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1 **Morphological variability of cushion plant *Lyallia kerguelensis* (Caryophyllales) in relation to**
2 **environmental conditions and geography in the Kerguelen Islands: implications for cushion**
3 **necrosis and climate change**

4
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18
19 **Abstract**

20 In recent decades climate change has been faster in various parts of the world. Within species, to
21 counter rapid climate changes shift of geographical area, individuals' plastic responses or populations'
22 genetic adaptation might occur. The sub-Antarctic islands are subject to one of the most rapid climate
23 changes on earth, with already visible impacts on native vegetation. Such might be the case of *Lyallia*
24 *kerguelensis* a cushion plant strictly endemic to the Kerguelen Islands. In *L. kerguelensis*, necrotic
25 parts were observed in cushions these last decades and possibly related to water stress. We analysed
26 morphological variability of *L. kerguelensis*, including necrosis extent, across 19 populations spanning
27 a wide range of environments across the Kerguelen Islands. Inter-population variations in the cushion
28 surface area, shape and compactness were well explained by topography, degree of wind exposure,
29 slope aspect, proportions of coarse sand and bare soil, and geographical distance between populations.
30 All these variables are related to wind intensity and water availability. Moreover, in cushions with less
31 than 10% necrosis in surface area, necrosis extent was positively correlated to soil sodium. Sodium
32 availability might reduce the plant's capacity for osmotic adjustment in face of other abiotic stresses,
33 such as water stress. We conclude that cushion morphology may have the capacity to adjust to
34 environmental variation, including aspects of climate change, but that cushion necrosis may be
35 accelerated in the driest and most saline environments.

37 **Keywords:** cushion plant, Kerguelen Islands, morphological variability, necrosis, photointerpretation,
38 sub-Antarctic

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42 and Education (France).

43

44 **Conflicts of interest/competing interests:**

45 No conflict of interest

46

47 **Availability of data and material:**

48 Images and R-Script are available at first author’s convenience. The datasets generated during the
49 current study are available online on Osuris geonetwork. <https://www.osuris.fr/geonetwork/srv/fre/catalog.sear ch#/meta data/7528f bbb-e1ac-4db2-a179-f20d3 f03ff 83>.

50

51
52 **Authors’ contributions:**

53 L.J.M, F.H, M.T. and T.D. conceived the ideas. F.H. and L.J.M. collected data. T.D. and Y.R. set up
54 the photointerpretation method. L.J.M. and T.D. analysed the data. L.J.M, F.H and M.T. led the
55 writing with a contribution from T.D. All authors contributed to discussions. Following comments
56 from the Editor and three reviewers, L.J.M., F.H. and M.T. revised the manuscript with contributions
57 from T.D. and Y.R. designed the map.

58

59 **Introduction**

60

61 In recent decades climate change has been faster in various parts of the world (IPCC 2013). Islands
62 have been particularly concerned which threatened a large part of the insular floras (Harter et al. 2015;
63 Veron et al. 2019). Indeed, within species, to counter rapid climate changes, shift of geographical area,
64 individuals’ plastic responses or populations’ genetic adaptation might occur (Hoffmann and Sgrò
65 2011; Noble et al. 2019). However geographical shift of area will be limited for native insular plant
66 species (Chen et al. 2011). Insular plants will thus have to respond and keep up with the speed of
67 climate change, which will be particularly challenging if they are living close to their physiological
68 limits (Moritz and Agudo 2013). This is eminently interesting in the sub-Antarctic islands where
69 climate change is extremely fast (Smith 2002; Convey 2007; Lebouvier et al. 2011) and plants are
70 living close to such physiological limits (Hennion et al. 2006b). In the near future, global climate
71 change is predicted to have particularly strong effects at higher latitudes in the (sub-)polar regions
72 (IPCC 2013, 2014). For instance, according to the Representative Concentration Pathway scenario
73 (RCP) 6.0, an increase in minimum temperatures of about +1 to +1.5°C is expected before the end of

74 the current century, along with up to 10.0% change in precipitation, which may cause considerable
75 stress for plants restricted to cold habitats (Harter et al. 2015). Temperature seasonality will also be
76 affected, inducing an earlier and longer growth period, lower frequency of freeze-thaw cycles, and
77 higher frequency of droughts (Boelhouwers et al. 2003; Lebouvier et al. 2011; IPCC 2013; Harter et
78 al. 2015). Such is the case of the Kerguelen Islands, where the climate is chronically cool and windy
79 year-round, as is typical for the sub-Antarctic islands generally (Convey 1996), with a mean annual
80 temperature of 4.84°C for the period 1976-2008 (Lebouvier et al. 2011). Overall since 1950 mean
81 annual temperature increased (+0.016 °C.year⁻¹). Rainfall tends to decrease across time with two long
82 periods of rainfall below the average (1962-1976 and 1991-2011) and two short periods of rainfall
83 around the average (1977-1991 and 2011 until now) (Météo-France, compilation IPEV 136 - UMR
84 6553). These climatic changes have led to the retreat of the Cook ice cap which is among one of the
85 most drastic glaciers retreats on Earth (Verfaillie et al. 2015; Favier et al. 2016).

86 The sub-Antarctic Islands form a biogeographical unit, even if there are variations in their origins and
87 locations (Shaw et al. 2010). Kerguelen Islands with three other archipelagos (Prince Edward Islands,
88 Crozet archipelago and Heard and Mc Donald Islands) form the South Indian Ocean Province with
89 unique biodiversity and a high degree of endemism (Hennion and Walton 1997; Van der Putten et al.
90 2010). Impacts of climate change on vegetation have rapidly become apparent in the sub-Antarctic
91 Islands with for instance occasional wilting of native plants, or dieback in several cushion plants
92 (Frenot et al. 2001; Hennion et al. 2006a; Le Roux and McGeoch 2008; Bergstrom et al. 2015). Here
93 we focus on the cushion plant *Lyallia kerguelensis* Hook.f. (Montiaceae), strictly endemic to
94 Kerguelen, a monotypic genus and phylogenetically isolated in its family (Wagstaff and Hennion
95 2007; Nyffeler and Egli 2010). Partial necrosis of *L. kerguelensis* cushions was first described by
96 Hennion (1992), being absent from all previous descriptions of the species (Hooker 1847; Werth 1911;
97 Chastain 1958), and thereby suggesting it might be a recent phenomenon in this species (Fig. 1).
98 Furthermore, as partly necrotic cushions were mostly observed in the drier parts of the island it was
99 suggested that this necrosis may be induced by dry conditions (Hennion 1992; Wagstaff and Hennion
100 2007). Therefore, necrosis in *L. kerguelensis* cushions appeared variable and possibly related to local
101 climatic conditions.

102 Cushion plants are often typical of areas that experience cold or cool climates, low precipitation and/or
103 strong winds in various regions of the Earth (Körner 2003, 2016; Boucher et al. 2016). Such growth
104 forms have a low surface area to volume ratio, which aids in reduction of heat and water losses
105 (Körner 2003; Aubert et al. 2014). Typically, in plants morphology is among the functional traits that
106 vary in response to environmental, including climatic conditions. A few examples show that
107 morphology of cushion plants may respond to environment. Indeed cushion size was in relation to
108 altitudinal gradient, a proxy of temperature and precipitation in alpine environments (Kleier et al.
109 2015; Zhao et al. 2018). *Azorella compacta* (Apiaceae) plants present a larger surface area on the
110 cushion part with northern exposure side which maximizes solar radiation (Kleier et al. 2015).

111 Moreover, air circulation and windblown sediment around cushions may explain the initial
112 development of the crescent shape in *Azorella selago* (Combrinck 2008; Combrinck et al. 2020).
113 Hence morphological variation in size and shape can be considered as a proxy of the response capacity
114 of cushion plants to environmental, including climate variation (Körner 2016). In contrast, when
115 changes are fast low response capacity is expected. Direct drought sensitivity was demonstrated
116 experimentally in Marion Island for the cushion plant *A. selago* (Le Roux et al. 2005), with earlier
117 senescence (i.e. stem death) apparent in cushions with lower water availability. Dieback, or large scale
118 necrosis, is defined as a process during which portions of the cushion, or even the entire cushion, can
119 no longer regenerate new foliage (Armesto et al. 1980). Studies of the spatial dynamics of dieback in
120 the congeneric plant *A. macquariensis* from Macquarie Island highlight a relation of the dieback to a
121 potential decrease in soil water availability under recent climate change rather than a pathogenic
122 origin. Nevertheless, stressed plants might be more sensitive to infections (Whinam et al. 2014;
123 Bergstrom et al. 2015; Dickson et al. 2019). Finally, necrosis can be related to wind intensity, with
124 more necrosis on the more exposed part of the cushion (Kleier and Rundel 2004). These observations
125 suggest that necrosis may be due to or enhanced by climate change.
126 Measuring the variability of necrosis extent and morphology in *L. kerguelensis* more generally could
127 provide a proxy for the response capacity of the plant to climate change. *L. kerguelensis* could be
128 considered as a model case to study response capacity of an endemic plant species to climatic changes.
129 In the current study, we assumed that the morphological traits of *L. kerguelensis* co-vary so as to
130 maintain a hemispherical shape that is optimal in harsh environments. We then predicted that
131 morphological variation, including necrosis extent would be present across individuals and
132 populations. We hypothesized that water availability, wind exposure and slope aspect were likely
133 primary drivers of necrosis. To test these hypotheses, we (i) searched relations between growth traits
134 and the entire morphology (further called allometry) in *L. kerguelensis* to select appropriate traits for
135 assessing inter-population variability, and (ii) sought to identify relationships between this inter-
136 population variability and environmental conditions on one hand and geographical distances on the
137 other hand. Finally, we (iii) studied the influence of necrosis on the cushion morphology and
138 attempted to identify which environmental conditions are related to necrosis.

