ranunculus biternatus*, while the three other

species were rare (Fig. S1).

3.2. Influence of abiotic parameters on the multidimensional trait space

Time ($F_{df=3/8} = 2.75$**) but not space ($F_{df=2/9} = 0.69$ ns) affected the communities' multidimensional trait spaces. This result indicates that communities were more functionally similar within years but not within sites (Fig. S4). The abiotic parameters influenced the communities' multidimensional trait spaces. The second (temperature) and third (pH and dissolved oxygen concentration) PCA axes significantly affected the similarity between hypervolumes, and the first axis (trophic status) tended to do so (PCA1, $F_{df=1/7} = 2.29$; PCA2, $F_{df=1/7} = 4.54$**; PCA3, $F_{df=1/7} = 2.41$*). These results indicate that more functionally similar communities had grown under more similar abiotic conditions (Fig. S4). The Simpson diversity index had no effect on hypervolume similarity ($F_{df=1/7} = 0.68$ ns).

3.3. Multidimensional trait space reduction with abiotic filter strengthening

The hypervolume volumes (reflecting the variability of community-level growth strategy) varied significantly through time ($Chisq_{df=3} = 20.43$***) but not through space ($Chisq_{df=2} = 2.31$ ns). Regarding abiotic parameters, volumes decreased linearly (with no significant quadratic effect) with increasing abiotic parameter values along the three PCA axes, with equivalent strength (similar slopes) among filters (Fig. 3, Table 1). This indicated lower variability in growth strategies at the community level, with increasing nutrient availability, temperature, and pH and dissolved oxygen concentration. The Simpson diversity index had no effect on the hypervolume volumes.

3.4. Variation in trait centroid positions and contributions to hypervolume shape

The centroid position and the contribution to hypervolume shape respectively informed on the trait mean and variability relatively to other traits.

