

1 **Turbulence-mediated facilitation of resource uptake in patchy stream macrophytes**

2 Authors:

3 Loreta Cornacchia^{1,5, a} loreta.cornacchia@nioz.nl, loreta.cornacchia@univ-lyon1.fr
4 Sofia Licci² sofia.licci@univ-lyon1.fr
5 Heidi Nepf³ hmnepf@mit.edu
6 Andrew Folkard⁴ a.folkard@lancaster.ac.uk
7 Daphne van der Wal^{1,6} daphne.van.der.wal@nioz.nl
8 Johan van de Koppel^{1,5} johan.van.de.koppel@nioz.nl
9 Sara Puijalon² sara.puijalon@univ-lyon1.fr
10 Tjeerd J. Bouma^{1,5} tjeerd.bouma@nioz.nl
11

12 Affiliations:

13 ¹ NIOZ Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems, and
14 Utrecht University, P.O. Box 140, 4400 AC Yerseke, the Netherlands.

15 ² Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622,
16 Villeurbanne, France

17 ³ Dept. of Civil and Environmental Engineering, Massachusetts Institute of Technology, 77
18 Massachusetts Ave., Bldg. 48-216D, Cambridge, MA 02139, USA.

19 ⁴ Lancaster Environment Centre, Lancaster University, Lancaster, UK

20 ⁵ Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700
21 CC Groningen, The Netherlands

22 ⁶ Faculty of Geo-Information Science and Earth Observation (ITC), University of Twente, P.O. Box
23 217, 7500 AE, Enschede, The Netherlands

24
25 ^a Present address: UMR 5023 LEHNA, Université Lyon 1, CNRS, ENTPE, Villeurbanne Cedex,
26 France

27 Corresponding author:

28 Loreta Cornacchia
29 Université Lyon 1
30 CNRS, UMR 5023 - LEHNA
31 Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés
32 6, rue Raphaël Dubois - Bât. Forel
33 F-69622 Villeurbanne Cedex FRANCE
34 e.mail: loreta.cornacchia@univ-lyon1.fr
35 Tel.: +33 (0)4 72 43 12 93
36 Fax: +33 (0)4 72 43 11 41
37
38

39 Running head: Turbulence-driven facilitation in macrophytes

40 Keywords: *submerged macrophytes; nutrient uptake; mass transfer*

41 **Abstract**

42 Many landscapes are characterized by a patchy, rather than homogeneous, distribution of vegetation.
43 Often this patchiness is composed of single-species patches with contrasting traits, interacting with
44 each other. To date, it is unknown whether patches of different species affect each other's uptake of
45 resources by altering hydrodynamic conditions, and how this depends on their spatial patch
46 configuration. Patches of two contrasting aquatic macrophyte species (i.e., dense canopy-forming
47 *Callitriche* and sparse canopy-forming *Groenlandia*) were grown together in a racetrack flume and
48 placed in different patch configurations. We measured $^{15}\text{NH}_4^+$ uptake rates and hydrodynamic
49 properties along the centerline and the lateral edge of both patches. When the species with a taller,
50 denser canopy (*Callitriche*) was located upstream of the shorter, sparser species (*Groenlandia*), it
51 generated turbulence in its wake that enhanced nutrient uptake for the sparser *Groenlandia*. At the
52 same time, *Callitriche* benefited from being located at a leading edge where it was exposed to higher
53 mean velocity, as its canopy was too dense for turbulence to penetrate from upstream. Consistent with
54 this, we found that ammonium uptake rates depended on turbulence level for the sparse *Groenlandia*
55 and on mean flow velocity for the dense *Callitriche*, but Total Kinetic Energy was the best descriptor
56 of uptake rates for both species. By influencing turbulence, macrophyte species interact with each other
57 through facilitation of resource uptake. Hence, heterogeneity due to multi-specific spatial patchiness
58 has crucial implications for both species interactions and aquatic ecosystem functions, such as nitrogen
59 retention.

60 **Introduction**

61 In many ecosystems, vegetation shapes entire landscapes by interacting with physical processes
62 (Dietrich and Perron 2006; Corenblit et al. 2011). In coastal and fluvial aquatic ecosystems, vegetation
63 modifies habitats through its effects on hydrodynamics and sedimentation (Leonard and Luther 1995;
64 Madsen et al. 2001; Schulz et al. 2003; Bouma et al. 2007), hence acting as an ecosystem engineer
65 (Jones et al. 1994). Many studies first considered interactions between hydrodynamics and
66 homogeneous vegetation (Kouwen and Unny 1973; Nepf 1999; Nepf and Vivoni 2000; Järvelä 2005;
67 Chen et al. 2013), and later focused on isolated or pairs of patches (Sand-Jensen and Vindbæk Madsen
68 1992; Folkard 2005; Bouma et al. 2009; Vandenbruwaene et al. 2011; Chen et al. 2012; Zong and Nepf
69 2012). Generally, vegetation patches locally reduce flow velocities, while increasing them in some
70 adjacent areas (Bouma et al. 2007; Chen et al. 2012; Schoelynck et al. 2012; Meire et al. 2014).

71 In aquatic ecosystems, the interaction between vegetation and hydrodynamics regulates important
72 ecological processes such as nutrient delivery and uptake by plants, as nutrients can be taken up from
73 the water column through plant shoots (Madsen and Cedergreen 2002; Bal et al. 2013). These
74 processes are crucial for community primary productivity and ecosystem function (Thomas et al. 2000;
75 Morris et al. 2008; Levi et al. 2015). Previous studies on uptake rates in relation to hydrodynamic
76 conditions mainly focused on seagrasses, using flume experiments with dissolved ¹⁵N-labeled
77 ammonium or nitrate (often the main inorganic nitrogen sources in natural conditions; Haynes and Goh
78 (1978)). These works identified the important effects of water velocity and flow alteration by seagrass
79 canopies on resource uptake (Thomas et al. 2000; Cornelisen and Thomas 2006), and the dependence
80 of uptake rates on the rate of mass transfer to the leaf surface under unidirectional flow (Cornelisen and
81 Thomas 2004). Further, Morris et al. (2008) identified spatial patterns in ammonium uptake within
82 seagrass patches, with higher uptake observed at the leading edge of the patch where the turbulent
83 kinetic energy and velocity within the patch were highest. In a study of nutrient uptake by river

84 macrophytes, Bal et al. (2013) found that ammonium uptake increased with flow velocity. Because the
85 diffusive boundary layer decreases with increasing velocity, the uptake rate also increases with
86 increasing velocity (Thomas et al. 2000; Cornelisen and Thomas 2004; Morris et al. 2008; Bal et al.
87 2013).

88 However, most of the previous studies dealt with monospecific canopies or focused on a single
89 species at a time, creating a monospecific community, while in reality natural landscapes are a diverse
90 community made up of multiple species. Different patches of single species are heterogeneously
91 distributed, and this patchiness is a common characteristic of aquatic habitats (Sand-Jensen and
92 Vindbæk Madsen 1992). A few examples are patchy seagrass meadows (Fonseca et al. 1983), and
93 streams characterized by a ‘pseudo-braided’ distribution of plant stands between areas of faster flow
94 (Dawson and Robinson 1984; Cotton et al. 2006; Wharton et al. 2006). This additional level of
95 complexity has just started to be integrated in studies of hydrodynamic-vegetation interactions. For
96 instance, Weitzman et al. (2015) focused on hydrodynamic implications of multi-specific canopies, but
97 considered canopy heterogeneity in the vertical dimension. Adhitya et al. (2014) focused on
98 hydrodynamics and spatial configurations of seagrass patches with different densities, but did not test
99 the consequences for resource uptake. Bal et al. (2013) focused on nutrient uptake rates within
100 monospecific patches of two species next to each other, but they only tested a single spatial
101 configuration and therefore did not investigate the effects of spatial patchiness. To date, it is still
102 unknown how patches of different species interact with each other by altering hydrodynamics and
103 uptake of resources, and how this depends on their landscape configuration.

104 Multispecies effects could be important for hydrodynamics and nutrient uptake because the
105 density, flexibility and canopy structure of different species affect hydrodynamics differently (Peralta
106 et al. 2008; Bouma et al. 2013). As we cannot easily predict the flow alteration by heterogeneous
107 species distributions, our understanding of the implications for species interactions and nutrient load

108 reduction in aquatic ecosystems is limited. Generally, the hydrodynamic controls on uptake rate are
109 expected to be dependent on the macro-scale rate of delivery (mean flow velocity; e.g. Cornelisen and
110 Thomas (2006)), or on the micro-scale processes that determine the concentration gradient at the leaf
111 boundary layer (turbulence; e.g. Morris et al. (2008)). However, in a diverse community there might be
112 cases where a single hydrodynamic parameter is not sufficient to describe uptake rates for multiple
113 species with different traits and effects on hydrodynamic conditions. For instance, turbulence can have
114 a significantly smaller scale in very dense canopies, compared to sparser ones (Nepf 2012). On the
115 other hand, the mean flow speed can be relatively constant within sparse canopies, but turbulence
116 might be locally variable. Therefore, understanding the interaction between multiple species in terms of
117 nutrient uptake, mediated by their hydrodynamic effects, is essential to gain a more realistic
118 understanding of species interactions and productivity in heterogeneous, multi-specific communities.

119 In this study, we use streams colonized by aquatic macrophytes as a model system. We
120 investigate how patches of two different species with contrasting morphological traits interact with
121 each other by influencing hydrodynamics, and thereby ammonium uptake. Moreover, we test how this
122 depends on their spatial configuration (patchiness). Here, we define multi-specific patchiness as a
123 community composed of patches of different species. Specifically, we study the interaction between
124 two macrophyte species that co-occur under field conditions and have contrasting density and canopy
125 structure. *Callitriche platycarpa* Kütz., 1842 forms very dense patches that exhibit increasing canopy
126 height with increasing patch length ('dense' species). *Groenlandia densa* (L.) Fourr. has a more open
127 canopy, and its canopy height is constant along the patch length ('sparse' species). In the field, the
128 dense patches of *Callitriche* are distributed quite regularly at a distance of about 8 meters, and
129 *Groenlandia* patches tend to aggregate around them (Cornacchia et al. 2018). Given the differences in
130 shoot density and canopy architecture between the two species (Table 1), we hypothesize that the
131 effects of the dense *Callitriche* patches on hydrodynamics may facilitate the delivery and uptake of

132 resources by the sparse *Groenlandia* patches. To test this hypothesis, patches of the two species were
133 arranged in different configurations in a laboratory flume. To investigate the role of spatial
134 configuration and reciprocal species effects on nutrient uptake, both the species upstream and the
135 relative location of the species downstream were varied. We discuss the implications of multi-specific
136 spatial patchiness on facilitation and aquatic ecosystem functions, such as nitrogen retention.

