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1 *4 figures (all in colors) + 2 tables + 6 supporting information*

2

3 **Warming drives feedback between plant phenotypes and ecosystem functioning in sub-Antarctic**
4 **ponds**

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39 Abstract

40 Ample evidence indicates that warming affects individuals in plant communities, ultimately threatening
41 biodiversity. Individual plants in communities are also exposed to plant–plant interaction that may affect
42 their performance. However, trait responses to these two constraints have usually been studied separately,
43 while they may influence processes at the ecosystem level. In turn, these ecological modifications may
44 impact the phenotypes of plants through nutrient availability and uptake. We developed an experimental
45 approach based on the macrophyte communities in the ponds of the sub-Antarctic Iles Kerguelen.
46 Individuals of the species *Limosella australis* were grown under different temperature × plant–plant
47 interaction treatments to assess their trait responses and create litters with different characteristics. The
48 litters were then decomposed in the presence of individual plants at different temperatures to examine
49 effects on ecosystem functioning and potential feedback affecting plant trait values. Leaf resource-
50 acquisition– and -conservation–related traits were altered in the context of temperature × plant–plant
51 interaction. At 13 °C, SLA and leaf C:N were higher under interspecific and intraspecific
52 interactions than without interaction, whereas at 23 °C, these traits increased under intraspecific
53 interaction only. These effects only slightly improved the individual performance, suggesting that plant–
54 plant interaction is an additional selective pressure on individuals in the context of climate warming. The
55 decay rate of litter increased with the Leaf Carbon Content at 13 °C and 18 °C, but decreased at
56 23°C. The highest decay rate was recorded at 18 °C. Besides, we observed evidence of positive
57 feedback of the decay rate alone, and in interaction with the temperature, respectively on the leaf C:N and
58 Leaf Dry Matter Content, suggesting that variations in ecological processes affect plant phenotypes. Our
59 findings demonstrate that warming can directly and indirectly affect the evolutionary and ecological
60 processes occurring in aquatic ecosystems through plants.

61 **Keywords**

62 Climate warming, ecosystem functioning, feedback, litter decay rate, plant–plant interaction, functional
63 traits

64 1. Introduction

65 Growing evidence indicates that climate change, in particular temperature increases, affects plant
66 communities and threatens biodiversity in general (Halloy and Mark 2003; Khare *et al.*, 2020; Harrison
67 2020). Consensus has been reached that climatic changes affect the physical and biological characteristics
68 of living organisms. Functional ecology has been advocated as a relevant framework for the study of such
69 changes' impacts on species traits and the identification of connections to individual fitness and ecological
70 consequences (McGill *et al.*, 2006).

71 Traits are morphological, phenological, and physiological features that are measurable at the
72 individual level (Violle *et al.*, 2007). Response traits reflect the modification of individual trait values due
73 to environmental variation, and effect traits reflect the consequent alteration of processes at higher
74 organizational levels up to the ecosystem (Lavorel and Garnier 2002; Violle *et al.*, 2007). In turn, the
75 modification of ecological processes can lead to selective pressure triggering species responses,
76 theoretically forming a feedback loop, although this phenomenon remains poorly studied (but see
77 Jacquemyn *et al.*, 2012; Gould *et al.*, 2014; Van Nuland *et al.*, 2016; terHorst and Zee, 2016). In
78 particular, studies considering both components of this feedback (individual-to-ecosystem and ecosystem-
79 to-individual) in plant communities with the integration of plant–plant interaction have not been
80 conducted so far.

81 Individuals in plant communities are exposed simultaneously to biotic and abiotic constraints,
82 although their trait responses have usually been studied separately (see, e.g., Dudley and Schmitt, 1996;
83 Greulich and Bornette, 1999; Suding *et al.*, 2008; Riis *et al.*, 2012). We thus have little understanding of
84 the importance and effects of plant–plant interaction in the governing of species responses to thermal
85 stress in the context of climate change. Thermal stress and plant–plant interaction (*i.e.*, competition and
86 facilitation) are environmental and ecological filters that drive individual phenotypes, and thus plant
87 community composition (Keddy 1992; Violle *et al.*, 2007). Previous studies have highlighted the
88 importance of intraspecific trait variability for species' ability to overcome these filters (Jung *et al.*, 2010;

89 [Violle et al., 2012](#)). For instance, competition induces increases in the specific leaf area (SLA) ([Bittebiere](#)
90 [et al., 2012](#)), leaf phosphorus and nitrogen concentrations ([Novotny et al., 2007](#)), and plant height
91 ([Bittebiere and Mony 2015; Yu et al., 2018](#)) to support individuals' competitive ability, whereas thermal
92 stress has the opposite effects, favoring individual resistance to restrictive conditions ([Wright et al., 2005;](#)
93 [Moles et al., 2009; Pallardy 2010; Reich 2014; Zhang et al., 2016; Bjorkman et al., 2018; Zhang et al.,](#)
94 [2019](#)). Overall, this antagonism between plant individual responses suggests the existence of an
95 intermediate, yet so far overlooked, strategy due to traits involved in thermal resistance and competitive
96 ability. In addition, individuals would invest in fewer but more performant ramets to support their
97 competitiveness, as they would have fewer resources under thermal stress conditions.

98 As plants are primary producers, their responses to plant–plant interaction \times thermal stress can
99 scale up through their effect traits to the ecosystem level ([Lavorel and Garnier 2002; Eviner and Chapin](#)
100 [2003; Quétier et al., 2007](#)), affecting functions such as carbon or nitrogen cycling. Intraspecific trait
101 variability in response to environmental and ecological filters may also play an important role in
102 ecosystem functioning, but this hypothesis remains poorly studied ([Pichon et al., 2022](#)). There is,
103 however, evidence supporting it, as litter decomposability is related strongly to physical and chemical
104 characteristics ([Fortunel et al., 2009; Yang et al., 2022](#)) and depends mostly on the “after-life effect” of
105 leaf trait values ([De Deyn et al., 2008; Makkonen et al., 2012](#)). In particular, it was found to correlate
106 negatively with the leaf dry matter content (LDMC) and leaf carbon content (LCC) and positively with the
107 SLA and leaf nitrogen content (LNC) ([Lecerf and Chauvet 2008; Cornwell et al., 2008; Freschet et al.,](#)
108 [2013; Tao et al., 2019](#)). Moreover, the litter decay rate depends not only on its characteristics, but also on
109 environmental conditions such as the temperature *via* the decomposers' activity ([Sulkava and Huhta](#)
110 [2003](#)). Thus, temperature may affect the litter decay rate directly or through litter characteristics resulting
111 from plant trait responses to warming.