The second PCA axis (thermal conditions) significantly affected all traits except the LDMC (Table 2, Fig. S5). It had negative linear effects on the height, SLA, and internode length; it and PCA3 displayed negative bell-curve relationships with the specific internode mass. The first
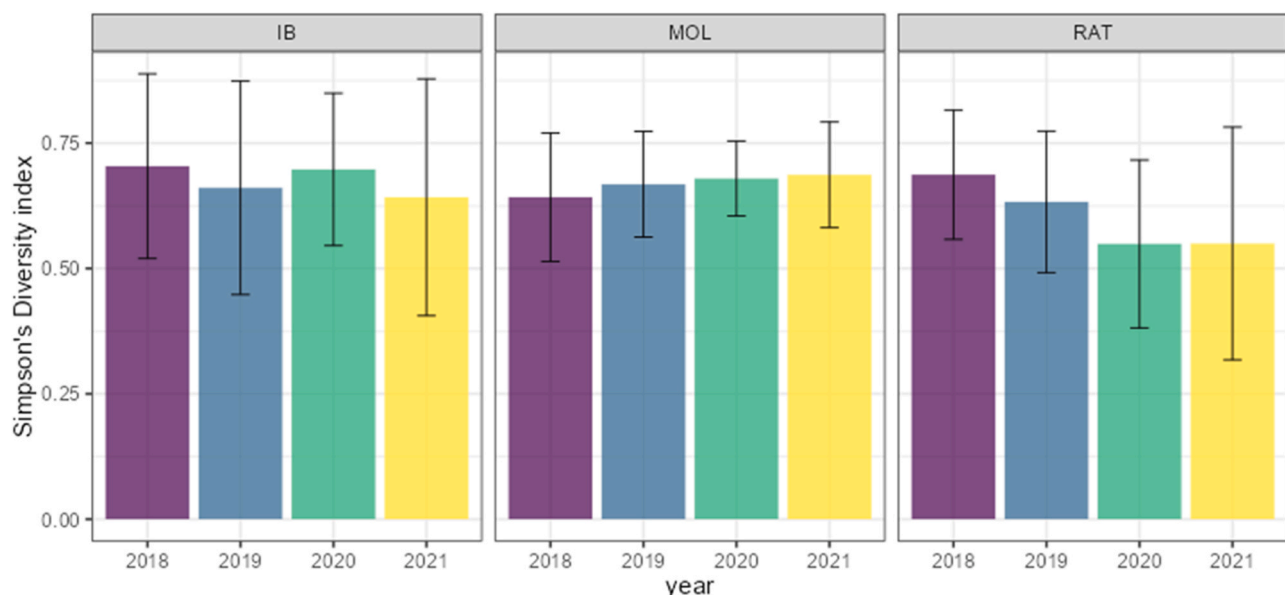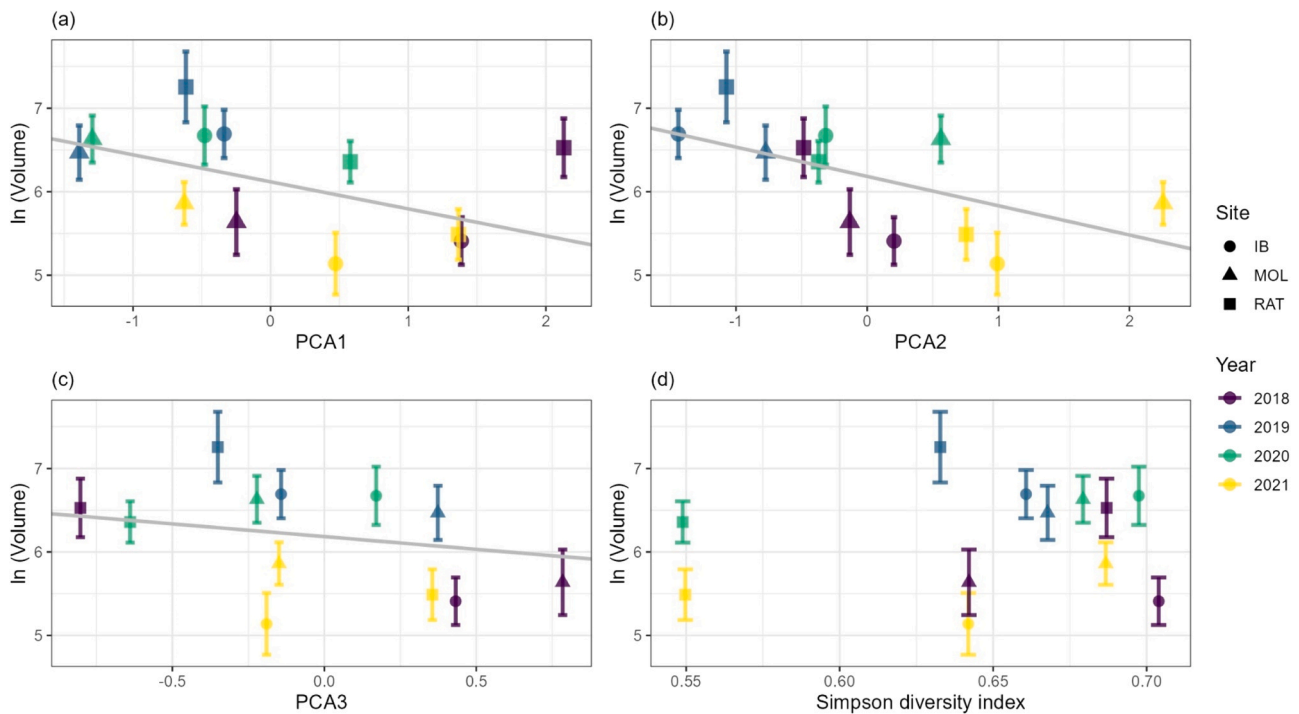

Fig. 2. Mean Simpson diversity index of each site for each year.

Fig. 3. Relationships between volumes of the hypervolumes and the habitat conditions. Relationships between volumes (means of ln-transformed values ± SDs) of the 12 hypervolumes calculated for aquatic plant communities through space and time and the three principal component (PCA) axes describing abiotic conditions (a–c) and the Simpson diversity index (d). Volumes indicate hypervolume sizes based on the five traits considered, and reflect the variability of community-level growth strategy. Gray lines reflect significant effects (p < 0.01) of explanatory variables in fitted linear mixed-effects models. PCA1, trophic status; PCA2, thermal conditions; PCA3, pH and dissolved oxygen concentration. SD, standard deviation.