137 **Materials and methods**

138 **Plant material**

139 We tested the effect of macrophyte patch species and configuration on ammonium uptake rates using
140 two submerged macrophytes species, *Callitriche platycarpa* and *Groenlandia densa*. Both species were
141 collected in February 2015 from a wetland on the Ain River, France (5.2825° E, 45.9855 N). Plants
142 were stored in plastic bags and transported to the laboratory in NIOZ Yerseke (The Netherlands) within
143 24 hours from collection. Until installation in the flume, the two macrophyte species were stored in a
144 green house, in tanks filled with freshwater that was continuously aerated, and exposed to natural light.
145 The macrophytes were allowed to recover for two days in the green house before starting the
146 experiments. In order to be used for the experimental setup, individual plants were transplanted in
147 stainless steel trays (30 × 29.5 × 5 cm). The trays were filled with a bottom layer of river sand (4.5 cm)
148 and a top layer (0.5 cm) of fine gravel (0.2 cm grain size). A false bottom in the flume allowed the trays
149 to be inserted with the soil surface at the same level as the flume bed. Based on the naturally occurring
150 densities of the two species in the field, we constructed patches of 97 ± 28 g DW m⁻² (mean ± SD) for
151 *Groenlandia* ('sparse' species) and 318 ± 67 g DW m⁻² for *Callitriche* ('dense' species) (Figure 1;
152 Table 1). The biomass of the constructed patches was estimated by collecting all plant material within
153 randomly selected 0.1 × 0.1 m quadrants ($n = 3$). The mean patch biomass for *Callitriche* is close to the

154 range of 208 – 256 g DW m⁻² reported in Sand-Jensen and Vindbæk Madsen (1992). The mean patch
155 biomass for *Groenlandia* corresponded to ca. 500 shoots m⁻², which represents a relatively low shoot
156 density in natural plant beds (Sheldon and Boylen 1977). We used a different patch length for each
157 species to resemble the typical lengths observed in the field, i.e. 2.7 m and 1.2 m on average for
158 *Groenlandia* and *Callitriche* respectively. These values are representative of average patch sizes
159 observed in field conditions (2.5 ± 1.7 m for *Groenlandia*, $n = 20$; 1.4 ± 0.8 m for *Callitriche*, $n = 20$;
160 Supporting Information Fig. S1). We used a total of 9 trays for *Groenlandia*, for a total patch coverage
161 of 2.7×0.3 m. For *Callitriche*, plants were rooted in two trays ($0.6 \times 0.3 \times 0.05$ m). When *Callitriche*
162 was placed upstream, three trays (filled with the same soil as the plant trays) were placed between the
163 two patches, to account for the presence of the typical overhanging canopy for this species. That is,
164 when the flume was running, a total coverage of 1.20×0.3 m² was observed due to shoots bending;
165 this region was considered as part of the *Callitriche* patch (see Figure 2). A distance of one tray (0.3 m)
166 between the two patches was used for the configurations in which *Groenlandia* was in the upstream
167 position. The flume section next to each patch was left open (without plants, but filled with the same
168 soil substrate used in the plant trays) in all configurations. Thus, the patches occupied one half of the
169 flume, rather than extending across the width of the flume. As patches in the field do not span the
170 whole channel, this configuration is representative of the typical distribution of vegetation patches in
171 streams, with an empty (unvegetated) zone next to the patch into which water flow is deflected and
172 accelerated around the patch (Fonseca et al. 1983; Gambi et al. 1990; Bouma et al. 2007; Follett and
173 Nepf 2012). The canopies of both species were fully submerged during the experiments. The relative
174 depth of submergence (H/h , ratio of water depth to maximum canopy height; Nepf (2012)) was
175 relatively constant along the *Groenlandia* patch due to its uniform height. Values of H/h ranged
176 between 8.75 and 4.3, corresponding to shallow submerged ($H/h < 5$). Instead, canopy height along the
177 *Callitriche* patch varied from $H/h = 17.5$ at the leading edge (i.e. deeply submerged, $H/h > 10$) to 3.0 in

178 the middle of the patch (indicating shallow submergence ($H/h < 5$), and even 1.30 at the downstream
179 end of the patch, which is very close to emergent conditions ($H/h = 1$).

180 **Flume setup and experimental configurations**

181 All experiments were performed within a unidirectional racetrack flume using a water depth of 0.35 m
182 and with a cross-sectionally-averaged velocity of $0.24 \pm 0.03 \text{ m s}^{-1}$. This is a moderate flow velocity,
183 representative of the summer flow conditions in streams typically colonized by *Callitriche* and
184 *Groenlandia* ($0.21 \pm 0.01 \text{ m s}^{-1}$, based on our field measurements in 2014 and 2015; Cornacchia et al.
185 (2018)). For a more detailed description of the flume, see Bouma et al. (2005). To test for the effects of
186 patch spatial configuration on ammonium uptake rates, the two patches were arranged one downstream
187 of the other, either on the same side of the flume ('aligned' configurations), or on opposite sides
188 ('staggered' configurations) (Figure 2). These different spatial configurations are both commonly
189 observed in natural streams, where patches grow downstream of other patches, or in a staggered
190 arrangement (L. Cornacchia, pers. obs.). Moreover, patches of different species in the field can be
191 found co-occurring at very short distances from each other, at the scale of 0.5 m (Cornacchia et al.
192 2018). To test for interactions between the two species, in terms of reciprocal effects on ammonium
193 uptake rates, we also switched the species located upstream for each of these configurations ('Sparse-
194 Dense' or 'Dense-Sparse' configurations).

195 **Measuring spatial patterns in $^{15}\text{N-NH}_4^+$ uptake rates and canopy hydrodynamics**

196 To determine spatial patterns of ammonium uptake rates by the macrophyte species, we measured
197 uptake rates at selected locations within the patches (Figure 2). Nutrient uptake rates were determined
198 inside the two patches at 10%, 50% and 90% of the patch length (0.27, 1.45 and 2.43 m from the
199 leading edge in *Groenlandia*; 0.12, 0.6 and 1 m from the leading edge in *Callitriche*) and, for each
200 location along the patch length, at 0.15 and 0.25 m of the patch width. For each incubation experiment,

201 macrophyte individuals were randomly selected from the tanks where they were kept with freshwater
202 and were transplanted into plastic pots (5 shoots per pot). Before transplantation in the flume, roots
203 were removed from the plants at the selected test locations, to prevent ammonium uptake by that means
204 from the labeled water that inevitably penetrated into the sand (following Bal et al. (2013)). Since the
205 sediment was not changed in between treatments (as that would have meant destroying and recreating
206 the patches), this avoided an effect of treatment order on uptake rates. While some nutrients are
207 obtained through roots in field conditions, the nutrient demands of many macrophyte species can be
208 satisfied by shoot nutrient uptake alone (Madsen and Cedergreen 2002). Although root removal may
209 have potentially affected the plant response to the flow, it was unlikely to affect their ability to resist
210 the flow during a short-term experiment (6 hours). Each plastic pot was then placed in one of the patch
211 locations described above, and inserted in the trays so that their upper part was in line with the
212 sediment level to avoid scouring effects. The pots were replaced after each incubation experiment and
213 new plants were transplanted. The renewal of plants between each run allowed us to avoid an effect of
214 treatment order on uptake rates, due to plants being exposed to the labeled water for a longer time.
215 Moreover, it provided natural variability in plant structure, while maintaining a constant patch structure
216 by keeping the trays forming the plant patches in the same positions between runs. The treatments were
217 run in the order shown in Figure 1.

218 In the incubation experiments, $^{15}\text{N-NH}_4^+$ was added to the water creating a 20 to 30 $\mu\text{mol-NH}_4^+\text{L}^{-1}$
219 solution, with 30% of the N as ^{15}N abundance, following Bal et al. (2013). This range of
220 values is representative of nutrient concentrations found in natural ecosystems: in summer 2015,
221 average ammonium levels recorded in the studied region were $24.5 \pm 28.54 \mu\text{mol-NH}_4^+\text{L}^{-1}$, with a
222 maximum value of $79.6 \mu\text{mol-NH}_4^+\text{L}^{-1}$. Such a high enrichment (30%) was chosen to minimize
223 dilution effects of the ^{15}N source pool over the course of the experiment. At the start and end of the
224 experiment, three replicate water samples were taken to measure NH_4^+ concentration in the water. The

225 same labeled water was used to perform four experiments, before replacing it with freshwater and a
 226 new label for the next runs (based on Bal et al. (2013)). Incubations were performed under artificial
 227 light conditions. Lamps were mounted above the flume tank throughout the test section to provide 14 h
 228 d⁻¹ of light (photosynthetic photon flux density of 550 μmol m⁻² s⁻¹; measured 35 cm above the
 229 sediment surface). The stable isotope was added near the paddles that drive the flow in the flume to
 230 ensure mixing. Each incubation experiment lasted for 6 hours, and two replicate runs were performed
 231 for each configuration. At the end of the 6 hours, macrophytes were collected from the test positions,
 232 rinsed with tap water to remove excess isotope from the plant surface, and folded into aluminum foil.
 233 In addition to the samples collected (*n* = 30 for each species), five specimens per species were
 234 randomly selected during the experiments from our species stock, to determine the background ¹⁵N
 235 signal. The plants were dried in the oven for 48 hours at 60° C, and individual biomass was weighed.
 236 Dried macrophytes were ground to a fine powder using a ball mill (MM 2000, Retsch, Haan,
 237 Germany). A subsample of about 3 mg of powder per plant was sent to the laboratory for mass
 238 spectrometry analysis of the isotope ratio. The samples were analysed for total N content and ¹⁵N-
 239 atomic percentage (as (¹⁵N/total N) × 100) with an Elemental Analyser (Thermo Electron FlashEA
 240 1112) and subsequent isotope ratio mass spectrometry (Thermo Delta V - IRMS). For recent guidelines
 241 on stable isotope notations, see Coplen (2011).

242 The ¹⁵N atomic fraction of the dissolved N source pool in the water column (*x*(¹⁵N)_{aq,N}) was
 243 calculated according to Morris et al. (2013):

$$x(^{15}\text{N})_{aq,N} = \frac{([\text{NH}_4^+]_{tracer}x(^{15}\text{N})_{tracer}) + ([\text{NH}_4^+]_{water}x(^{15}\text{N})_{initial})}{[\text{NH}_4^+]_{tracer} + [\text{NH}_4^+]_{water}} \quad (1)$$

244 where *x*(¹⁵N)_{tracer} is the atomic fraction of the added tracer (0.98), [NH₄⁺]_{water} is 20.7 ± 3.1 μmol-
 245 NH₄⁺L⁻¹ (mean ± SE), and *x*(¹⁵N)_{initial} is the atomic fraction of the initial water column (assumed to

246 reflect ^{15}N of atmospheric N, 3.7×10^{-3}). To provide an estimate of the change in $^{15}\text{NH}_4^+$ ($\mu\text{mol-}$
 247 $\text{NH}_4^+\text{L}^{-1}$) concentrations between runs (i.e., $[\text{NH}_4^+]_{\text{tracer}}$), mean $^{15}\text{NH}_4^+$ uptake rates ($\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$)
 248 for each species were multiplied by their total estimated biomass (g DM m^{-2}) and by the incubation
 249 time (6 hours). Given the large volume of the flume water, the estimated $^{15}\text{NH}_4^+$ tracer concentrations
 250 remained high, between 8.0 and 8.8 $\mu\text{mol-NH}_4^+\text{L}^{-1}$, corresponding to an increase in total water column
 251 $[\text{NH}_4^+]$ of between 27.5% and 29.7%.