112 The litter decay rate is a key driver of nutrient cycling ([Freschet et al., 2013](#)), as it determines the
113 dynamics of soil labile organic matter and influences nutrient release and flows in the ecosystem ([Kaye](#)
114 [and Hart 1997; Schimel and Bennett 2004](#)). Warming can accelerate nitrogen mineralization ([Epstein et](#)

115 *al.*, 2000; Rustad *et al.*, 2001) and plant nutrient uptake (Bassirrad 2000; Epstein *et al.*, 2000), especially
116 in cold biomes, where the decay rate is often limited by cool conditions (Hobbie *et al.*, 2002; Robinson
117 2002). Consequently, changes in nutrient availability and uptake should create a feedback toward the
118 mineral nutrition of plants, affecting their growth and trait values (Wardle *et al.*, 2004; Freschet *et al.*,
119 2013). In particular, the SLA and leaf nutrient concentrations are known to increase in response to nutrient
120 availability (Westoby *et al.*, 2002; Cornelissen *et al.*, 2003), and the alteration of plant trait values is thus
121 expected in warmer environments and/or habitats in which the litter decay rate and nutrient availability are
122 altered.

123 To address these assumptions, we took an experimental approach based on a model of pond
124 ecosystems in the sub-Antarctic region. We recreated at small (mesocosm) scale the conditions in these
125 pond ecosystems. In the first phase of the experiment, individuals of the sub-Antarctic plant species
126 *Limosella australis* were grown under different temperature \times plant–plant interaction treatments and their
127 trait responses were assessed. In the second phase, litters of varying characteristics were decomposed at
128 different temperatures, enabling examination of the effects on ecosystem functioning and potential
129 feedback involving plant trait values. Specifically, we tested the following hypotheses (Fig. 1):

130 1. that competitive interaction would increase with the warming up to optimal thermal conditions,
131 especially when individuals are growing with similar functional neighbors, suggesting that plant
132 traits converge toward values supporting competitive abilities (e.g., increases in height, SLA, and
133 LNC to maintain plant performance), and that thermal stress (i.e., warming exceeding the
134 optimum thermal range) would induce smaller phenotypes and more resource conservation to
135 favor thermal resistance (e.g., decreases in height, SLA and LNC and increases in LDMC and
136 LCC, reducing plant performance, as well as the production of fewer but more performant ramets
137 to support competitiveness);

138 2. that the litter decay rate would depend on both temperature and litter characteristics, increasing
139 with warming, especially in case of litter produced from individuals with high SLA and LNC and
140 low LCC and LDMC; and

141 3. that the decay rate combined with the warming would affect the LNC, LCC, SLA, and LDMC
142 of plant individuals growing in the ecosystem, with higher values stimulating nutrient cycling and
143 thus individual's deployment of an acquisitive strategy (i.e., high SLA and LNC, low LDMC and
144 LCC).

145

146 2. Material and methods

147 2.1. Studied system and plant species

148 Our experiment was based on a model of the ponds of Iles Kerguelen (sub-Antarctic region, South Indian
149 Ocean, 48°30–50°S, 68°27–70°35E). These ponds are shallow freshwater systems supplied by rainfall and
150 regularly enriched with nutrients from marine fauna such as seabirds and elephant seals (Smith 2008).
151 Warming is occurring particularly rapidly in this region (Walther *et al.*, 2002; Leihy *et al.*, 2018), where
152 the native biota has adapted to cold temperatures (mean air temperature during the year = 4.6°C) (Frenot
153 *et al.*, 2006; Lebouvier 2007) and abundant precipitation (500–3200 mm along an east–west gradient;
154 Frenot *et al.*, 1998; Meteo France). Average water temperature in summer during daytime (plant growth
155 season) is 13 °C, but higher water temperatures are regularly recorded, depending on the water depth (up
156 to 23°C, on a regular basis). Plant communities are made up of few species, simplifying plant–plant
157 interaction, and are less impacted by anthropic influences than are other regions of the world. This system
158 model is thus particularly relevant for the inferring of mechanisms of plant community assembly and
159 ecosystem functioning, especially under climate change (Bergstrom and Chown 1999).

160 These ponds provide habitats for aquatic plant (*i.e.*, macrophyte) communities composed of six
161 native perennial species, which can co-occur locally: *L. australis* R.Br. (Scrophulariaceae), *Callitriche*

162 *antarctica* Engelm (Plantaginaceae), *Juncus scheuchzerioides* Gaudich. (Juncaceae), *Ranunculus*
163 *biternatus* Smith, *Ranunculus pseudotrullifolius* Skottsbo., and *Ranunculus moseleyi* Hook.f (all
164 Ranunculaceae). *Limosella australis* was the target species in the present study, as its population seems to
165 have declined in recent years and its extirpation from several localities suggests that it is more sensitive
166 than other species to current climate changes in the region (Douce *et al.*, 2023). The five other species
167 were used as neighboring species. *Limosella australis* has a network architecture forming a clone
168 composed of related ramets (short, erect stems with leaves and roots) connected through stolons.

