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Running head: Macrophyte communities in the Iles Kerguelen

Functional characteristics rather than co-occurrences determine the outcome of interactions between neighbouring plants in sub-Antarctic ponds: consequences for macrophyte community biomass.

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Abstract

1. Understanding of the mechanisms underlying species coexistence within plant communities is crucial to predict their fate given the current context of biodiversity loss. Freshwater ecosystems are among the most abiotically constrained habitats because they harbor clonal macrophyte communities. Strong habitat filtering in these ecosystems influences the functional composition and diversity of macrophyte communities, determining the outcome of interactions between neighbours and ultimately affecting local spatial arrangement between neighbours (LSA). This influence may be modulated by environmental conditions in abiotically constrained habitats, such as freshwater ecosystems.
2. We focused on macrophyte communities living in ponds in the Iles Kerguelen, in the sub-Antarctic. These freshwater ecosystems are especially abiotically constrained (cold climate), and their plant communities are remarkably species-poor, simplifying the study of interactions between neighbours. We measured several abiotic variables in the ponds, species LSA and interspecific interactions (using the Log Response Ratio metric), and the functional composition of the community using aerial, root and clonal traits. We also determined the biomass of the whole macrophyte community.
3. Our results showed that LSA does not effectively assess interactions between neighbours at very small scales, neither at the community (one species *versus* all neighbouring species) nor the species level (between pairs of species). Secondly, aerial (leaf and stem) and root traits related to resource acquisition played a more important role in interactions between neighbours than clonal traits (*i.e.* internode length and specific internode mass related to space acquisition and resource storage, respectively).

4. Depending on the target species, (i) interactions responded positively or negatively to mean trait and functional diversity of the community, and (ii) different traits of neighbours (aerial or root traits) triggered an interaction response. Lastly, abiotic variables, in particular water temperature and light intensity, influenced macrophyte community biomass and plant community structure (*i.e.* species richness, functional diversity and LSA), either directly or through the modulation of other abiotic variables.
5. Our results lead to the two following conclusions: (i) interactions between neighbours do not reflect their local spatial arrangements but are strongly associated with abiotic variables and neighbourhood functional traits (depending on species), (ii) joint integration of biotic and abiotic variables in multivariate analyses enables better inference of biodiversity responses to environment, and the subsequent consequences for ecosystem function, especially in the context of climate change.

Keywords

Functional traits, community performance, abiotic filters, species coexistence, local spatial arrangement.

Introduction

Determining the mechanisms underlying species coexistence within plant communities is crucial to predict their fate in the current context of climate change and biodiversity loss (Chapin, 2003). Both abiotic and biotic drivers are known to structure local assemblages within communities (Cadotte & Tucker, 2017; Kraft, Adler, et al., 2015). Indeed, species that do not possess the functional traits allowing them to resist particular abiotic conditions are filtered out, leading to similar phenotypes among co-occurring species. Moreover, at finer scales, plants permanently interact with their immediate neighbours (*e.g.* competition, facilitation), also ultimately shaping specific and functional composition of the community (Connell, 1983; Goldberg & Barton, 1992; Tilman, 1982). Abiotically constrained habitats exacerbate the importance of interactions between neighbours (Choler, Michalet, & Callaway, 2001), with facilitative interactions being more pronounced under stressful and/or resource-limited conditions (Williams, Zeldin, Semski, Hipp, & Larkin, 2021; Zhang, Wang, & Qi, 2017). Freshwater ecosystems are among the most abiotically constrained, often harboring particular plant communities. They host macrophyte (*i.e.* aquatic plant) communities, dominated by clonal plants (Klimeš, Klimešová, Hendriks, & van Groenendael, 1997; Santamaría, 2002) that interact in both horizontal (for space) and vertical (for resources) directions (Gioria & Osborne, 2014). Altogether, the underlying mechanisms involved in interactions between neighbours and that support species coexistence may vary within a particular freshwater ecosystem, including within abiotically constrained habitats, although this has been poorly tested, especially regarding facilitative interactions (Silknetter et al., 2020).

Strong habitat filtering in aquatic ecosystems (Santamaría, 2002) affects the functional composition and diversity of macrophyte communities (Bornette & Puijalon, 2011; Fu et al., 2014; Zhang, Liu, Luo, Dong, & Yu, 2019), which may in turn play significant roles in interactions between neighbours (Suzuki, Rivero, Shulaev, Blumwald, & Mittler, 2014). The outcome of interactions between neighbours is not only driven by individual functional traits

96 (Gaudet & Keddy, 1988), but may also be determined by the difference between the functional
97 trait values of neighbouring competitors, as predicted by recent theories of species coexistence
98 (Cadotte & Tucker, 2017; Kraft, Godoy, & Levine, 2015). The traits of neighbours are expected
99 to have different effects on the outcome of interactions, in particular when trait values differ
100 from those of the focal plant (Kraft, Crutsinger, Forrestel, & Emery, 2014), and according to
101 their role in competitive strategies (tolerance *vs.* competing traits) (Novoplansky, 2009). On
102 the one hand, coexistence is often assumed to arise from high different functional trait values,
103 which alleviate competitive interactions (limiting similarity). On the other hand, small
104 differences in functional traits arising from competitive hierarchies may reduce differences in
105 competitive ability, thereby promoting coexistence of species with similar trait values (Kraft,
106 Crutsinger, Forrestel, & Emery, 2014). In abiotically constrained habitats, high functional
107 convergence between species is expected due to environmental filtering (Cornwell, Schwilk,
108 & Ackerly, 2006; Grime, 2006), suggesting reduced importance of mechanisms involved in
109 traits differentiation. Moreover, clonal traits influencing space acquisition could act as tolerance
110 traits to abiotic constraints as they provide opportunities to find more suitable environmental
111 conditions, while aerial (*e.g.* height or Specific Leaf Area) and root traits should be crucial for
112 resource competition (Kunstler et al., 2016; Lau, Shaw, Reich, & Tiffin, 2014). Thus, aerial and
113 root traits (vertical traits) should be more strongly involved in interactions between neighbours
114 than clonal (horizontal) traits.