252 To calculate the NH_4^+ uptake rate (V in $\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$) of each sample, we followed the
 253 equation in Morris et al. (2013):

$$V = [N]_{\text{DM_sample}} \cdot \frac{(x^{\text{E}(^{15}\text{N})_{\text{DM_sample}}})}{(x(^{15}\text{N})_{\text{aq.N}} \cdot \Delta t)} \quad (2)$$

254 where $x^{\text{E}(^{15}\text{N})_{\text{DM_sample}}}$ is the ^{15}N excess atom fraction, calculated as the difference between the atomic
 255 fraction measured in the biomass of the sample after incubation ($x(^{15}\text{N})_{\text{DM_sample}}$) and the background
 256 ^{15}N abundance $x(^{15}\text{N})_{\text{DM_nat.ab}}$ measured on five background specimens for each species ((3.70 ± 0.008)
 257 $\times 10^{-3}$ for *Callitriche*, $(3.69 \pm 0.018) \times 10^{-3}$ for *Groenlandia*); Δt (h) is the incubation time (6 h) and
 258 $[N]_{\text{DM_sample}}$ is the N content of the dry biomass ($\mu\text{mol g}^{-1}$ (dry mass (DM)) of each sample.

259 Hydrodynamic measurements

260 To test the relationship between hydrodynamic parameters and nutrient uptake, vertical profiles of
 261 velocity were measured with a 3D acoustic Doppler velocimeter (ADV, Nortek) over 30 s at 10 Hz.
 262 Within each profile, velocity was measured at seven vertical locations at 2, 5, 10, 12, 15, 17 and 27 cm
 263 above the channel bed. The profiles were measured in the same streamwise and lateral locations as the
 264 plant samples collected for nutrient uptake estimation, i.e. at 10%, 50% and 90% of the length of each
 265 patch in the streamwise (x) direction, and at 0.15 and 0.25 m of the patch width in the spanwise (y)

266 direction (Figure 2). To minimize interference by vegetation structures within the sampling volume of
 267 the ADV probe, the probe started at the lowest measuring point for each vertical profile within the
 268 vegetation. This prevented the canopy from being compressed as the probe moved towards the bed. To
 269 ensure that measurements were based on reliable data points, spikes and low-quality data points (i.e.,
 270 correlation below the standard quality threshold of 70%) were removed during post-processing. The
 271 height of the vegetation canopy in each location was measured with a ruler in cm. The canopy height
 272 (h) was 0.17 ± 0.08 m for *Callitriche*, and 0.07 ± 0.01 m for *Groenlandia* (Table 1). Freshwater
 273 macrophytes are flexible, mesh-like structures (Sand-Jensen 2005), often with highly branched stems
 274 that get entangled in each other. Their flexibility and complex morphology make it very challenging to
 275 measure individual plant parameters like shoot height, frontal area, shoot density or average distance
 276 between shoots. Thus, the frontal area per water volume (a , m^{-1}) and frontal area per bed area (ah ,
 277 dimensionless) for the two species were calculated from water depth (H) and canopy length (l), width
 278 (y) and height (h) measurements (Table 1) through the following equations:

$$a = \frac{h y}{H y l} = \frac{h}{H l} \quad (3)$$

$$ah = \frac{h y}{y l} = \frac{h}{l} \quad (4)$$

279 As the frontal area of flexible submerged macrophytes is highly variable (i.e. their shape and canopy
 280 height change with flow velocity; Sand-Jensen (2005)), the values are indicative for the incoming flow
 281 velocity of 0.24 m s^{-1} used in the experiments.

282 The instantaneous velocity ($u(t), v(t), w(t)$) measured in the streamwise, lateral, and vertical
 283 directions, respectively, were separated into time-averages ($\bar{U}, \bar{V}, \bar{W}$), and instantaneous turbulent
 284 fluctuations ($u'(t), v'(t), w'(t)$), e.g. as $u'(t) = u(t) - \bar{U}$, and similarly for v and w . The vertical
 285 average of the time-averaged velocity in the streamwise direction was used to calculate the depth-

286 averaged velocity ($\langle \bar{U} \rangle$, m s⁻¹) at each profile position. The Total Kinetic Energy (Total KE) per unit
 287 mass is defined from the instantaneous velocities (u, v, w), defined as:

$$Total\ KE = \frac{1}{2} (\overline{u^2} + \overline{v^2} + \overline{w^2}) = Turbulent\ KE + Mean\ KE \quad (5)$$

288 which can be partitioned into turbulent kinetic energy (Turbulent KE) and mean kinetic energy (Mean
 289 KE), defined as (e.g. Kundu et al. (2004)):

$$Turbulent\ KE = \frac{1}{2} (\overline{u'^2} + \overline{v'^2} + \overline{w'^2}) \quad (6)$$

$$Mean\ KE = \frac{1}{2} (\overline{U^2} + \overline{V^2} + \overline{W^2}) \quad (7)$$

290 The Total Kinetic Energy (m² s⁻²) provides a better metric for the instantaneous velocity,
 291 because it reflects both the time-mean and turbulent fluctuations, and as such it is more relevant to
 292 boundary layer dynamics, especially in cases with low time-mean velocity but high Turbulent KE.
 293 Specifically, previous studies have suggested that strong instantaneous velocity and/or plant motion can
 294 periodically strip away the diffusive sub-layer, which, if frequent enough, will enhance flux to the plant
 295 surface (Koch 1994; Stevens and Hurd 1997; Huang et al. 2011).

296 Reynolds shear stress (τ_{xz} , Pa) at the top of the canopy at each location was calculated as:

$$\tau_{xz} = -\rho \overline{u'(t)w'(t)} \quad (8)$$

297 in which $\rho = 1000$ kg m⁻³ is the density of the flume water.

298 Volumetric flow rate of water through the patches (Q_c , m³ s⁻¹) was calculated as:

$$Q_c = \sum_0^h Q_i \quad \text{and} \quad Q_i = y(h_i - h_{i-1})\bar{u}_{h_i} \quad (9)$$

299 in which h is the canopy height, Q_i the volumetric flow rate of water through the layer ($h_i - h_{i-1}$), y is
300 the patch width (0.3 m) and \bar{u}_{h_i} the double-averaged u component (i.e., averaged in time and spatially
301 averaged in the two lateral positions) of the velocity at depth h_i .

302 **Measuring channel-scale patterns of ammonium uptake**

303 To investigate how the relationship between hydrodynamic parameters and ammonium uptake
304 develops at the scale of a whole channel, we tested the correlation between the total in-patch NH_4^+
305 uptake rates and in-patch average hydrodynamic parameters (mean velocity, Turbulent KE and Total
306 KE). This allowed us to test whether spatial patch configurations that generated higher mean flow
307 velocity, Total KE or Turbulent KE levels within the canopies promoted higher uptake at the channel
308 scale. The total in-patch NH_4^+ uptake rate for each configuration was calculated as the sum of the
309 uptake rates estimated in all sampling points ($n = 6$ per species; Figure 2). This total uptake was used as
310 an estimate of channel-scale uptake, but is not necessarily a measure of total ammonium uptake rates
311 per biomass or aerial cover.

312 **Statistical analyses**

313 The flume incubation experiments yielded $n = 30$ samples per experimental run (i.e. from 3 x -positions
314 \times 2 y -positions \times 5 shoots per position) for each species, and two replicate runs were performed for
315 each configuration. As we were interested in differences in uptake rates among positions within
316 patches, the average uptake rates of the 5 shoots per each position were used in subsequent analyses.
317 Friedman's rank-sum test was used to test for the presence of trends in NH_4^+ uptake rates from the
318 upstream to downstream positions along the patches in all replicate runs. The tests were run separately
319 for each species, both for the centerline and for the edge measurement points. To account for the fact
320 that within-patch measurements were not independent from each other, statistical differences in NH_4^+
321 uptake rates for each species under four flume spatial configurations were tested using nested ANOVA

322 (with replicate run as a nested factor within the configuration treatment). As Friedman's rank-sum tests
323 showed no significant trend in ammonium uptake neither along the centerline nor along the edge
324 positions within patches, measurement position was considered a random effect in the model. The data
325 were log-transformed to meet the ANOVA test assumptions of normality and homogeneity of variance.
326 Pearson's correlation coefficient was used to test for significant correlation between NH_4^+ uptake rates
327 ($\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$) and hydrodynamic parameters (depth-averaged velocity $\langle \bar{U} \rangle$ (m s^{-1}); Reynolds
328 shear stress τ_{xz} (Pa); Turbulent KE ($\text{m}^2 \text{s}^{-2}$); Total KE ($\text{m}^2 \text{s}^{-2}$); and volumetric flow rate, Q_c ($\text{m}^3 \text{s}^{-1}$),
329 and between channel total NH_4^+ uptake rates and average hydrodynamic parameters within both
330 species patches (mean velocity, Turbulent KE and Total KE). P values of less than or equal to 0.05
331 were considered to be significant. All statistical analyses were performed in R 3.1.2 (R Core Team
332 2015).

333 **Results**

334 *Relationship between canopy hydrodynamic parameters and nutrient uptake*

335 We found that the two macrophyte species affected each other's ammonium uptake rates by altering
336 mean flow velocity ($\langle \bar{U} \rangle$) and turbulence (Turbulent KE). Ammonium uptake rates depended on either
337 mean flow velocity (*Callitriche*) or turbulence (*Groenlandia*), but Total Kinetic Energy (Total KE) was
338 the single best descriptor of uptake rates for both species (Figure 3; Table 2). Specifically, NH_4^+ uptake
339 rates for the sparse *Groenlandia* were significantly correlated with Turbulent KE ($r = 0.68, p < 0.001$),
340 but not with mean flow velocity ($r = -0.20, p = 0.35$) (Figure 3; Table 2). The opposite was true for the
341 dense *Callitriche*: uptake rates were significantly correlated with mean flow velocity ($r = 0.42, p =$
342 0.04), but not with Turbulent KE ($r = 0.34, p = 0.1$) (Figure 3; Table 2). However, Total KE, which is
343 more representative of the instantaneous velocity, described uptake for both species ($r = 0.79, p < 0.001$

344 for *Groenlandia*; $r = 0.45$, $p = 0.03$ for *Callitriche*; $r = 0.54$, $p < 0.001$ for both species together)
345 (Figure 3A; Table 2). No significant relationship was found between ammonium uptake rates and either
346 Reynolds shear stress or Q_c (Table 2).

347 Effects of patch spatial configurations on nutrient uptake

348 When located upstream, the dense *Callitriche* patch increased turbulence and thereby enhanced the
349 uptake of resources by the sparse *Groenlandia* patch located downstream. The ammonium uptake rates
350 were influenced by both macrophyte species and spatial patch configuration (order and alignment).
351 Importantly, the Dense-Sparse (D-S) configurations led to higher uptake rates for both species. The
352 NH_4^+ uptake rates for the sparse *Groenlandia* were $2.63 \pm 1.33 \mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$, almost double than
353 for the dense *Callitriche* ($1.44 \pm 0.78 \mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$). Testing for the presence of patterns in NH_4^+
354 uptake rates from upstream to downstream within the patches showed no significant trend in uptake
355 rates along the patch centerline (*Friedman* $\chi_2^2 = 3$, $p = 0.22$ for *Callitriche*; *Friedman* $\chi_2^2 = 1$, $p = 0.60$
356 for *Groenlandia*), nor along the patch edge (*Friedman* $\chi_2^2 = 0.25$, $p = 0.88$ for *Callitriche*; *Friedman* χ_2^2
357 $= 3$, $p = 0.22$ for *Groenlandia*). This indicates there was no significant pattern in stable isotope
358 concentration from upstream to downstream within patches.