169 170 2.2. Biological material

171 Seeds of *L. australis* and ramets of the other five macrophyte species were collected from different
172 localities of the main island of the Iles Kerguelen (10 localities for the seeds, six localities for the ramets;
173 Appendix A.1). These localities were at least 10 km apart, and a total of 75 ramets and of 30 seeds were
174 collected from different ponds per locality, to maximize the genetic variability. *Limosella australis* ramets
175 were grown from the seeds and multiplied clonally under controlled conditions of substrate (50% sand and
176 50% compost; 250 g.m⁻³ N, 120 g.m⁻³ P₂O₅, and 80 g.m⁻³ K₂O), water supply, temperature (13°C, which is
177 the mean water temperature recorded during the day in Iles Kerguelen ponds, during the growth season),
178 and light (12/12 h). This approach allowed us to limit maternal effects and obtain ramets with similar
179 growth histories. In addition, clonal individuals produce genetically identical ramets, enabling the control
180 of genotype effects on the responses measured under the different experimental treatments. All ramets
181 were cleaned and size standardized before being transplanted into the mesocosms.

183 184 2.3. Responses of functional and performance traits to temperature and plant–plant interaction

185 The first phase of the experiment was conducted in mesocosms in regulated rooms of the Laboratoire
186 d'Ecologie des Hydrosystèmes Naturels et Anthropisés, Villeurbanne, France. The biological material
187 obtained from prior cultures realized under controlled conditions was used to establish three plant–plant
188 interaction treatments: (i) *L. australis* cultivated alone (no interaction), (ii) *L. australis* cultivated with

189 conspecifics (intraspecific interaction), and (iii) *L. australis* cultivated together with the five other species
190 (interspecific interaction; Fig. 2a). This design allowed us to assess the effects of intra. vs. interspecific
191 plant-plant interactions on plant responses. To examine the impact of temperature increases on plant
192 responses during their growing season, the plant-plant interaction treatments were carried out at three
193 temperatures (Riis *et al.*, 2012): (i) 13°C (mean of daily water temperatures in ponds during the growing
194 season), (ii) 18°C (low warming of water temperatures), and (iii) 23°C (extreme warming of water
195 temperatures) (Fig. 2a).

196 For all treatment modalities, pots of 9 cm diameter and 8 cm height and the type of substrate used
197 for culture were used. All planted ramets (targets and neighbors) were adult and were transplanted with
198 one stolon internode (with reserves to facilitate growth after transplantation; Stuefer and Huber, 1999).

199 In the interspecific and intraspecific treatments, ramets ($n = 18/\text{pot}$) were planted in a hexagonal
200 pattern (Fig. 2a) to ensure balanced plant-plant interaction with neighbors (Birch *et al.*, 2007). To create
201 these competitive assemblages, competitor individuals from different localities were mixed; there was no
202 relationship between the original localities and those of the *L. australis* seeds. In each pot, we also planted
203 three target ramets with the same genotype and an equal distribution of neighboring ramets (species
204 positioned randomly in the interspecific treatment) at constant total density (Fig. 2a).

205 To ensure that they were well established, neighbors were transplanted 15 days before the *L.*
206 *australis* target ramets and all neighbors that died during this period were replaced. This delay allowed
207 the neighbors to be well-established when targets were transplanted. After target transplantation, the pots
208 were maintained at the optimal growth temperature of 13°C for 10 days to allow recovery before they
209 were exposed to the experimental temperatures. Ten replicates of each temperature \times plant-plant
210 interaction treatment were established (total, 90 pots). One genotype was assigned to each replicate for the
211 assessment of plastic responses as genotype reaction norms. A 12/12-h (2780 lux/dark) light regime was
212 used. Each pot was placed individually in a tray filled with water (12 cm depth of water; water mean
213 nutrient content: 8.0 $\mu\text{g/L}$ N-NH₄⁺, 47.1 $\mu\text{g/L}$ N-NO₃⁻, and 1.140 mg/L P-PO₄³⁻), which was refilled

214 weekly. In each temperature-regulated room (one per tested temperature), the pot positions were
215 randomized every 2 weeks.

216 After 13 weeks of cultivation, cultures were harvested. The *L. australis* target ramets produced
217 new connected daughters of similar genotype (hereafter referred to as clones) through clonal growth,
218 enabling us to control for genotype effects when measuring traits. We measured functional and
219 performance traits on *L. australis* plants at the clone and ramet levels to (i) determine the ramet responses
220 to temperature × plant-plant interactions and (ii) assess the influence of potential modifications of trait
221 values on plant growth. To that aim, we randomly selected one of the three target clones per pot to assess
222 the efficiency of clonal growth. The total dry mass of the ramet (*i.e.*, sum of the biomasses of stems,
223 leaves, roots, and one clonal internode) was measured as a proxy of its performance. At the clone level,
224 the total dry mass and number of ramets were measured as proxies of clone performance. The dry mass
225 was measured after the plant parts had been oven dried at 65°C or freeze dried for 48 h. All plants were
226 cleaned before measurement. In addition, functional traits were measured at the ramet level. One newly
227 produced and adult ramet of the clone was used for height measurements. Another ramet was used for the
228 following leaf trait measurements : SLA, LDMC, LCC, LNC, and leaf C:N ratio which characterize
229 resource acquisition and conservation strategies, as these traits are known to respond to temperature and
230 plant–plant interaction (Cornelissen *et al.*, 2003) and to be effect traits for the litter decay rate (Santiago
231 2007; Quested *et al.*, 2007). The SLA and LDMC were measured following Cornelissen *et al.*, (2003) on
232 one randomly selected healthy, mature leaf per ramet. The LCC and LNC were measured on several
233 leaves from the same ramet, pooled to obtain the required mass (1 mg ± 10% of the leaf dry biomass) and
234 encapsulated in tin capsules after being weighed. The capsule contents were then analyzed using an
235 elemental analyzer (Vario PyroCube, Elementar, Villeurbanne, France).

236 The remaining ramets of this clone and the other two *L. australis* target clones were used to create
237 litter for the second experiment.