115 Within plant communities, individuals are not randomly distributed. Their spatial
116 distribution can result either from stochastics events (Hubbell, 2011), or from environmental
117 heterogeneity, dispersal, and interactions between neighbours (Herben & Hara, 2003).
118 Therefore, the observed local spatial arrangement between neighbours (hereafter referred as
119 to LSA), would be the outcome of environmental filtering and of their interactions as commonly
120 demonstrated (Blanchet, Cazelles, & Gravel, 2020). Besides, inter-specific interactions
121 between plants are known to depend on abiotic characteristics (Martin & Coetzee, 2014;
122 Shields & Moore, 2016), with a shift from competition to facilitation in harsh conditions

(Bertness & Callaway, 1994, stress gradient hypothesis). Facilitation allows for a better recruitment and survival by improving abiotic conditions at local scales, which is expected to reflect spatial aggregation between plants (Bertness & Callaway, 1994; Kikvidze et al., 2005; Tirado & I. Pugnaire, 2005). Conversely, studies have shown that competition for resources leads better competitors to displace other species, commonly reflecting segregated LSA (Pottier, Marrs, & Bédécarrats, 2007; C. Schöb, Kammer, Kikvidze, Choler, & Veit, 2008; Seabloom, Bjørnstad, Bolker, & Reichman, 2005). As a consequence, spatial aggregation and segregation may indicate facilitation and competition respectively in constrained habitats (Eccles, Esler, & Cowling, 1999; Kikvidze et al., 2005; Malkinson, Kadmon, & Cohen, 2003; Raventós, Wiegand, & Luis, 2010). This assertion has never been tested within aquatic habitats where resource distribution differs strongly from other constrained habitats (for instance arid systems), due to the major effect of water depth on light availability.

Studies on joint effects of biotic and abiotic filters on macrophyte communities remain limited (Shields & Moore, 2016, but see: Anderson & Kalff, 1988; Chambers & Prepas, 1990; Gopal & Goel, 1993; McCreary, 1991), and this highly fragmented knowledge necessarily leads to inconsistencies in the reported effect of abiotic variables on the outcome of interactions between neighbours. In particular, this literature gap does not enable the respective roles of abiotic and biotic variables or their interactions to be determined for the taxonomic and functional composition of the aquatic plant community, and subsequently for its biomass. The biomass of the aquatic plant community can indeed be affected by abiotic variables either directly through their effects on plant physiology [*e.g.* aquatic system morphology, water or sediment chemistry (*i.e.* nutrient cycling) (Dhir, 2015; Hossain et al., 2017; MacKay et al., 2009; Velthuis et al., 2018; Wrona et al., 2006; Zhang et al., 2020)] or indirectly through species selection caused by environmental filtering (Kraft, Godoy, & Levine, 2015) combined with interactions between neighbours (stress gradient hypothesis, Bertness 1994), and functional traits (Dar, Pandit, & Ganai, 2014; James, Fisher, Russell, Collings, & Moss, 2005; Kim & Nishihiro, 2020; Mouchet, Villéger, Mason, & Mouillot, 2010). In ponds,

water temperature, dissolved nutrients, and light intensity are expected to be the main abiotic variables acting directly on plant community biomass and indirectly through the modulation of plant community structure.

In this study, we focused on macrophyte communities living in the ponds of the Iles Kerguelen, located in the sub-Antarctic region. These ponds are particularly useful for testing questions about interactions between neighbours in the context of abiotically constrained habitat, as the climate is very cold, yet warming (Lebouvier et al., 2011), and the remarkably low plant richness provides simplified natural communities (Frenot, Gloaguen, Massé, & Lebouvier, 2001; Van der Putten, Macel, & Visser, 2010). To that aim, within each pond, we measured several abiotic variables, plant species LSA, interactions between neighbours, and the functional composition of the community. We additionally assessed the biomass of the whole macrophyte community in each pond. Through this field sampling approach, we tested the following hypotheses: (i) interactions between neighbours can be inferred by LSA because spatial segregation should reflect negative effects of the neighbour's cover on target species biomass, thus indicating competition; (ii) vertical functional traits (*i.e.* aerial and root traits) influence interactions between neighbours, while horizontal traits (*i.e.* clonal traits) are less significant, so functional characteristics of neighbours influence their interactions; (iii) abiotic variables (water temperature, dissolved nutrients, and light intensity) should influence plant community biomass, either directly or through the modulation of plant community structure (*i.e.* species richness, functional diversity, and LSA).

Materials and methods

Study model

The study was carried out *in situ*, at the Iles Kerguelen in the French sub-Antarctic (South Indian Ocean) (48°30–50°S,68°27–70°35E). The climate of this archipelago is characterized by cold temperatures (annual mean of 4.6°C with few variations - Frenot et al., 2006; Lebouvier et al., 2011), and abundant precipitations (range from 500 mm to 3200 mm along an East-West gradient - Frenot, Gloaguen, Cannavacciuolo, & Bellido, 1998, and Meteo France). Although remarkably well adapted to cold temperatures, native macrophyte communities are characterized by very low species richness (zero to four co-occurring species per pond) (Frenot et al., 2006). They thus constitute ideal simplified models to infer mechanisms of plant community assembly, especially within constrained abiotic environments (Bergstrom & Chown, 1999).

The study was conducted in ponds at three sites located along the shore of the main island of the archipelago (Fig. 1a): Cap Molloy, Isthme Bas and Cap Ratmanoff. These three sites are less than 40 km apart, and display similar climates. Conversely, abiotic conditions are more variable within ponds than between sites. The ponds investigated have relatively small sizes (average area = 181.57 ± 382.39 m² except for one pond 180800 m², Table S1). They are shallow freshwater systems, enriched by nutrient inputs from marine fauna like seabirds and seals owing to their proximity to the ocean littoral (Smith, 2008). At each site, 15 ponds of varying area were selected to represent the variation in pond size, which influences water temperatures (Bornette & Puijalon, 2011). In contrast, mean water depth did not differ among ponds (19.03 ± 9.12 cm).