139

140 **Materials and methods**

141

142 *Lyallia kerguelensis* Hook.f. (Nyffeler and Eggli 2010), Montiaceae, is a long-lived perennial herb,
143 persisting at least 16 years (Wagstaff and Hennion 2007). It forms roughly round-shaped cushions
144 (Fig. 1) 20 – 40 cm across, exceptionally up to 1 m, in small and sparse populations (Hennion and
145 Walton 1997; Wagstaff and Hennion 2007). The root system is strong and deep, composed of a main
146 thick deep root branching out with numerous fine roots (Werth 1911; Chastain 1958). Furthermore, we
147 often observed aerial and slightly flexible roots that radiate from cushions and penetrate the soil at a

148 distance, likely functioning as guys to anchor the plant in the face of strong winds. *L. kerguelensis*
149 distribution in Kerguelen is sparse, with an altitude range from sea level to around 500 m a.s.l.
150 (Hennion and Walton 1997; Wagstaff and Hennion 2007; Réserve Naturelle TAF, IPEV Subanteco
151 and PlantEvol, unpublished) (Fig. 1). The species is restricted to windswept stony habitats in fellfields
152 or moraines (Wagstaff and Hennion 2007). Fellfields (or "wind deserts") are extensive, sterile, rocky
153 areas present from the shore to the highest elevations, and more generally characteristic of polar
154 regions (Aubert de la Rüe 1964). Vegetation is patchy, mainly composed of lichens and bryophytes
155 (Smith 1984; Block et al. 2009).

156 Our study was based on four field campaigns in the Kerguelen Islands (48°30' - 50°S, 68°27' -
157 70°35'E ; Lebouvier and Frenot 2007). The first three campaigns were from December to January
158 (2015-2016, 2016-2017 and 2017-2018), the last campaign was from December 2018 to March 2019.
159 In the current study, we analysed 319 plants from 19 populations (Fig. 2, Online Resource Table 1) in
160 three different regions of Kerguelen Islands: the northern part with Port Christmas (two populations)
161 and Ile MacMurdo (two populations), the south-western part with one population at Péninsule Rallier
162 du Baty, and the south-eastern part including populations in Vallée des Souilles in Presqu'île Ronarch
163 (three), Ile Australia north (three) and south (four), Ile Longue (two) and Plateau du Vent in Presqu'île
164 Jeanne d'Arc (two).

165 For each population, general environmental characteristics were recorded regarding types of fellfield
166 (slope, scree slope, plateau, summit, outwash plain), topography (flat, terrace, base or mid or top of
167 slope, summit, other); wind exposure (very sheltered, sheltered, exposed, very exposed); slope;
168 distance to sea; slope aspect; visual estimation of cover in percentage of blocks (>20cm), pebbles (2cm
169 to 20 cm), gravel (2mm to 2 cm), bare soil (<2mm), bryophytes and herbs. Soil conductivity, water
170 saturation and temperature were measured with a TRIME (Time Domain Reflectometry with
171 intelligent Micro Elements) probe. Altitude was determined using GPS (eTrex 10, Garmin). For each
172 sampled population, three samples of bare soil, 200 mL in total, were collected at different locations
173 around cushions to provide a composite soil sample. Half of the soil sample was immediately stored at
174 -20°C for subsequent determination of nitrate concentration (Laboratoire d'Analyse des Sols, INRA,
175 Arras, France). A small portion of the remaining fresh soil was mixed with 30 mL of distilled water
176 and then left for 18-24 h to permit the sedimentation of soil particles, and pH was then determined
177 using a pH meter (BASIC 20 PLUS CRISON, resolution 0.01 pH) (Hermant et al. 2013). The
178 remaining soil was dried at 105°C for 48 h, being weighed before and after drying. The dried soil was
179 used to determine soil texture and composition (Laboratoire d'Analyse des Sols, INRA, Arras, France)
180 (Online Resource Table 2). The studied cushions were selected following categories identified in an
181 earlier study (Dorey 2017, unpublished). Dorey (2017, unpublished) applied a random sampling of 83
182 *L. kerguelensis* cushions in 11 populations selected for their contrasted environments. With
183 exploratory analyses they observed that the percentage of explanation of environmental variables was
184 reduced with the increase of necrosis extent. They found that cushions above a threshold of 10%

185 necrotic surface area have lower relationship with environmental variables than below this threshold
186 (Online Resource Fig.1). In our study, we sampled cushions below and above this threshold to better
187 characterize the relationship between the necrosis extent and specific environmental variables for each
188 group. Within each population, we selected the same number of cushions from each category, defining
189 these as ‘vigorous cushion’ (visually less than 10% of necrotic extent), and ‘necrotic cushion’
190 (visually 10% to 80% of necrotic extent). The maximum proportion of necrosis retained in the study
191 was arbitrarily set at 80%, above which we considered the cushion as too affected to be reactive.
192 For each cushion, pictures were taken vertically from above the cushion and with a scale, without
193 shade on the cushion, allowing to see the top of each apex. An extraction protocol to measure
194 morphological traits by photointerpretation (Dorey 2017, unpublished) was then applied. The cushion
195 height was measured in the field for 229 cushions (data not available for AUS23, AUSN1, AUSN2
196 and AUSN4 populations). Image analyses were performed with Arcgis 10.6.1. We determined the
197 perimeter of the cushion (Online Resource Fig. 2a), the total surface area of the cushion (Online
198 Resources Fig. 2b), the percentage of neighbouring plants (Online Resource Fig. 2c), the necrotic
199 extent (Online Resources Fig. 2e); the shorter, longer radius and the cushion shape (Online Resources
200 Fig. 2f). Finally, we calculated a cushion compactness proxy (Cranston et al. 2015) using the
201 following formula:

$$\frac{\text{Compactness}}{\text{apex number}}$$

202
203
204 We calculated also two ratios, height and short radius and height and long radius of the cushion to
205 provide a proxy of the 3D shape of the cushion. A total of 11 morphological and biotic traits were
206 recorded and their mean values and standard deviations per population are provided in Table 1.
207 All statistical analyses were carried out in the open-source programming language R, version 3.4.2.
208 Graphs were produced with the *ggplot2* package (Wilkinson 2005). Random distributions of
209 morphological traits were verified within both necrotic categories and were then pooled except for the
210 necrotic extent trait. Spearman correlogram (*PerformanceAnalytics* package) was used to determine
211 the allometry of the traits of the 319 individuals, n=279 for variables using height. Based on these
212 allometric relationships, only the surface area, compactness and shape traits were used in subsequent
213 analyses. To determine the significance of inter-population variation in morphological traits, a
214 Kruskal-Wallis test was applied. To study the relationships between cushion morphology and
215 environment, the environmental conditions were divided into six categories (topography and habitat,
216 slope aspect, surface texture, soil texture, soil chemical composition and soil physical characteristics)
217 as shown in Table 2. In each category, Spearman correlogram was used to determine the covarying
218 variables. A multivariate model was established between each morphological trait and the
219 environmental categories. Normality and heteroscedasticity were checked respectively with the

220 Shapiro test (Royston 1982) and the *ncvTest* (package *car*, Fox and Weisberg 2019) and, if necessary,
221 a *box-cox* transformation was applied (package *MASS*, Venables and Ripley 2002). Then an AIC
222 backward (package *MASS*) analysis was applied to obtain a minimum adequate model. For the
223 multivariate cushion surface area and shape model with topography and habitat, a *post hoc* Emmeans
224 test was applied with the Tukey method (*emmeans* package). Finally, to study geographical distance
225 between populations a Mantel test (*Ade4* package) was performed; Euclidian distance for the trait,
226 Manhattan distance for the geographical coordinates, and 999 permutations for robustness of the p-
227 value were chosen.

228

229 **Results**

230

231 **Allometry of traits and morphological variability**

232 The surface area, perimeter, and height of the cushions were strongly positively correlated one to each
233 other (Table 3). However, the cushion compactness was correlated only with the cushion height and
234 the cushion shape was correlated to none of the other morphological traits. Mean cushion shape ratio
235 (relation between short and long diameter) was 0.75 ($n = 319$, $sd = 0.01$) with low variation indicating
236 that cushions approximate an ovoid cushion shape. Moreover, the ratios between height and short or
237 long radius were also close to 1 ($n = 279$, mean \pm sd; 0.85 ± 0.03 and 1.17 ± 0.04 respectively). For
238 vigorous and non-vigorous cushions the relationships between the necrosis extent and the three
239 morphological traits (cushion surface area, shape, and compactness) were not significant.

240 Biotic traits relating to the neighbouring plant community (epiphyte proportion and neighbouring plant
241 proportion) were positively correlated one to each other but also with most of the morphological traits,
242 except for cushion height (not correlated with the proportion of epiphytes) and shape (correlated with
243 none of these biotic traits) (Table 3).

