How does trait variance partitioning help us to understand plant community assembly? The example of pond communities in the Kerguelen Islands

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We focused on the macrophyte communities living in the ponds of the Iles Kerguelen (sub-Antarctic region). Partitioning trait variance allows to detect at which scale operate the decisive processes in plant community assembly. In addition, we simultaneously considered biotic and abiotic variables to better understand the effects of environmental variations on traits, subsequently impacting plant performance and species fate.

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Abstract

Question: in the current context of biodiversity erosion, functional approaches to the examination of community assembly mechanisms and better prediction of plant species fates have emerged. The assessment of trait variation patterns should be a powerful means of identifying community assembly mechanisms. However, most studies of trait variations and their consequences for individual performance (*i.e.*, vegetative biomass) are usually incomplete as they focused on single ecological scales or filters, with no consideration of relationships between traits. Such research has provided a fragmented view of plant community assembly.

Location: We examined macrophyte communities living in ponds of the sub-Antarctic Iles Kerguelen.

Methods: We measured traits related to resource acquisition and conservation on all occurring species, and examined their variation across temporal (years), spatial (sites), and taxonomic (between- and within-species) scales and in response to multiple abiotic and biotic habitat variables. The consequences of these trait variations and the effects of their correlation for plant individual performance were also explored.

Results: Trait distributions were fairly conserved among sites, whereas we observed a large amount of intraspecific trait variation enabling individuals to resist filters. Responses to biotic and/or abiotic variables were trait dependent, and simultaneous trait responses should enable individual plants to face several simultaneous constraints. Almost all traits had direct or indirect effects on individual performance, indicating the need to consider trait relationships.

Conclusion: The partitioning of trait variance is a relevant approach to the identification of the scale at which the most decisive processes for plant community assembly operate without the interference of scale dependency issues, and should orient further research. In addition, several biotic and abiotic variables should be considered in future studies to better understand the effects of environmental changes on plant communities.

Keywords

Functional trait, plant performance, variance partitioning, intraspecific trait variability, macrophyte, plant community assembly, filter, pond ecosystem

Introduction

In the current context of biodiversity erosion, it is crucial to improve our understanding of the mechanisms underlying plant community dynamics for the prediction of plant species fates, particularly in aquatic ecosystems, which are especially sensitive to ongoing changes (Pan et al., 2023). Two decades ago, functional approaches emerged that allowed us to rebuild community ecology and establish general principles regarding assembly mechanisms (Calow, 1987; McGill et al., 2006). Since then, studies based on functional traits (morphological, physiological, and phenological characteristics that directly or indirectly impact individual performance through growth, reproduction, or survival) have been conducted in terrestrial (*e.g.*, Garnier et al., 2001; Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Violle et al., 2007), and aquatic plant communities (Chmara et al., 2021; Fu et al., 2013, 2014; Luo et al., 2016; Ma et al., 2022; Su et al., 2019; Yang et al., 2004; Zhang et al., 2019). Functional approaches have revealed that marked trait variation occurs in the field at inter- and intraspecific levels in response to a range of biological processes operating at different spatial and temporal scales, ultimately leading to species coexistence (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Messier et al., 2010; Taudiere & Violle, 2016).

Individual trait variation is usually observed independently through the lens of space, time, or taxonomy, resulting in a fragmented view of community assembly, with the exception of a few studies in which two of these scales have been considered (Fu et al., 2013; Fyllas et al., 2020; Johnson & Toprak, 2021; Kim & Nishihiro, 2020). Temporal trait variation is reported as a part of a seasonal strategy allowing plants to permanently adjust trait performance to deal with external stresses; examples are the adjustment of physiological (*e.g.*, photosynthetic capacity; Grassi et al., 2005; Muraoka et al., 2010) and morphological (*e.g.*, leaf thickness; Fullana-Pericas et al., 2017) traits. Spatial scales also shape overall trait variations, which can arise as species-specific responses to various environmental filtering processes. In macrophytes species for example, shoot height and branch length have been found to vary primarily among lakes (in connection with trophic status and water depth), whereas the root/shoot ratio and leaf number are linked to within-lake variations (Fu et al., 2013).The

decomposition of trait variations across taxonomic scales (McGill, 2008; Swenson et al., 2006) allows for the consideration of inter- *vs*. intraspecific trait variations to determine whether species identity is a critical filtering factor, or whether individuals are filtered out according to their trait values. Overall, studies providing information on the scale that carries the most important trait variations are of particular interest, as the results should aid the understanding of many community assembly patterns and processes (McGill, 2008; Taudiere & Violle, 2016; Violle et al., 2007, 2012) and the assessment of the scale dependency issue in community ecology (*e.g.*, Cavender-Bares et al., 2009; Swenson et al., 2006).

In the last 10 years, studies reported the major role of intraspecific trait variability (ITV) in ecological processes, and showed that ITV can account for up to 40% of trait variance in plant communities (Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Jung et al., 2010). ITV would allow a better resistance to filters (Jung et al., 2010; Violle et al., 2012) through adaptation (genetic variability) and/or phenotypic plasticity (Albert et al., 2011; Byars et al., 2007; Ghalambor et al., 2007). In aquatic plant communities, the high investment of macrophyte species in clonal growth suggests that resistance to filters mainly relies on plastic responses (De Wilde et al., 2014; Gao et al., 2021; Han et al., 2021; Li et al., 2019; Pilon & Santamaría, 2002; Wolfer & Straile, 2004). Most plant morphological traits are key for coping with environmental filters (see, *e.g.*, Lavorel & Garnier, 2002). Responses to both biotic and abiotic filters have been evidenced extensively in macrophyte traits involved in growth or resource acquisition [*i.e.*, the specific leaf area (SLA), height, and root and internode lengths; Fu et al., 2013; Gao et al., 2021; Pilon & Santamaría, 2002; Wolfer & Straile, 2004] and in resource conservation [*i.e.*, the leaf dry matter content (LDMC) and specific connection mass; Elger & Willby, 2003; Gao et al., 2021; Koleszár et al., 2022; Pilon & Santamaría, 2002]. How traits respond to simultaneously varying biotic and abiotic conditions, however, remains unclear (Chalmandrier et al., 2022). This may lead to the partial interpretation or even misinterpretation of trait variation patterns, especially in *in-situ* studies with such simultaneous variation (Cadotte & Tucker, 2017; Kraft et al., 2015). Indeed, similar patterns of trait variations (convergence or divergence in trait values) can be related to abiotic and/or biotic conditions (Cadotte & Tucker,

2017). We thus argue that the partitioning of intraspecific trait variations should aid the determination of the roles of traits in species' biotic and abiotic resistance to environmental filters (Le Bagousse-Pinguet et al., 2017; Liu et al., 2018). We expect traits to respond simultaneously to biotic and abiotic conditions, but with varying strength depending on the trait category (resource conservation *vs.* acquisition). In particular, we expect traits related to resource acquisition to respond to water, sediment nutrients, and biotic conditions, determining competitive abilities (Garnier et al., 2004; Reich, 2014; Violle et al., 2007; Wright et al., 2004), and those related to resource conservation to respond mostly to harsh abiotic conditions, conferring individual plant resistance to environmental constraints (Funk et al., 2021; Levitt, 1980; Reich, 2014).