238

239 2.4. Response of the decay rate to temperature and litter characteristics

240
241 The aboveground biomass (*i.e.*, leaves, stems, and clonal connections) of the *L. australis* target clones
242 remaining after the first phase of the experiment was oven dried at 65°C for 48 h, and the dry material
243 (pooled and mixed homogenously for each treatment) was used to create litter bags. As litter
244 characteristics usually depend on living plant traits, we assumed that the physical and chemical
245 characteristics of the litter would differ among the nine treatments designed for the first phase of the
246 experiment (temperature × plant-plant interactions), resulting in nine litter characteristics. Dry
247 aboveground biomass originating from *L. australis* ramets from the same experimental treatment was
248 pooled and homogeneously mixed, before being dispatched into different litter bags. We thus assumed
249 that litter bags from the same treatment had the same litter characteristics and could be considered as
250 replicates. Each litter bag (nylon, fine mesh to focus on microbial decomposition; 6 × 4 cm, pore area
251 1000 µm²) contained 5 mg ± 10% dry aboveground biomass. To determine the effects of temperature on
252 litter decay rate, five replicates of litterbags with the same litter characteristics were placed at each of
253 three temperatures (13°C, 18°C, and 23°C) in respective rooms in 250-mL glass pots (9.5 cm diameter, 11
254 cm height; Fig. 2b). In total, 27 experimental treatments (9 litter characteristics × 3 temperatures) and 135
255 mesocosms (9 litter characteristics × 3 temperatures × 5 replicates) were established. To estimate the
256 timing of experiment termination, we placed three additional pots containing litter bags with random
257 characteristics at each temperature and monitored the loss of mass from these bags over time.

258 To recreate the conditions of sub-Antarctic pond ecosystems, the pots were filled with 150 mL
259 ultra-pure sterilized water (to avoid microbial contamination and the addition of exogenous nutrients) and
260 100 mL sedimentary substrate (1:3 mixture of Iles Kerguelen sediments and sterilized sand). The
261 sediments had been collected previously at various field locations on the main island of the Iles Kerguelen
262 and mixed to ensure colonization by microorganisms identical to those occurring *in situ*. They were
263 brought from the field to the laboratory at 4°C to keep the microorganisms alive, in sealed cans to avoid
264 external contamination. The substrate was inoculated with the mixed sediments for 1 week to ensure full

265 microorganism colonization. In addition, one *L. australis* ramet was transplanted into each pot 1 week
266 before the litter bag was introduced to further evaluate the combined effects of temperature and the litter
267 decay rate on its trait values (Fig. 2b). One genotype was assigned to each of the five replicates, *i.e.*, 27
268 ramets originating from the same clone and standardized by height, were distributed among the 27
269 treatments to control for genotype effects on *L. australis* responses. A 12/12-h (2780 lux/dark) light
270 regime was used.

271 This second phase of the experiment ended after 56 days, when all litter bags had lost at least 50%
272 of their mass. The litter bags were collected, cleaned, and freeze dried for 2 days before being weighed.

273 We calculated the litter decay rate for each litter bag following an exponential decay model
274 (Olson 1963):

$$275 \quad Mf = Mi * e^{-k*x},$$

276 where *Mf* is the litter dry mass remaining after *x* days, *Mi* is the initial litter dry mass (5 mg ± 10%), and *k*
277 is the litter decay rate per day (.days⁻¹) (Makkonen *et al.*, 2012; Zhang *et al.*, 2019):

$$278 \quad k = -\frac{1}{x} \ln \left(\frac{Mf}{Mi} \right).$$

279 2.5. Feedbacks effects of temperature and litter characteristics on plant growth

280

281

282 At the end of the second phase of the experiment, we measured functional and performance traits on *L.*
283 *australis* plants at the clone and ramet levels to assess the influence of potential modifications of the
284 decomposition process on plant growth. We measured the same functional and performance traits that the
285 one measured at the end of the first phase of the experiment. To that aim, clones were harvested and
286 cleaned. One ramet per clone was used for the measurement of traits at the ramet level; one fresh leaf was
287 frozen at -20 °C for nutrient analyses and the remaining biomass of the ramet was freeze dried for 2 days.
288 At the ramet level, we thus measured the height, SLA, LDMC, LCC, LNC, leaf C:N ratio, as well as the

289 total dry mass of the ramet as a proxy of its performance. The remaining biomass of the clones was oven
290 dried at 65°C for 48 h for clone-level measurements that is the total dry mass and number of ramets as
291 proxies of clone performance.

292

293 2.6. Statistical analyses

294 We examined correlations between all pairs of traits using Spearman rank correlation tests. We detected a
295 strong negative correlation (*i.e.*, $r > 0.7$; [Dormann *et al.*, 2013](#)) between the LNC and leaf C:N ratio only.
296 We retained the leaf C:N ratio over the LNC for further analyses because it satisfied the application
297 conditions of the tests performed.

298 To identify morphological and performance traits that responded to temperature \times plant–plant
299 interaction (fixed factors), we used linear mixed-effects models and the "lme4" package ([Bates, 2010](#);
300 *glmer.nb* function for the number of ramets and *lmer* function for all other traits). The clone genotype was
301 included in the models as a random factor to detect trait plastic responses as genotype reaction norms. The
302 trait data were normalized (log transformed) as needed. When the interaction between temperature and
303 plant–plant interaction was not significant, an additive model was fitted instead. When the effects of
304 temperature and/or plant–plant interaction were significant, differences in trait means among treatments
305 were examined using *post-hoc* tests and the *diffsmeans* function of the "lmerTest" package ([Kuznetsova
306 *et al.*, 2017](#)) with adjusted *p* values (Bonferroni correction).

307 We assessed the combined effects of temperature and litter characteristics on the litter decay rate.
308 As leaf traits are known to influence litter physical and chemical characteristics ([De Deyn *et al.*, 2008](#);
309 [Makkonen *et al.*, 2012](#)), we reduced the leaf traits (LCC, leaf C:N ratio, SLA, and LDMC) to the first two
310 axes in a principal component analysis (PCA), in which data were centered and standardized, for litter
311 characterization (Appendix B.1, Appendix C.1), to increase the degree of freedom in the following
312 analysis. Then, we ordered the characteristics of the litters produced from the nine temperature \times plant-
313 plant interaction treatments through the PCA axes (Appendix D.1, Appendix E.1). As all of the dry

314 aboveground biomass originating from each temperature \times plant–plant interaction treatment was pooled
315 and homogenized, we assumed that the corresponding litter bags had the same characteristics. The
316 interactive effects of temperature (categorical variable) and litter characteristics (quantitative variables;
317 first two axes in the PCA) on the litter decay rate were examined. The trait data were normalized by
318 square root transformation. Stepwise selection of the most parsimonious model based on the Akaike
319 information criterion (AIC) was performed using the *dredge* function of the “MuMIn” package (Bartoń,
320 2013). The significance of model factors was determined using type-II analysis of covariance
321 (ANCOVA).