244 To determine inter-population variability in plant morphological traits, Kruskal-Wallis tests were
245 performed. Significant variation between populations was detected for the cushion surface area (Chi-
246 squared test, $X_{318} = 94.011$, $p < 0.0001$), compactness (Chi-squared test, $X_{318} = 134.47$, $p < 0.0001$)
247 and shape (Chi-squared test, $X_{318} = 29.292$, $p = 0.0377$). Between populations, for vigorous cushions
248 the necrosis extent varied significantly (Chi-square test, $X_{18} = 35.943$, $p = 0.0072$). In contrast, for
249 necrotic cushions inter-population variations of necrosis extent were not significant (Chi-square test,
250 $X_{18} = 16.348$, $p = 0.5683$).

251

252 **Relationships between cushion morphology and environment or geography**

253 The variability of the cushion surface area across populations was well explained by the topography
254 and habitat, slope aspect and soil texture models, explaining 75%, 54% and 19% of overall variation
255 respectively (Table 4). In the first model, two conditions were significant, topography and wind

256 exposure, without significant interaction. A *post-hoc* test showed that larger cushions were present
257 mid-slope rather than on flat areas (Fig. 3a). A non-significant trend of larger surface area with a
258 decrease of wind exposure was found. For the slope aspect model, the *post hoc* test did not identify
259 any significant slope aspect influencing the cushion surface area. Finally, soil texture was positively
260 related to the cushion surface area, with a larger percentage of coarse sand being correlated to a larger
261 cushion surface area. Inter-population variability in cushion shape was explained (52% of variation)
262 by the univariate model with slope aspect variable (Table 4), with a lower circular shape preferentially
263 observed with south-east slope aspect compared to locations with south-west or north-east slope
264 aspects or flat locations (Fig. 3b). Besides, variability in cushion compactness was significantly related
265 to the surface texture model (18% of variation; Table 4), and was positively correlated to the
266 proportion of bare soil (Pearson correlation, $r = 0.478$, $n = 19$, $p = 0.039$). To determine relationships
267 between population morphology and geography, we applied Mantel tests separately for each
268 morphological trait. For cushion surface area and shape the results of the Mantel tests were
269 insignificant, respectively, $r = -0.178$, $p = 0.933$ and $r = -0.022$, $p = 0.441$. The results were significant
270 only for the cushion compactness ($r = 0.320$, $p = 0.011$), where longer distances across populations
271 were related to higher inter-population variability of cushion compactness but not of cushion shape or
272 surface area.

273

274 **Relationship between cushion necrosis and environment or geography**

275 We investigated whether environmental variables explained necrosis extent across populations. For
276 necrotic cushions models were insignificant (data not shown). For vigorous cushions, only the sodium
277 concentration (ANOVA, $F_{14} = 0.081$, $p = 0.0219$) was significant in the soil composition model
278 (*adjusted R*² = 27%, Fig. 4) Mantel tests of the necrosis / geographic distance relationships were
279 significant for neither vigorous nor necrotic cushions ($r = -0.05$, $p = 0.645$; and $r = -0.05$, $p = 0.530$,
280 respectively).

281

282 **Discussion**

283

284 Cushion allometry was observed for most of the morphological traits analysed. Three traits were
285 selected as representative of the allometry: cushion surface area, shape and compactness. For each
286 trait, the variation among the populations could be explained by environmental and geographical
287 variables. Finally, necrosis extent did not vary with morphological traits but in vigorous cushions
288 inter-population variation was related to soil composition.

289

290 **Allometry of traits and morphological variability**

291 A previous study indicated a strong relationship between height and diameter in *L. kerguelensis*
292 (Hermant et al. 2013). Here we determined that along with height and diameter, shape and

293 compactness were positively correlated. Similar allometry has been reported elsewhere in other
294 species of cushion plants (Niklas 1994). Besides, shape ratio showed low variation suggesting a
295 conserved circular shape, and height-radius ratio close to 1 strengthened the hemispherical shape of *L.*
296 *kerguelensis* cushions. Our study confirms the position of *L. kerguelensis* in the class C1
297 (hemispherical, compact and hard cushion) of Aubert et al. (2014). Positive correlations were also
298 observed between cushion morphology and biotic variables, suggesting that larger cushions of *L.*
299 *kerguelensis* (surface area, perimeter and compactness) provide greater opportunity to trap dispersing
300 seeds and are favorable environments for other plant species. Furthermore larger and older cushions
301 might have provided a longer period of colonization opportunities for epiphytes. Similar results were
302 observed for various cushion plants in the high Andes (Arredondo-Núñez et al. 2009).
303 The degree of necrosis was not related to the morphological traits studied, suggesting that necrosis is
304 not encouraged by a particular morphology, contrary to our initial expectation that necrosis would
305 cause sagging and change in cushion shape leading to lower cushion compactness as observed in
306 *Azorella macquariensis* (Bergstrom et al. 2015). Vigorous cushions (<10% necrosis) showed inter-
307 population variability in mean necrosis, varying from 0.70% to 5.18%. This suggests that some
308 populations are less subject to necrosis or that recovery can occur, as has been noted in a previous
309 survey (Dorey, 2017 unpublished). However, for necrotic cushions (>10% necrosis) inter-population
310 variation was not significant, confirming the presence of necrosis in all the populations studied
311 without influence of specific environmental conditions.

312

313 **Relationships between environment, geography and morphology**

314 The surface area of cushions was related to topography and wind exposure, with larger cushions
315 predominantly developing mid-slope rather than on flat areas, and a trend of larger cushions in less
316 wind-exposed populations. In the fragmented landscape and harsh climate of Kerguelen, topography
317 and wind are two major environmental components. The hilly topography of the island (Fig. 2)
318 generates heterogeneity in rainfall, water retention and wind exposure (Aubert de la Rüe 1964;
319 Wagstaff and Hennion 2007). Mid-slope areas receive runoff water from higher altitude and at the
320 time drain to lower altitude, unlike flatter areas, while wetlands usually develop at the base of slopes.
321 The Kerguelen Islands, like other sub-Antarctic islands, are considered to have moist climates
322 (Hennion et al. 2006b) and sub-Antarctic plants are known for their requirement of water for growth
323 (Dorne and Bligny 1993; Hennion and Walton 1997). Thus, mid-slope may provide optimal water
324 supply for the growth of *L. kerguelensis*. Furthermore, wind exposure induces mechanical stress and
325 can accelerate transpiration of plants (Körner 2003; Hausmann et al. 2009; Gardiner et al. 2016).
326 Plants from *L. kerguelensis* developing in less windy environments such as mid-slope may be less
327 subject to extreme meteorological events like storms or severe frost. Finally, contents of coarse sand in
328 the underlying soil was positively correlated to cushion surface area. Sandy soils are generally well

329 draining, with low water storage capacity and a high usable fraction (Körner, 2003). This finding
330 suggests that ease of water uptake favours larger cushions.

331 Variation in cushion shape between populations was mainly explained by slope aspect. In Kerguelen,
332 north and north-west slope aspects provide the greatest solar exposure but are also the most exposed to
333 wind, and vegetation is more luxurious away from these slope aspects (south or east aspect) (Werth
334 1911; Aubert de la Rüe 1964). Our data indicated lower occurrence of circular cushions on the south-
335 east aspect, less exposed to wind, suggesting that the circular shape might be associated with wind
336 exposure in *L. kerguelensis*. This finding is in agreement with the recent air flow dynamics model on
337 *A. selago* where cushions with more pronounced crescent shapes were in habitats with less airflow
338 turbulence (Combrinck et al. 2020).

339 Variability in cushion compactness was partly explained by the proportion of bare soil and geographic
340 distance between populations. Greater cushion compactness was correlated with a higher proportion of
341 bare soil. This may indicate lower protection against wind than on rocky ground, possibly in relation
342 to greater exposure to cold or desiccation stressed. It is interesting to note that compactness in cushion
343 plants generally co-varies with altitude, that may be correlated to temperature and humidity variation
344 (He et al. 2014; Cranston et al. 2015; Zhao et al. 2018). However, *L. kerguelensis* did not show
345 compactness variation across the altitudinal gradient examined here. In summary, cushion surface
346 area, shape and compactness were all driven primarily by two major environmental variables: wind
347 intensity and water availability.

348

349 **Relationships between environment, geography and necrosis**

350 The only environmental variable significantly linked with variation in necrosis was soil sodium
351 content for cushions with low necrosis extent only. The nearest distance to the sea was negatively
352 related to soil sodium concentration ($t_{17} = 2.27$, $p = 0.036$), and a decrease with altitude was observed.
353 Salt is carried in wind-blown sea spray from which it enters the soil, and in the sub-Antarctic marine
354 salt may be found far from the coast due to permanent strong winds (Smith 1987; Jenkin 1997).
355 Furthermore, in Marion Island salinity gradient with altitude and distance from the sea is observed
356 (Conradie and Smith 2012). The mean soil sodium concentration was similar in our sites in Kerguelen
357 to that in Marion Island (Conradie and Smith 2012), supporting the hypothesis of a similar marine
358 influence in both islands. Nevertheless necrosis extent in *L. kerguelensis* was not directly related to the
359 nearest distance to the sea ($t_{17} = -1.43$, $p = 0.170$).