Macrophyte communities colonizing ponds are composed of six native species that can all co-occur locally: *Limosella australis* R.Br. (Scrophulariaceae), *Callitriche antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), together with three

196 Ranunculaceae species: *Ranunculus biternatus* Smith, *R. pseudotrullifolius* Skottsb., and *R.*
197 *moseleyi* Hook.f. These species are only found in the sub-Antarctic region, and *R. moseleyi*
198 may even be endemic to Iles Kerguelen. All species are perennial, displaying a clonal network
199 structure (*i.e.* plants are composed of related ramets (shoots with leaves and roots) that are
200 connected through plagiotropic stems). *Callitriche antarctica, L. australis, R. pseudotrullifolius*
201 and *R. moseleyi* are hydrophytes, while *R. biternatus* and *J. scheuchzerioides* are helophytes.
202 Only *C. antarctica* develops a floating canopy, while the five other species possess a rosette
203 growth form rooted in pond sediments. *Ranunculus pseudotrullifolius, R. moseleyi,* and *L.*
204 *australis* are mostly submerged (Hennion et al. 1994; Chau et al. 2021). However, *R.*
205 *pseudotrullifolius* may also produce floating leaves (Figure S1). *Ranunculus biternatus* and *J.*
206 *scheuchzerioides* can also be entirely submerged, depending on variations in pond water level
207 (Figure S1). Most ramets of these species were therefore submerged within ponds (ramet
208 height = 6.02 ± 3 cm, water depth = 19.03 ± 9 cm).

209 Abiotic and biotic characterization of ponds

210 We characterized abiotic conditions every three months over a year, starting from February
211 2020 and ending in March 2021 (Fig. 1b). At each sampling date and pond, water and sediment
212 samples were collected from three zones and mixed to obtain one composite water sample
213 (30 mL) and one composite sediment sample (50 mL) taking into account potential spatial
214 heterogeneity within each pond. As other abiotic conditions may also vary spatially in the pond,
215 we randomly positioned three (pond area < 5 m²) to five (pond area > 5 m²) quadrats (1 m²).
216 In these quadrats, three abiotic variables were measured: water depth (calculated as the
217 average of three measurements within the quadrats), electric conductivity (EC), and
218 concentration of dissolved oxygen (DO) (calculated as the average of three measurements
219 performed below water surface, in the middle of the water column, and at the pond bottom)
220 using a multiparameter HQ40D HACH sensor (EC ± 0.1 $mS.cm^{-1}$, DO ± 0.01 $mg.L^{-1}$). In
221 addition, light intensity and water temperature were continuously recorded in each pond, every

half hour since September 2020, using loggers (Hobo MX2202) positioned in the middle of the water column. Based on this dataset, water temperatures and light intensity fluctuations were then simulated for the period of February 2020 to August 2020 (winter season) which was not monitored. Water temperatures were simulated using their relationship with air temperatures recorded by Meteo France (2020 records, Port-aux-Français), and winter luminosity from its relationship with summer luminosity (Table S2). Finally, pond area (length × width) and proximity to the closest pond were also measured in March 2021.

For the measurements of water nutrient and chlorophyll-a concentrations, water samples were filtered through GF/F filters (0.7 µm pore size, Whatman GF/C) to eliminate coarse and fine particles within the 24 hours after field sampling. All samples (filtered water and sediments) and GF/F filters were then stored at -20°C for several weeks before analyses. Chlorophyll a pigments collected on GF/F Whatman filters were quantified using the Unesco method (Vohra, 1966) with a spectrophotometer. This measure was used to estimate the quantity of phytoplankton per volume of water for each pond. $N–NH_4^+$, $N–NO_3^-$ and $P–PO_4^{3-}$ concentrations of water samples were determined using standard colorimetric methods (Grasshoff, Ehrhardt, Kremling, & Anderson, 1999) with a sequential analyzer (SmartChem200, AMSAlliance).

In sediment samples, organic carbon to nitrogen ratio (C:N) was measured using the "capsule method" (Brodie et al., 2011). For each sample, five mg ± 10% of dry sediment previously lyophilized and homogenized were weighted in a silver capsule and acidified with HCl (2 $mol.L^{-1}$) to eliminate carbonates. Capsule liquids were evaporated on a 65°C hot plate for 12 hours, before capsules were oven-dried at 80°C for 48 hours. Organic carbon and nitrogen total content were then measured with an elementary analyzer (FlashEA; 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 with NaOH (1 M). Then the supernatant was collected, its pH was stabilized with HCl (3.5 M), and its concentration was quantified using the molybdate/ascorbic acid blue method.

Local spatial arrangements of macrophyte species

In December 2020, within each of the 45 ponds, spatial distribution of all plant species was recorded using five square lattices of 50 × 50 cm², randomly positioned on vegetation. The lattice was divided into 5 × 5 cm² cells (100 cells in total) and the presence/absence of each macrophyte species within each cell was recorded (Fig. 1b). Non-floating species (*i.e.* all species except *C. antarctica*) were considered as present when a ramet was rooted in the target cell, whereas *C. antarctica* was considered as present when a ramet was observed at the cell vertical. The cell size was selected as it corresponds to the scale at which plants are likely to interact (Purves & Law, 2002).

We calculated the species by species co-occurrence matrix in each lattice. In this matrix, the intersection between species i and j indicates the number of times both species co-occur in a cell of the lattice. We used the matrix to characterize local spatial arrangements between neighbours at two scales: (i) for all pairs of species (species scale), (ii) and for one species *versus* all neighbouring species (community scale). LSA corresponded to the difference between the observed number of co-occurrences within a quadrat and the expected number of co-occurrences at the pond level based on species cover (number of cells where species is present/total number of cells in the pond, considering all pond lattices simultaneously). Thus, negative values of LSA indicate local spatial segregation while positive values indicate local spatial aggregation. For the species scale, the observed number of co-occurrences was the total number of cells where a pair of species i and j co-occurred, and for the community scale, the total number of cells where species i co-occurred with any other species. Besides, for the species scale, the expected number of co-occurrences N_{exp} between species i and j were calculated by pooling the five lattices of each pond as follows:

$$N_{exp} = coverspecies_i \in thepond \times coverspecies_j \in thepond \times totalnumberofcells \in thepond$$

274 where the cover of a given species is the number of cells in which the species occurred divided
275 by the total number of cells in the pond. For the community scale, the expected number of co-
276 occurrences was the sum of the expected number of pairwise co-occurrences between species
277 i and all the other species present in the pond.