Table 1

Effects of principal component (PCA) axes and the Simpson diversity index on hypervolume volumes, reflecting the variability of community-level growth strategy.

	DF	Estimate	SE	Adjusted SE	Z value	Pr(>|z|)
PCA1	**1**	**-0.323**	**0.089**	**0.105**	**3.056**	**0.002**
PCA1[a]	1	0.050	0.079	0.087	0.579	0.562
PCA2	**1**	**-0.351**	**0.084**	**0.101**	**3.464**	**<0.001**
PCA2[a]	1	0.009	0.039	0.046	0.194	0.846
PCA3	**1**	**-0.304**	**0.083**	**0.100**	**3.042**	**0.002**
Simpson diversity index	1	0.009	0.038	0.044	0.213	0.831

Data are for full averages of the best-fitting linear mixed-effects models, selected by Akaike information criterion comparison. Significant values are in bold, asterisks indicate significant effect: **p < 0.01; ***p < 0.001.

[a] Quadratic effect; SE, standard error; Pr(>\|z\|), p value from the Z test. PCA1, trophic status; PCA2, thermal conditions; PCA3, pH and dissolved oxygen concentration.

(trophic status) and third (pH and dissolved oxygen concentration) axes had negative linear effects on the height and positive quadratic effects on the SLA (*i.e.*, with minimal values at intermediate axis positions). The Simpson diversity index affected the height (Table 2).

The aerial trait (height, SLA, and LDMC) variability differed significantly from the null model for four aquatic plant communities through space and time; such significant effects of clonal traits were found for only two communities (Fig. 4, S3). The variability of height was significantly more than expected for a community with low scores on the three PCA axes, and significantly less than expected for communities with high scores on the three axes. The variability of the LDMC was significantly more than expected for a community with a low PCA1 (trophic status) and high PCA2 (temperature) axis score, and

significantly less than expected for communities with high PCA1 and low PCA2 axis scores. The opposite pattern was observed for the SLA. No clear pattern of variability was observed for the clonal traits (Fig. 4, S3).

3.5. Influence of trait means and variability on community performance

We found a significant positive effect of the mean height (centroid) on the CWM biomass (Table 3), which was the only mean trait effect on community performance detected. The trait variability (contribution) significantly affected the CWM biomass for the SLA (negatively) and specific internode mass (positively; Table 3). The LDMC and internode length had no significant effect on community performance.

4. Discussion

4.1. Convergence of community strategies along abiotic filter strengthening

In this study, the comparison of hypervolumes through space and time revealed that abiotic filter variations between years, affected aquatic plant strategies at the community level. In particular, abiotic environmental conditions affected the variability of plant strategies and the similarity of trait spaces between communities.

Reductions in and/or displacement of species' multidimensional trait spaces have been reported at local scales and over very short terms [≤2 years (Carmona et al., 2015; Rodríguez-Alarcón et al., 2022)]. Studies conducted at larger spatiotemporal scales have not involved the examination of multidimensional trait spaces and have focused only on terrestrial ecosystems (*e.g.,* Rota *et al.*, 2017 for 3-year sampling). Through our approach, we demonstrated that aquatic communities under similar abiotic constraints displayed similar strategies, suggesting that individual functional responses to interannual variations were homogeneous at the regional scale (King et al., 2017), and thus reflecting stabilizing selection. This short-term response suggests the occurrence of

Table 2
Effects of principal component (PCA) axes on centroid coordinates, reflecting trait means.