322 To determine whether functional and performance traits responded to the litter decay rate (*i.e.*,
323 ecosystem process) and temperature, we fitted linear mixed-effect models with the temperature
324 (categorical variable) and decay rate (quantitative variable) serving as fixed interactive factors and the
325 eight traits studied serving as response variables. Because one genotype was attributed to each replicate,
326 the models also included the clone genotype as a random factor to detect trait plastic responses as
327 genotype reaction norms. We used the *glmer.nb* function of the “lme4” package (Bates, 2010) for the
328 number of ramets and the *lmer* function for all other traits. The trait data were normalized by log
329 transformation. Stepwise selection of the most parsimonious model based on the AIC was performed
330 using the *dredge* function of the “MuMIn” package (Bartoń, 2013). The significance of the model factors
331 was assessed using type-II ANCOVA. When a significant effect of temperature was detected, pairwise
332 comparison of trait means among temperatures was performed using the *dunn_test* function of the “statix”
333 package with adjusted *p* values (Bonferroni correction).

334 All statistical analyses were carried out with R 4.0.3 (R Core Team, 2023).

335 3. Results

336 3.1. Functional and performance trait responses to temperature and plant–plant interaction

337 Three of the five functional traits (the leaf C:N ratio, SLA, and LDMC) responded to temperature \times plant–
338 plant interaction (Table 1, Fig. 3). Thus, temperature changed the functional responses of these traits in a
339 plant–plant interaction context, and *vice versa*. In the absence of plant–plant interaction and in comparison
340 with individuals grown at 18 and 23°C, individuals of *L. australis* grown at 13°C had similar leaf C:N
341 ratios, lower LDMC values, and contrasting SLA values that tended to increase with increasing
342 temperatures. Plant–plant interaction modified these response patterns. The LDMC increased with
343 temperature under intraspecific interaction, but remained similar to that observed in the absence of
344 interaction under interspecific interaction (Fig. 3b). Variation in the leaf C:N ratio was also observed, with
345 both intra- and interspecific interaction leading to increases at 18°C in comparison with the values
346 observed at 13°C (Fig. 3d).

347 At 13°C (optimal growth temperature of *L. australis* plants in natural environments), the LDMC
348 did not vary with plant–plant interaction, but the SLA and leaf C:N ratio were higher with interspecific
349 and intraspecific interaction, respectively, than with no interaction. At higher temperatures, this response
350 pattern was modified, with the LDMC and leaf C:N ratio displaying similar responses (Fig. 3b, d). At
351 18°C, the values of these two traits were higher under inter- and intraspecific interaction than under no
352 interaction; at 23°C, they increased only under intraspecific interaction. The LCC and height responded
353 only to plant–plant interaction (Table 1, Fig. 3).

354 The two performance traits measured at the clone level (clone dry mass and number of ramets)
355 responded to temperature \times plant–plant interaction. The number of ramets increased significantly with the
356 temperature, except under intraspecific interaction. Similarly, the clone dry mass remained constant under
357 intraspecific interaction, regardless of the temperature, whereas it increased with the temperature under no
358 and interspecific interaction. In contrast, at the ramet level, the temperature and plant–plant interaction had
359 only additive effects on the ramet dry mass, and the effect of plant–plant interaction was much stronger

360 than that of the temperature (Table 1, Fig. 3). Whereas the 23°C treatment altered the ramet dry mass only
361 slightly, intraspecific interaction increased it significantly relative to the other two interaction treatments.

362 3.2. Response of the decay rate to temperature and LCC

363 A PCA of the leaf traits was performed to reduce the dimensions (Appendix B.1, Appendix C.1), and the
364 coordinates on PCA axes 1 and 2 were used as proxies of litter characteristics. PCA axis 1 (48.4% of
365 accounted variance) was related negatively to the SLA and positively to the LDMC and leaf C:N ratio.
366 PCA axis 2 (24.3% of accounted variance) was related positively to the LCC. PCA axis 1 was not related
367 significantly to the decay rate, alone or in interaction with the temperature, and was excluded during
368 model selection based on the AIC. However, we found an interactive effect of the temperature and PCA
369 axis 2 on the decay rate (ANCOVA: $F_{df=2} = 6.02$, $p = 0.003$; Fig. 4). The decay rate increased with the
370 PCA axis 2 value (*i.e.*, the LCC) at 13°C and 18°C, but decreased with increasing LCC at 23°C (Appendix
371 F.1). With similar LCC values, the decay rate was significantly higher at 18°C than at 13°C (Tukey
372 contrast test: $t = 13.15$, $p < 0.001$) and 23°C ($t = -13.90$, $p < 0.001$).

373

374 3.3. Decay rate feedback effects on the plant phenotype

375 Three of the five functional traits (the SLA, LCC, and height) did not respond to the decay rate or
376 temperature (Table 2). The LDMC was explained by the decay rate and temperature, with no significant
377 interaction detected, and the leaf C:N ratio was affected positively by only the decay rate (Table 2). More
378 precisely, the LDMC increased significantly with the decay rate, with values higher at 13°C and 23°C than
379 at 18°C (Table 2).

380 The clone dry mass and number of ramets were affected only by the temperature; clones produced
381 more and heavier ramets at 23°C than at 13°C and 18°C (Table 2). The ramet dry mass did not respond to
382 the decay rate or temperature.