Variation in functional traits should ultimately influence individual performance (*i.e.*, vegetative biomass production; Geber & Griffen, 2003), and thus species fate in the plant community (Ghalambor et al., 2007), but with varying intensity depending on the trait. Moreover, several traits co-vary and/or are subjected to tradeoffs in individual plants to coordinate different biological functions (Maire et al., 2013; Valladares et al., 2007; Violle et al., 2007). For instance, resource conservation– and acquisition-related traits have been found to negatively co-vary (Fort et al., 2013; Garnier et al., 2001; Kleyer et al., 2019; Reich et al., 1997, 1999); low SLAs are generally associated with high LDMCs, reflecting a functional relationship with the leaf life span (Roche et al., 2004; Wright et al., 2004). However, such trait relationships, which can indirectly influence individual performance, are usually neglected in relevant studies. The identification of the direct and indirect influences of traits on performance likely imposes hierarchies among plant traits, which can be revealed with structural equation modeling [SEM; Ackerly et al., 2000; Dwyer & Laughlin, 2017; Saiz et al., 2018; Vile et al., 2006]. We expect resource conservation–related traits to have more direct impacts on individual biomass than do resource acquisition–related traits, as they are related directly to individual size and thus affect individual performance.

A growing number of theories and concepts in ecology has been tested recently in the sub-Antarctic Iles Kerguelen region, considered to contain sentinel ecosystems and open-air

laboratories (Bergstrom & Chown, 1999). Climate change, particularly warming, is especially rapid in this region (Walther et al., 2002) and has strong impacts on aquatic ecosystems, including ponds that harbor remarkably species-poor macrophyte communities (Douce et al., 2023a). In this study, we used macrophyte communities to construct a simple model that is more realistic than the use of mesocosms (which include all variations in abiotic and biotic conditions). We measured traits related to resource acquisition and conservation and performance in all macrophyte species. Trait variations were studied across spatial, temporal, and taxonomic scales, and covered multiple abiotic and biotic habitat conditions. Consequences for individual plant performance were also explored. We tested the following hypotheses (Fig. 1):

i. that the partitioning of trait variance among spatial, temporal, and taxonomic scales would enable the detection of mechanisms involved in plant community assembly, revealing a large amount of ITV related to coexistence mechanisms and within-site heterogeneity;

ii. that all traits would respond to both biotic and abiotic conditions, but with trait-dependent intensity, with traits related to resource acquisition (SLA, height, and root and internode length) responding to water, sediment nutrients, and biotic conditions and those related to resource conservation (LDMC and specific root and internode masses) responding mostly to harsh abiotic conditions; and

iii. that traits related to resource conservation would affect individual vegetative biomass more directly than those related to resource acquisition, with the potential modulation of relationships between traits, *i.e.*, negative co-variation of resource acquisition– and conservation-related traits, modifying their role in individual performance.

Materials and methods

Study model

The study was carried out in the field at the French sub-Antarctic Iles Kerguelen (South Indian Ocean; 48°30–50°S, 68°27–70°35E). The climate on this archipelago is characterized by cold

temperatures (annual mean of 4.6°C with little variation; Frenot et al., 2006; Lebouvier et al. 2011) and abundant precipitation (500–3200 mm along an east–west gradient; Frenot et al., 1998; Meteo France). Plant communities in polar regions are paucispecific (and thus have simplified plant–plant interaction) and subjected to highly reduced anthropogenically induced environmental pressure. As such, they constitute simplified models relative to temperate plant communities, which is especially relevant for the inference of mechanisms of community assembly in constrained abiotic environments (Bergstrom & Chown, 1999).

The study was conducted in ponds at three sites located along the shore of the archipelago's main island (Appendix S1): Cap Molloy, Isthme Bas, and Cap Ratmanoff. These three sites are less than 40 km apart and have similar climates, and their overall abiotic conditions are more variable locally than among sites (Appendix S2; Douce et al., 2023a). At each site, 15 ponds of variable areas were selected to overcome bias related to system size, which influences the water temperature (Bornette & Puijalon, 2011). All but one of the ponds investigated were small (average area = 181.57 ± 382.39 m²; exception, 180,800 m²; Douce et al., 2023a). They are shallow freshwater systems enriched by nutrient inputs from marine fauna, such as seabirds and seals, due to their littoral proximity (Smith, 2008). The ponds' water depth was similar (average of the 45 ponds = 17.29 ± 8.28 cm).

The macrophyte communities at the study sites were composed mainly of six native species that can all locally co-occur: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), *Ranunculus biternatus* Smith, *Ranunculus pseudotrullifolius* Skottsb., and *Ranunculus moseleyi* Hook.f (all Ranunculaceae). All of these species are perennials (*i.e.*, they remain present during winter) with clonal network structures, *i.e.*, the plants are composed of related ramets (shoots with leaves and roots) that are connected by plagiotropic stems. These clonal structures display slow growth rate, and ramet lifespan generally exceed two years with low investment in sexual reproduction. *C. antarctica, L. australis, R. pseudotrullifolius*, and *R. moseleyi* are hydrophytes, and *R. biternatus* and *J. scheuchzerioides* are helophytes. Only *C.*

200 *antarctica* is caulescent and harbors a floating canopy; the other five species have rosette
201 architectures and are rooted in pond sediments (Douce et al. 2023a). As the water level in
202 ponds is highly variable (Douce et al 2023a), individual leaves can be alternately submerged
203 or emerged, without any variations in their morphology. Individuals then display leaves of
204 homogeneous morphology (Appendix S3). These macrophyte communities may experience
205 different episodes of disturbances through the year, as for instance, the freezing of pond
206 surface in winter (although this phenomenon remains limited to the first 5-10 cm of water
207 column), the temporary drying in summer (for less than a month), and the seal trampling, that
208 may altogether lead to the low macrophyte cover in ponds (low community resilience).
209 Nevertheless, the studied communities remain very stable through years and seasons (Douce
210 et al. 2023a).
211
212 ## Field sampling
213 The study was conducted in 2017, 2018, 2019, and 2020, with plant ramet sampling at the
214 three sites conducted each year in November. In each pond, we randomly positioned three to
215 five 1 × 1-m quadrats, depending on the pond area, and usually including pond edges. In each
216 quadrat, we collected one mature ramet of each of the six studied species, when present, for
217 the measurement of plant traits. One ramet was composed of leaves, roots, and one
218 connection internode for the five rosette species, and a fully developed caulescent structure
219 (with attached leaves and roots and no ramification arising from axillary buds), and one
220 connection internode for the caulescent species. All collected ramets, including those of the
221 helophyte species, were submerged completely in the ponds (mean ramet height = 7.14 ± 2.99
222 cm, mean water depth = 17.29 ± 8.28 cm). Given the low variability in water depth between
223 ponds, the ramets were collected at similar depths. In addition, we recorded species
224 abundances in each quadrat.
225 Pond abiotic conditions were monitored every 3 months from November 2019 to
226 November 2020. For each sampling date and pond, water and sediment samples were hand
227 collected at similar depths for nutrient and phytoplankton concentration analyses. These