359 The upstream-downstream order and spatial patch alignment of the species significantly
360 affected uptake rates for both the sparse *Groenlandia* (nested ANOVA, $F_{3,4} = 6.87$, $p = 0.04$) and the
361 dense *Callitriche* (nested ANOVA, $F_{3,4} = 12.57$, $p = 0.017$; Figure 4). We generally found that when
362 the denser species (*Callitriche*) was located upstream of the sparser one (*Groenlandia*), ammonium
363 uptake rates for both species increased significantly, compared to patch configurations in the Sparse-
364 Dense order (Figure 4). This significant increase in uptake rates was related to the hydrodynamic
365 effects of different configurations, and particularly the traits of *Callitriche* (i.e. density and canopy
366 height, which blocks a larger fraction of flow depth). When the dense patch of *Callitriche* was

367 upstream, it generated higher Turbulent KE that influenced the downstream patch of *Groenlandia*
368 (Figure 2), enhancing its uptake rates (Figure 3). Also, when the dense *Callitriche* was upstream, its
369 leading edge was exposed to higher mean velocity compared to when it was trailing behind the sparse
370 patch (Figure 2), thereby increasing its uptake rates (Figure 3). Specifically, for the dense *Callitriche*,
371 uptake rates within the Sparse-Dense order were higher in the staggered than in the aligned
372 configuration (Tukey's HSD, $z = -2.66$, $p < 0.05$). In the Dense-Sparse configurations, no significant
373 difference in uptake rates was found between the staggered or aligned arrangement (Tukey's HSD, $z =$
374 -0.50 , $p > 0.05$). However, uptake rates were significantly higher in the Dense-Sparse staggered
375 configuration than in both the S-D configurations (Tukey's HSD, $z = -2.83$, $p < 0.05$). For the sparse
376 *Groenlandia*, uptake rates within the Sparse-Dense aligned and staggered configuration were not
377 significantly different from each other (Tukey's HSD, $z = -1.92$, $p < 0.05$). In the Dense-Sparse
378 configurations, no significant difference in uptake rates was found between the staggered or aligned
379 arrangement (Tukey's HSD, $z = 0.51$, $p > 0.05$). Uptake rates in the D-S aligned configuration were
380 significantly higher than in the S-D aligned configuration (Tukey's HSD, $z = -2.69$, $p < 0.05$), but were
381 not significantly different from the S-D staggered case (Tukey's HSD, $z = -0.77$, $p > 0.05$).

382 We found that the vegetation distributions that generated higher Total Kinetic Energy levels
383 within the patches promoted higher total uptake at the channel scale (Figure 5). Testing for the
384 hydrodynamic parameter-uptake relationships at the channel scale revealed a significant positive
385 relationship between the in-patch Total Kinetic Energy (average of both patches in each configuration)
386 and the channel total ammonium uptake ($r = 0.98$, $p = 0.01$; Figure 5). Channel total ammonium uptake
387 was also significantly related to in-patch Turbulent KE ($r = 0.97$, $p = 0.03$), but not to mean flow
388 velocity ($r = 0.93$, $p = 0.07$).

389 **Discussion**

390 The interaction between vegetation and hydrodynamics regulates important ecological processes such
391 as nutrient delivery and uptake by aquatic plants, which are crucial for community primary productivity
392 (Thomas et al. 2000; Cornelisen and Thomas 2006; Morris et al. 2008). We found that, by generating
393 turbulence, dense macrophyte patches facilitate resource uptake by neighboring sparse patches. Flume
394 measurements showed that the dense *Callitriche* had a strong hydrodynamic effect, creating high-
395 turbulence regions in its wake that facilitated nutrient uptake by the sparse *Groenlandia*, which had a
396 weaker hydrodynamic effect. While the sparse vegetation benefited from the high turbulence generated
397 in the wake of a dense patch, the dense vegetation benefited from being located at a leading edge,
398 where it was exposed to higher mean velocity, compared to when it was located downstream of another
399 patch (Figure 2; Figure 6). We identified Total Kinetic Energy as the best descriptor of the nutrient
400 removal capacity of streams, especially in heterogeneous multi-species communities. Overall, spatial
401 configurations that lead to higher Total Kinetic Energy within the patches were the ones that led to
402 higher total ammonium uptake. Hence, our results highlight the importance of turbulence as an agent of
403 interaction between different species. Moreover, this study suggests that accounting for interactions
404 between heterogeneous, multi-specific patchy vegetation is crucial to understand aquatic ecosystem
405 functions such as nitrogen retention.

406 *Implications of resource uptake in mono- and multi-species communities*

407 Previous studies of macrophytes generally found that nutrient uptake rates increased with mean flow
408 velocity (Cornelisen and Thomas 2006; Bal et al. 2013). Morris et al. (2008) found that Turbulent KE
409 was associated with spatial variation in uptake, and volumetric flow rate explained differences in
410 uptake between contrasting species. Yet, in our study, neither of these traditional hydrodynamic
411 parameters could accurately describe uptake rates for both species. However, direct comparison with
412 these previous studies is limited to some extent by differences in treatments. While previous

413 experiments tested the effect of changing bulk flow velocity on uptake rates, we tested a single bulk
414 flow velocity that represented the average flow conditions in the study sites where *Callitriche* and
415 *Groenlandia* coexist. We thus focused on within-patch flow variability, and how the interaction
416 between the two species was determined by their spatial arrangement and flow modification. Using a
417 single bulk flow condition resulted in a relatively narrow range of velocities experienced by the sparse
418 *Groenlandia* ($0.13 - 0.27 \text{ m s}^{-1}$), whereas the flow alteration ability of the dense *Callitriche* led to a
419 higher flow variability ($0.002 - 0.24 \text{ m s}^{-1}$). This factor may partly explain the lack of significant
420 correlation between flow velocity and uptake rates for *Groenlandia*. Further research is needed to test
421 how changes in mean flow conditions affect the interaction between the two species.

422 We identified Total Kinetic Energy as the parameter that explained most of the variability in
423 uptake rates for both species. To our knowledge, this parameter has not been related before to nutrient
424 uptake rates by aquatic vegetation. Previous studies have suggested that Turbulent KE may influence
425 nutrient uptake (Anderson and Charters 1982; Koch 1994), and the total energy parameter captures this
426 influence. Specifically, when Turbulent KE is weak, flux is controlled by the time-mean diffusive sub-
427 layer thickness, which is a function of the time-mean velocity (e.g. Hansen et al. (2011); Rominger and
428 Nepf (2014); Lei and Nepf (2016)). However, when the Turbulent KE is high, periodic disturbances of
429 the diffusive sub-layer by the turbulence can create instantaneously higher concentration gradients at
430 the surface and, thus, higher flux (e.g. Stevens and Hurd (1997); Huang et al. (2011); Rominger and
431 Nepf (2014)). By reflecting the magnitude of both the time-mean velocity and Turbulent KE, the total
432 kinetic energy captures both regimes of flux. The Total Kinetic Energy is particularly suitable in
433 heterogeneous systems where upstream Turbulent KE generation (e.g. by larger, denser patches) can
434 influence flux downstream, i.e. the Turbulent KE is not locally generated and thus uncorrelated with
435 the local time-mean velocity. In the dense *Callitriche* patches, the canopy is often too dense for
436 turbulence to form within the patch or to penetrate from the free stream. Under these low Turbulent KE

437 conditions, the flux is correlated by the local time-mean velocity, which sets the scale of the diffusive
438 sub-layer. For the sparse *Groenlandia*, time-mean flow velocity is relatively constant in the canopy and
439 we found no correlation between within-patch flow variations and uptake rates. However, the within-
440 patch Turbulent KE is elevated both by local stem generation and the penetration of turbulence
441 generated upstream. Under these high Turbulent KE conditions, the uptake rates have a high correlation
442 with the Turbulent KE intensity. In landscapes made up of patches of different species, regions with
443 flux controlled by $\langle \bar{U} \rangle$ and regions controlled by Turbulent KE are heterogeneously distributed, so that
444 neither $\langle \bar{U} \rangle$ nor Turbulent KE can capture the channel-scale nutrient uptake. Because it can describe
445 both regions of low Turbulent KE (uptake controlled by mean velocity) and high Turbulent KE (uptake
446 controlled by Turbulent KE intensity), we propose Total Kinetic Energy as a useful parameter to
447 describe nutrient uptake capacity in heterogeneous landscapes, which could be used to estimate
448 ecosystem services of nutrient retention by vegetation.

449 In contrast to the findings of Morris et al. (2008) and Bal et al. (2013), we did not find a
450 significant relationship between ammonium uptake rates and volumetric flow rate, likely because the
451 two species have different flexibility and density traits that affect patch compression (Table 1). The
452 canopies of the two species, and the relative importance of flow velocity and turbulence within them,
453 are consistent with the sparse and dense canopy regimes described in Nepf (2012). As expected for a
454 dense canopy condition ($ah > 0.1$), canopy-scale turbulence in *Callitriche* is generated at the top of the
455 canopy and can be transported downstream, while stem-scale turbulence is much smaller. Instead,
456 *Groenlandia* is representative of a sparse canopy condition ($ah < 0.1$), where stem-scale turbulence is
457 generated within the canopy, but the velocity profile remains logarithmic.

458 Our results reveal the important role of patch spatial configuration and the resulting
459 heterogeneity in influencing species interactions and the nutrient uptake capacity of the landscape. The
460 generation of turbulence by a *Callitriche* patch led to a 59% nutrient uptake enhancement effect on

461 *Groenlandia*, increasing it from an ammonium uptake rate of $2.03 \pm 0.85 \mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$ in the
462 Sparse-Dense configurations (where *Groenlandia* was not exposed to turbulence generation by
463 *Callitriche*), to $3.23 \pm 0.37 \mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$ in the Dense-Sparse configurations (where it was
464 exposed to turbulence generation by *Callitriche*). These findings are in line with a field study showing
465 that spatial heterogeneity, created by the interaction of canopy morphology, sediment topography and
466 hydrodynamics, controlled nutrient transport and uptake rates in a patchy seagrass landscape (Morris et
467 al. 2013). While we found clear effects of the upstream-downstream patch arrangement on ammonium
468 uptake rates, we only observed a significant effect of patch arrangement (staggered vs. aligned) in the
469 Sparse-Dense configurations. Vegetation patches in the flume experiment did not span the whole width
470 of the channel, leading to water flow deflection and acceleration around the lateral edges of patches.
471 This flow acceleration effect around the patches is in general agreement with experimental evidence in
472 field and laboratory studies (Vandenbruwaene et al. 2011; Schoelynck et al. 2012; Bouma et al. 2013),
473 suggesting that the conclusions of this work could be generally applied to field conditions. In addition
474 to the role of spatial configuration, it is likely that the distance between the patches governs the
475 intensity of the interaction between them. The stronger interactions between patches likely occur when
476 the distance between them is less than the wake length of the upstream patch (Folkard 2005). It might
477 be expected that the wake length is in turn related to patch density, because density determines at what
478 distances the patch effects will dissipate (Zong and Nepf 2012). Further studies should be undertaken to
479 investigate the detailed hydrodynamic consequences of different spatial patch configurations, testing
480 for the effects of a wider range of distances and its interactive effect with patch density.