278 Assessing neighbours' interactions within ponds

279 In March 2021 (*i.e.* at the end of the growing season), for each macrophyte species in each
280 pond, we collected mature ramets with and without interspecific plant interactions (*i.e.*
281 presence of other individuals in their neighbourhood) (Fig. 1b). Ramet neighbourhood was
282 characterized within a surrounding circle of 20 cm diameter (Purves & Law, 2002). We
283 considered 10% of vegetation cover in the neighbourhood as a threshold for the occurrence of
284 interactions between neighbours (*i.e.* target ramet with interactions had neighbourhood cover
285 > 10% while ramet without interactions (control ramet) had neighbourhood cover < 10%).
286 Nevertheless, we further checked that this threshold value of 10% had no influence on our
287 results (threshold value of 35%, see Table S3). For all target ramets, neighbouring species
288 abundances were also recorded (within 5% precision), along with bare soil to take into account
289 the overall interaction intensity.

290 For each ramet collected, we measured total biomass, *i.e.* including the leaves, stems,
291 roots, and one internode of clonal connection. When present, fruits were also included in ramet
292 biomass although their biomass was negligible (only 9% of collected ramets had fruits)
293 compared to vegetative growth, in line with previous works conducted on macrophyte species
294 (Barrat-Segretain, 1996; Barrett, Eckert, & Husband, 1993). Measurements of biomass were
295 performed after oven-drying ramets for 48 hours at 65°C. Ramet biomass was used as a proxy
296 of its performance. The effect of neighbouring species on species i ramet in pond j on site k
297 was used as a proxy of interactions between neighbours and was estimated using the Log
298 Response Ratio (hereafter referred as to biomass LRR) (Hedges, Gurevitch, & Curtis, 1999)
299 as follows:

$$\text{Biomass LRR}_{i,j,k} = log\left(\frac{Biomass\ of\ ramet\ of\ species_i \in pond_j\ on\ site_k}{Average\ biomass\ of\ control\ ramets\ of\ species_i\ on\ site_k}\right)$$

Neighbourhood functional characteristics

To assess the functional characteristics of plant neighbourhood, we collected one ramet (with its leaves and roots, and one connection internode) of each of the six above-mentioned species when present, within each quadrat of each pond (n = 3 to 5 quadrats per pond). Collection occurred in November 2020, and three categories of traits were measured on the ramets: (i) above-ground competition traits: aerial traits including height, Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC) to characterize the plant photosynthetic efficiency and tissue conservation; (ii) below-ground competition traits: root traits including maximum root length and specific root mass to characterize nutrient uptake; (iii) competition for horizontal space traits: clonal traits including internode length to characterize the avoidance response, and specific internode mass to characterize ramet investment into resource storage.

To measure SLA and LDMC following Cornelissen et al. (2003), one healthy mature leaf was randomly selected per ramet. Internode length was measured on one of the internodes attached to the ramet. Specific internode mass was calculated as the ratio between internode dry mass and length ($g.cm^{-1}$). Specific root mass was calculated as the ratio between root dry mass and maximum root length ($g.cm^{-1}$). Measurements of dry masses were performed after oven-drying plant parts for 48 hours at 65°C. All plants were cleaned before measurements were taken.

We tested for correlations between all pairs of traits using Spearman rank correlations to detect possible co-variations among traits. We did not detect significant correlations between any pair of traits (Spearman's rho < 0.7, Dormann et al., 2013). The functional neighbourhood of the plant community of each target ramet was characterized by two types of metrics: the community weighted mean (CWM) (Lavorel et al., 2007) of each trait calculated using each species cover and mean trait values at the pond level (we expected plant traits to

differ between ponds with different abiotic conditions), and the functional dispersion of traits (then referred as FDis), calculated using the *fdisp* function of package FD (Laliberté & Legendre, 2010), of each of the three trait categories (aerial, clonal, and root traits).

Data analyses

The means of daily (day and night) water temperatures and light intensity from February 2020 to March 2021 were calculated for each pond, and all abiotic variables were averaged at the pond scale. Abiotic dimensions describing pond conditions were reduced to the first-three axes of a Principal Component Analysis (PCA) performed on abiotic variables, and in which data were centered and standardized by standard deviation (Figure S2).

Association between interactions between neighbours and their local spatial arrangement

Firstly, we used linear models to test for the effects of local spatial arrangements between neighbours at the community scale (between a target species and all its neighbouring species) and pond abiotic conditions on the biomass LRR for five out of the six macrophyte species (*L. australis* omitted due to a lack of points). We included LSA and the first three axes of the PCA performed on abiotic variables as explanatory variables in the full model. Then we applied a stepwise model selection based on the AIC criteria (MuMIn package), and selected the most parsimonious model using an ANOVA test (type II). The same procedure was applied to test relationships between biomass LRR of target species i and LSA calculated at the species level (*i.e.* between species i and j). To that purpose, we only chose biomass LRR values calculated for ramets of species i having species j in their neighbourhood.

Responses of interactions between neighbours to their traits

We tested the response of biomass LRR for three out of the six macrophyte species (due to a lack of points), to its functional neighbourhood at community level. That is, the CWM of the

349 traits of all neighbours and FDis of aerial, clonal, and root traits, together with pond abiotic
350 conditions (first-three axes of the PCA performed on pond abiotic variables), and bare soil (to
351 take into account the overall interaction intensity) using linear models. We started with the full
352 model and then applied a model selection procedure through a stepwise selection based on
353 AIC criteria (see previous model).