		DF	Estimate	SE	Adjusted SE	Z value	Pr(>|z|)
Height	**PCA1**	1	**-0.206**	**0.028**	**0.036**	**5.730**	**< 0.001**
	PCA1[a]	1	0.042	0.032	0.037	1.118	0.263
	PCA2	1	**-0.086**	**0.026**	**0.033**	**2.626**	**0.008**
	PCA2[a]	1	0.009	0.017	0.020	0.453	0.651
	PCA3	1	**-0.157**	**0.026**	**0.032**	**4.804**	**<0.001**
	PCA3[a]	1	-0.006	0.016	0.020	0.302	0.762
	Simpson diversity index	1	**-0.126**	**0.027**	**0.034**	**3.724**	**<0.001**
SLA	PCA1	1	0.005	0.021	0.025	0.217	0.828
	PCA1[a]	1	**0.131**	**0.034**	**0.041**	**3.206**	**0.001**
	PCA2	1	**-0.215**	**0.037**	**0.044**	**4.864**	**<0.001**
	PCA2[a]	1	0.021	0.028	0.031	0.682	0.495
	PCA3[a]	1	**0.128**	**0.034**	**0.041**	**3.070**	**0.002**
	Simpson diversity index	1	0.004	0.018	0.021	0.202	0.839
LDMC	PCA1	1	-0.035	0.066	0.070	0.499	0.618
	PCA1[a]	1	-0.063	0.077	0.083	0.765	0.444
	PCA2	1	0.037	0.064	0.069	0.543	0.587
	PCA[a]	1	0.065	0.061	0.066	0.984	0.325
	PCA3	1	0.004	0.025	0.028	0.171	0.864
	PCA3[a]	1	-0.031	0.059	0.063	0.498	0.618
	Simpson diversity index	1	0.062	0.075	0.081	0.766	0.443
IN length	PCA1	1	-0.056	0.048	0.054	1.043	0.297
	PCA1[a]	1	-0.042	0.044	0.049	0.867	0.385
	PCA2	1	**-0.156**	**0.045**	**0.053**	**2.899**	**0.003**
	PCA2[a]	1	0.063	0.038	0.043	1.445	0.148
	PCA3	1	-0.080	0.045	0.051	1.559	0.118
	Simpson diversity index	1	-0.008	0.023	0.027	0.319	0.749
Spe. IN mass	PCA1	1	-0.004	0.017	0.020	0.211	0.833
	PCA1[a]	1	-0.003	0.015	0.017	0.193	0.847
	PCA2[a]	1	**-0.095**	**0.026**	**0.031**	**3.090**	**0.002**
	PCA3	1	-0.043	0.038	0.042	1.015	0.310
	PCA3[a]	1	**-0.161**	**0.034**	**0.041**	**3.926**	**<0.001**
	Simpson diversity index	1	0.001	0.011	0.014	0.080	0.937

Data are for full averages of the best-fitting linear mixed-effects models, selected by Akaike information criterion comparison. Significant values are in bold, asterisks indicate significant effect: **p < 0.01; ***p < 0.001.

[a] Quadratic effect; SE, standard error; Pr(>\|z\|), p value from the Z test. PCA1, trophic status; PCA2, thermal conditions; PCA3, pH and dissolved oxygen concentration; IN, internode; Spe., specific.
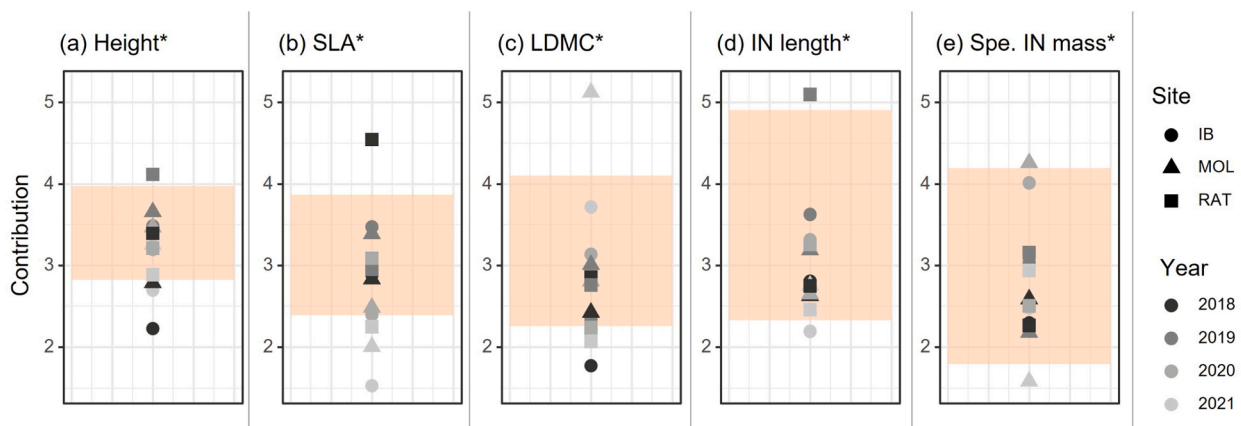
Fig. 4. Contributions of traits to hypervolume shape. Each trait's contribution is related to its variability relatively to that of the other four traits and was calculated as the ratio between volume of the hypervolume considering all traits to the one of the hypervolume considering all traits but the trait of interest. The symbols of different shades of grey represent the 12 hypervolumes calculated for aquatic plant communities through space and time (*i.e.* site × year combinations). The orange areas correspond to the confidence intervals for trait values built from simulated hypervolumes with all years and sites considered, by selecting the 2.5th and 97.5th percentiles of simulated values. For each trait, contribution values falling outside the confidence interval are significantly higher (+) or lower (−) than expected from simulation. Traits of which contribution values calculated for some site × year combinations are significantly higher or lower than expected from simulation, are indicated by the asterisk. IN, internode; Spe., specific.