481 *Turbulence-mediated species interactions: implications for species distributions and nutrient load*
482 *reduction*

483 The study of turbulence-mediated interactions between macrophyte species suggests a possible
484 mechanism behind the co-occurrence of *Groenlandia* patches around *Callitriche* in the field. Recently,
485 it has been shown that *Groenlandia* shoots grow better around *Callitriche* patches than on bare,
486 unvegetated sediment (Cornacchia et al. 2018). The wake of the *Callitriche* patches is both a high-
487 turbulence and low-velocity region (Sand-Jensen 1998). Thus, a combination of enhanced resource
488 uptake by turbulence, and reduced biomass losses by flow velocity, might be the conditions behind the
489 improved growth rates of *Groenlandia* plants around *Callitriche* patches. As the sparse *Groenlandia*
490 tends to surround the dense *Callitriche* patches in regularly spaced aggregations every 8 m (Cornacchia
491 et al. 2018), the interaction between the two species might enhance the overall nutrient removal
492 capacity of the river. The facilitative effect of *Callitriche* on *Groenlandia* could switch to competition,
493 as the high biomass *Callitriche* might have a competitive advantage by reducing resource availability
494 for the sparser species (*Groenlandia*). On the other hand, competition could be lessened through root
495 uptake from the nutrient pool in the sediment. The balance between facilitation and competition can be
496 clarified by considering additional variables such as root uptake and nutrient availability in the water
497 column and in sediment. Moreover, care must be taken when upscaling the relationship between
498 hydrodynamics and resource uptake at the channel scale. In our incubations, we focused only on uptake
499 rates of a single nutrient (ammonium), which is energetically less costly, but some species might invest
500 in nitrate uptake. This is an interesting aspect that should be explored in future studies of channel-scale
501 nitrogen uptake by vegetation. As a future perspective, we might be able to use the knowledge on these
502 types of species interactions as tools to enhance restoration success of degraded (eutrophic) sites.

503

504 **References**

505 Adhitya, A. and others 2014. Comparison of the influence of patch-scale and meadow-scale
506 characteristics on flow within seagrass meadows: a flume study. *Marine Ecology Progress*
507 *Series* **516**: 49-59.

508 Anderson, S. M., and A. Charters. 1982. A fluid dynamics study of seawater flow through *Gelidium*
509 *nudifrons*. *Limnology and Oceanography* **27**: 399-412.

510 Bal, K. D. and others 2013. Influence of hydraulics on the uptake of ammonium by two freshwater
511 plants. *Freshwater Biology* **58**: 2452-2463.

512 Bouma, T. and others 2005. Trade-offs related to ecosystem engineering: A case study on stiffness of
513 emerging macrophytes. *Ecology* **86**: 2187-2199.

514 Bouma, T., M. Friedrichs, B. Van Wesenbeeck, S. Temmerman, G. Graf, and P. Herman. 2009.
515 Density-dependent linkage of scale-dependent feedbacks: A flume study on the intertidal
516 macrophyte *Spartina anglica*. *Oikos* **118**: 260-268.

517 Bouma, T. and others 2013. Organism traits determine the strength of scale-dependent bio-geomorphic
518 feedbacks: A flume study on three intertidal plant species. *Geomorphology* **180**: 57-65.

519 Bouma, T. and others 2007. Spatial flow and sedimentation patterns within patches of epibenthic
520 structures: Combining field, flume and modelling experiments. *Continental Shelf Research* **27**:
521 1020-1045.

522 Chen, Z., C. Jiang, and H. Nepf. 2013. Flow adjustment at the leading edge of a submerged aquatic
523 canopy. *Water Resources Research* **49**: 5537-5551.

524 Chen, Z., A. Ortiz, L. Zong, and H. Nepf. 2012. The wake structure behind a porous obstruction and its
525 implications for deposition near a finite patch of emergent vegetation. *Water Resources*
526 *Research* **48**.

527 Coplen, T. B. 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-
528 ratio measurement results. *Rapid communications in mass spectrometry* **25**: 2538-2560.

529 Corenblit, D. and others 2011. Feedbacks between geomorphology and biota controlling Earth surface
530 processes and landforms: a review of foundation concepts and current understandings. *Earth-*
531 *Science Reviews* **106**: 307-331.

532 Cornacchia, L., J. van de Koppel, D. van der Wal, G. Wharton, S. Puijalon, and T. J. Bouma. 2018.
533 Landscapes of facilitation: how self-organized patchiness of aquatic macrophytes promotes
534 diversity in streams. *Ecology*.

535 Cornelisen, C. D., and F. I. Thomas. 2004. Ammonium and nitrate uptake by leaves of the seagrass
536 *Thalassia testudinum*: impact of hydrodynamic regime and epiphyte cover on uptake rates.
537 *Journal of Marine Systems* **49**: 177-194.

538 ---. 2006. Water flow enhances ammonium and nitrate uptake in a seagrass community. *Marine*
539 *Ecology Progress Series* **312**: 1-13.

540 Cotton, J., G. Wharton, J. Bass, C. Heppell, and R. Wotton. 2006. The effects of seasonal changes to
541 in-stream vegetation cover on patterns of flow and accumulation of sediment. *Geomorphology*
542 **77**: 320-334.

543 Dawson, F., and W. Robinson. 1984. Submerged macrophytes and the hydraulic roughness of a
544 lowland chalkstream. *Verhandlung Internationale Vereinigung Limnologie* **22**.

545 Dietrich, W. E., and J. T. Perron. 2006. The search for a topographic signature of life. *Nature* **439**: 411-
546 418.

547 Folkard, A. M. 2005. Hydrodynamics of model *Posidonia oceanica* patches in shallow water.
548 *Limnology and oceanography* **50**: 1592-1600.

549 Follett, E. M., and H. M. Nepf. 2012. Sediment patterns near a model patch of reedy emergent
550 vegetation. *Geomorphology* **179**: 141-151.

551 Fonseca, M. S., J. C. Zieman, G. W. Thayer, and J. S. Fisher. 1983. The role of current velocity in
552 structuring eelgrass (*Zostera marina* L.) meadows. *Estuarine, Coastal and Shelf Science* **17**:
553 367-380.

554 Gambi, M. C., A. R. Nowell, and P. A. Jumars. 1990. Flume observations on flow dynamics in *Zostera*
555 *marina* (eelgrass) beds. *Marine ecology progress series*: 159-169.

556 Hansen, A. T., M. Hondzo, and C. L. Hurd. 2011. Photosynthetic oxygen flux by *Macrocystis pyrifera*:
557 a mass transfer model with experimental validation. *Marine Ecology Progress Series* **434**: 45-
558 55.

559 Haynes, R., and K. M. Goh. 1978. Ammonium and nitrate nutrition of plants. *Biological Reviews* **53**:
560 465-510.

561 Huang, I., J. Rominger, and H. Nepf. 2011. The motion of kelp blades and the surface renewal model.
562 *Limnology and Oceanography* **56**: 1453-1462.

563 Järvelä, J. 2005. Effect of submerged flexible vegetation on flow structure and resistance. *Journal of*
564 *Hydrology* **307**: 233-241.

565 Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers, p. 130-147.
566 *Ecosystem management*. Springer.

567 Koch, E. 1994. Hydrodynamics, diffusion-boundary layers and photosynthesis of the seagrasses
568 *Thalassia testudinum* and *Cymodocea nodosa*. *Marine Biology* **118**: 767-776.

569 Kouwen, N., and T. E. Unny. 1973. Flexible roughness in open channels. *Journal of the Hydraulics*
570 *Division* **99**.

571 Kundu, P. K., I. M. Cohen, and H. H. Hu. 2004. *Fluid mechanics*, 6th ed. ISBN: 978-0-12-405935-1.
572 Elsevier Press, Boston.

573 Lei, J., and H. Nepf. 2016. Impact of current speed on mass flux to a model flexible seagrass blade.
574 *Journal of Geophysical Research: Oceans* **121**: 4763-4776.

575 Leonard, L. A., and M. E. Luther. 1995. Flow hydrodynamics in tidal marsh canopies. *Limnology and*
576 *oceanography* **40**: 1474-1484.

577 Levi, P. S. and others 2015. Macrophyte complexity controls nutrient uptake in lowland streams.
578 *Ecosystems* **18**: 914-931.

579 Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch, and D. F. Westlake. 2001. The interaction
580 between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* **444**:
581 71-84.

582 Madsen, T. V., and N. Cedergreen. 2002. Sources of nutrients to rooted submerged macrophytes
583 growing in a nutrient-rich stream. *Freshwater Biology* **47**: 283-291.

584 Meire, D. W., J. M. Kondziolka, and H. M. Nepf. 2014. Interaction between neighboring vegetation
585 patches: Impact on flow and deposition. *Water Resources Research* **50**: 3809-3825.

586 Morris, E. P., G. Peralta, F. G. Brun, L. Van Duren, T. J. Bouma, and J. L. Perez-Llorens. 2008.
587 Interaction between hydrodynamics and seagrass canopy structure: Spatially explicit effects on
588 ammonium uptake rates. *Limnology and Oceanography* **53**: 1531-1539.

589 Morris, E. P. and others 2013. The role of hydrodynamics in structuring in situ ammonium uptake
590 within a submerged macrophyte community. *Limnology and Oceanography: Fluids and*
591 *Environments* **3**: 210-224.

592 Nepf, H. 1999. Drag, turbulence, and diffusion in flow through emergent vegetation. *Water resources*
593 *research* **35**: 479-489.

594 Nepf, H., and E. Vivoni. 2000. Flow structure in depth-limited, vegetated flow. *Journal of Geophysical*
595 *Research: Oceans* **105**: 28547-28557.

596 Nepf, H. M. 2012. Flow and transport in regions with aquatic vegetation. *Annual Review of Fluid*
597 *Mechanics* **44**: 123-142.

598 Peralta, G., L. Van Duren, E. Morris, and T. Bouma. 2008. Consequences of shoot density and stiffness
599 for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic
600 flume study. *Marine Ecology Progress Series* **368**: 103-115.

601 R Core Team. 2015. R: A Language and Environment for Statistical Computing (Version 3.1. 2): R
602 Foundation for Statistical Computing. Vienna, Austria. URL <http://www.R-project.org>.

603 Rominger, J. T., and H. M. Nepf. 2014. Effects of blade flexural rigidity on drag force and mass
604 transfer rates in model blades. *Limnology and Oceanography* **59**: 2028-2041.

605 Sand-Jensen, K. 1998. Influence of submerged macrophytes on sediment composition and near-bed
606 flow in lowland streams. *Freshwater Biology* **39**: 663-679.

607 Sand-Jensen, K., and T. Vindbæk Madsen. 1992. Patch dynamics of the stream macrophyte, *Callitriche*
608 *cophocarpa*. *Freshwater Biology* **27**: 277-282.

609 Sand-Jensen, K. 2005. Aquatic plants are open flexible structures—a reply to Sukhodolov. *Freshwater*
610 *Biology* **50**: 196-198.