samples were collected at three points per pond and then mixed together to account for possible heterogeneity in nutrient spatial distribution. One composite water sample (30 mL) and one composite sediment sample (50 mL) were obtained per pond. The sediment was a mixture of sand and organic matter, with similar grain and composition among ponds. As abiotic variables are likely to vary within ponds, in each quadrat at the ramet collection points, we measured the mean water depth (based on three measurements) and mean dissolved oxygen (DO) concentration (based on measurements taken at three water depths). We also measured the pH and electrical conductivity (EC), since they are not related to the phytoplankton concentration in the studied systems (Douce et al., 2023b). These measurements were performed using a multiparameter HQ40D HACH sensor (EC ±0.1 $mS.cm^{-1}$, DO concentration ±0.01 $mg.L^{-1}$). From September 2020 onward, whole-pond water temperatures were recorded every 30 minutes using loggers (Hobo MX2202) positioned in the middle of the water column. Water temperatures in November 2019–August 2020 were simulated using their relationship to air temperatures recorded by Meteo France (2020 records, Port-aux-Français; see Douce et al., 2023b). Each pond area (length × width) was measured in November 2019. All of these measured parameters have been found to structure the studied communities (Douce et al., 2023a).

Trait measurements

Seven functional traits of the mature ramet samples were measured, following Cornelissen et al. (2003). The selected traits characterize ramet growth strategies and are known to be responsive to biotic and abiotic conditions (Table 1), especially in macrophyte species (Dalla Vecchia et al., 2020). They are related to individual resource acquisition (height, SLA, and internode and root lengths) and conservation (LDMC and internode and root specific masses; see Table 1 for details).

For each sampled ramet, the SLA and LDMC of one randomly selected healthy mature leaf were first measured. Second, the length and specific mass of one randomly selected attached internode were measured. The specific internode mass was calculated as

the ratio between the internode dry mass and length ($g.cm^{-1}$). Then, the longest primary root attached to the ramet was used to measure the maximum root length and specific root mass [calculated as the ratio between the dry mass and root length ($g.cm^{-1}$)]. We also estimated ramet performance resulting from its growth strategy by measuring its total biomass (*i.e.*, dry masses of leaves, stems, roots, and one connection internode; see, *e.g.*, Adomako et al., 2021; Keser et al., 2014; Younginger et al., 2017; Zhao et al., 2020). Dry mass measurements were performed after the plant parts had been dried for 48 hours in an oven at 65°C. All plants were cleaned before measurement.

Measurement of nutrient and phytoplankton concentrations

For the measurement of water nutrient and phytoplankton concentrations (as reflected by the amount of chlorophyll a per milliliter water), water samples were passed through GF/F filters (0.7 µm; Whatman) to remove coarse and fine particles and phytoplanktonic organisms within 24 hours of sampling. All samples (filtered water and sediments, and filters) were stored at –20°C for several weeks before chemical analysis in metropolitan France.

Chlorophyll a pigments were quantified from the GF/F Whatman filters using the Unesco method (Vohra, 1966) and a spectrophotometer. $N–NH_4^+$, $N–NO_3^-$, and $P\text{-}PO_4^{3-}$ concentrations in the water samples were determined using colorimetric methods and a sequential analyzer (SmartChem 200; AMS Alliance) (Grasshoff et al., 1999). The organic C:N ratio in sediment samples was measured using the capsule method (Brodie et al., 2011). An aliquot of 5 mg ± 10% homogeneous sediment sample was acidified into 100 µL 2 M HCl in silver capsules to eliminate carbonates. The capsule liquids were evaporated on a 65°C hot plate for 12 hours, and the capsules were then oven dried at 80°C for 2 days. The total organic C and N contents were then measured with an elementary analyzer (FlashEA 1112 NC Analyzer®; Thermo Fisher Scientific, Waltham, MA, USA). The bioavailable P concentration in sediments was determined following the protocol of Ni et al. (2016). Bioavailable P was extracted from 50 mg dry sediment samples with 5 mL NaOH (1 M). Then, the supernatant was collected, its pH was stabilized with HCl (3.5 M), and the extracted P that had been

converted to orthophosphate was quantified using the molybdate/ascorbic acid blue method (Murphy & Riley, 1962); results are reported as milligrams of available P per gram dry sediment.

Data analysis

We tested for correlations between all pairs of traits using Spearman rank correlation analysis. We detected no strong correlation ($r < 0.7$) between traits (Dormann et al., 2013). Thus, each trait was indicative of a part of a global growth strategy.

Abiotic and biotic characterization of ponds

To characterize the abiotic conditions within ponds, the mean of daily (day and night) water temperatures from November 2019 to November 2020 was calculated for each pond (Douce et al., 2023b). Abiotic variables measured at the quadrat scale were averaged at the pond scale. Depending on the analysis, we performed several reductions of abiotic variables. Water nutrient dimensions ($N\text{-}NH_4^+$, $N\text{-}NO_3^-$, and $P\text{-}PO_4^{3-}$) were reduced to the first axis of a principal component analysis (PCA), in which data were centered and standardized by standard deviation (Appendix S4), hereafter referred to as "PCAwater." PCAwater axis 1 (42.06%) was related negatively to the $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$ concentrations. Similar dimension reduction was performed for sediment nutrients (C:N ratio and bioavailable P; Appendix S5), hereafter referred to as "PCAsediments." PCAsediments axis 1 (58.59%) was related negatively to the C:N ratio and positively to the bioavailable P concentration.

To characterize the biotic conditions within ponds, we calculated two non-correlated indices: macrophyte species richness and Pielou evenness. Biotic dimensions describing plant species abundances in each pond were reduced to the first three axes of a factorial correspondence analysis ("FCAplants"; Appendix S6). The first FCAplants axis (33.81%) was driven positively by the abundance of *R. moseleyi* and negatively by that of *C. antarctica*. The

second axis (24.99%) related positively with the abundance of *R. pseudotrullifolius* and negatively with that of *J. scheuchzerioides*. The third axis (16.99%) was related positively to the abundance of *L. australis* and negatively to that of *R. biternatus*. To assess the functional characteristics of pond communities, we calculated the overall functional dispersion (FDis) using seven traits (height, SLA, LDMC, internode length, specific internode mass, maximum root length, and specific root mass) and the *fdisp* function of the FD package (Laliberté & Legendre, 2010).