354 ***Direct and indirect associations between abiotic and biotic variables and macrophyte***
355 ***community biomass***

356 Macrophyte community biomass, was calculated at the pond level using the sum of the mean
357 ramet biomass per species, and the cover of each species at the pond scale (total number of
358 cells in which the species occur / total number of cells, considering all quadrats). We used
359 Structural Equation Modeling (SEM) (Grace, Anderson, Olff, & Scheiner, 2010) to decipher
360 direct and indirect effects of abiotic and biotic variables on community biomass. We included
361 variables thought to affect macrophyte community biomass, either directly or through the
362 modulation of interactions between neighbours. The variables were: nutrient concentration in
363 water and sediments (Dar et al., 2014; Schneider, Cunha, Marchese, & Thomaz, 2015), pond
364 morphometry [pond area (Rolon & Maltchik, 2006), water depth (Wang, Zhang, Xu, & Yu,
365 2016)], and water quality variables [electric conductivity (Lévesque, Hudon, James, &
366 Legendre, 2017), O_2 concentration (Morris, Harrison, Bailey, & Boon, 2004), mean temperature
367 (Dar et al., 2014), light intensity (Su et al., 2019)]. We added chlorophyll a concentration to
368 reflect competition between macrophytes and phytoplankton (Phillips, Willby, & Moss, 2016).
369 Distance to the closest pond was also included as a proxy of the degree of proximity between
370 ponds, as this is known to impact plant species dispersal, and thus plant community richness
371 and functional diversity (Favre-Bac, Mony, Burel, Seimandi-Corda, & Ernoult, 2017). Finally,
372 biotic variables such as richness, FDis, and LSA allowed us to quantify macrophyte community
373 structure and test for an association with biomass (Hooper et al., 2005; Monzeglio & Stoll,
374 2005; Qi et al., 2021). All possible relationships between variables were built based on the
375 literature (Figure S3).

To build these relationships, LSA was calculated at the pond scale, taking the total number of co-occurrences between all pairs of species at the pond scale into account. FDis was calculated at the pond scale (calculated by pooling all lattices), including all measured traits and species cover. Nutrient concentrations in water ($N\text{-}NH_4^+$, $N\text{-}NO_3^-$, $P\text{-}PO_4^{3-}$) and in sediments (C:N ratio, bioavailable P) were each reduced to the first axis of a PCA analysis, in which data were centered and standardized. Variables were normalized (log or square-root transformations) and standardized before analysis. 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 carried out with R 4.0.3.

Results

A Principal Component Analysis (PCA) was performed on abiotic parameters measured at the pond level to reduce abiotic dimensions (Figure S2). PCA Axis 1 was positively related to the light intensity in ponds which was highest when nutrient availability in sediments was low. PCA Axis 2 was positively related to the concentration of $N\text{-}NH_4^+$ in the water column and negatively to the density of phytoplankton (represented by the concentration of chlorophyll a per mL of water), especially when habitat temperatures were cold. PCA Axis 3 was positively related to $N\text{-}NO_3^-$ concentration in water and conductivity.

Local spatial arrangements between neighbours did not reflect their interactions

At the community scale (interactions with all species in neighbourhood), we found no significant relationship between biomass LRR and LSA in all species ("All" in Table 1). Pond abiotic conditions, however, significantly explained biomass LRR in two out of the five species tested, either positively or negatively. Water nutrient concentration (PCA Axes 2 and 3) was strongly associated with interactions for *C. antarctica* and *R. moseleyi* (Table 1). At the species scale (LSA of pairwise combinations of species, including the target species), biomass LRR was significantly associated with LSA (species aggregation or segregation) for only one out of the five target species (Table 1). In *J. scheuchzerioides,* spatial aggregation had a positive effect on the biomass LRR of *R. moseleyi*. Biomass LRR was nevertheless mostly predicted by pond abiotic conditions in the tested species, except in *R. pseudotrullifolius* (Table 1). In particular, biomass LRR of *C. antarctica* and *J. scheuchzerioides* were predicted by the dissolved $N\text{-}NH_4^+$ concentration (PCA Axis 2), likely depending on the presence of phytoplankton. Conversely, biomass LRR of *R. biternatus* and *R. moseleyi* was impacted by the water $N\text{-}NO_3^-$ concentration and electric conductivity (PCA Axis 3).

Interactions depend on the functional characteristics of neighbours

Biomass LRR significantly responded to functional characteristics of neighbours in two out of the three target species (Table 2). Indeed, CWM of the neighbours' traits explained a total of 23.5% of biomass LRR variations in *J. scheuchzerioides*, and FDis of neighbours' traits contributed to 76.2% of biomass LRR variations in *R. biternatus*. More specifically, biomass LRR of these two species was only associated with CWM of aerial traits (Table 2), which had positive (describing facilitation) and negative (describing competition) effects, depending on the target species. However, this effect was limited in *R. biternatus* (tCWM_SLA= -0.02*, tCWM_LDMC= -0.006*, both traits explaining about 3.5% of biomass LRR variations). Much of biomass LRR variations in *R. biternatus* were actually explained by FDis (68.88%). More precisely, FDis of aerial and root traits displayed respectively positive (t=2.61***) and negative effects (t=-2.55***) on *R. biternatus* biomass LRR (Table 2).

Direct and indirect effects of abiotic and biotic variables characterizing ponds on macrophyte community biomass

Five out of the 13 variables tested did not have any direct or indirect effects on macrophyte CWM biomass (*i.e.* community biomass) (Fig. 2): distance to pond (*i.e.* between-pond proximity), pond area, and concentrations of dissolved O_2, water and sediment nutrients. Regarding the eight variables that were significantly associated with community biomass, four had direct effects: water temperature (-0.32***), chlorophyll a (-0.46***), richness (0.36***) and LSA (-0.49***). A negative association between LSA macrophyte community biomass indicated that the more species were aggregated, the lower the community biomass.

There were also multiple indirect effects on community biomass. Firstly, several abiotic variables modulated the effect of other abiotic variables. For example, light intensity increased water temperature (0.51***), thereby indirectly decreasing macrophyte community biomass. Secondly, biotic variables modulated each other, amplifying indirect biotic effects (Fig. 2). FDis was correlated with species richness (0.65***) and had a negative effect on LSA (-0.28*),

435 thereby indirectly increasing community biomass. In addition, biotic variables were influenced
436 by abiotic variables, strengthening indirect abiotic effects on macrophyte community biomass
437 (Fig. 2). FDis was negatively affected by water depth (-0.34**), while LSA was positively
438 affected by electric conductivity (0.45***). Ultimately, water depth and electric conductivity
439 indirectly decreased macrophyte community biomass.