383 4. Discussion

384 4.1. Plant functional responses to warming are modified by the community context

385 As the planet warms, plant–plant interaction and thermal constraints are expected to have increasing
386 important influences on the biological and ecological performance of individual plants. However, the
387 effects of these two factors on plant trait responses have been examined only independently (see, e.g.,
388 [Dudley and Schmitt, 1996](#); [Greulich and Bornette, 1999](#); [Suding *et al.*, 2008](#); [Riis *et al.*, 2012](#)). We
389 explored the functional responses of the macrophyte *L. australis* under a range of plant–plant interaction
390 and temperature conditions. Our original experimental design allowed us to obtain evidence that resource-
391 acquisition– and -conservation–related traits were altered in the context of temperature \times plant–plant
392 interaction, and that these effects had impacts on individual biomass production. Furthermore, individual
393 plants developed different response strategies in warmer environments according to the type of plant–plant
394 interaction (intra- vs. interspecific).

395 Under optimal thermal conditions (13°C), the mean phenotype of *L. australis* under no plant
396 interaction was characterized by a short stature, small SLA, high LDMC, and intermediate leaf C:N ratio.
397 Temperature and plant–plant interaction strongly affected this phenotype, and had interactive effects on
398 the three functional traits involved in the leaf economics spectrum (the leaf C:N ratio, SLA, and LDMC),
399 that is, individual strategies for nutrient investment and conservation in leaves ([Wright *et al.*, 2004](#)).
400 Phenotypic variation depended on neighbors' functional traits, the degree of similarity between
401 individuals is well known to be a driver of competition strength ([Kraft *et al.*, 2014](#); [Kraft *et al.*, 2015](#);
402 [Cadotte and Tucker 2017](#)). In the absence of plant–plant interaction, the SLA and LDMC increased and
403 decreased, respectively, with increasing temperature, suggesting enhancement of the acquisitive strategy,
404 contrary to the expectation ([Bjorkman *et al.*, 2018](#)). Under intraspecific interaction, the SLA remained
405 constant along the temperature gradient, while the LDMC and leaf C:N ratio increased, reflecting the
406 development of a resistance strategy to adjust the plant biology to unfavorable habitats ([Keddy *et al.*,](#)
407 [1998](#)). Under interspecific interaction, trait variations in response to increasing temperature were more

408 similar to those observed in the absence of interaction. This result suggests that competitive interaction
409 was less intense over the temperature gradient, and that individual plants with different functional
410 characteristics used resources more efficiently (Kraft *et al.*, 2014). Taken together, these findings suggest
411 that the ability of plant species to successfully respond to increasing temperatures depends strongly on the
412 presence of functionally similar or dissimilar competitors in the plant community. This response was
413 based on most leaf traits that were investigated here. To deepen our conclusions on warming influence on
414 plant growth, we suggest that the response of other leaf dimensions should additionally be studied. Indeed,
415 although SLA captures one of the major axes of leaf physiology (Poorter and Bongers, 2006), other leaf
416 dimensions e.g., area and length, are important indicators of plant growth (Hirose *et al.*, 1997; Monteith *et*
417 *al.*, 1997; Ewert 2004; Farooq *et al.*, 2010).

418 The context-dependent plastic responses developed by *L. australis* individuals in this study had
419 biological costs. In the absence of plant–plant interaction, individuals produced more ramets with very
420 slightly different dry masses at higher temperatures, enabling clones to colonize the space more rapidly
421 (Fahrig *et al.*, 1994; Stuefer *et al.*, 2002). Nevertheless, this beneficial effect of warming on plant growth,
422 reported by other researchers (Hollister *et al.*, 2005; Fu *et al.*, 2015; Baruah *et al.*, 2017), was abolished by
423 plant–plant interaction. Clone and ramet performance remained constant and only slightly improved,
424 respectively, with increasing temperature under intra- and interspecific interaction. This result strongly
425 suggests that the observed functional trait responses to temperature \times plant–plant interaction were not
426 adaptive (Ghalambor *et al.*, 2007) and that plant–plant interaction is an additional selective pressure on
427 individual plants in the context of climate change. Importantly, our current predictions of species fate
428 under climatic warming are likely inaccurate in the absence of knowledge of the community context. As
429 increasing temperatures additionally modify individual responses to neighbors and determine the outcome
430 of plant–plant interaction (Armas and Pugnaire 2011; Bilas *et al.*, 2021; Hao *et al.*, 2023), we emphasize
431 that higher temperatures may modify the roles of functional traits in species coexistence at the community

432 level. Different species displaying different responses to plant-plant interactions based on their traits
433 ([Bittebiere et al., 2019](#)), further studies are needed with additional target species.

434

435 4.2. The LCC drives the litter decay rate, depending on the temperature

436 Variations in litter characteristics, in particular the LCC, affected the litter decay rate in interaction with
437 the temperature in this study, consistent with findings from a stream experiment performed by [Lecerf and](#)
438 [Chauvet \(2008\)](#). This result emphasizes the importance of considering intraspecific trait variability when
439 studying ecosystem functioning, contrary to the historical assumption that species representation by mean
440 trait values alone is sufficient ([Albert et al., 2010](#)). Unexpectedly, greater LCCs enhanced litter
441 decomposition at 13°C and 18°C, similar to the results obtained by [Coûteaux et al., \(1991\)](#) for chestnut
442 leaves. These authors showed that the decay rate of litter with a high nitrogen (and low carbon) content
443 was initially high and had declined at the end of the experiment, in relationship to the decomposer
444 community composition; they expected such litter to have favored the development of organisms able to
445 degrade resistant compounds during the late stages of decomposition ([Couteaux et al., 1991](#)). High
446 temperatures (e.g., 23°C) may reduce the importance of the decomposer community composition in
447 decomposition. Surprisingly, variations in the SLA, LDMC, and leaf C:N ratio were not sufficient to
448 impact the decay rate in this study. The *L. australis* litter likely remained of overall good quality, an
449 assumption supported by previous works showing that macrophyte species produce easily decomposable
450 tissues, with little lignin ([Hanlon 1982](#); [Kögel-Knabner 2002](#)). In addition, variations in litter
451 characteristics may have been related to traits that we did not consider here, in particular, the Leaf
452 Phosphorus Content (LCP) ([Kurokawa and Nakashizuka 2008](#); [Parsons and Congdon 2008](#); [Cornwell et](#)
453 [al., 2008](#); [Schindler and Gessner 2009](#)). Further studies are then needed to assess how LCP could interact
454 with warming, to determine the decay rate of macrophyte litter.