Variance partitioning across nested scales

We used trait measurements from 2017–2020 to partition trait variance across four nested scales. The trait data were normalized (log or square-root transformed) when needed, and standardized to equalize the weight of each trait dimension. A variance component analysis was performed for each of the seven studied traits using the *Parvart* procedure (Cati package) across temporal (four years), spatial (three sites), and taxonomic (inter- and intraspecific variance) scales introduced into the model (including measurement error) in that order. As individuals do not display any heterophyllia, the intraspecific trait variation only accounts for trait variations between individuals. The significance of the variance components was assessed by determining 95% confidence intervals (CIs) through bootstrapping. We randomly selected 700 of the 1430 individuals in our dataset with replacement (Messier et al., 2010), and partitioned the trait variance among the four nested scales. We repeated this procedure 500 times to ultimately calculate a 95% CI for each variance component. To get rid of the imperfect nesting of species within sites (Appendix S7), we ran alternative models of variance partitioning without the species scale, and obtained similar results (Appendix S8). Similarly, as some species were less abundant (*R. moseleyi*, *R. pseudotrullifolius,* and *L. australis*; Appendix S7), we ran alternative tests of variance partitioning without the individual data of these scarce species, to test the robustness of our results. We obtained similar results with and without the inclusion of scarce species data (Appendix S9).

Analysis of trait responses to biotic and abiotic filters

We aimed to determine which traits and categories of traits were involved in plant biotic and/or abiotic resistance. We considered univariate responses and tested for the effects of abiotic and biotic variables measured or calculated at the pond scale on trait values measured in November 2020 and averaged at the pond scale for all ramets of all species. In the full models, we included as explanatory variables the species identity (a categorical variable indicating the ramet species), macrophyte species richness, Pielou evenness, community FDis, first three FCAplants axes (Appendix S6), and phytoplankton concentration for biotic variables, and the water depth, pH, EC, DO concentration, mean temperature, pond area, and first PCAwater and PCAsediments axes (Appendices S3 and S4) for abiotic variables. The trait data were normalized (log or square-root transformed) as needed and standardized. We applied stepwise model reduction based on the Akaike information criterion (AIC) using the MuMIn package (Bartoń, 2013) to select the most parsimonious full model, and performed a type II analysis of variance.

A similar procedure was applied to test for the effects of the above-listed abiotic and biotic variables on traits grouped into multivariate-response resource acquisition (height, SLA, internode length, and maximum root length), and resource conservation (LDMC, specific root mass, and specific internode mass) categories. The trait data were normalized (log or square-root transformed) as needed and standardized. We selected variables by backward elimination from the full model, removing those with non-significant effects, and then performed a type II multivariate analysis of variance (yielding the Pillai statistic) of the reduced model.

Analysis of trait and abiotic variable effects on species performance

The ramet total biomass (reflecting performance) and trait values recorded in November 2020 were averaged for each species at the pond level (n = 97) and standardized to eliminate

variance due to species identity. We tested for direct and indirect effects of the seven traits on individual performance using SEM (Grace et al., 2010). All possible relationships between traits, based on the literature (Appendix S10), were included. We performed a path analysis with the lavaan package (Rosseel, 2012), and reduced the full model by variable selection based on AIC values.

All statistical analyses were performed with R 4.0.3.

Results

Traits varied primarily within macrophyte species

All studied traits exhibited larger variances within sites than between sites, since space (site) had no influence at all. Time (year) had little influence (explaining less than 8% of variance in all traits) when significant. Conversely, taxonomy explained most of the variance within sites (Fig. 2). Most traits (with the exception of internode mass and LDMC) exhibited higher trait variance at the intra- as compared with the interspecific scale. The intraspecific variance of the trait was even maximal in the internode length (79.47%) and the maximum root length (65.52%).

The variation of most traits was affected by abiotic and biotic variables

Within ponds, growth strategies relied on resource acquisition and conservation traits. Resource acquisition traits as a whole responded to the abiotic variables of water nutrients (PCAwater) and depth. Resource conservation traits were impacted by biotic and abiotic variables, namely the phytoplankton concentration, species abundance, and sediment nutrients (PCAsediments; Table 2).

Four traits responded to only abiotic (height, SLA, and internode length, respectively explaining 3.15%, 14.31%, and 5.03% of the variance) or biotic (specific internode mass, explaining 10.28% of the variance) pond variables (Table 2). Variation in the LDMC, maximum root length, and specific root mass was influenced by both biotic and abiotic variables (Table

2). The responses of these three traits to the variables examined were trait dependent, with a greater cumulative influence of biotic variables (Table 2). The LDMC and maximum root length were predicted largely by species abundances (explaining 5.90% and 4.37%, respectively, of the variance), and the specific root mass was predicted mostly by the phytoplankton concentration (explaining 10.49% of the variance). To lesser extents, the water physico-chemistry (*i.e.*, temperature, pH, and nutrients) influenced both root traits and sediment nutrients (PCAsediments) influenced the LDMC.

Plant traits directly and indirectly affected individual performance

We identified multiple direct or indirect effects of all traits, except that the LDMC did not affect the individual total biomass (Fig. 3). Traits directly influencing the individual total biomass (height and all clonal and root traits) had positive effects, with the height (0.38, $p < 0.001$) and specific internode mass (0.43, $p < 0.001$) having the strongest influence. These direct effects on individual performance were modulated (*i.e.*, amplified or reduced) by their correlations (Fig. 3). For example, the internode length and specific root mass correlated with height, indirectly supporting their total positive effect on individual performance. The SLA had no direct effect on individual performance, but had a negative influence through its relationship with the specific internode mass (–0.20, $p < 0.05$). When total trait effects on individual performance were considered (Fig. 3b), the SLA had a negative impact and all other traits had overall positive effects.

Discussion

Taxonomy explains most trait variance

The linking of patterns to processes in community ecology is often challenging, especially in field-based studies. Several authors have suggested that trait variance be used to infer

community assembly mechanisms (McGill, 2008; Taudiere & Violle, 2016; Violle et al., 2007, 2012). To tease apart the multiple factors that drive community assembly in aquatic systems, we partitioned the variance of several traits among three distinct, yet interacting, scales (space, time, and taxonomy). Studies in which different scales are taken into account simultaneously remain rare (but see, *e.g.*, Henn et al., 2018; Liu et al., 2018; Luo et al., 2016), and to our knowledge, none of them was performed over several years.