Discussion

Interactions between neighbours depend on abiotic variables and their functional characteristics in polar ponds

Interactions between neighbours shape plant communities, and thus drive variations in their biomass. Indeed, a reduction in competitive interactions, or an increase in facilitative interactions between species, can lead to complementary effects, subsequently increasing community biomass (Callaway, 2007; Mulder, Uliassi, & Doak, 2001). We observed that interactions between neighbours depend on the functional traits of the target ramet and of its neighbours, as well as on abiotic variables (Schneider et al., 2015; Zhang et al., 2020).

In these sub-polar ponds, the direction and strength of interactions were mostly associated with patterns in abiotic variables, reemphasizing the need to consider abiotic factors as major influences on interactions between neighbours (Biswas & Wagner, 2014; Eränen & Kozlov, 2008). Changes in the net outcome of interactions caused by abiotic stressors could be inferred from fine scale observations of species spatial co-occurrences within communities (Kikvidze et al., 2005). Similarly, we expected interactions between the different species and their neighbours to be inferred from their LSA, both at the community and species scales. However, LSA did not reflect changes in the interactions between neighbours at very small scales, neither at the community (multispecies interactions) nor the species level. Our results are in line with Delalandre & Montesinos-Navarro (2018), who showed that LSA does not capture the underlying processes involving pairwise interactions at patch scale (about 0.05m²). Several non-exclusive hypotheses may explain these results. Firstly, the very low species richness of the Ile Kerguelen macrophyte community (four species at most) might cause more species segregation (Delalandre & Montesinos-Navarro, 2018). Indeed, we showed that more than 70% of the significant LSA at the pond scale represented species segregations (Table S5). Secondly, different processes may generate similar LSA *in situ* (MacKenzie, Bailey, & Nichols, 2004; McIntire & Fajardo, 2009; Rayburn & Monaco, 2011).

466 Segregation may indeed reflect competitive interactions but also habitat heterogeneity,
467 allowing species with different abiotic preferences to establish within different suitable micro-
468 sites. Similarly, aggregation is usually interpreted as facilitation but can also indicate species
469 aggregation within the same, most suitable micro-site in an heterogeneous habitat (Blanchet
470 et al., 2020). Finally, LSA calculation *in situ* has limitations. For example, if two species have
471 opposite effects on each other (*i.e.* one species is facilitated by another that in turn competes
472 with the first one), these will result in null LSA (we recorded 53 null LSA out of the 156 tested
473 ones, Table S5). Moreover, the indirect effect of a third species on pairwise species
474 interactions (Castillo, Verdu, & Valiente-Banuet, 2010; Christian Schöb, Armas, & Pugnaire,
475 2013) or asymmetric interactions (Delalandre & Montesinos-Navarro, 2018) are not
476 measurable despite affecting the outcome of interactions between neighbours, and thus the
477 resulting patterns of co-occurrence.

478 In abiotically constrained habitats, high functional convergence between species is
479 expected, resulting from habitat filtering (Cornwell et al., 2006; Grime, 2006). Yet, coexistence
480 within a community (*i.e.* the outcome of interactions) could be due to two possible processes,
481 both based on differences in trait values between species: limiting similarity (Kraft, Godoy, &
482 Levine, 2015; Turcotte & Levine, 2016) and the competitive hierarchy (Chesson, 2000;
483 Mayfield & Levine, 2010). As expected, vertical traits (*i.e.* aerial and root traits related to
484 resource acquisition) appeared to play a stronger role in interactions between neighbours than
485 horizontal traits (clonal traits), in two out of the three species. Originally, we highlighted that
486 there are two possible processes of species coexistence occurring within macrophyte
487 communities, based on different traits and relationships with interacting species identities.
488 Furthermore, these results indicate that the balance between competition and facilitation within
489 abiotically constrained habitat, results from functional characteristics of neighbours related to
490 resource acquisition, not just from functional characteristics of target species. More
491 specifically, CWM of height had positive effects on *J. scheuchzerioides* biomass LRR
492 (explaining 24% of its variation), that is, tall neighbours have facilitative effects on this species.

493 *Juncus scheuchzerioides* stands among the tallest species, and its neighbourhood is mostly
494 composed of conspecifics (34.8 ± 18.1%, Figure S4). Since most contacts between *J.*
495 *scheuchzerioides* ramets are intra-specific, and likely intraclonal, we conclude that intraspecific
496 facilitation or even intra-clonal cooperation [physiological integration (Wang et al., 2021)] are
497 important for this species. In *R. biternatus*, ramets responded more to the variability of aerial
498 and root traits than to their average within the neighbourhood (68.88% against 7.3% of biomass
499 LRR variation). More precisely, *R. biternatus* is facilitated by a high aerial and a low root
500 functional diversity, indicating above-ground resource partitioning (*i.e.* niche differentiation
501 along the aerial trait axis). Thus, functionally redundant species can coexist at the community
502 scale if their neighbourhood comprises species displaying different trait values (Maire et al.,
503 2012). For example, *R. moseleyi* and *R. pseudotrullifolius*, two species closely related to *R.*
504 *biternatus* and sharing similar resource use and functional roles, are very rare in its
505 neighbourhood composition (Figure S4).

506 In conclusion, we confirmed that both abiotic and biotic characteristics are related to
507 interactions between neighbours at species level. Multiple assembly processes operate
508 simultaneously within the macrophyte community (Spasojevic & Suding, 2012) either through
509 community weighted mean or neighbour dissimilarity (Copeland & Harrison, 2017) depending
510 on traits. Ultimately, this shows the importance of multi-trait approaches to better infer
511 community assembly processes (Kraft, Godoy, & Levine, 2015). Plus, we emphasize that LSA
512 does not reflect interactions between neighbours. Therefore, interpreting significant spatial co-
513 occurrences as evidence of interactions between neighbours should be done cautiously. By
514 specifically focusing on interactions, mesocosm experiments are one way to control for multiple
515 abiotic factors and environmental heterogeneity that can modulate interactions between
516 neighbours and produce similar LSA (Bittebiere, Saiz, & Mony, 2019; Brazeau & Schamp,
517 2019). Consequently, community-level characterization of LSA is needed as well as pairwise
518 relationships. Furthermore, biotic and abiotic variables, either jointly or separately, should

519 indirectly influence community biomass through their modulations of interactions between
520 neighbours, and thereby also influence species biomasses.