360 From a physiological point of view, sodium induces adjustment of osmotic potential in plants through
361 various mechanisms (Navarro et al. 2007; Shabala 2013). Ion homeostasis (partly with sodium) is
362 achieved during abiotic stress and allows to keep an osmotic potential sufficient for water absorption
363 and then sustain turgor of the cells (Pardo and Quintero 2002). Furthermore, sodium at high
364 concentration can reduce stomata density and then alter photosynthesis (Orsini et al. 2011). In the sub-
365 Antarctic region, studies of salt stress have been performed on several plant species some of which are

366 spread from the coast up to fellfields, concluding that such plants could be defined as glycophytes
367 tolerant of salt stress (Smith 1978; Hennion and Bouchereau 1998; Hummel et al. 2004). For *L.*
368 *keruelensis*, higher sodium concentrations in soil may add to other abiotic stresses in their habitats
369 and increase their sensitivity to other osmotic stresses such as drought as was found in other plants
370 (Jamshidi Goharrizi et al. 2020). Taken together, our data suggest that necrosis may be related to water
371 availability, although a pathogenic origin cannot be excluded. Our results are consistent with the
372 findings on *A. macquariensis* where dieback was related to summer water availability (Whinam et al.
373 2014; Bergstrom et al. 2015; Dickson et al. 2019) and do not support a pathogenic origin.

374

375 **Possible impact of climate change on *L. kerguelensis***

376 In summary, cushion surface area, shape and compactness were primarily driven by two
377 environmental variables: wind intensity and water availability. Cushion necrosis also seems to be
378 linked with multiple stresses and mainly osmotic stresses such as drought. However environmental
379 changes expected with the RCP 6.0 model include an overall +1.26 to + 1.50°C temperature increase
380 by 2081-2100, along with 0.1% to 10.0% lower water availability (Harter et al. 2015), which will
381 increase stress for plant populations already facing low water availability or unfavorable slope aspect,
382 exposing them to higher wind desiccation. Indeed, change already observed in precipitation in the
383 Kerguelen Islands over the past 60 years (Lebouvier et al. 2011) may have triggered necrosis or
384 enhanced the process, as observed on Macquarie Island with increased wind speed, hours of sunshine
385 and evapotranspiration over 17 years (Bergstrom et al. 2015; Dickson et al. 2019). Under the scenario
386 outlined above cushion necrosis in *L. kerguelensis* may therefore become increasingly frequent.

387

388 **Conclusions**

389

390 Our study confirms that *L. kerguelensis* cushions tend to form a hemispherical shape. The size and
391 compactness of the plant vary with environmental conditions (topography, slope aspect, wind
392 exposure and soil texture) and geography, all of which are related to wind intensity and/or water
393 availability. The occurrence of necrosis in cushions was related partly to soil salinity. Higher sodium
394 concentrations in soil may worsen the impacts of other osmotic stresses such as drought, resulting in
395 necrosis increase. Our results suggest that, under current climate change trends in the Kerguelen
396 Islands, cushion morphology may have the capacity to change to adjust to environmental variation.
397 However, in the future, cushion necrosis may be accelerated in the driest and most saline
398 environments. *In situ* experiments are required to better understand the drivers of necrosis, coupled
399 with long-term monitoring to document the dynamics of necrosis and any potential recovery.

400

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606 **Figures and Tables**

607

608 **Table 1:** Morphological traits of *L. kerguelensis* and biotic traits per population (mean +/- standard
609 deviation): number of individuals, cushion surface area, cushion perimeter, cushion compactness,
610 cushion shape, cushion height, ratio height/short radius, ratio height/long radius, proportion of
611 neighbouring plants in contact with the perimeter, proportion of epiphytes across the cushion surface
612 area, necrosis extent for vigorous cushions (defined with less than 10% necrosis extent) and necrosis
613 extent for necrotic cushions (defined with more than 10% necrosis extent). NA= data not available.
614 For necrosis extent of vigorous and necrotic cushions mean and standard deviations were calculated
615 per category per population.

616

617 **Table 2:** Environmental characteristics used in the multivariate models of the 19 populations of *L.*
618 *kerguelensis* studied. Topography and type of habitat: altitude, type of fellfield (slope, scree slope,
619 plateau, summit, outwash plain), topography (flat, terrace, base or mid or top of slope, summit, other),
620 wind exposure (very sheltered, sheltered, exposed, very exposed), range of slopes (0°,]0-3°,]3-
621 10°,]10-30°,]30-80°); slope aspect (N, NW, W, SW, S, SE, E, without dominate slope aspect);
622 visual estimation of surface texture: pebbles (2cm to 20 cm), bare soil (<2mm) and herbaceous cover
623 in percentage; soil texture: clay and coarse sand percentage; soil chemical composition: Na, Mn, Al
624 cmol.kg⁻¹, P and N g.kg⁻¹, ratio C.N⁻¹; soil physical characteristics: pH, organic matter and soil
625 humidity.

626

627 **Table 3:** Spearman correlations and *p*-values for correlations of each morphological and biotic trait.
628 Cushion surface area, cushion perimeter, cushion height, cushion shape, cushion compactness,
629 proportion of epiphytes across the cushion surface area and proportion of neighbouring plants in
630 contact with the cushion perimeter. For volume and height *n* = 229, the other traits *n* = 319. Asterisks
631 indicate the significance of the correlation * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001

632

633 **Table 4:** Minimum adequate multivariate linear models of morphological traits and environmental
634 conditions; *n* = 19, adjusted *R*² (*ad. R*²), degree of freedom (*df*), *F*-value and *p*-value are presented.
635 Cushion surface area model with variables of topography and habitat, of slope aspect and of soil
636 texture; cushion shape model with variable of slope aspect; cushion compactness model with variable
637 of texture surface; bold numbers indicate significant variables.

638

639 **Figure 1:** *Lyallia kerguelensis* cushion. An epiphytic *Festuca contracta* T. Kirk plant is present in the
640 cushion, the neighbouring plants on the left of the picture are *Agrostis magellanica* Lam.. Necrotic
641 and vigorous apices are shown (respectively red and white arrows).

642

643 **Figure 2:** Locations of the 19 studied populations of *Lyallia kerguelensis* (black triangles) in
644 Kerguelen Islands on an altitudinal background (NASA – SRTM 30M, 2005); the black dot indicates
645 the research station, labels indicate important features in the island. Top right map: distribution of *L.*
646 *kerguelensis* on Kerguelen Islands (black dot) in April 2018; data from the Réserve Naturelle Terres
647 Australes Françaises and Institut Polaire Français, programs 136 and 1116) map background from IGN
648 1/200 000 georeferenced with spatial adjustment (D. Fourcy, unpublished). The small globe sets the
649 Kerguelen Islands in the South Indian Ocean. ArcGIS 10.8.1

650
651 **Figure 3:** a: Prediction of cushion surface area (m²) with various topographies. The black dot
652 represents the value of the linear model and the grey shape the 95% confidence interval. Different
653 letters indicate significant differences ($p < 0.05$) with topography. b: Prediction of shape with various
654 slope aspects. The black dot represents the value of the linear model and the grey shape the 95%
655 confidence interval. Different letters indicate significant differences ($p < 0.05$) between slope aspects.

656
657 **Figure 4:** Relationship between soil sodium concentration and mean necrosis extent (%); a panel:
658 linear regression $t_{14} = 2.922$, $p = 0.0112$, $n=16$ The grey strips represent the 95% confidence interval.