In the present study, variance partitioning among the scales examined was similar among traits, indicating that similar processes determined the different trait values. Community assembly mechanisms operating over time (year) and space (region) were responsible for a small percentage of the total trait variance, in line with the observations of Fu et al. (2013). Those authors partitioned trait variance across spatial scales alone, and found that a large spatial scale (*i.e.*, a regional scale including different lakes) did not account for much variance in the root/shoot ratio and leaf number for the macrophyte *Potamogeton maackianus* (Fu et al., 2013). In our work, trait distributions were fairly conserved among sites, which suggests exchanges, therefore dispersion, between studied sites. The small size of the study area probably explains the occurrence of most variance within and not among sites; a larger study area should be considered in future research. Intrasite variance (at inter- and intraspecific scales) overwhelmingly dominated intersite variance, for all traits. Thus, a mechanism participated in the spreading of trait values around the optimum within sites. This pattern may arise from several non-exclusive processes. First, adaptation to habitat heterogeneity within sites can lead to differences in optimal trait values at the micro-site scale. Second, biotic interactions can disperse trait values to limit similarity among individuals, thereby reducing competition. As highlighted by Messier et al. (2010), niche and neutral theories can contribute significantly to the explanation of community assembly.

Interestingly, taxonomy accounted for most variance in all traits, with in particular intraspecific trait variance being greater (56.29% on average) than interspecific variance for most traits. However, the relative importance of interspecific *versus* intraspecific trait variability

442 was trait dependent, consistent with previous findings (Albert, Thuiller, Yoccoz, Douzet, et al.,
443 2010; Fajardo & McIntire, 2010; Roche et al., 2004). We found LDMC and specific internode
444 mass to vary more between species than within species This indicates that traits related to
445 resources conservation are highly conserved among species, allowing different macrophyte
446 species to specialize and co-occur along habitat gradients (different conditions among ponds).
447 However, resource acquisition traits (height, SLA, internode length, maximum root length)
448 varied more within species than between species, in line with Siefert et al. (2015) who found
449 that "whole-plant traits" (*i.e.* plant height, and architecture) were more variable within
450 population than between species in a global-scale meta-analysis. This high amount of
451 intraspecific trait variability would mostly rely on phenotypic plasticity, already known to allow
452 macrophyte individuals to resist to filters, and to environmental heterogeneity at very fine scale
453 (within-pond habitat variances) (Fu et al., 2012, 2013; L. Ni, 2001; Yang et al., 2004). Another
454 hypothesis is that, in macrophytes, architectural traits can display multiple trait values since
455 individuals are much less constrained by gravitational force than terrestrial species (Fu et al.,
456 2013).

457 We confirmed that partitioning trait variance is a relevant approach to detect at which
458 scale operate the most decisive processes in plant community assembly without scale
459 dependency issues (McGill, 2008). Moreover, we underlined the strong importance of ITV in
460 shaping community assembly (Jiang et al., 2016; Violle et al., 2012), and we then argue that
461 not only species mean and community-aggregated trait values (Schamp et al., 2007; Stubbs
462 & Bastow Wilson, 2004), but also trait distributions have to be analyzed when studying
463 community dynamics and structure (de la Riva et al., 2016; Henn et al., 2018). Including ITV
464 into community ecology can improve the detection of processes underlying species
465 coexistence at local scale (Doudová & Douda, 2020; Fu et al., 2014; Violle et al., 2009).

466

Intraspecific trait variation occurred in response to biotic and abiotic variables

As studies on aquatic systems overall focus on macrophyte species responses to a specific, and usually limited, number of environmental variables (Barker et al., 2008; Fu, 2020; Fu et al., 2014; Li et al., 2018; Ma et al., 2022a; Martin & Coetzee, 2014; Shields & Moore, 2016), our vision of ITV in the context of multiple constraints remains partial. With this study, we sought to fill this gap by simultaneously examining trait responses to multiple abiotic and biotic variables.

Contrary to our expectations, not all traits of the pond-dwelling individuals responded to both abiotic and biotic variables. Three resource acquisition traits (height, SLA, and internode length) and one resource conservation trait (specific internode mass) were influenced by abiotic or biotic variables alone, although they are known to usually respond to both variable types (Fu et al., 2013; Gao et al., 2021; Pilon & Santamaría, 2002). However, all other trait variations (*i.e.*, the LDMC, maximum root length, and specific root mass) responded to biotic and abiotic variables as predicted. This difference in trait response patterns indicates that individual plants do not respond as a whole, but instead that each trait has a singular role, in the context of multiple constraints. This finding challenges the validity of conclusions that assume responses at the whole-plant level (De Kroon et al., 2005), and suggests that survival within multi-constrained habitats relies on low phenotypic integration (Murren, 2002), enabling the expression of multivariate phenotypes. Overall, our findings underline the relevance of multi-trait approaches integrating biotic and abiotic variables, as also stated by Chalmandrier et al. (2022), to efficiently capture plant response strategies and ultimately identify mechanisms of species coexistence at local scales. In addition, our observations suggest that patterns of trait variation measured *in situ* should be interpreted carefully, as they may not reflect responses to only biotic or abiotic filters (Duarte et al., 1986; Kõrs et al., s. d.; Su et al., 2019).

In the ponds of the Iles Kerguelen, each trait category was involved in the response to specific habitat variables. First, traits related to resource acquisition, as a whole, responded to water nutrients. The SLA decreased when water nutrients increased, suggesting that

494 macrophyte species are plastic, maximizing either light capture when higher nutrient
495 concentrations stimulate phytoplankton growth, reducing light penetration into water (Rabalais,
496 2002), or nutrient capture (Zervas et al., 2019). In addition, the root length, also involved in
497 nutrient acquisition, was impacted positively by species abundances. Competition for nutrient
498 acquisition favors root trait divergence and forces plants to optimize resource uptake
499 (Ferguson et al., 2016; Manschadi et al., 2006). This result indicates that the consideration of
500 root trait variation can aid the detection of responses to biotic competition, although it is not
501 incorporated well into field studies due to the difficulty of sampling (Colom & Baucom, 2020).
502 Lastly, internodes elongated with water depth, probably as part of a strategy to avoid harsh
503 conditions (Bittebiere & Mony, 2015; Callaghan et al., 1992; Louâpre et al., 2012). Second,
504 traits related to resource conservation (the LDMC and specific internode and root masses)
505 were impacted negatively by competition. Resource storage in connection internodes and
506 roots decreased in response to species abundance and/or phytoplankton biomass, likely
507 reflecting a lack of available resources. To a lesser extent, the LDMC responded to sediment
508 nutrients, consistent with previous findings (Fu, 2020; Garnier et al., 2001). Previous studies
509 have suggested that an increase in nutrient availability induces leaf trait variability toward low
510 nutrient conservation, for instance by reducing the LDMC (Poorter & Garnier, 2007).

511 Based on our results, we recommend that several biotic and abiotic variables should
512 be considered in future studies to better understand the effects of environmental changes on
513 plant communities (Cavieres et al., 2014; Crain et al., 2004; Kim & Nishihiro, 2020; Klanderud
514 et al., 2015; Mitchell et al., 2017; Morris et al., 2020; Wood et al., 2012).