611 Schoelynck, J., T. De Groote, K. Bal, W. Vandenbruwaene, P. Meire, and S. Temmerman. 2012. Self-
612 organised patchiness and scale-dependent bio-geomorphic feedbacks in aquatic river vegetation.
613 *Ecography* **35**: 760-768.

614 Schulz, M., H.-P. Kozerski, T. Pluntke, and K. Rinke. 2003. The influence of macrophytes on
615 sedimentation and nutrient retention in the lower River Spree (Germany). *Water Research* **37**:
616 569-578.

617 Sheldon, R. B., and C. W. Boylen. 1977. Maximum depth inhabited by aquatic vascular plants.
618 *American midland naturalist*: 248-254.

619 Stevens, C. L., and C. L. Hurd. 1997. Boundary-layers around bladed aquatic macrophytes.
620 *Hydrobiologia* **346**: 119-128.

- 621 Thomas, F. I., C. D. Cornelisen, and J. M. Zande. 2000. Effects of water velocity and canopy
622 morphology on ammonium uptake by seagrass communities. *Ecology* **81**: 2704-2713.
- 623 Vandenbruwaene, W. and others 2011. Flow interaction with dynamic vegetation patches: Implications
624 for biogeomorphic evolution of a tidal landscape. *Journal of Geophysical Research: Earth*
625 *Surface* **116**.
- 626 Weitzman, J. S., R. B. Zeller, F. I. Thomas, and J. R. Koseff. 2015. The attenuation of current-and
627 wave-driven flow within submerged multispecific vegetative canopies. *Limnology and*
628 *Oceanography* **60**: 1855-1874.
- 629 Wharton, G. and others 2006. Macrophytes and suspension-feeding invertebrates modify flows and fine
630 sediments in the Frome and Piddle catchments, Dorset (UK). *Journal of Hydrology* **330**: 171-
631 184.
- 632 Zong, L., and H. Nepf. 2012. Vortex development behind a finite porous obstruction in a channel.
633 *Journal of Fluid Mechanics* **691**: 368-391.

634 **Acknowledgments**

635 The authors gratefully acknowledge Bert Sinke, Lennart van IJzerloo, Lowie Haazen and Jeroen van
636 Dalen for their technical assistance in the flume. We thank Peter van Breugel and members of the
637 analytical lab of NIOZ-Yerseke for the stable isotope analyses. We thank Siebren Wezenberg for
638 helping during the experiments. This work was supported by the Research Executive Agency, through
639 the 7th Framework Programme of the European Union, Support for Training and Career Development
640 of Researchers (Marie Curie - FP7-PEOPLE-2012-ITN), which funded the Initial Training Network
641 (ITN) HYTECH 'Hydrodynamic Transport in Ecologically Critical Heterogeneous Interfaces',
642 N.316546. Data associated with this study is available from 4TU.Centre for Research Data at:
643 10.4121/uuid:e4678efa-426f-483a-b74a-c6ab4df53354

644 **Figure legends**

645 Figure 1: (A) Natural patches of *Callitriche* and (B) *Groenlandia* in the field. (C, D) Lateral view of the
646 two patches, with the black outline indicating canopy height at increasing distance from the patch
647 leading edge.

648 Figure 2: Schematic diagram of the four spatial configurations of aquatic macrophytes in the test
649 section of the flume. Light green indicates patches of *Groenlandia* (sparse canopy), and dark green
650 indicates patches of *Callitriche* (dense canopy). Diagonal lines indicate the boxes in which plants were
651 rooted. Black circles are locations of plant specimens removed after the incubations experiments for
652 assessment of NH_4^+ uptake rates, and of Acoustic Doppler Velocimeter (ADV) profile measurements.
653 Numbers indicate mean (\pm SE) water velocity \bar{U} (m s^{-1}) and Turbulent Kinetic Energy (Turbulent KE)
654 ($\text{m}^2 \text{s}^{-2}$) within each species patch.

655 Figure 3: Scatter plots of NH_4^+ uptake rates ($\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$) against Total Kinetic Energy (Total
656 KE) ($\text{m}^2 \text{s}^{-2}$), depth-averaged velocity $\langle \bar{U} \rangle$ (m s^{-1}) and Turbulent Kinetic Energy (Turbulent KE) ($\text{m}^2 \text{s}^{-2}$)
657 for the sparse *Groenlandia* (black circles) and the dense *Callitriche* (white diamonds). Black lines
658 are linear regression lines for the *Groenlandia* (solid line) and *Callitriche* (dotted line) data separately
659 and represent significant relationships ($p \leq 0.05$).

660 Figure 4: Boxplots of the distribution of NH_4^+ uptake rates ($\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$) within patches of the
661 dense *Callitriche* (a) and the sparse *Groenlandia* (b) in each spatial configuration (S indicating sparse
662 vegetation, D indicating dense vegetation, see Figure 2). Letters denote significant differences (Tukey's
663 HSD, $p < 0.05$).

664 Figure 5: Scatter plots of channel total NH_4^+ uptake rates ($\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$) in each spatial
665 configuration against Total Kinetic Energy ($\text{m}^2 \text{s}^{-2}$) averaged within patches of *Callitriche* and

666 *Groenlandia* in each spatial configuration (S indicating sparse vegetation, D indicating dense
667 vegetation, see Figure 2). Error bars represent standard error of the mean.

668 Figure 6: Schematized drawing of the effects of multispecific spatial patchiness on hydrodynamics and
669 nutrient uptake rates. In Sparse-Dense configurations (a), the sparse vegetation is exposed to high mean
670 flow but low turbulence, and does not benefit from being located at the leading edge. Similarly, the
671 dense vegetation is exposed to low mean flow speed due to sheltering by the patch upstream, and hence
672 has lower uptake rates. Instead, in Dense-Sparse configurations (b), uptake rates of both species are
673 higher: the dense vegetation benefits from being at the leading edge and exposed to high mean flow
674 speed (which increases uptake rates); at the same time, the sparse vegetation benefits from the high
675 turbulence created in the wake of the dense patch.

676

677

678

679 **Tables**

680 **Table 1** Summary of patch characteristics [mean \pm SD (*n*)] of the two species at the incoming flow
 681 velocity of 0.24 m s⁻¹ used in the flume experiments: biomass (g DW m⁻²; measured), canopy height (*h*,
 682 m; measured), frontal area per water volume (*a*, m⁻¹; calculated from Eq. 3), frontal area per bed area
 683 (*ah*, dimensionless; calculated from Eq. 4).

	Biomass (g DW m ⁻²)	Canopy height (<i>h</i> , m)	Frontal area per water volume (<i>a</i> , m ⁻¹)	Frontal area per bed area (<i>ah</i> , dimensionless)
<i>Groenlandia</i>	97 \pm 28 (3)	0.070 \pm 0.010 (9)	0.090 \pm 0.007 (2)	0.031 \pm 0.003 (2)
<i>Callitriche</i>	318 \pm 67 (3)	0.170 \pm 0.080 (5)	0.571 \pm 0.101 (2)	0.200 \pm 0.035 (2)

684

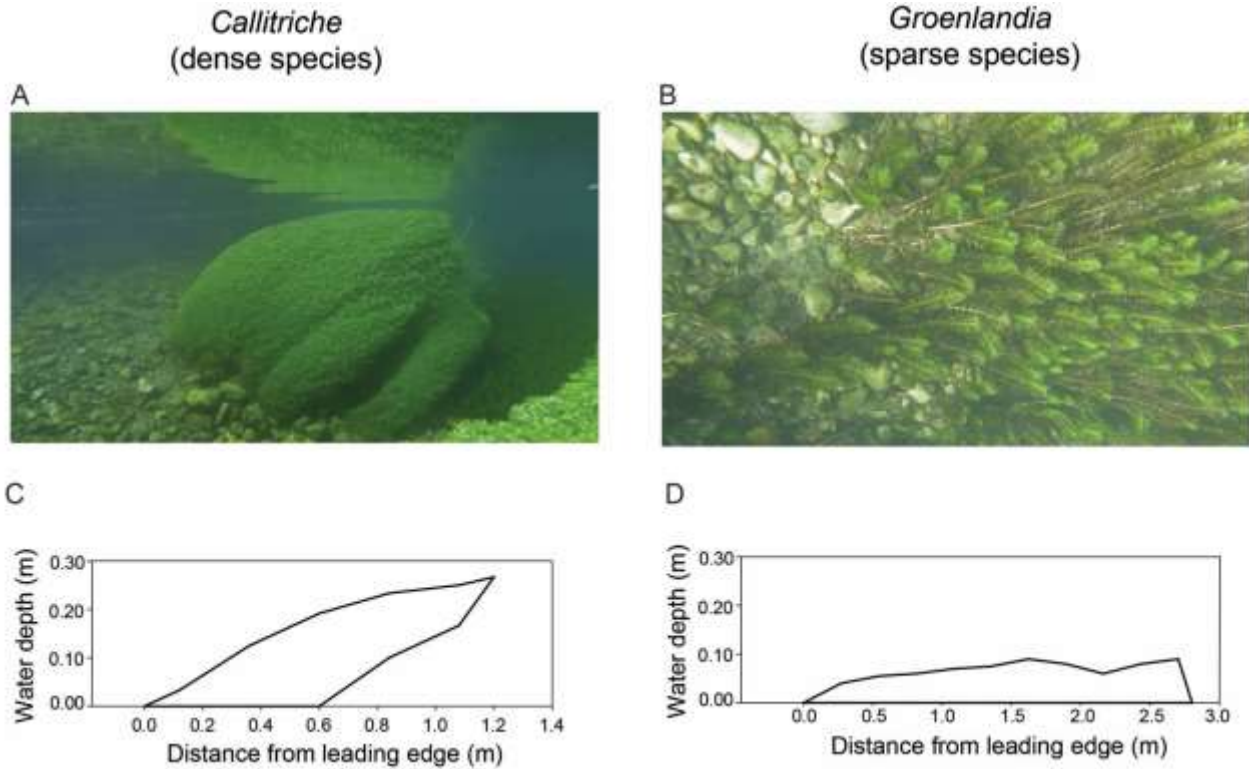
685 **Table 2** Pearson's correlation coefficients between NH_4^+ uptake rates ($\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$) and canopy
686 height (cm) or hydrodynamic parameters (depth-averaged velocity $\langle \bar{U} \rangle$ [m s^{-1}]; Reynolds shear stress
687 τ_{xz} [Pa]; Turbulent Kinetic Energy (Turbulent KE) [$\text{m}^2 \text{s}^{-2}$]; Total Kinetic Energy (Total KE) [$\text{m}^2 \text{s}^{-2}$]
688 and canopy water flow Q_c [$\text{m}^3 \text{s}^{-1}$]) for *Groenlandia*, *Callitriche* and both species considered together.
689 Correlation coefficients in bold are significant at $p \leq 0.05$.