455 Temperature explained most of the variance in the litter decay rate in this study, consistent with
456 previous findings that environmental factors, such as the mean annual temperature and rainfall, explain the

457 largest proportions of this variance (Lavelle *et al.*, 1993; Hättenschwiler *et al.*, 2005; García-Palacios *et*
458 *al.*, 2016). Litter decomposition was most efficient at 18°C, suggesting that it is stimulated with increasing
459 temperatures from 13°C to 18°C, but is limited at temperatures that are too high (i.e., 23°C). This result
460 confirms our assumption about microbial decomposer activity and emphasizes that the relationship
461 between temperature and the litter decay rate followed a bell curve peaking at 18 °C in our experimental
462 system based on the Iles Kerguelen ponds. The apparent discrepancy between our results and those of
463 others (but see Bradford *et al.*, 2017) can be explained by differences in experimental design. In previous
464 studies, the effects of temperature increases were generally assessed along latitudinal or altitudinal
465 gradients *in situ* (Aerts 2006; García-Palacios *et al.*, 2013; García-Palacios *et al.*, 2016; Follstad Shah *et*
466 *al.*, 2017; Amani *et al.*, 2019) or in a controlled experiment with a temperature gradient insufficiently
467 large to obtain such a bell curve (+2.8°C; Ferreira *et al.*, 2015). Our findings call into question the current
468 understanding of the fate of polar decomposer communities and subsequent impacts on nutrient cycling at
469 temperatures superior to 18°C, which have already been recorded at different localities in the sub-
470 Antarctic region, including the Iles Kerguelen (Meteo France, Douce *et al.*, 2023) and Marion Island
471 (Nyakatya and McGeoch 2007).

472
473 **4.3. Feedback effects of temperature and litter decomposition on plant phenotype**
474 Our findings partially confirm our hypothesis that decomposition efficiency (represented by the decay
475 rate) together with temperature would ultimately affect plant trait variation at the ecosystem level. No trait
476 was impacted by temperature × decay rate interaction. The LDMC responded to their additive effects and
477 the leaf C:N ratio responded to the decay rate alone, confirming the existence of nutrient cycling feedback
478 effects on the functional traits of *L. australis*. Litter decomposition mediates many ecosystem parameters,
479 such as carbon sequestration and the amount of mineralized and bioavailable nutrients (Kaye and Hart
480 1997; Regina 2001; Schimel and Bennett 2004; Aponte *et al.*, 2012; Yang *et al.*, 2022). Litter
481 decomposition was stimulated with increasing temperatures up to 18°C in this study. As warming
482 stimulates microorganism efficiency, N mineralization was likely accelerated (Rustad *et al.*, 2001). This

483 effect should have been particularly pronounced in our system, which mimics cold biomes where
484 decomposition is strongly limited (Hobbie *et al.*, 2002; Robinson 2002). The resulting increase in N
485 availability should have increased plant nutrient uptake, contributing to the explanation of the observed
486 low LDMC (Wardle *et al.*, 2004; Freschet *et al.*, 2013). These alterations of the leaf economics spectrum
487 (Reich *et al.*, 1997; Wright *et al.*, 2004) characterize individuals with nutrient acquisition strategies, in line
488 with findings from similar studies of systems with high resource availability (Ordoñez *et al.*, 2009;
489 Stanisci *et al.*, 2020). By contrast, the higher LDMC values recorded at 13°C and 23°C, *i.e.*, when
490 decomposition (and probably nutrient mineralization) were less efficient, indicate that *L. australis*
491 individuals switched their nutrient allocation strategies toward conservation. Considering that the ramet
492 dry mass did not change with the temperature or litter decomposition, the highlighted functional variations
493 in ramet strategies enabled the maintenance of ramet performance. At the clone level, temperature
494 increases were beneficial, stimulating ramet production, regardless of the litter decomposition process.

495 Studies of the effects of variations in ecological processes on organisms' phenotypic variation
496 remain rare (but see Bull *et al.*, 2006; Becks *et al.*, 2012; Brunner *et al.*, 2017), and have not been
497 conducted with plants. The findings of this study suggest that feedback between ecological properties and
498 trait expression ultimately results in evolutionary processes in aquatic ecosystems. If the observed LDMC
499 and leaf C:N ratio variations are heritable, ecological properties should lead to the further selection of
500 individuals with the most adapted trait values in response to thermal changes (De Meester *et al.*, 2019),
501 resulting in evolutionary changes in aquatic plant phenotypes. The feedback involving the individual,
502 community, and ecosystem levels observed in this study reflects eco-evolutionary dynamics (Hendry
503 2016).

504

505 5. Conclusions

506 This study showed that the community context is key for plant responses to climate warming in cold
507 ecosystems, with simple plant-plant interaction network (*i.e.* with low species richness). Our functional

508 approach allows us to easily generalize our results to other cold ecosystems of the world (at high latitudes
509 or altitudes), independently of the taxonomic identity of the studied species (McGill *et al.*, 2006). Working
510 on this cold and simple system then constitutes a first step towards the understanding of the impact of
511 warming on biodiversity and ecosystem functioning. However, future studies are now needed to deepen
512 our conclusions, with the study of more complex systems (in terms of species richness), adapted to
513 warmer temperatures.