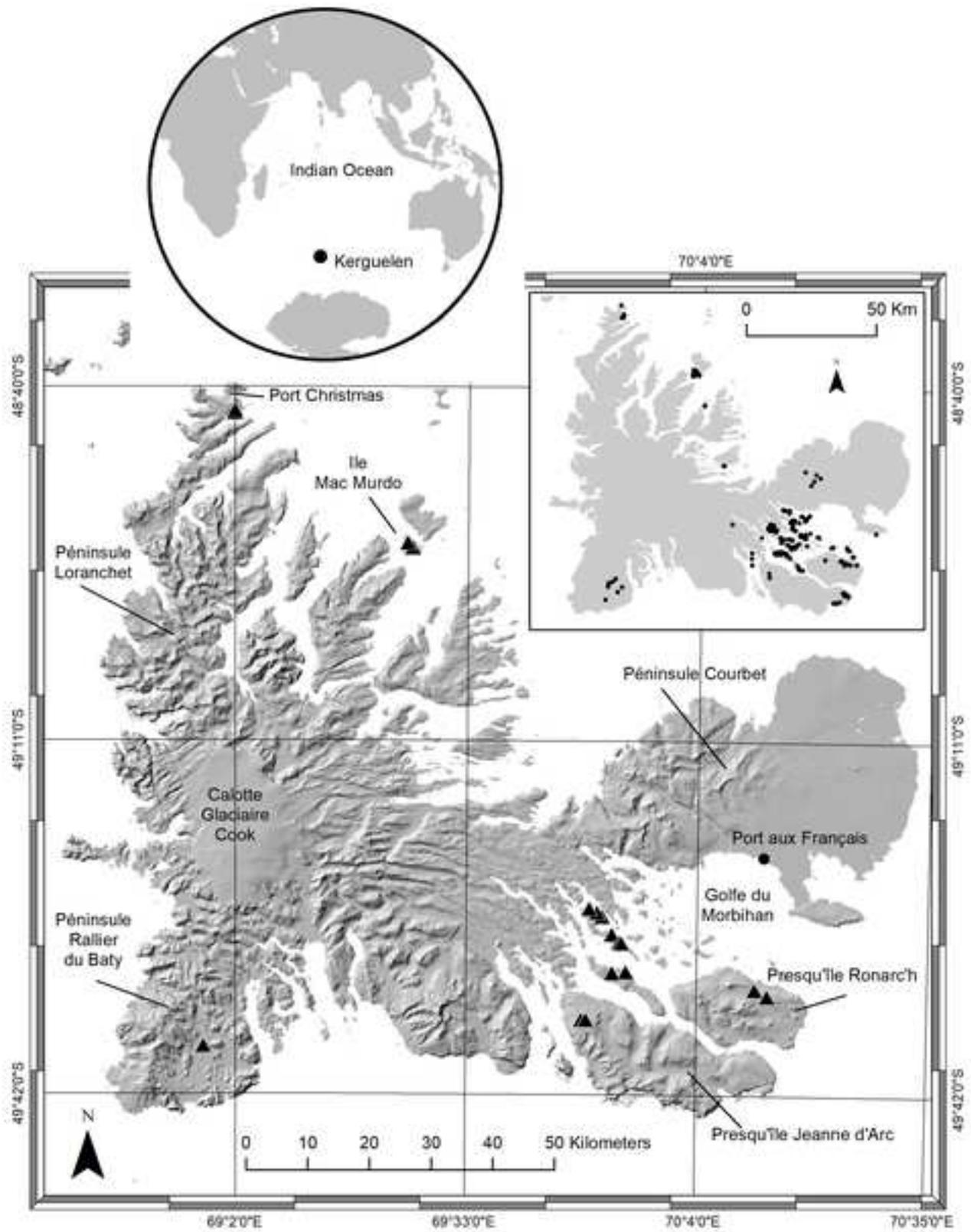


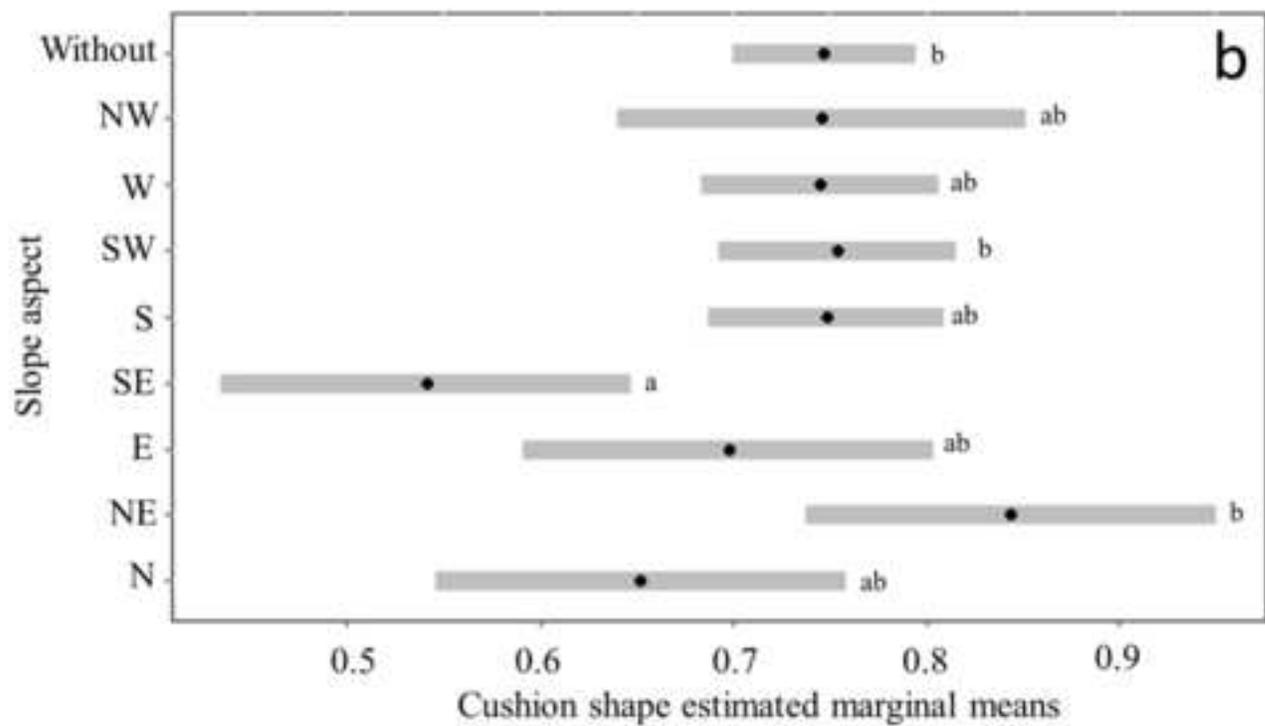
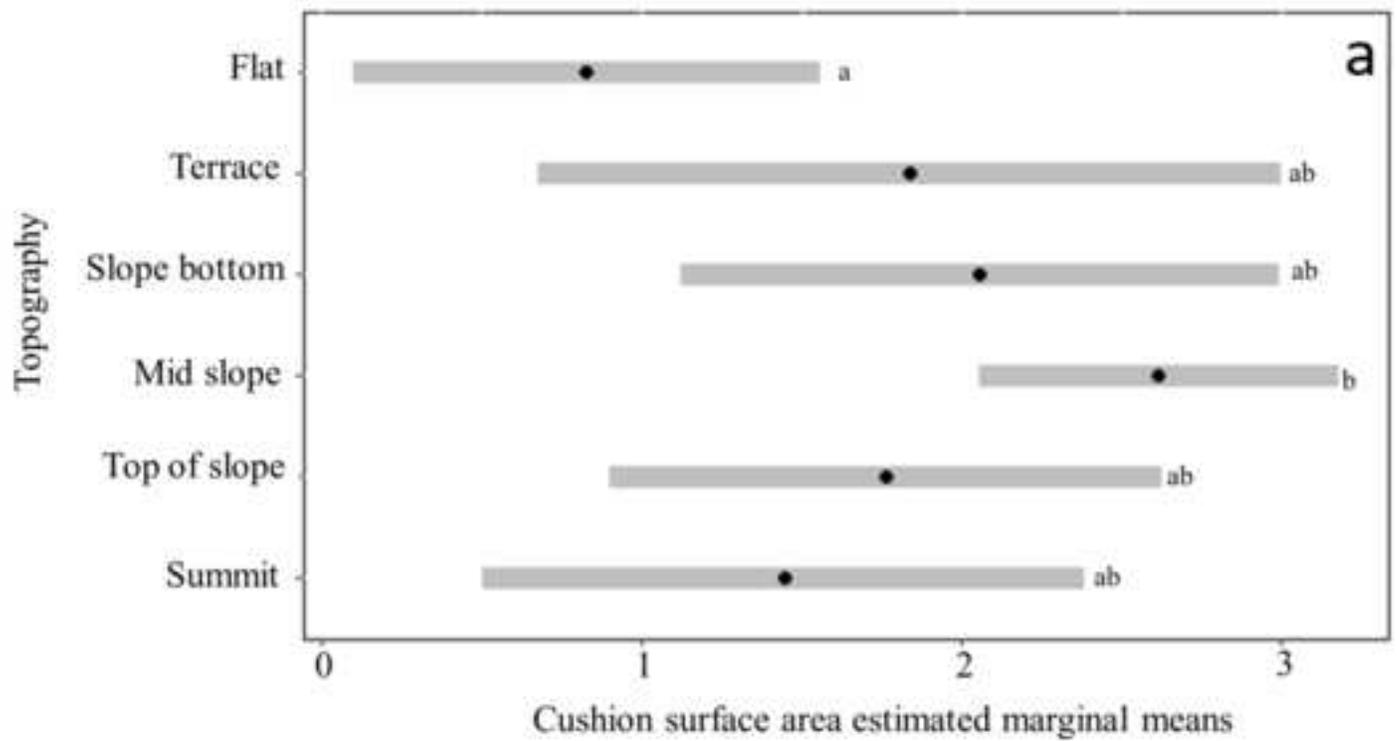
Necrotic apex

