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## Do non-native plants affect terrestrial arthropods in the sub-Antarctic Kerguelen Islands?

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### Abstract :

Biological invasions are a major threat to the terrestrial ecosystems of the sub-Antarctic islands. While non-native plants generally have negative impacts on native arthropods, few studies have investigated how both native and non-native arthropods and plants interact in the sub-Antarctic islands. This was the aim of our study, which was conducted on three islands of the Kerguelen archipelago. The design was based on the spatial proximity of areas dominated by non-native or native plant species. Trait-based indices were calculated to characterize the functional structure of plant communities, considering plant stature and leaf traits. Native and non-native vegetation had contrasting functional composition but their functional diversity was similar. The effects of the type of vegetation, native or non-native, and plant functional diversity on arthropods were tested. Native macro-arthropod richness and abundance were similar or higher in non-native vegetation, and benefited from greater plant functional diversity. Abundances of macro-herbivores, macro-decomposers and macro-predators were also similar or higher in non-native vegetation. Conversely, the abundances of micro-arthropods, Symphypleona springtails and Oribatida mites, were higher in native vegetation but we also found that plant functional diversity had a negative effect on Symphypleona. Our results suggest that non-native plants can affect micro-arthropods directly or indirectly, likely through their effects on abiotic factors. By affecting macro-arthropod abundances across different trophic groups and by depleting micro-arthropods, non-native plants can alter trophic interactions, functional balances and the functioning of whole ecosystem.

**Keywords :** Biodiversity, Biological invasions, Species richness, Vascular plants, Functional traits

79 **INTRODUCTION**

80 The Kerguelen Islands are located in the South Indian Ocean, and include a main island of 6675  
81 km<sup>2</sup> and about sixty other islands (1 km<sup>2</sup>-200 km<sup>2</sup>) (Fig 1). Like the other sub-Antarctic islands,  
82 their terrestrial ecosystems are characterized by strong geographical and historical isolation.  
83 They harbor a small number of sub-Antarctic species for both flora and fauna due to low levels  
84 of immigration from nearby continents and harsh environmental conditions (Chown et al.  
85 1998). Terrestrial ecosystems are very simple, natively lacking some taxonomic groups such as  
86 mammals, amphibians and reptiles. Low plant diversity at the species and botanical family  
87 levels characterizes the native flora, which is composed of 29 species of vascular plants (Frenot  
88 et al. 2001). Native macro-arthropod communities are composed of 22 native insect species and  
89 two native spider species (Hullé and Vernon 2021), while micro-arthropod communities which  
90 are dominated by Oribatida mites and springtails are respectively composed of 24 and 18 native  
91 species (Deharveng and Travé 1981). It should be noted that micro-arthropod diversity may be  
92 underestimated and that some ‘undiscovered’ or cryptic species are likely to be found using  
93 recent advances in molecular biology in Antarctic (Collins et al. 2020). Macro-arthropod  
94 communities are unbalanced, some trophic groups being absent or not abundant such as  
95 herbivores, pollinators and decomposers such as flies dominate macro-arthropod communities  
96 due to the large amounts of marine mammal and seabird excretions (Chown and Convey 2016).  
97 Despite the geographical isolation of the Kerguelen Islands, many species among plants,  
98 arthropods and mammals have been introduced, voluntarily or involuntarily, due to human  
99 activities, and have established. For instance, there are currently as many non-native as native  
100 macro-arthropod species (Hullé and Vernon 2021), while few non-native micro-arthropod  
101 species have been recorded (Deharveng and Travé 1981; Greenslade and Convey 2012). For  
102 plants, the number of species in some sites historically frequented by humans has become three

103 times greater than the number of native species (Frenot et al. 2005), having potentially  
104 important impacts on ecosystem processes.

105 Biological invasions are widely recognized as being one of the most significant threats  
106 to biodiversity and are expected to increase with global warming (Shaw et al. 2010; McGeoch  
107 et al. 2015). Sub-Antarctic islands are deeply affected by climate change (Lebouvier et al. 2011)  
108 which makes their ecosystems more suitable to less stress-adapted non-native species (Pertierra  
109 et al. 2017). In addition, some established non-native species may become invasive (Frenot et  
110 al. 2005), exacerbating their impact on biodiversity and ecosystems due to the disruption of  
111 interaction networks (Dunn and Hatcher 2015). In general, invasive plants reduce the diversity  
112 of native plant species and are predicted to also negatively impact native arthropod diversity  
113 (review in Spafford et al. 2013) through different mechanisms such as the alteration of  
114 vegetation structure or the loss of some plant species which host specialist arthropods. Few  
115 native specialist arthropods are present on the Kerguelen Islands, e.g., the moth *Embryonopsis*  
116 *halticella* which feeds on *Poa cooki* (Crafford and Scholtz 1986), and the fly *Calycopteryx*  
117 *moseleyi* (Tréhen et al. 1986), the weevils *Bothrometopus angusticollis* and *Canonopsis sericea*  
118 which feed on *Pringlea antiscorbutica* (Voisin et al. 2017), and the loss of their host-plant might  
119 particularly affect them.