trait plasticity over local adaptation, which would enable communities to respond to changing environmental conditions (Arnold et al., 2019; Matesanz et al., 2010). Previous studies have revealed positive associations between phenotypic plasticity and temporal variability in temperature and precipitation (Vázquez et al., 2017), especially in relation to interannual variation (Stotz et al., 2021).

We detected a linear decrease in strategy variability in communities along gradients of abiotic conditions, with no additional effect of community diversity [indeed, the pond community composition was stable over space and time during the survey period (Douce et al., 2023)]. We observed important variation across site × year in the temperature, N–NH$_4^+$ concentration and dissolved oxygen concentration. These results

Table 3

Effects of trait means (centroids) and variability (contributions) on plant community performance (log community weighted mean biomass).

	DF	Estimate	SE	Adjusted SE	z value	Pr(>|z|)
Height						
Centroid	**1**	**0.406**	**0.058**	**0.058**	**7.032**	**<0.001**
Contribution	1	0.006	0.025	0.025	0.237	0.813
SLA						
Centroid	1	-0.093	0.052	0.052	1.773	0.076.
Contribution	**1**	**-0.034**	**0.016**	**0.016**	**2.057**	**0.040**
LDMC						
Centroid	1	_	_	_	_	_
Contribution	1	-0.007	0.013	0.013	0.554	0.580
IN length						
Centroid	1	0.070	0.054	0.054	1.278	0.201
Contribution	1	-0.002	0.020	0.020	0.090	0.928
Spe. IN mass						
Centroid	1	0.090	0.080	0.080	1.125	0.261
Contribution	**1**	**0.027**	**0.012**	**0.012**	**2.307**	**0.021**
Simpson diversity index	1	0.001	0.011	0.014	0.080	0.937

Data are for full averages of the best-fitting linear mixed-effects models, selected by Akaike information criterion comparison. Significant values are in bold, asterisks indicate significant effect: **p < 0.01; ***p < 0.001. [2] Quadratic effect; SE, standard error; Pr(>\|z\|), p value from the Z test. IN, internode; Spe., specific.

confirmed the concept that aquatic systems are characterized by multiple constraints, which could explain their particular sensitivity to climate changes through the modification of several abiotic parameters (Santamaría, 2002). In addition, we found that the relationships between strategy variability and filter stringency were linear, rather than quadratic, suggesting a gradual response to increasing temperature, trophic status, pH, and dissolved oxygen concentration. The decrease in strategy variability in response to the strengthening of each of the three detected abiotic filters suggests the existence of different adaptive phenotypes to cope with increased stringency. One could wonder about the possibility that a single phenotype enabling species to respond to the simultaneous strengthening of different filters could develop, as found in drylands, where traits related to drought tolerance and defense against herbivory are the same (Lin et al., 2023). High values along these abiotic gradients– *i.e.* high temperatures and high nutrient concentrations – are those expected for the upcoming years, due to climate changes. More frequent episodes of high temperatures and low precipitations should reduce water depth in ponds and thus entail increases in dissolved nutrient concentrations (Lebouvier et al., 2011b; Smith, 2002). The community responses to interannual variations in abiotic parameters observed in this short-term study – *i.e.,* reduced strategy variability - can thus be expected on the long-term with climate changes.