Vigorous apex

05/01/2016

2cm





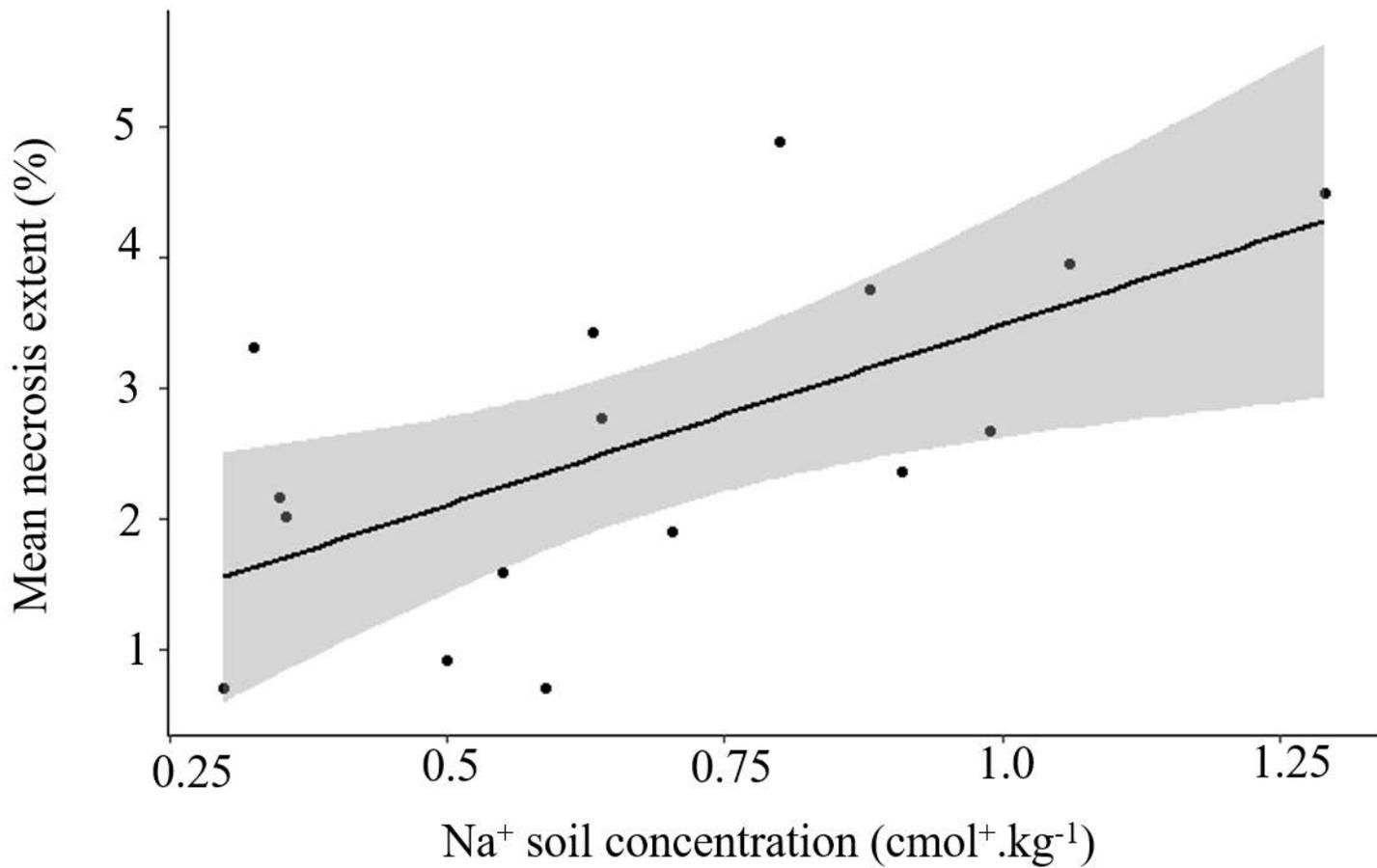


Table 1:

Population	Cushion						Necrotic extent (%)						
	Number of individuals	surface area (cm ²)	Cushion perimeter (cm)	Cushion compactness	Cushion shape	Height / short radius	Height/ long radius	Proportion of neighbouring plants	Proportion of epiphytes	for vigorous cushion	Necrotic extent (%) for necrotic cushion		
AUS23	12	215.80 ± 46.83	88.94 ± 14.64	4.58 ± 0.48	0.65 ± 0.03	NA	NA	NA	31.57 ± 7.19	0.0008 ± 0.0007	0.92 ± 0.11	32.40 ± 6.05	
AUS25	20	122.73 ± 21.63	56.39 ± 5.20	7.53 ± 0.77	0.71 ± 0.05	5.95 ± 0.55	0.89 ± 0.09	1.24 ± 0.10	63.99 ± 6.63	0.0002 ± <0.0001	2.91 ± 0.99	32.30 ± 8.22	
AUS30	20	162.33 ± 44.01	50.38 ± 7.00	5.85 ± 0.28	0.76 ± 0.04	7.52 ± 1.04	0.65 ± 0.52	0.86 ± 0.05	32.13 ± 6.53	0.0002 ± 0.0001	0.70 ± 0.33	21.24 ± 3.13	
AUS32	19	97.26 ± 13.21	42.98 ± 3.41	5.49 ± 0.38	0.70 ± 0.05	7.00 ± 0.74	0.65 ± 0.41	0.92 ± 0.07	34.72 ± 5.88	<0.0001 ± <0.0001	3.96 ± 0.86	22.16 ± 3.91	
AUSN1	10	250.69 ± 62.95	84.82 ± 11.25	6.69 ± 0.82	0.77 ± 0.04	NA	NA	NA	41.30 ± 5.60	0.0009 ± 0.0003	2.37 ± 1.69	25.50 ± 7.46	
AUSN2	10	301.46 ± 50.83	95.83 ± 13.31	7.74 ± 0.27	0.84 ± 0.02	NA	NA	NA	44.67 ± 8.89	0.0020 ± 0.0008	4.89 ± 1.24	15.48 ± 3.34	
AUSN4	8	168.21 ± 69.98	57.58 ± 14.82	6.37 ± 0.84	0.69 ± 0.08	NA	NA	NA	14.90 ± 5.05	0.0005 ± 0.0004	3.76 ± 1.44	20.00 ± 2.83	
LON11	12	29.78 ± 6.65	24.49 ± 2.62	6.89 ± 0.46	0.70 ± 0.05	4.21 ± 0.66	0.63 ± 0.08	0.93 ± 0.11	19.46 ± 7.12	<0.0001 ± <0.0001	1.90 ± 1.45	26.29 ± 5.81	
LON30	20	62.26 ± 9.01	36.36 ± 3.54	5.48 ± 0.32	0.80 ± 0.04	6.35 ± 0.44	0.54 ± 0.03	0.71 ± 0.04	24.09 ± 6.10	0.0001 ± <0.0001	2.78 ± 0.94	25.52 ± 2.74	
MAC1	19	126.66 ± 24.90	51.91 ± 5.82	3.76 ± 0.18	0.68 ± 0.06	6.20 ± 0.52	0.71 ± 0.07	1.08 ± 0.09	20.09 ± 5.09	<0.0001 ± <0.0001	3.43 ± 0.89	21.70 ± 3.56	
MAC3	20	99.15 ± 14.91	44.06 ± 3.51	4.25 ± 0.20	0.81 ± 0.04	5.93 ± 0.56	0.81 ± 0.06	1.02 ± 0.07	11.23 ± 3.37	<0.0001 ± <0.0001	2.67 ± 0.26	25.19 ± 1.14	
PI21	20	39.55 ± 5.48	30.50 ± 2.43	6.48 ± 0.27	0.75 ± 0.05	2.41 ± 0.25	1.24 ± 0.14	1.75 ± 0.19	0.46 ± 0.45	<0.0001 ± <0.0001	3.32 ± 0.27	23.13 ± 0.72	
PI22	10	122.30 ± 31.35	69.51 ± 7.43	5.50 ± 0.23	0.54 ± 0.06	4.40 ± 0.56	1.14 ± 0.21	2.16 ± 0.31	40.13 ± 8.38	0.0010 ± 0.0004	4.06 ± 1.17	21.29 ± 6.11	
PI23	20	100.61 ± 20.06	47.30 ± 5.47	6.55 ± 0.42	0.73 ± 0.03	7.90 ± 0.92	0.59 ± 0.07	0.81 ± 0.09	18.60 ± 6.31	<0.0001 ± <0.0001	4.49 ± 0.36	37.10 ± 4.77	
PCR1	20	68.99 ± 11.91	172.84 ± 136.32	4.60 ± 0.26	0.81 ± 0.03	4.35 ± 0.81	0.85 ± 0.09	1.11 ± 0.11	28.00 ± 5.43	<0.0001 ± <0.0001	1.60 ± 0.23	29.25 ± 1.69	
PCR2	18	146.18 ± 55.67	51.17 ± 9.00	4.28 ± 0.35	0.74 ± 0.05	7.23 ± 0.58	0.83 ± 0.06	1.11 ± 0.08	15.90 ± 3.62	0.0001 ± <0.0001	2.16 ± 0.91	37.36 ± 6.58	
PJDA2	20	162.06 ± 68.53	40.88 ± 11.57	5.45 ± 0.33	0.75 ± 0.04	4.05 ± 0.22	1.49 ± 0.13	1.96 ± 0.17	12.98 ± 4.97	0.0001 ± <0.0001	0.70 ± 0.54	51.39 ± 6.75	
PJDA6	20	261.61 ± 65.94	80.82 ± 13.68	5.40 ± 0.17	0.77 ± 0.03	5.68 ± 0.64	0.76 ± 0.07	0.95 ± 0.07	24.00 ± 4.88	<0.0001 ± <0.0001	2.01 ± 0.79	28.59 ± 3.09	
RBA5	20	162.15 ± 26.47	74.74 ± 7.93	6.51 ± 0.23	0.76 ± 0.02	4.89 ± 0.13	0.88 ± 0.08	1.14 ± 0.10	27.26 ± 4.99	0.000 ± 0.000	5.18 ± 1.33	32.70 ± 5.22	