515

516 ## Effects of trait values and their relationships on macrophyte performance

517 The SEM approach allowed us to demonstrate that all traits considered except the LDMC had
518 direct or indirect effects on individual performance. This observation is especially important, as
519 the relationships between traits can influence individual performance (Engbersen et al., 2022;

Pywell et al., 2003), in particular in macrophyte species (Fu et al., 2014; Ma et al., 2022b). Our findings support the current view in functional ecology of the relevance of multi-trait approaches in which trait relationships are taken into account (Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Bittebiere et al., 2019; Blonder et al., 2014; Gustafsson & Norkko, 2019).

As traits are interrelated, adjustments in trait values must be coordinated to produce properly functioning organisms; in addition, patterns of trait correlation can vary greatly across environments (Murren, 2002). To maintain optimal fitness, functionally related traits of individual plants should correlate more strongly (*i.e.*, high level of integration within the functional unit) than do functionally different traits (*i.e.*, among functional units), conferring flexibility as well as coordination (Nicotra et al., 1997). This pattern is consistent with our results, as we detected the strongest correlations among traits related to resource conservation (the specific internode and root masses) and leaf traits (the SLA and LDMC).

With the pooling of direct and indirect effects, we found that height and resource conservation traits (the specific internode and root masses) had stronger positive effects than did the other resource acquisition traits (root and internode lengths and SLA), consistent with the results reported by Wildová et al. (2007). Individual growth and resource conservation traits are related directly to individual size, thus affecting the individual biomass, whereas resource acquisition traits are related more to colonization ability and allocation between organs, thus affecting individual performance more indirectly (Wildová et al., 2007). Thus, individuals would prioritize investment in resource conservation in constrained habitats, such as sub-Antarctic ponds.

Finally, abiotic variables can have cascading effects on individual performance through their influence on trait variation. Seasonal and annual changes in abiotic values in constrained habitats such as polar ponds would greatly impact plant trait values. For example, an increase in the water temperature reduces root length, indirectly and negatively affecting individual performance. Thus, although increases in the water temperature can stimulate macrophyte performance within the optimum thermal range (Dar et al., 2014), they may have negative

impacts in sub-Antarctic ponds, suggesting that the optimal thermal range can be exceeded (Frenot et al., 2006). Similarly, variation in water depth affects plant performance through its effect on internode length. With continued increases in the water temperature and reductions in precipitation (Walther et al., 2002), one can predict that the consequences for the macrophyte community structure and its productivity will be severe.

Conclusion

The partitioning of trait variance among multiple ecological scales provides a less fragmented picture of variables that drive community assembly and avoids the misinterpretation of trait variation in field studies. This study underlines the strong importance of ITV in the shaping of community assembly (Jiang et al., 2016; Violle et al., 2012), and more precisely, in species coexistence and responses to multiple abiotic filters. We recommend the simultaneous consideration of several biotic and abiotic variables in future studies to better understand the effects of environmental changes on plant communities (Cavieres et al., 2014; Crain et al., 2004; Klanderud et al., 2015; Mitchell et al., 2017; Morris et al., 2020; Wood et al., 2012). Additionally, we emphasize the relevance of multi-trait approaches in which trait relationships are taken into account in the examination of trait effects on individual performance.

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Author contributions

A-K.B. and D.R. acquired the financial support for the study. A-K.B. and D.R. lead the administration of the project (Management and coordination responsibility for the research activity planning and execution, including obtention of sampling permits). P.D. and A-K.B. conceived the ideas and designed methodology. P.D. and A-K.B. collected the data. P.D., L.S.,

F.M-B., F.V. and A-K.B. performed the nutrient analyses. P.D. and A-K.B. analyzed the data. P.D., D.R., L.S., F.M-B. and A-K.B. led to the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest

The authors declare that they have no conflict of interest.

Data availability statement

The data that support the findings of this study are openly available in figshare at https://figshare.com/articles/dataset/Data_ponds_Kerguelen/21904257

Supporting information

Appendix S1. Locations of the three sampling sites in the French sub-Antarctic Iles Kerguelen.

Appendix S2. Means ± standard deviations for abiotic and biotic variables at the site scale.

Appendix S3. Photos of the aerial parts of the six studied macrophyte species showing the absence of heterophylly.

Appendix S4. Eigenvector scores for the first axis of a principal component analysis (PCA 1) of water nutrient parameters measured at the pond level.

Appendix S5. Eigenvector scores for the first axis of a principal component analysis (PCA 1) of abiotic parameters measured at the pond level.

Appendix S6. Eigenvector scores for the first three axes of a factorial correspondence analysis (FCAs 1–3) of water nutrient parameters measured at the pond level.

Appendix S7. Numbers of collected and measured samples per species, site, and year.

Appendix S8. Variance partitioning of individual traits across three nested scales: year, site, and within-site.

Appendix S9. Variance partitioning of individual traits across three nested scales: year, site, and within-site when deleting the less abundant species.

598 Appendix S10. Theoretical structural equation model representing the direct and indirect
599 effects of trait values measured in ponds on individual performance (total biomass).