4.2. Importance of traits related to plant metabolism in response to increasing temperature, trophic status, pH, and dissolved oxygen concentration

Trait responses to the three spatiotemporal gradients of abiotic parameters considered in this study (*i.e.*, temperature, trophic status, and pH and dissolved oxygen concentration) did not support our hypothesis that mean aerial and clonal trait values would decrease and increase, respectively, with abiotic filter strengthening and show the converse pattern with less-stringent abiotic filters. The shape of the mean response is actually trait dependent, with no connection to the trait category (*i.e.*, clonal or shoot/foliar). Traits related to plant metabolism (SLA, specific internode mass) and to three-dimensional space exploration (height, internode length) displayed quadratic and linear responses, respectively, to the three spatiotemporal abiotic gradients (with the exception of the linear relationship between the SLA and temperature). The quadratic relationships of the SLA and specific internode mass to the abiotic filters can be attributed to the efficiency of underlying enzymatic

(metabolic) reactions, which usually display optimums for intermediate level of habitat conditions (Foyer et al., 2002; Salvucci and Crafts-Brandner, 2004). The SLA has usually been found to increase linearly with the trophic status to allow individuals to switch from a relatively conservative toward an acquisitive resource strategy (Poorter and de Jong, 1999). The decrease in the SLA observed in this study may follow this principle and be related to the balance between N-NH$_4^+$ and N-NO$_3^-$. Although the overall nutrient availability was greater, this balance changed with the reduction of the NH$_4^+$ concentration, and thus likely the quantity of bioavailable nitrogen for plant growth. Beyond the switching point in the relationship, nutrient concentrations are very to extremely high, which causes turbidity and explains individuals' investment in larger leaves to support light acquisition, especially under higher nutrient availability (Freschet et al., 2015). Similarly, the specific internode mass increases or decreases depending on whether temperature stimulates [mild temperature, more carbohydrate storage (Herrmann et al., 2019)] or constrains [stressful temperature, less carbohydrate storage (Lippmann et al., 2019)] metabolism efficiency. In addition, the SLA and specific internode mass were related to the pH and dissolved oxygen concentration, with an opposite pattern of response, in this study. The pH is generally agreed to control the available forms of dissolved inorganic carbon [CO_2 *vs.* HCO$_3^-$ (Burton, 1987)], thereby affecting carbon uptake and photosynthesis (Titus and Stone, 1982). As aquatic plants have greater affinity for CO_2 than for HCO$_3^-$ (Allen and Spence, 1981), higher pHs induce stress, resulting in an increased SLA and resource storage in clonal internodes. However, higher oxygen concentrations slow carbon fixation (Van et al., 1976), resulting in less carbohydrate storage. As a consequence, individuals invest in greater SLAs to support carbon uptake through larger exchange areas.

Slight variations in abiotic filters did not positively affect the height or internode length in this study. Instead, the height decreased linearly in response to all abiotic filters and the internode length responded negatively to the temperature. In addition, the SLA decreased linearly in response to increasing temperature. Overall, these findings suggest that plant growth decreased in all ecological situations (increasing temperature, trophic status, pH, and dissolved oxygen concentration), probably related to the passive response of growth delay [rather than an active avoidance strategy (Gong et al., 2020; Jenks and Hasegawa, 2008; Seleiman, 2019)], which would decrease the efficiency of light and space acquisition at the community scale.