Table 2:

category	Topography and type of habitat				Slope aspect		Surface texture		Soil texture			Soil chemical composition					Soil physical characteristic			
	Populati on	Altitu de (m)	Type of fellfield	Topography	Wind exposure	Slope	Slope aspect	Pebble (2 to 20cm) cover (%)	Soil (< 2mm) cover (%)	Herbaceous cover (%)	% clay	% coarse sand	Na cmol kg ⁻¹	Mn cmol kg ⁻¹	Al cmol kg ⁻¹	P g kg ⁻¹	N g kg ⁻¹	C N ⁻¹	pH	Organic matter g kg ⁻¹
AUS23	137	slope	mid slope	exposed	[3-10]	N	10	0	30	5.5	92.6	0.50	0.054	0.481	0.015	2.27	12.9	6.54	29.1	55.32
AUS25	125	scree slope	mid slope	very exposed	[10-30]	NW	20	20	30	4.9	57.6	1.66	0.039	0.546	0.011	1.85	12.9	6.12	23.9	24.27
AUS30	15	plateau	Slope base	very exposed	[3-10]	NW	30	10	20	5.3	65.5	0.59	0.015	0.542	0.009	1.85	12.3	6.12	22.7	17.67
AUS32	60	plateau	flat	very exposed	[0-3]	E	30	10	30	6.5	50.6	1.06	0.015	0.071	0.017	3.25	11.0	6.70	35.9	5.77
AUSN1	14	slope	mid slope	intermediate	[10-30]	SW	30	10	20	5.4	58.5	0.91	0.017	0.080	0.009	2.37	13.0	6.80	30.9	25.86
AUSN2	32	slope	mid slope	intermediate	[10-30]	NE	30	10	20	4.7	73.7	0.80	0.013	0.064	0.010	1.81	13.2	6.90	23.8	26.65
AUSN4	22	plateau	summit	exposed	0	S	30	10	10	4.2	24.2	0.88	0.005	0.159	0.013	2.02	12.2	6.40	24.6	32.02
LON11	84	plateau	flat	very exposed	0	Without	15	5	5	7.9	44.5	0.70	0.015	0.882	0.019	2.92	11.5	5.25	33.5	52.98
LON30	154	plateau	flat	very exposed	0	Without	15	5	5	8.5	35.7	0.64	0.021	1.710	0.027	3.66	11.4	5.52	41.7	34.99
MAC1	55	plateau	summit	very exposed	0	Without	10	5	5	7.3	45.0	0.63	0.020	0.809	0.014	2.66	12.9	6.34	34.3	23.67
MAC3	153	summit	top of slope	very exposed	[10-30]	S	25	2	15	3.6	61.5	0.99	0.014	0.903	0.005	0.67	12.5	6.80	8.35	32.00
P121	250	slope	top of slope	very exposed	[0-3]	S	70	2	10	6.0	35.9	0.33	0.010	1.290	0.025	2.04	11.6	5.77	23.6	33.00
P122	320	slope	Slope base	very exposed	[0-3]	SE	70	0	30	5.4	40.6	0.23	0.030	1.520	0.021	1.97	11.7	5.75	23.1	19.67
P123	340	scree slope	top of slope	very exposed	[3-10]	SW	10	5	10	5.2	58.4	1.29	0.010	0.160	0.036	0.43	11.7	6.36	5.04	6.78
PCR1	238	plateau	flat	exposed	0	Without	40	5	20	4.1	74.5	0.55	0.031	0.503	0.025	1.35	11.4	6.58	15.4	18.89
PCR2	216	plateau	flat	exposed	0	without	30	5	20	5.0	51.5	0.35	0.013	0.202	0.024	1.42	11.0	5.62	15.6	21.71
PJDA10	520	plateau	terrace	very exposed	[3-10]	NW	40	5	40	4.2	71.0	0.30	0.019	0.764	0.025	1.12	11.9	6.04	13.4	14.53
PJDA6	482	plateau	mid slope	very exposed	[10-30]	W	30	10	15	4.9	66.8	0.35	0.019	0.755	0.038	0.80	10.7	6.21	8.53	14.00
RBA5	71	outwash plain	flat	exposed	0	SW	35	0	20	0.4	78.4	0.21	0.016	0.145	0.003	0.25	10.7	6.55	4.24	17.53

Table 3:

	Cushion surface area	Cushion perimeter	Cushion height	Cushion shape	Cushion compactness	Proportion of epiphytes	Proportion of neighbouring plants
Cushion surface area	1	0.94***	0.68***	0.05	-0.04	0.37 ***	0.40***
Cushion perimeter		1	0.60***	-0.10	-0.01	0.44***	0.42***
Cushion height			1	0.08	-0.12*	0.05	0.33***
Cushion shape				1	0.10	-0.04	0.01
Cushion compactness					1	0.20***	0.19***
Proportion of epiphytes						1	0.34***
Proportion of neighbouring plants							1

Table 4:

Cushion surface area				
	<i>Ad. R²</i>	<i>df</i>	<i>F-value</i>	<i>p-value</i>
Topography & habitat	75%	8		
Topography			9.153	0.0037
Wind exposure			9.403	0.0154
Type of fellfield			1.913	0.2017
Slope aspect	64%	10		
Slope aspect			4.978	0.001
Soil texture	19%	17		
Coarse sand			2.273	0.0363
Cushion shape				
	<i>Ad. R²</i>	<i>df</i>	<i>F-value</i>	<i>p-value</i>
Slope aspect	52%	10		
Slope aspect			4.455	0.0352
Cushion compactness				
	<i>Ad. R²</i>	<i>df</i>	<i>F-value</i>	<i>p-value</i>
Surface texture	18%	17		
Bare soil			4.974	0.0395

ELECTRONIC SUPPLEMENTARY MATERIAL

Online Resource Table 1: environmental characteristics of the 19 populations of *L. kerguelensis* studied. At population scale: longitude; latitude; altitude; type of fellfield (slope, scree slope, plateau, summit, wall, fault, outwash plain); topography (flat, terrace, base or mid or top of slope, summit, other); wind exposure (very sheltered, sheltered, exposed, very exposed); range of slope (0° ,] $0-3^\circ$],] $3-10^\circ$],] $10-30^\circ$],] $30-80^\circ$]); distance to the closest sea shore; slope aspect (N, NW, W, SW, S, SE, E, without dominant slope aspect); visual estimation of blocks (>20cm), pebbles (2cm to 20 cm), gravel (2mm to 2 cm), bare soil (<2mm), bryophyte and herbaceous cover in percentage.

Online Resource Table 2: soil characteristics of the 19 populations of *L. kerguelensis* studied; soil texture (clay, sand, silt), soil chemical composition (Na, Mn, Al, CEC, P, N, $C.N^{-1}$, NO_3^- , NH_4^+) and soil hydric characteristics (pH, conductivity and soil water saturation).

Online Resource Table 3: quantitative description of physical attributes and environmental parameters of the 19 populations studied. Topography and type of habitat: altitude, type of fellfield (slope, scree slope, plateau, summit, wall, fault, outwash plain), topography (flat, terrace, base or mid or top of slope, summit, other), range of slope (0° ,] $0-3^\circ$],] $3-10^\circ$],] $10-30^\circ$],] $30-80^\circ$],), slope aspect (N, NW, W, SW, S, SE, E, without dominant slope aspect); distance to the sea and wind exposure (very sheltered, sheltered, exposed, very exposed); visual estimation of surface texture: mineral block (>20cm), pebbles (2cm to 20 cm), gravel (2cm to 2mm), bare soil (<2mm), bryophyte and herbaceous cover in percentage; soil texture: clay, silt (fine + coarse) and sand (fine + coarse) percentage; soil chemical composition: Ca^{2+} , P, N, ratio C N^{-1} , Mn, Al, Na, CEC, NO_3^- , NH_4^+ , Fe; soil physical characteristics: conductivity, pH, soil water saturation and organic matter.