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Tables and figures

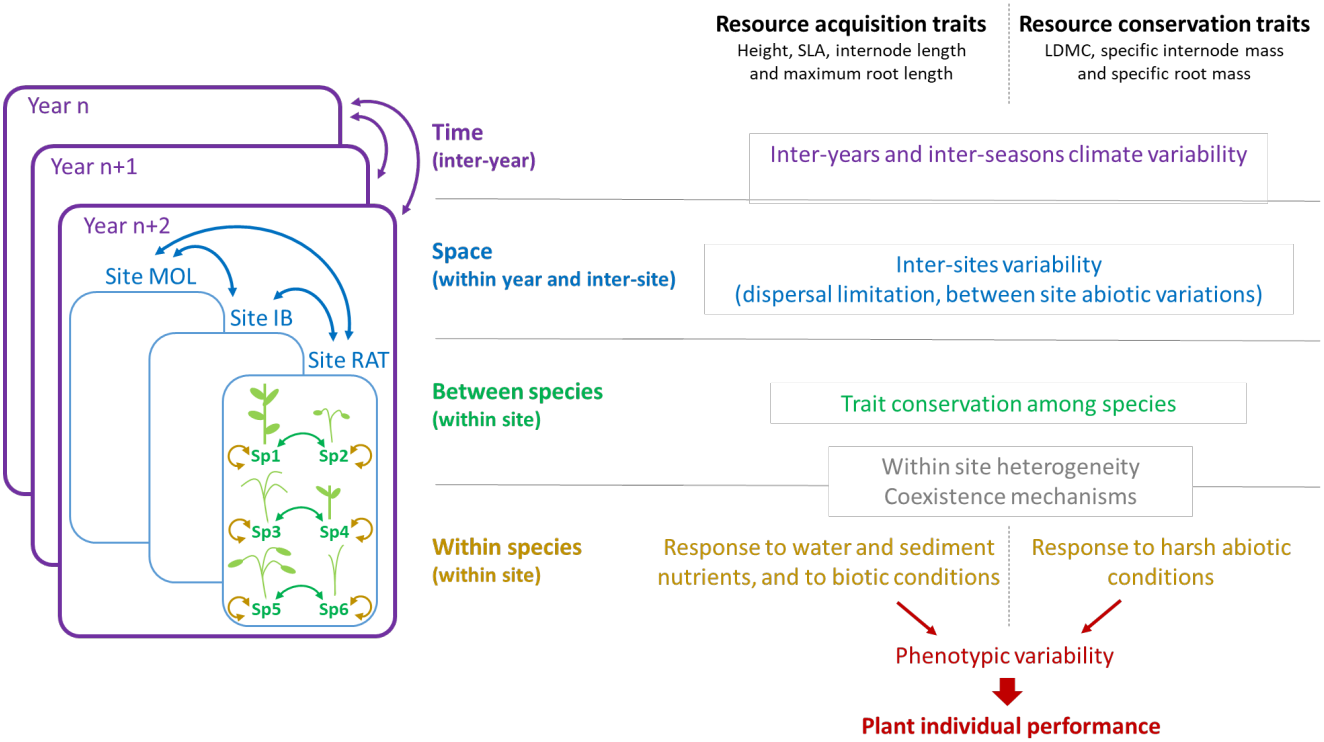
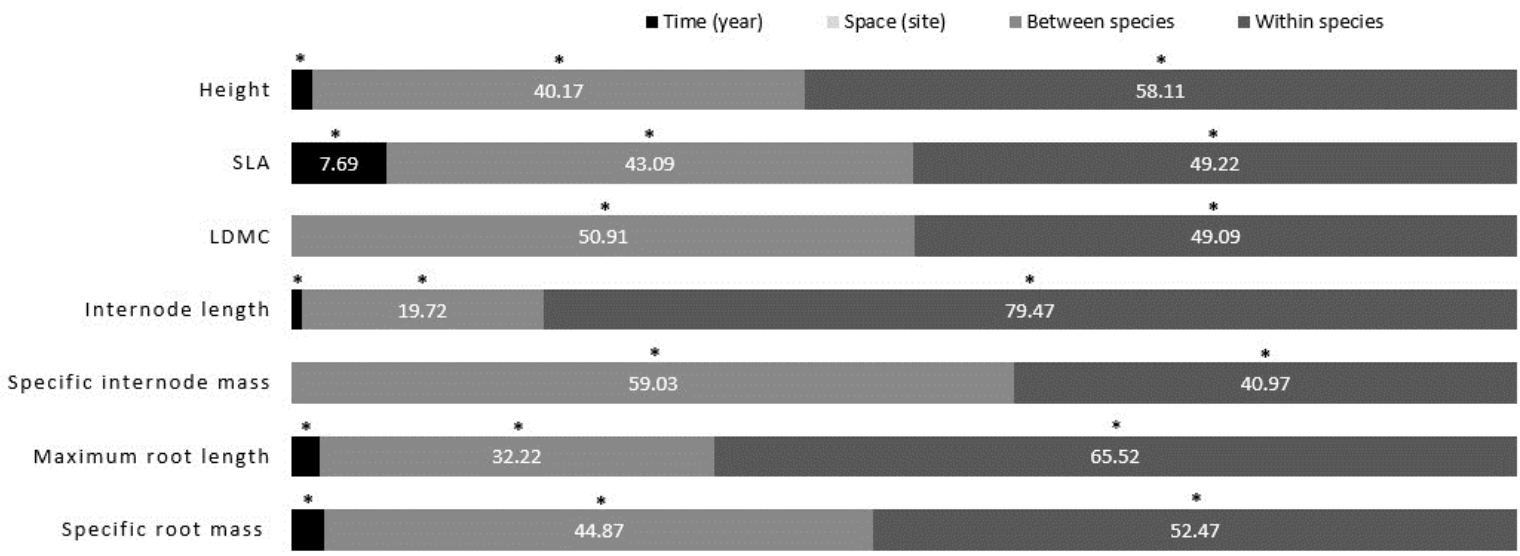


Figure 1. Conceptual graphic setting hypotheses.

Table 1. Measured plant functional traits and associated responses to abiotic and biotic conditions.

Traits	Description	Calculation	Abiotic variables with evidenced trait shifts	Biotic interactions with evidenced trait shifts
Resource acquisition traits				
Specific Leaf Area (SLA)	Proxy of plant photosynthetic capacity and resource acquisition	Ratio of area and dry mass of leaf ($mm^2.mg^{-1}$)	Temperature [a, ab, b, c, d], nutrients [a, e, ab], moisture [f, g], light [ac]	Competition for light [h, i], above-ground competition [j, g], facilitation [i]
Height	Allow optimal light exposure	Shortest distance between the upper limit of the main photosynthetic tissues and the ground level (cm)	Temperature [a, n], water availability [o, p, g], water depth [q], soil nutrients [a, r]	Aerial competition [m, i], belowground competition [i, g], facilitation [i]
Internode length	Plant ability to exploit local environment and to disperse at short distance	Distance between two successive ramets (cm)	Soil nutrients [t, u, v, s], light [ac, ae, af, w]	Spatial competition [m, x, s]
Maximum root length	Acquisition of nutrients	Length of the longest root (cm)	Temperature [a, ad, n], soil nutrients [a, e]	Competition [y]
Resource conservation traits				
Leaf Dry Matter Content (LDMC)	Proxy of physical resistance of leaves and resources storage	Ratio of dry and fresh masses of leaf ($mg.g^{-1}$)	Temperature [b, c], moisture [k, g], soil nutrients [e, k], water nutrients [l]	Competition [m, g]
Specific internode mass	Proxy of resources allocation for clonal multiplication and storage	Ratio of dry mass and length of connection ($mg.cm^{-1}$)	Soil nutrients [s, t]	Competition [m]
Specific root mass	Proxy of resources storage	Ratio of dry mass and length of root ($mg.cm^{-1}$)	Temperature [a, q], nutrients [a, e], Moisture [a, n]	

a = (Cornelissen et al., 2003); ab = (Gong & Gao, 2019); ac = (Santamaría, 2002); ad = (Freschet et al., 2017); ae= (Xiao et al., 2006) ; af= (Puijalon et al., 2008) ; b = (Meng et al., 2015); c = (Dostálek et al., 2020); d = (Poorter et al., 2009); e = (Lavorel & Garnier, 2002); f= (Jung et al., 2010); g = (Loughnan & Gilbert, 2017); h = (Violle et al., 2009); l = (Butterfield & Callaway, 2013); j = (Rooney & Kalff, 2000); k = (Wehn et al., 2017); l = (Fu et al., 2018); m = (Bittebiere & Mony, 2015); n = (Gray & Brady, 2016); o = (Moles et al., 2009); p = (Tao et al., 2016); q = (Wang et al., 2016); r = (Martinez-Almoyna et al., 2020); s = (Hutchings et al., 1997); t = (Rusch et al., 2011); u = (Louâpre et al., 2012); v = (Slade & Hutchings, 1987b); w = (Slade & Hutchings, 1987a); x = (Bittebiere et al., 2019); y = (Colom & Baucom, 2020).