521 Joint effects of biotic and abiotic variables on macrophyte community 522 biomass

523 Five out of the 13 abiotic and biotic variables tested had no direct or indirect effect on
524 macrophyte community biomass, confirming the need to study pond systems as a whole. The
525 distance to the closest pond (*i.e.* between-pond connectivity), pond area, dissolved O_2
526 concentration, and (contrary to our expectations) water and sediment nutrient concentrations,
527 do not have any direct or indirect effects on macrophyte community biomass. Ponds may not
528 be limited by nutrients, since inputs by marine fauna are frequent, especially during summer
529 (Smith, 2008), leading to minimal impact on biomass. Indeed, the species studied tended to
530 have relatively high SLA and low LDMC (Figure S5), making them nutrient acquisitive, in line
531 with similar studies of systems with high resource availability (Stanisci et al., 2020).

532 Our holistic approach confirmed our third hypothesis, demonstrating that abiotic
533 variables were associated with macrophyte community biomass, either directly or through the
534 modulation of inextricably connected biotic variables (*i.e.* the local spatial arrangement of the
535 macrophyte community and its functional diversity, also related to its species richness). This
536 is consistent with Sanaei, Sayer, Saiz, Yuan, & Ali (2021), who showed that biotic and abiotic
537 variables are important drivers of plant assemblages and community biomass in relationships
538 with nutrients and spatial co-occurrences within arid systems (semi-steppe rangelands). In our
539 case, abiotic and biotic variables had negative and positive effects on community biomass,
540 respectively.

541 We demonstrated that few variables were directly associated with macrophyte
542 community biomass: water temperatures, phytoplankton quantity (chlorophyll a), species
543 richness, and the LSA. Spatial structure with segregated species supports macrophyte
544 community biomass by limiting competitive interactions with superior competitors (Porensky,

545 Vaughn, & Young, 2012). Furthermore, richness was positively associated with the
546 macrophyte community biomass. Several studies have already demonstrated that higher
547 species richness leads to higher community biomass because of the complementary use of
548 resources among species, and of the sampling effect (increased probability of sampling highly
549 productive species) (Engelhardt & Ritchie, 2001; Loreau & Hector, 2001; Schmid, 2002;
550 Tilman, Lehman, & Thomson, 1997a). In addition, higher species richness leads to better
551 ecosystem functioning (Loreau et al., 2001; Schwartz et al., 2000; Tilman, Knops, et al.,
552 1997b), and maintains some abiotic conditions beneficial to the growth of macrophytes.
553 Importantly, macrophyte community biomass is negatively affected by increased water
554 temperatures. The importance of water temperature is not surprising since macrophyte species
555 in the sub-Antarctic are adapted to cold temperatures. Indeed, although rising water
556 temperatures can stimulate increases in macrophyte community biomass within the optimum
557 thermal range (Dar et al., 2014), their negative impact suggests that this optimal thermal range
558 has already been exceeded at the Iles Kerguelen (Frenot et al., 2006). As water temperatures
559 continue to warm, the consequences for macrophyte community structure and its biomass will
560 likely be severe. We found that light intensity increased water temperatures leading to an
561 indirect negative impact on macrophyte community biomass. This observation calls into
562 question results from the literature where only the positive direct effect of light intensity on plant
563 growth rate in aquatic ecosystems was considered, and thus effects on community biomass
564 were not reported (Jin, Ibrahim, Muhammad, Khan, & Li, 2020). Furthermore, since
565 macrophytes greatly influence ecosystem-level processes in ponds (Iacarella, Barrow, Giani,
566 Beisner, & Gregory-Eaves, 2018; Lürig, Best, Dakos, & Matthews, 2021; Mo, Deng, Gao, Guo,
567 & Yu, 2015), climate warming could negatively affect trophic chains and ecosystem function
568 (Gutt et al., 2021).

569 Finally, very few studies in freshwater ecosystems have thoroughly assessed both
570 abiotic and biotic variables in habitats (but see Wood, Stillman, Clarke, Daunt, & O'Hare, 2012
571 and Liu et al., 2020). This gap in the literature limits our understanding of the fate of macrophyte

572 species concomitantly exposed to abiotic and biotic filters, especially in a context of climate
573 change. The interconnection between abiotic and biotic variables shown here raises questions
574 about the sequential influence of abiotic and biotic filters on plant community assembly (Keddy,
575 1992; Violle et al., 2012; but see Cadotte & Tucker, 2017). In addition, we provide strong
576 evidence for the urgent need to approach biodiversity structure and its influence on ecosystem
577 function, by jointly integrating biotic and abiotic variables in multivariate analyses
578 (Chalmandrier et al. 2022).

Conclusion

Our study brings new insights into the mechanisms involved in interactions between neighbours that supports species coexistence within freshwater ecosystems and other abiotically constrained habitats. In particular, we showed that abiotic variables had a stronger effect on species interactions than the spatial structure of macrophyte communities. In addition, we provided new evidence that biotic and abiotic variables influencing the assembly of macrophyte communities are interconnected, and we encourage reseachers to consider their combined effects in future studies to get a better picture of the processes underlying plant community assembly. Longer-term studies will be needed to better assess changes in plant communities, especially within poorly studied freshwater systems vulnerable to climate changes.

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Conflict of interest

The authors declare that they have no conflict of interest.

Data availability statement

All data are available in figshare (https://doi.org/10.6084/m9.figshare.21187183.v1).

Author Contributions

Conceptualization: P.D., H.S., M-L.B., A-K.B. Developing methods: H.S., M-L.B., A-K.B. Conducting the research: P.D., F.M-B., L.S., F.V., Y.O., M.F., A-K.B. Data analysis and interpretation: P.D., H.S., M-L.B., A-K.B. Preparation figures and tables, and writing: P.D., H.S., M-L.B., F.M-B., L.S., D.R., F.V., Y.O., M.F., A-K.B.