Online Resource Table 1

Population	Latitude	Longitude	Altitude (m)	Type of fellfield	Topography	Wind exposure	Slope (°)	Distance to the sea (hm)	Slope aspect	Block cover (%)	Pebble cover (%)	Gravel cover (%)	Soil cover (%)	Bryophyte cover (%)	Herbaceous cover (%)
AUS23	69.877	-49.465	137	slope	mid slope	exposed	[3-10]	3	N	80	10	0	0	0	30
AUS25	69.876	-49.466	125	scree slope	mid slope	very exposed	[10-30]	4	NW	20	20	20	20	5	30
AUS30	69.893	-49.477	15	plateau	bottom of slope	very exposed	[3-10]	3	NW	40	30	20	10	0	20
AUS32	69.898	-49.478	60	plateau	flat	very exposed	[0-3]	1	E	50	30	10	10	10	30
AUSN1	69.854	-49.440	14	slope	mid slope	intermediate	[10-30]	2	SW	50	30	0	10	5	20
AUSN2	69.843	-49.434	32	slope	mid slope	intermediate	[10-30]	2	NE	50	30	0	10	20	20
AUSN4	69.825	-49.428	22	plateau	summit	exposed	0	2	S	60	30	0	10	20	10
LON11	69.908	-49.520	84	plateau	flat	very exposed	0	4	without	70	15	5	5	70	5
LON30	69.877	-49.521	154	plateau	flat	very exposed	0	10	without	70	15	0	5	75	5
MAC1	69.427	-48.902	55	plateau	summit	very exposed	0	5	without	80	10	10	5	0	5
MAC3	69.416	-48.895	153	summit	top of slope	very exposed	[10-30]	8	S	50	25	20	2	10	15
P121	70.200	-49.545	320	slope	top of slope	very exposed	[0-3]	16	S	20	70	10	2	0	10
P122	69.197	-49.545	250	slope	bottom of slope	very exposed	[0-3]	20	SE	10	70	0	0	10	30
P123	70.224	-49.554	340	scree slope	top of slope	very exposed	[3-10]	20	SW	80	10	5	5	5	10
PCR1	69.033	-48.705	238	plateau	flat	exposed	0	6	without	60	40	0	5	0	20
PCR2	69.033	-48.701	216	plateau	flat	exposed	0	9	without	60	30	10	5	0	20
PJDA10	69.809	-49.591	520	plateau	terrace	very exposed	[3-10]	27	NW	20	40	20	5	0	40
PJDA6	69.820	-49.590	482	plateau	mid slope	very exposed	[10-30]	35	W	30	30	30	10	5	15
RBA5	68.962	-49.630	71	outwash plain	flat	exposed	0	8	SW	10	35	35	0	10	20

Online Resource Table 2

Population	% clay	% silt	% sand	Na cmol kg ⁻¹	Mn cmol kg ⁻¹	Al cmol kg ⁻¹	CEC	P g kg ⁻¹	N g kg ⁻¹	C N ⁻¹	NO ³ mg kg ⁻¹	NH ⁴ mg kg ⁻¹	pH	Conductivity μs cm ⁻¹	Water saturation (%)
AUS23	5.5	9.5	56.2	0.50	0.054	0.481	4.61	0.015	2.27	12.9	0.82	14.6	6.54	560.00	55.32
AUS25	4.9	7.5	40.1	1.66	0.039	0.546	4.16	0.011	1.85	12.9	1.83	4.75	6.12	291.57	24.27
AUS30	5.3	7.7	39.7	0.59	0.015	0.542	7.23	0.009	1.85	12.3	1.13	3.53	6.12	171.45	17.67
AUS32	6.5	11.4	35.4	1.06	0.015	0.071	22.41	0.017	3.25	11.0	1.31	2.81	6.7	491.60	5.77
AUSN1	5.4	10.4	37.0	0.91	0.017	0.080	8.71	0.009	2.37	13.0	0.46	4.58	6.8	996.00	25.86
AUSN2	4.7	6.0	41.7	0.80	0.013	0.064	11.37	0.010	1.81	13.2	0.61	5.93	6.9	360.00	26.65
AUSN4	4.2	23.1	24.9	0.88	0.005	0.159	3.91	0.013	2.02	12.2	0.59	2.93	6.4	588.00	32.02
LON11	7.9	13.9	32.2	0.70	0.015	0.882	3.466	0.019	2.92	11.5	1.52	4.17	5.25	239.75	52.98
LON30	8.5	19.1	26.7	0.64	0.021	1.710	5.8458	0.027	3.66	11.4	1.33	2.57	5.52	188.95	34.99
MAC1	7.3	10.2	36.2	0.63	0.020	0.809	5.7921	0.014	2.66	12.9	1.32	6.81	6.34	269.88	23.67
MAC3	3.6	4.5	43.8	0.99	0.014	0.903	11.844	0.005	0.67	12.5	0.98	1.75	6.8	85.76	32.00
P121	6.0	21.1	25.9	0.33	0.010	1.290	3.2056	0.025	2.04	11.6	1.24	2.69	5.77	123.92	33.00
P122	5.4	18.1	29.2	0.23	0.030	1.520	3.4387	0.021	1.97	11.7	1.19	1.48	5.75	85.20	19.67
P123	5.2	11.4	36.0	1.29	0.010	0.160	5.82	0.036	0.43	11.7	0.93	0.933	6.36	421.62	6.78
PCR1	4.1	6.6	41.4	0.55	0.031	0.503	6.68	0.025	1.35	11.4	0.46	1.48	6.58	420.00	18.89
PCR2	5.0	14.1	33.4	0.35	0.013	0.202	1.3196	0.024	1.42	11.0	1.02	1.02	5.62	237.29	21.71
PJDA10	4.2	8.35	39.6	0.30	0.019	0.764	2.4108	0.025	1.12	11.9	1.00	0.995	6.04	129.82	14.53
PJDA6	4.9	8.75	38.8	0.35	0.019	0.755	3.4619	0.038	0.80	10.7	0.99	0.989	6.21	122.89	14.00
RBA5	0.4	2.0	47.8	0.21	0.016	0.145	0.76	0.003	0.25	10.7	0.54	2.33	6.55	50.00	17.53

Online Resource Table 3:

Category	Variable	Description
Topography & habitat	Altitude	14-520 m a.s.l.
	Types of fellfield	slope, summit, plateau, glacial outwash plain
	Topographical position	Bottom of slope, mid slope, top of slope, summit, flat area, terrace
	Slope aspect	Present at all slope aspects
	Slope	always less than 30%, with populations also occurring on flat areas
	Wind exposure	Intermediate, windy and very windy
	Distance to the sea	0.1 km to 3.5 km
Surface texture	Mineral cover	Block cover (10 to 80%) and pebbles (10 to 70%) were predominant and alternative one to each other. Proportions of gravel and bare soil were always below 20%
	Vegetation cover	herbaceous species: 5 to 40%, bryophytes: 0 to 20% ; except Ile Longue where bryophytes were in the majority (70-75%)
Soil texture		organo-mineral, 24 to 57 % sand, less than 9% clay and up to 23 % silt
Soil chemical composition	Calcium	0.3 to 2.7 cmol kg ⁻¹
	Phosphorous	0.005 to 0.038 cmol kg ⁻¹
	Total nitrogen	0.25 to 3.66 cmol kg ⁻¹
	C N ⁻¹ ratio	10.7 to 13.2
	Manganese	0.005 to 0.054 cmol kg ⁻¹
	Aluminium	0.064 to 1.71 cmol kg ⁻¹
	Sodium	0.206 to 1.66 cmol kg ⁻¹
	Effective cation exchange capacity	0.76 to 22.41
	Nitrates	0.46 to 1.83 cmol kg ⁻¹
	Ammonium	0.93 to 14.6 cmol kg ⁻¹
	Iron	0.003 to 0.06 cmol kg ⁻¹
	Manganese	0.005 to 0.054 cmol kg ⁻¹
Soil physical characteristics	Conductivity	50 μs cm ⁻¹ to 996 μs cm ⁻¹
	pH	5.2 to 6.9.
	Water saturation	5.77% to 60.79%.
	Organic matter	7.34 to 72.1 g kg ⁻¹

Online Resource Figure 1: Redundancy analysis (RDA) explanation percentage; from Dorey 2017, unpublished; cushions were selected randomly and determination of necrosis extent was done with the same methods as in our study detailed in Online Resource Figure 2; two groups are defined: 0-10% necrosis extent (n=42) and 10-100% necrosis extent (n=41). Black dots represent RDA explanation percentage for environmental variables (altitude, slope, % block cover, % pebbles cover, % gravel cover, % bare soil cover, % bryophyte cover, % herbaceous cover, mean height of neighbouring plants, neighbouring plant proportion) and black triangles represent RDA explanation percentage for soil variables (soil water content, pH, conductivity, soil depth, clay, fine silt, coarse silt, fine sand, coarse sand, C N⁻¹, organic matter, CEC, NH₄⁺, NO₃⁻). Other thresholds were tried but were less significant (Dorey 2017, unpublished).

Online Resource Figure 2: Analyses were done with Arcgis 10.6.1, using a WDS_1994_World_Mercator spatial reference. (a) The rule with a 90° angle, next to the cushion is used to calibrate the system as the length between the red crosses is indicated on the rule. (b) Polygonal entity was created to determine the perimeter of the cushion (blue line) and the surface area. (c) The proportion of the perimeter merging with other plants, referred to as the percentage of neighbouring plants (orange line). (d) Each apex is composed of an apical meristem, terminal leaves visible on the pictures and older leaves hidden inside the cushion (thus not visible on the picture). Point features were used to determine the number of vigorous (green) and necrotic (red) apices. (e) A circular area surrounding each point entity was created per apex category with a fixed size, then merged to create a unique area entity, avoiding potential superposition of the circular areas; vigorous surface area (light pink) and necrotic surface area (magenta) were determined respectively, then a ratio between the total surface area of the cushion and the necrotic surface area was done and further called percentage of necrosis extent. (f) A cushion shape proxy was generated, the smallest rectangle (white) where the cushion fit was automatically defined around the perimeter polygon, the middle of the rectangle is defined as the centroid of the cushion (red cross). Cushion diameters (short and long) were assessed by measurement of the two orthogonal diameters at the centroid up to the perimeter polygon (yellow lines) (extension *ET GeoWizards*), short and long radius are respectively half of the short and long diameter. If necessary another polygonal feature was applied to delimit the surface area of the epiphytes (plants growing on the cushion) which are present on some cushions.