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1095 **Figure 2.** Partitioning of individual trait variance across four nested scales, obtained using the Partvar procedure on
1096 the data collected from 2017 to 2020. All data were log or square-root transformed when needed, and standardized
1097 to equalize the weight of each trait dimension. *p < 0.05 (bootstrapping, *n* = 1430). SLA, specific leaf area; LDMC,
1098 leaf dry matter content. Time: four years of sampling; space: three sampled sites *i.e.* Cap Molloy, Isthme Bas, and
1099 Cap Ratmanoff; Between species: the six different macrophyte species of pond communities *i.e. Callitriche*
1100 *antarctica*, *Limosella australis*, *Juncus scheuchzerioides*, *Ranunculus biternatus, R. pseudotrullifolius,* and *R.*
1101 *moseleyi*; Within species: intraspecific trait variation.

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1103

1104 **Table 2.** Trait responses to abiotic and biotic pond habitat variables.

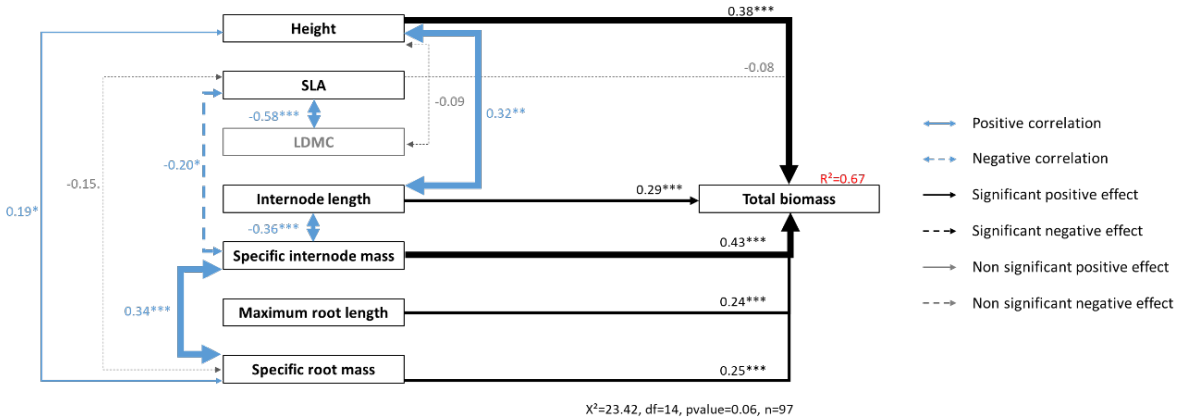
Trait		Explanatory variables of selected model				
	n	Predictor	F	d.f.	Model predictors coefficient	Part of explained variance (%)
Resource acquisition						
All	99	**Species identity**	**8.80*** **	5		
		PCAwater	**8.67*** **	1		
		Water depth	**2.64***	1		
Height	101	Functional diversity	3.49.	1	0.12	1.55
		pH	8.77**	1	-0.20	3.15
		Species richness	3.30.	5	-0.13	1.46
		Species identity	23.62***	1		52.24
		Water depth	3.06.	1	0.12	1.35
		Residuals		91		40.25
SLA	102	FCAplants 2	3.50.	1	-0.14	1.97
		Electric conductivity	8.66**	1	0.27	4.86
		Water temperature	4.56*	1	0.18	2.57
		Phytoplankton concentration	2.38 n.s.	1	-0.13	1.34
		PCAwater	12.24***	1	-0.32	6.88
		Species identity	11.54***	5		32.40
		Residuals		89		49.98
Internode length	100	pH	2.33 n.s.	1	-0.11	1.78
		Species richness	3.71.	1	-0.15	2.83
		Species identity	5.79***	5		22.20
		Water depth	6.22*	1	0.19	5.03
		Residuals		89		68.16
Maximum root length		**FCAplants 1**	9.21**	1	0.24	4.37
		FCAplants 3	3.61.	1	-0.14	1.71
		Water temperature	7.70**	1	-0.21	3.66
		Species identity	19.10***	5		45.39
		Water depth	2.42	1	0.11	1.18
		Residuals		92		43.69
Resource conservation						
All	97	**Species identity**	8.34***	5		
		Phytoplankton concentration	3.33*	1		
		FCAplants 3	7.13***	1		
		PCAsediments	5.37**	1		

LDMC		**FCAplants 3**	9.87**	1	-0.23	5.90
		Functional diversity	2.65 n.s.	1	0.11	1.58
		PCAsediments	7.62**	1	-0.22	4.55
		Species identity	11.22***	5		33.56
		Residuals		91		54.41
Specific internode mass	98	**FCAplants 1**	5.60*	1	-0.17	2.71
		Water conductivity	2.89.	1	-0.12	1.39
		Phytoplankton concentration	7.33**	1	-0.18	7.57
		Species identity	18.37***	5		44.37
		Residuals		91		43.96
Specific root mass	102	**pH**	4.11*	1	-0.15	1.92
		Phytoplankton concentration	22.42***	1	-0.41	10.49
		Pielou evenness	3.77.	1	-0.13	1.76
		PCAwater	7.26**	1	-0.24	3.40
		Species identity	17.03***	5		39.85
		Residuals		91		42.58

Water and sediment nutrient dimensions were reduced to first principal component axes (PCAwater and PCAsediments; Appendices S3 and S4). To account for the influence of within-pond species abundance, FCAplants represents the first three axes from a factorial correspondence analysis (Appendix S5). Variables in bold had significant effects. *$p < 0.05$, **$p < 0.01$, ***p < 0.001, "." $0.05 < p < 0.1$, n.s. not significant ($p > 0.1$), multivariate (all) and individual analyses of variance of the most probable models (2020 data). *n*, number of points used to calculate the relationship. Height and maximum root length were square-root transformed and all other data were log transformed. FCAplants 1 is related positively to the abundance of *R. moseleyi* and negatively to the abundance of *C. antarctica*, FCAplants 2 is related positively to the abundance of *R. pseudotrullifolius* and negatively to the abundance of *L. australis*, and FCAplants 3 is related positively to the abundance of *L. australis* and negatively to the abundance of *R. biternatus*.

Figure 3. a) Structural equation model representing the direct and indirect pond-level effects of trait values on individual performance of all species [November 2020 data, reduced model (lavaan package, variable selection based on Akaike information criteria); full model presented in Appendix S8]. Trait values were standardized for each species to eliminate variance due to species identity. Standardized path coefficients are given with *p* values: ***$p < 0.001$, **$p < 0.01$, "." $0.05 < p < 0.1$, no asterisk $p \geq 0.1$. Line widths represent relationship strength. R^2 values reflect the proportion of response variable variance explained. b) Absolute direct and indirect effects of trait values on individual performance.

a)



b)