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Tables

Table 1. Results of ANOVAs performed on the most probable models determined based on the AIC selection method, and relationships between biomass LRR of each target species and the local spatial arrangements calculated between this target species and (i) all species in its neighbourhood without distinction (community scale), or (ii) one particular neighbouring species (species scale). See Materials and Methods section for more details on the calculation of local spatial arrangements between neighbours. To characterize the abiotic conditions of the ponds and test their effects on biomass LRR (without interactions with LSA), we used the first-three axes of a PCA performed on abiotic variables (Figure S2). Some species pairwise combinations were not tested because of a lack of observations, and thus do not appear in the table.

Biomass LRR of the target species	Neighbouring species	Explanatory variables of selected model					
		n	Predictor	F	d.f.	Model coefficient and its significance	Local spatial arrangements between the target species and neighbouring species
C. ant	All	21	**Axis2**	29.4	1	0.21***	None
	J. sch	18	**Axis2**	24.07	1	0.30***	None
	R. bit	16	**Axis2**	28.42	1	0.18***	None
J. sch	All	30	Axis2	2.73	1	-0.17 (n.s.)	None
	C. ant	15	**Axis2**	7.62	1	-0.29*	None
	R. bit	30	Axis2	4.09	1	-0.19.	None
	R. mos	8	**LSA**	13.03	1	0.14*	**Aggregation**
	R. pseudo	8	x	x	x	x	None
R. bit	All	28	x	x	x	x	None
	C. ant	13	x	x	x	x	None
	J. sch	30	x	x	x	x	None
	R. mos	8	x	x	x	x	None
	R. pseudo	10	**Axis3**	21.41	1	0.33**	None
R. mos	All	8	**Axis3**	8.94	1	-0.81*	None
	J. sch	8	**Axis3**	8.94	1	-0.81*	None
	R. bit	7	**Axis3**	11.44	1	-0.78*	None
R. pseudo	All	8	x	x	x	x	None
	J. sch	8	x	x	x	x	None
	R. bit	9	x	x	x	x	None

Notes: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; '.' $0.05 < p < 0.1$; n.s. = not significant ($p > 0.1$). 'x' none of the tested predictors actually influenced the response variable (model selection). *C. ant* = *C.*

antarctica; J. sch = J. scheuchzerioides; R. bit = R. biternatus; R. mos = R. moseleyi; R. pseudo = R. pseudotrullifolius. 'LSA' local spatial arrangements. 'n' number of points to calculate relationship.

Table 2. Results of ANOVAs performed on the most probable models determined based on AIC selection method, and testing responses of biomass LRR calculated for each target species to functional characteristics (*i.e.* CWM and FDis of traits) of their neighbours. Predictors in bold characters were significantly associated with biomass LRR. Functional characteristics were calculated on ramets within the 20cm neighbourhood of each target ramet, and included the CWM of seven traits and FDis calculated for three types of traits (aerial, root, and clonal). To characterize abiotic conditions and to test for their effects on biomass LRR (without interactions with functional characteristics), we used the first-three axes of a PCA performed on abiotic variables (Figure S2). Biomass LRR response was not tested in three species (*L. australis, R. moseleyi,* and *R. pseudotrullifolius*), because of a lack of observations (n=4), thus these species are not presented in the table.

Biomass LRR of the target species	Explanatory variables of selected model					
	n	Predictor	F	d.f.	Model coefficient and its significance	Part of explained variance (%)
C. ant	24	CWM max. root length	3.31	1	0.05.	7.91
		Axis2	14.0	1	0.31**	33.39
		Bare soil	4.61	1	0.01*	11.01
		Residuals		20		47.69
J. sch	24	**CWM height**	8.07	1	0.11**	23.51
		Bare soil	5.26	1	0.008*	15.33
		Residuals		21		61.16
R. bit	27	**CWM SLA**	5.17	1	-0.02*	3.56
		CWM LDMC	5.44	1	-0.006*	3.74
		FDis aerial traits	47.14	1	2.61***	32.43
		FDis root traits	55.89	1	-2.55***	36.45
		Axis3	13.63	1	0.28**	9.38
		Residuals		21		14.44

Notes: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; '.' $0.05 < p < 0.1$. 'x' none of the tested predictors actually influenced the response variable (model selection). C*. ant = C. antarctica; J. sch = J. scheuchzerioides; R. bit = R. biternatus; R. mos = R. moseleyi; R. pseudo = R. pseudotrullifolius*. Max. root length = maximum root length. 'n' number of points to calculate relationship.

Figure captions

Figure 1. a) Locations (red points) of the three sampled sites and their associated ponds on the French sub-Antarctic Iles Kerguelen (48°30–50°S,68°27–70°35E). b) Sampling design within each pond: abiotic variables, neighbours' traits to assess neighbourhood functional characteristics, species co-occurrences to calculate local spatial arrangements between neighbours, targets biomass to calculate LRR and finally the neighbouring species abundance (%).

Figure 2. a) Structural equation model representing the direct and indirect effects of abiotic and biotic variables characterizing ponds, on macrophyte community biomass. The initial model is presented in the Supplementary Information and was reduced with lavaan package through variable selection based on AIC criteria. All variables were calculated at pond level. CWM biomass was calculated based on the mean of biomass per species and their cover at pond level. Water and sediment nutrient dimensions were each reduced to the first axis of a PCA analysis. Single dark headed arrows indicate direct effects. Double headed blue arrows indicate correlation between two model variables. Standardized path coefficients are given in blue for correlations and in black for direct effects with their *p*-values: ***$p < 0.001$; **$p < 0.01$; '.' $0.05 < p < 0.1$; no asterisk $p \geq 0.1$ not significant. The widths of the lines are proportional to the strength of relationships (values of path coefficients). Solid and dashed lines respectively indicated positive or negative direct effects. Grey paths and grey variables indicated paths and variables that did not have significant direct or indirect effects on CWM biomass. R^2 values were the variance proportion of response variables explained by their explanatory variables. Local spatial arrangements between neighbours were calculated at pond scale, taking into account the total number of co-occurrences between all pairs of species. FDis was calculated at pond scale (taking into account all present species per pond), including aerial, clonal and root traits. b) Absolute direct and indirect effects of abiotic and biotic variables on macrophyte community biomass.