We expected to observe aerial and clonal trait convergence toward values that allowed individuals to better cope with environmental changes, especially when the constraints increased. We confirmed this hypothesis for height in response to increasing temperature, trophic status, pH, and dissolved oxygen concentration; under mild conditions, values diverged. The plant height response is thus integrative with respect to the three gradients examined. We also confirmed this hypothesis for the SLA, with a convergence of values in response to higher temperatures and lower trophic status, and for the LDMC in response to lower temperatures and higher trophic status. The convergence of the SLA and height toward lower means in response to increasing temperatures is in line with previous findings that interannual climatic variations resulted in greater plasticity in traits related to size or allocation (Alpert and Simms, 2002; Botero et al., 2015; Pigliucci et al., 1999).

4.3. Impacts of current environmental changes on community performance

Three of the five traits examined in this study influenced macrophyte community productivity, through their mean value (height) or variability (SLA and specific internode mass). The aerial traits (height and SLA) influenced the community performance more strongly than did the clonal trait (specific internode mass).

Abiotic variables should have cascading effects on macrophyte performance through their influences on trait dispersion caused by environmental filtering (Dar et al., 2014; James et al., 2005; Kim and

Nishihiro, 2020; Kraft et al., 2015; Mouchet et al., 2010). Changes in abiotic values, such as increases in temperature and trophic status in constrained habitats like polar ponds, can greatly and negatively impact macrophyte community performance. In the present case, the convergence in height toward lower means in response to increasing temperature, trophic status, pH, or dissolved oxygen concentration implies a negative effect on community productivity. As water temperatures continue to increase, which is known to stimulate nitrogen mineralization and thus the trophic status (Rustad et al., 2001), the consequences will likely be doubly severe for macrophyte communities. Moreover, the positive effect of a low degree of SLA variation on community performance implies that the observed high functional convergence of SLA values among species in response to higher temperatures and trophic status should be positive and negative, respectively. On the contrary, the high functional convergence of specific internode mass values among species had negative effects on macrophyte community performance. Thus, space and resource storage partitioning among species would help to maintain good performance at the community level, especially in constrained habitats like sub-Antarctic ponds. As a consequence, the height, SLA, and specific internode mass responses act as traits affecting community productivity. As macrophytes are primary producers, their responses can greatly influence ecosystem-level processes (Iacarella et al., 2018; Lürig et al., 2021; Mo et al., 2015), implying that future climate changes could have severe impacts on trophic chains.

5. Conclusion

This study demonstrates that hypervolumes are a powerful tool for the inference of community strategies in response to rapid and short-term environmental change. The examination of interannual abiotic variations over 4 years was sufficient to detect rapid responses toward resistance (tolerance or avoidance) when abiotic conditions change, with likely reliance on phenotypic plasticity. Moreover, our findings may inform the characterization of future functional changes in the aquatic plant communities of Iles Kerguelen and the sub-Antarctic region in which similar species are found (Bergstrom and Selkirk, 2000; Chau et al., 2021), through the explicit association of key functional traits with the trophic status, temperature, pH, and mean dissolved oxygen concentration. In particular, this study underlines the importance of accounting for increasing temperatures (Chaudhry and Sidhu, 2022; Harrison, 2020; Khare et al., 2020), as they influence changes in traits and thereby affect community performance. The mechanism underlying the observed short-term trait variation likely corresponds to plasticity. This finding raises questions about possible longer-term community adaptations, especially in a scenario in which extreme temperatures are more frequent and precipitation decreases (*i.e.*, abiotic filter strengthening), as observed in the Iles Kerguelen. Several studies have revealed positive relationships between phenotypic plasticity and the mean annual temperature, reflecting the reduced ability of plants from cold regions to cope with the increasing frequency of extreme climatic events (Stotz et al., 2021). Longer-term research extended to other cold regions (e.g. in the Arctic) would thus be of interest to observe emerging trends in the functional responses of aquatic plant communities. In addition, further investigations are needed to precisely characterize response strategies at the species level and to improve our understanding of the processes underlying plant community assembly in the context of abiotic filter strengthening.

CRediT authorship contribution statement

Anne-Kristel Bittebiere: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Félix Vallier:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **Pauline Douce:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Pauline Eymar-Dauphin:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Florian Mermillod-Blondin:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Laurent Simon:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Hugo Saiz:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Formal analysis, Conceptualization. **David Renault:** Writing – review & editing, Writing – original draft, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2024.125798.

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