	<i>Groenlandia</i> ($n = 24$)	<i>Callitriche</i> ($n = 24$)	All ($n = 48$)
Height	0.17	-0.18	-0.30
$\langle \bar{U} \rangle$	-0.20	0.42	0.40
τ_{xz}	0.01	-0.18	0.03
Turbulent KE	0.68	0.34	0.53
Total KE	0.79	0.45	0.54
Q_c	-0.07	0.19	-0.09

690

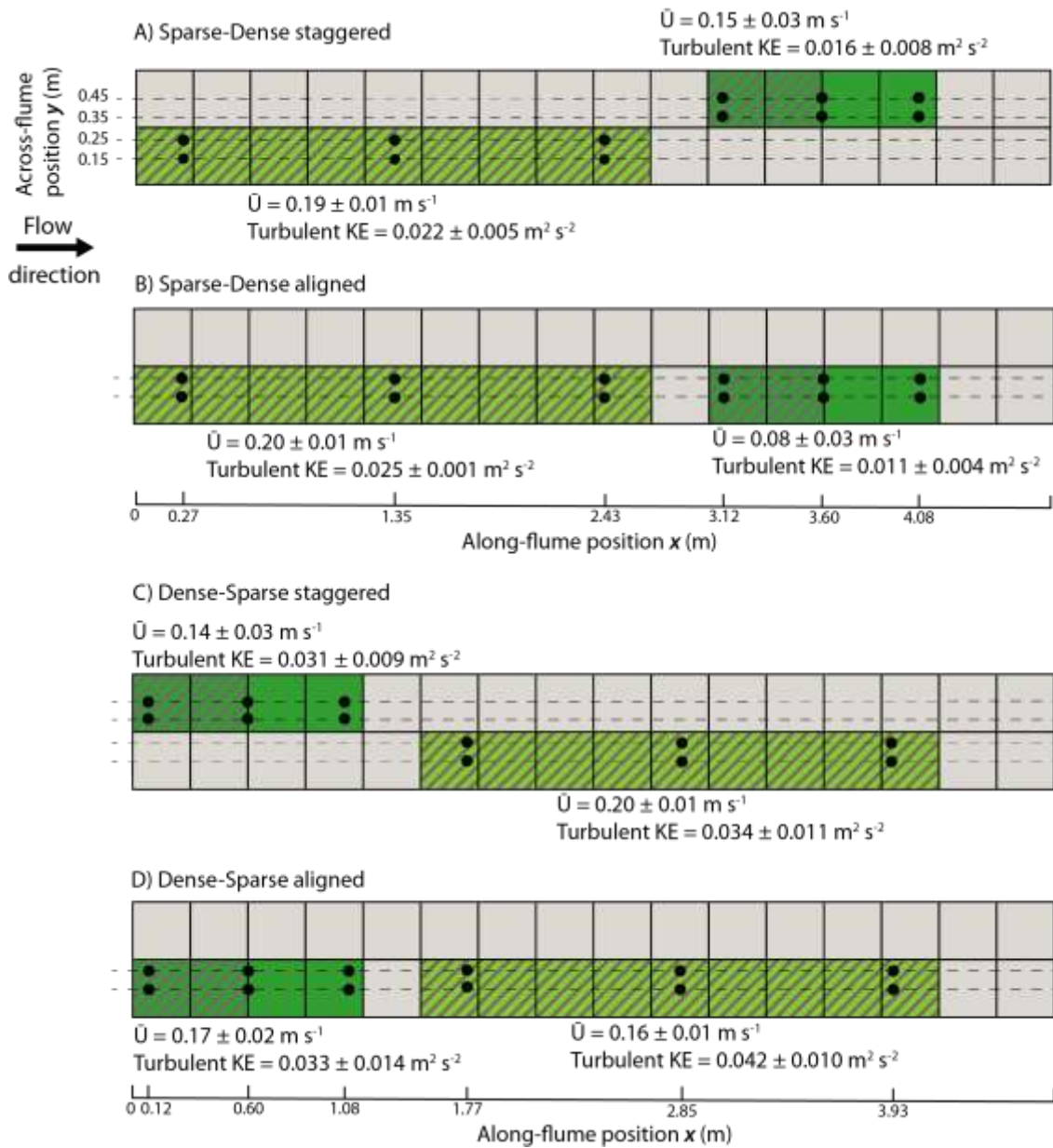
691

692 **Figures**



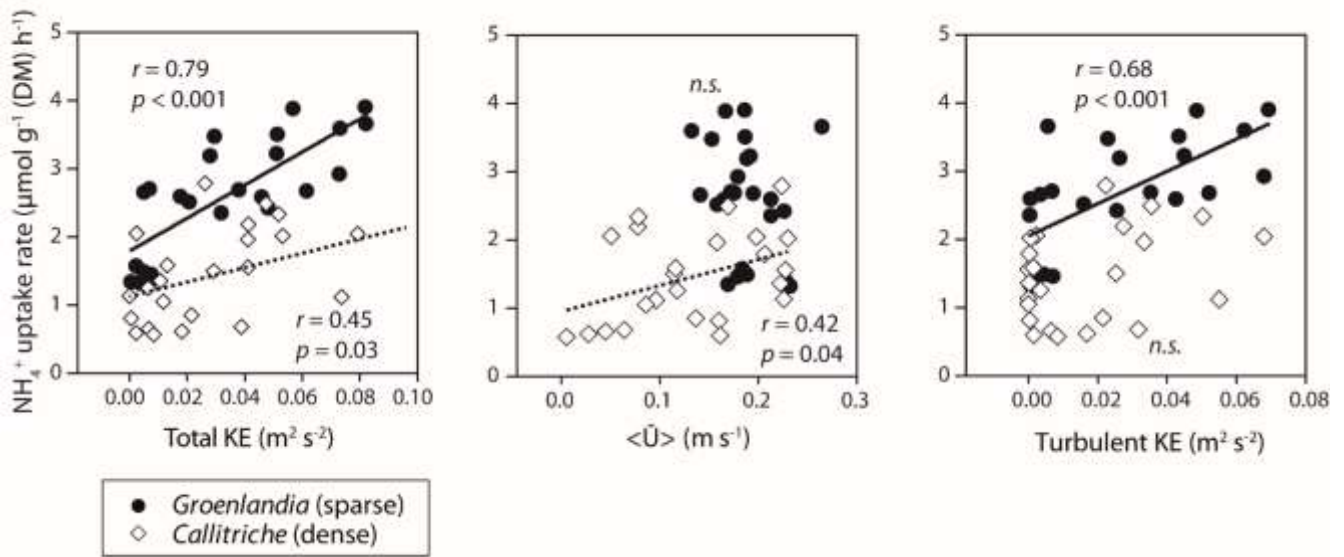
693

694 **Figure 1** (A) Natural patches of *Callitriche* and (B) *Groenlandia* in the field. (C, D) Lateral view of the
695 two patches, with the black outline indicating canopy height at increasing distance from the patch
696 leading edge.



697

698 **Figure 2** Schematic diagram of the four spatial configurations of aquatic macrophytes in the test
 699 section of the flume. Light green indicates patches of *Groenlandia* (sparse canopy), and dark green
 700 indicates patches of *Callitriche* (dense canopy). Diagonal lines indicate the boxes in which plants were
 701 rooted. Black circles are locations of plant specimens removed after the incubations experiments for
 702 assessment of NH_4^+ uptake rates, and of Acoustic Doppler Velocimeter (ADV) profile measurements.
 703 Numbers indicate mean (\pm SE) water velocity \bar{U} (m s^{-1}) and Turbulent Kinetic Energy (Turbulent KE)
 704 ($\text{m}^2 \text{ s}^{-2}$) within each species patch.