514 We also showed that temperature is directly and indirectly (through litter characteristics and the
515 decay rate) involved in ecological and evolutionary processes, bringing new insight into the mechanisms
516 underlying the effects of increasing temperatures on plant biodiversity and aquatic ecosystems. However,
517 we only worked on the effects of stable temperatures, while climate warming also implies the increase in
518 the frequency of extreme temperature events (Diffenbaugh *et al.*, 2017; Wang *et al.*, 2017; Gu *et al.*,
519 2022). Plant responses to temperature fluctuations thus needs to be more deeply investigated in the future,
520 as plant studies considering it remained really rare in the literature so far (Slein *et al.*, 2023), although it
521 would aggravate the deleterious effects of warming (Stoks *et al.*, 2017; Bernhardt *et al.*, 2018; Denny
522 2019; Slein *et al.*, 2023). For instance, it has been shown that the reproductive stage of plants is
523 particularly vulnerable, with both male and female organs of the flower being sensitive to temperature
524 fluctuations, resulting in lower fruit and seed set (Hedhly 2011). In addition, temperature fluctuations and
525 high temperature stress significantly affect plant growth (Kotak *et al.*, 2007; Scheepens *et al.*, 2018),
526 suggesting probable consequences on plant performance and survival.

527 Finally, the effects of warming on ecosystem functioning should be examined in greater detail by
528 additionally considering intraspecific trait variability. Most studies have involved the examination of the
529 effects of mean species traits on ecological processes (Orwin *et al.*, 2010; Garnier and Navas 2012; Lienin
530 and Kleyer 2012); recent studies have provided evidence of feedback between community shifts and
531 ecosystem processes (Lecerf and Chauvet 2008; Reich 2014; Moran *et al.*, 2016; Lu *et al.*, 2017; Berzaghi
532 *et al.*, 2020). More work is thus needed to clarify how intraspecific trait variability impacts higher-order

533 ecological processes (Yang *et al.*, 2018; Swenson *et al.*, 2020; Westerband *et al.*, 2021; Yang *et al.*, 2021),
534 and how it could then determine eco-evolutionary dynamics. Indeed, variations in individual functional
535 traits induce shifts in populations dynamics, in community assembly *via* changes in the whole plant
536 performance and in the environmental filtering processes, and at a larger scale, in ecosystem functions
537 through the effect traits (Westerband *et al.*, 2021).

538

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540
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550 **Declaration of competing interest**

551 None declared.

552 **CRedit authorship contribution statement**

553 **Pauline Douce:** Conceptualization, Methodology, Formal analysis, Investigation, Writing– Original draft.
554 **Laurent Simon:** Conceptualization, Methodology, Investigation, Writing – Review & Editing. **Fanny**
555 **Colas:** Conceptualization, Methodology, Investigation, Writing – Review & Editing. **Florian Mermillod-**
556 **Blondin:** Conceptualization, Methodology, Investigation, Writing – Review & Editing. **David Renault:**
557 Funding acquisition, Writing – Review & Editing. **Cécile Sulmon:** Funding acquisition, Writing – Review
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559 Methodology, Investigation, Writing – Review & Editing. **Anne-Kristel Bittebiere:** Conceptualization,
560 Methodology, Investigation, Writing – Original draft, Supervision, Funding acquisition.

561 **Data availability**

562 Data are available at: <https://doi.org/10.6084/m9.figshare.24049887.v1>

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1007

1008 **Figure legends**

1009
1010 **Fig. 1.** Schematic representation of the hypotheses tested in this study at the species and
1011 ecosystem levels. SLA, Specific Leaf Area; LDMC, Leaf Dry Matter Content; LCC, Leaf Carbon
1012 Content; LNC, Leaf Nitrogen Content; Hyp., Hypothese.

1013
1014 **Fig. 2.** The two-phase experimental design. a) In the first phase, plant trait and performance
1015 responses to combined effects of temperature and plant–plant interactions were examined. Three
1016 temperatures and three plant–plant interactions treatments were tested. *L. australis* target ramets
1017 are indicated in blue on the plantation pattern; b) In the second phase, the combined effects of
1018 temperature and litter characteristics on litter decay rates, and subsequently plant growth (traits
1019 and performance), were examined. Qi, characteristics of litter obtained from ramets grown under
1020 the i^{th} treatment in phase 1.

1021
1022 **Fig. 3.** Mean (\pm SDs) functional (a–e) and performance (f–h) traits of *Limosella australis*
1023 cultivated at three temperatures and under three types of plant–plant interaction ($n = 90$). The
1024 number of ramets and clone dry mass were measured at the clone level; all other traits were
1025 measured at the ramet level. Letters indicate the results of pairwise comparison of means among
1026 temperatures within each plant–plant interaction treatment (*difflsmeans* function). Different
1027 shades of yellow, pink, and purple indicate significant differences in means from pairwise
1028 comparisons among plant–plant interaction treatments for each temperature (*difflsmeans*
1029 function). The leaf C:N ratio obtained at 13°C under interspecific interaction is colored in two
1030 shades of yellow, indicating that it did not differ from those observed under the other plant–plant
1031 interaction treatments, at this temperature. T×I, significant temperature and plant–plant

1032 interactions interactive effect; T+I, significant temperature and plant-plant interactions additive
1033 effect; I, significant plant-plant interaction effect alone; SLA, Specific Leaf Area; LDMC, Leaf
1034 Dry Matter Content; LCC, Leaf Carbon Content; Ram., ramet; Cl., clone. * $p < 0.05$, ** $p < 0.01$,
1035 *** $p < 0.001$.

1036

1037 **Fig. 4.** Decay rate (k) as a function of the Leaf Carbon Content (PCA axis 2 values) under the
1038 three temperature treatments ($n = 135$). The straight lines represent the adjustment of the linear
1039 model to the data. Significant regression results are presented in Appendix F.1.

1040

1041 [Supporting information](#)

1042

1043 **Appendix A.1.** Locations of the sampling sites on the French sub-Antarctic Iles Kerguelen.

1044 **Appendix B.1.** Eigenvector scores for the first axis of a principal component analysis (PCA) of leaf traits.

1045 **Appendix C.1.** PCA results for the four leaf traits and temperature x plant–plant interaction.

1046 **Appendix D.1.** ANOVA results indicating significant differences among temperature × plant–plant
1047 interaction treatments in litter characteristics.

1048 **Appendix E.1.** Mean characteristics (\pm SD) of the litters produced from the nine temperature × plant–
1049 plant interaction treatments.

1050 **Appendix F.1.** Decay rates as functions of the leaf carbon content (PCA axis 2).

1051