705

706

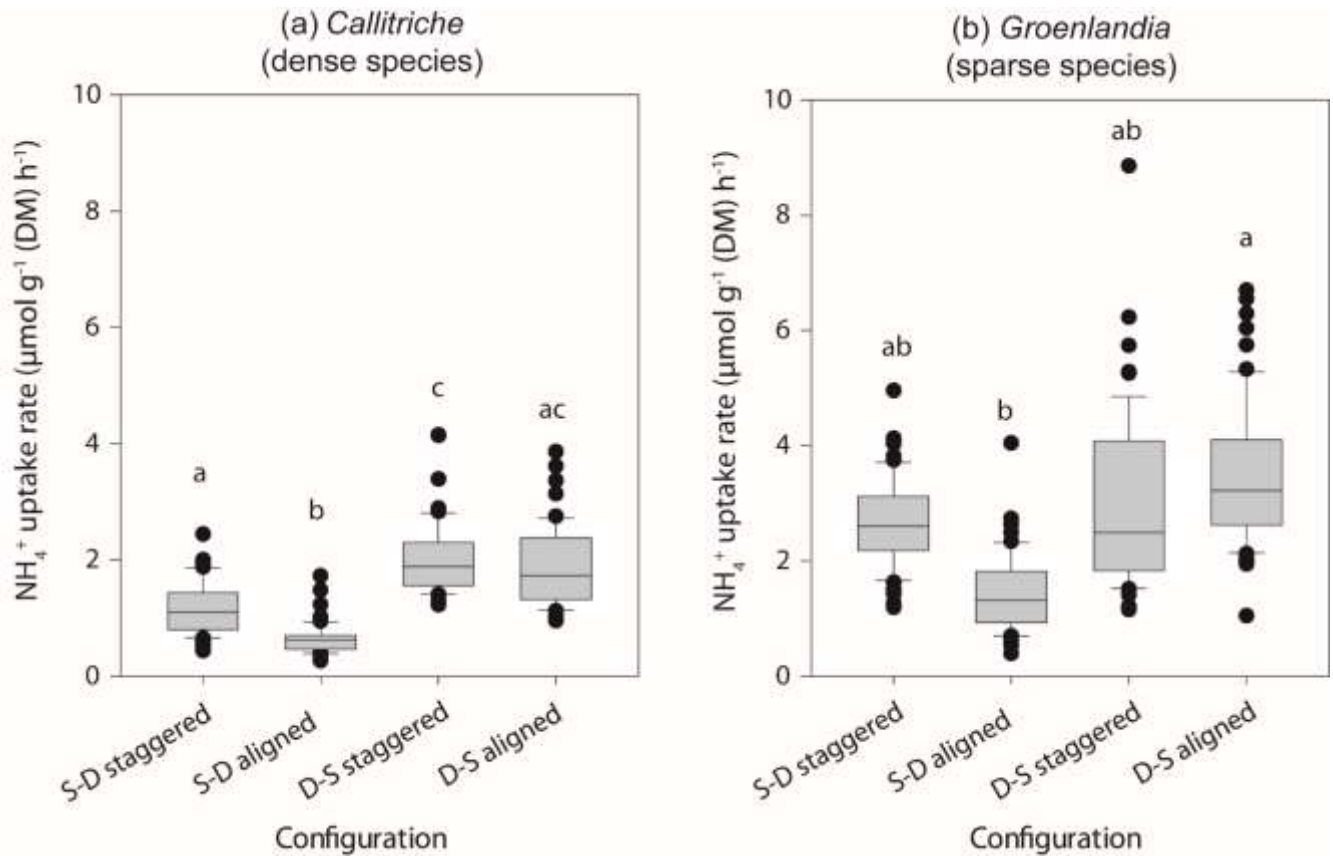
707

708

709

710

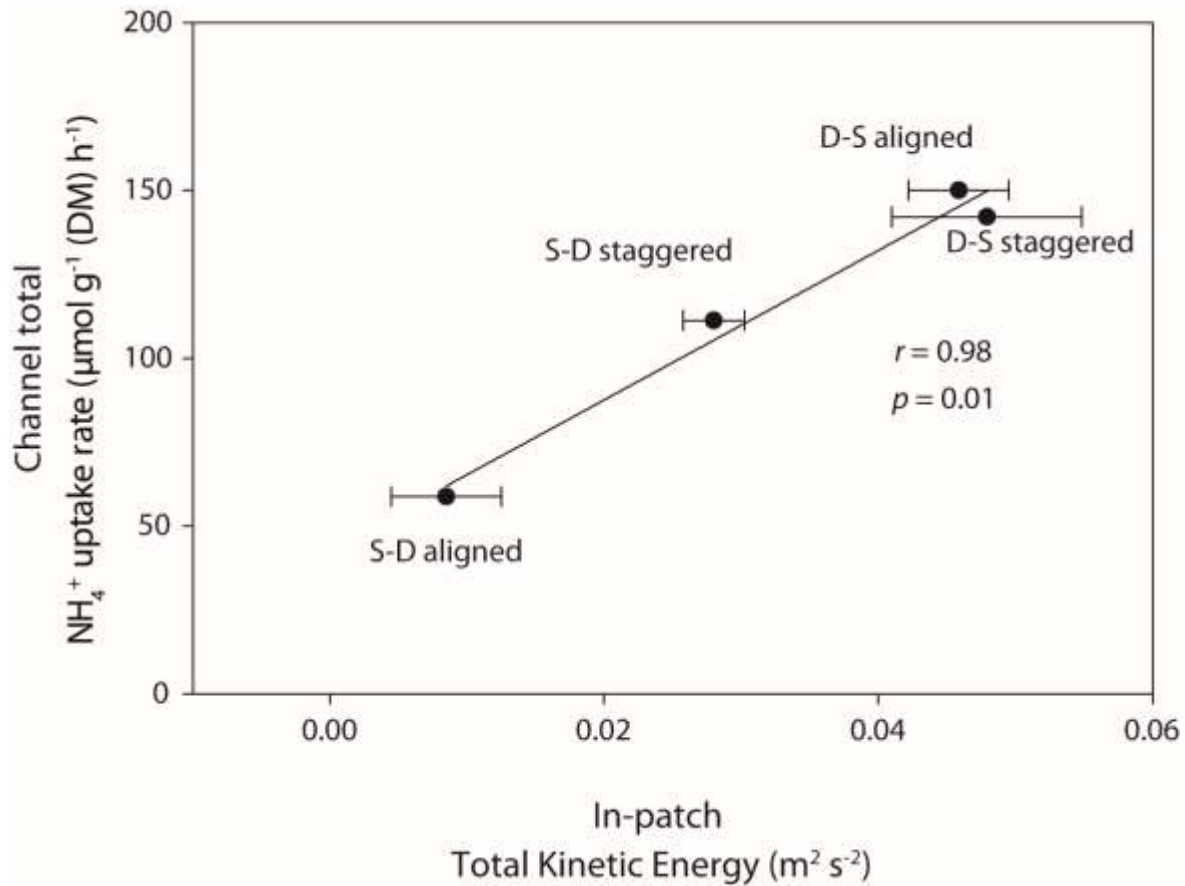
Figure 3 Scatter plots of NH_4^+ uptake rates ($\mu\text{mol g}^{-1} (\text{DM}) \text{h}^{-1}$) against Total Kinetic Energy (Total KE) ($\text{m}^2 \text{s}^{-2}$), depth-averaged velocity $\langle \bar{U} \rangle$ (m s^{-1}) and Turbulent Kinetic Energy (Turbulent KE) ($\text{m}^2 \text{s}^{-2}$) for the sparse *Groenlandia* (black circles) and the dense *Callitriche* (white diamonds). Black lines are linear regression lines for the *Groenlandia* (solid line) and *Callitriche* (dotted line) data separately and represent significant relationships ($p \leq 0.05$).



711

712 **Figure 4** Boxplots of the distribution of NH₄⁺ uptake rates (μmol g⁻¹ (DM) h⁻¹) within patches of the
 713 dense *Callitriche* (a) and the sparse *Groenlandia* (b) in each spatial configuration (S indicating sparse
 714 vegetation, D indicating dense vegetation, see Figure 2). Letters denote significant differences (Tukey's
 715 HSD, $p < 0.05$).

716

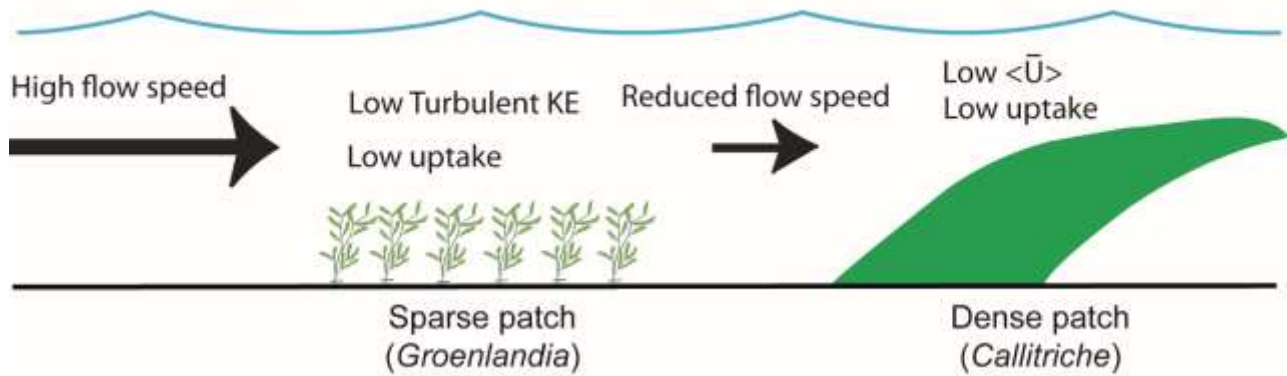


717

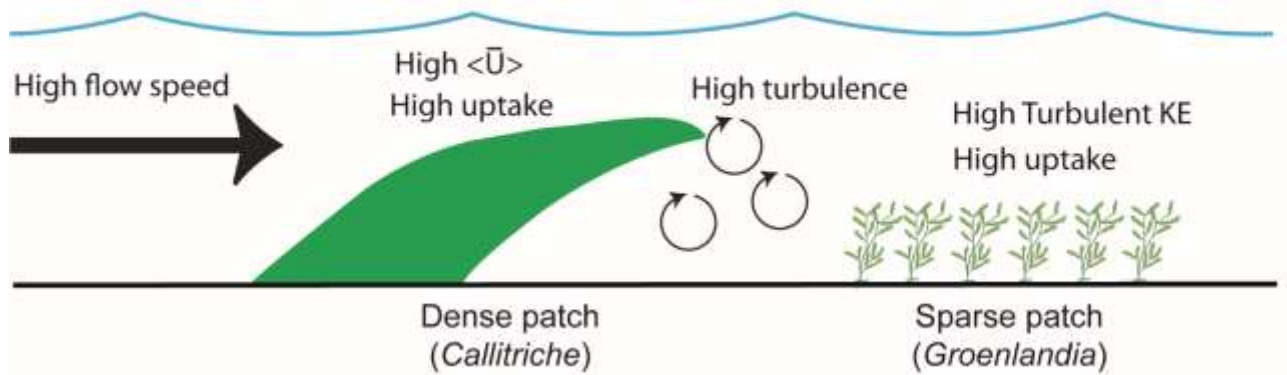
718 **Figure 5** Scatter plots of channel total NH_4^+ uptake rates ($\mu mol g^{-1} (DM) h^{-1}$) in each spatial
 719 configuration against Total Kinetic Energy ($m^2 s^{-2}$) averaged within patches of *Callitriche* and
 720 *Groenlandia* in each spatial configuration (S indicating sparse vegetation, D indicating dense
 721 vegetation, see Figure 2). Error bars represent standard error of the mean.

722

(a) Sparse-Dense species configurations



(b) Dense-Sparse species configurations



723

724

725

726

727

728

729

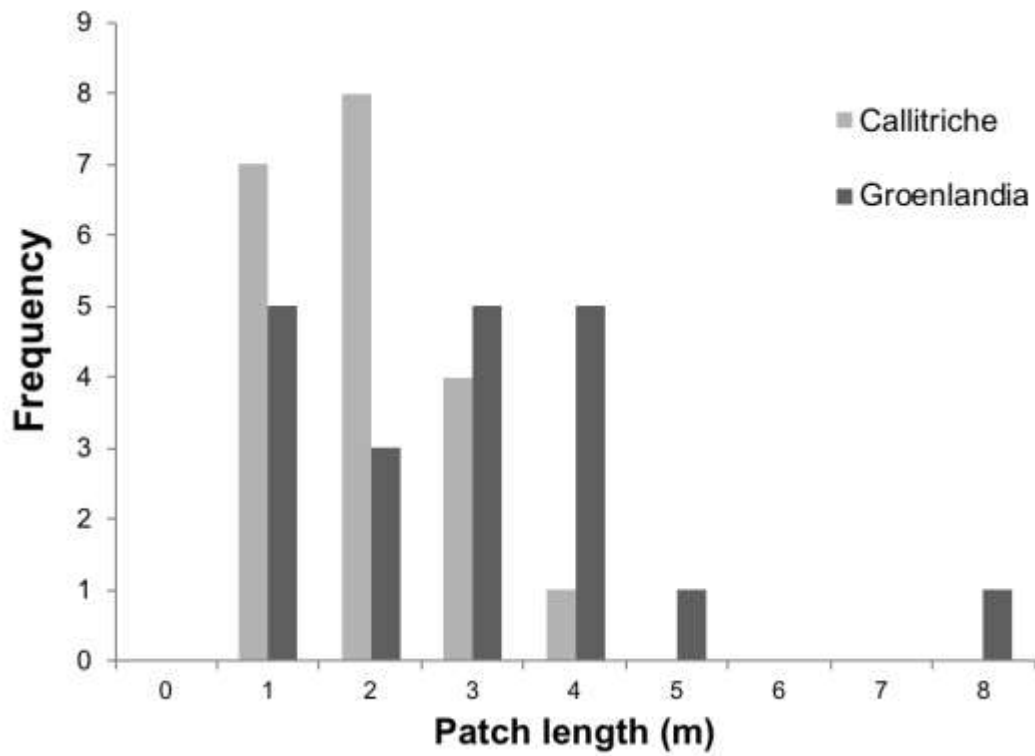
730

731

732

Figure 6 Schematized drawing of the effects of multispecific spatial patchiness on hydrodynamics and nutrient uptake rates. In Sparse-Dense configurations (a), the sparse vegetation is exposed to high mean flow but low turbulence, and does not benefit from being located at the leading edge. Similarly, the dense vegetation is exposed to low mean flow speed due to sheltering by the patch upstream, and hence has lower uptake rates. Instead, in Dense-Sparse configurations (b), uptake rates of both species are higher: the dense vegetation benefits from being at the leading edge and exposed to high mean flow speed (which increases uptake rates); at the same time, the sparse vegetation benefits from the high turbulence created in the wake of the dense patch.

733 Supporting Information



734

735 **Figure S1:** Frequency distribution of patch length (m) for *Callitriche* and *Groenlandia* ($n = 20$) in field
736 conditions.