120 Arthropods are highly dependent on plants (Schaffers et al. 2008; Joern and Laws 2013)  
121 and different components of plant community features affect them, such as plant composition,  
122 or morphological and physical attributes. For instance, plant height and lateral spread as well  
123 as leaf dimensions characterize plant architecture and determine the availability of different  
124 micro-habitat conditions allowing or not arthropods to choose optimal conditions of  
125 temperature, protection against wind, rain or predators (Spafford et al. 2013; Gardarin et al.  
126 2018). By providing attachment points for spider webs, architectural traits may have an impact  
127 on predator hunting efficacy, depending on predator hunting strategy and on predator-prey

128 interactions (Pearson 2009). Vegetation stature also influences the distribution of soil-dwelling  
129 arthropods likely through its correlation with litter quantity (Gardarin et al. 2018). For  
130 herbivores, which have direct interactions with plants since they feed on them, Carmona et al.  
131 (2011) showed that morphological and physical plant traits may act as a physical barrier and  
132 are often more important for plant-herbivore interactions than chemical traits. For instance,  
133 traits related to the biomechanical properties, such as cuticle thickness, specific leaf area  
134 (Ordonez et al. 2010), or leaf dry matter content (Deraison et al. 2015) have been shown to  
135 impact herbivore choice when selecting their food plant.

136         How arthropod communities reliant on native vegetation on sub-Antarctic islands, are  
137 impacted by non-native plants is yet to be tested (Houghton et al. 2019) and is difficult to  
138 predict. This is due to the absence or low richness of many insect groups (Gressit 1970; Vernon  
139 et al. 1998), and to the high interactions at play between native and non-native plants, native  
140 and non-native arthropods and between plants and arthropods (Houghton et al. 2019). Trait-  
141 based approaches have been proposed as useful tools to study plant-arthropod interactions at  
142 the community level (Lavorel et al. 2013; e.g., Deraison et al. 2015; Le Provost et al. 2017) and  
143 to understand community responses to biotic disturbance induced by non-native species (Gross  
144 et al. 2013; Mouillot et al 2013). This study aimed to investigate the effects of plant  
145 communities dominated by native or non-native plant species on macro- and micro-arthropod  
146 communities on three islands of the Kerguelen archipelago. On each of the studied islands, we  
147 selected relatively large areas of the two types of vegetation, i.e., native and non-native, that  
148 were close to each other. By considering plant traits involved in plant-arthropod interactions,  
149 i.e., plant architecture and leaf attributes, we assessed whether the plant functional community  
150 structure differed between the two types of vegetation using complementary indices, the  
151 functional dispersion and the community-weighted mean of traits (Mouillot et al. 2013).  
152 Secondly, we estimated the taxonomic diversity of macro-arthropods and their abundances as

153 well as the abundances of epigaeic micro-arthropods in both types of vegetation. We then  
154 investigated whether these components of arthropod communities differed between native and  
155 non-native plant communities and whether plant functional diversity and community-weighted  
156 means of traits explained a significant part of their variability.

157

## 158 MATERIAL AND METHODS

### 159 STUDY AREA AND SAMPLING DESIGN

160 The study was conducted during the summer 2017-2018 on three islands of the *Golfe du*  
161 *Morbihan* in the Kerguelen archipelago (48° 30'–50° S, 68° 27'–70° 35' E): *Île Australia*, *Île*  
162 *aux Cochons* and *Île Mayes* (Fig. 1). Originally, plant communities were dominated by *Acaena*  
163 *magellanica*, *Azorella selago*, *Festuca contracta* and *P. antiscorbutica*. These plant assemblies  
164 covered *Île Australia* and *Île Mayes* until the 2010s. From these years, following climate  
165 change, non-native Poaceae and Asteraceae developed, in particular *Poa pratensis* and  
166 *Taraxacum gr. ruderalis*. These plants have expanded widely on *Île Mayes*, where meadows of  
167 *P. pratensis* covered large areas in 2016. On *Île Australia*, non-native Poaceae communities (*P.*  
168 *pratensis*, *Vulpia bromoides*) were still localized in 2016. *Île aux Cochons* differed from the  
169 other two islands by the presence of rabbits (*Oryctolagus cuniculus*) until 1997, when they were  
170 eradicated (Chapuis et al. 2001). This mammal resulted in the rarefaction of *P. antiscorbutica*  
171 and *A. selago*, replaced by *A. magellanica*, which covered more than 90% of the island in 1997  
172 (Chapuis et al. 2001; Chapuis et al. 2002). During the years 2000-2010, the increase in  
173 temperature and especially the low summer precipitations (Lebouvier et al. 2011) resulted in  
174 the significant regression of *A. magellanica* and the development of non-native Asteraceae  
175 (*Taraxacum erythrospermum*, *T. gr. ruderalia*) and Poaceae (in particular *P. pratensis*).  
176 Currently, the communities dominated by native species, i.e., *A. magellanica*, occupy small

177 areas. All three islands have been colonized by mice, which have heavily predated and damaged  
178 their invertebrate fauna (Chapuis et al. 2002).

179 The sampling design consisted of areas of native- or non-native-dominated vegetation  
180 that were close to each other (a few tens of meters). It was implemented in herbaceous habitats  
181 which are the main habitats colonized by non-native plants. Sites corresponding to these criteria  
182 were preselected using a remote sensing based cartography of the vegetation on the three  
183 studied islands (Fourcy et al. 2018) (Fig. 2; see Online Resource 1 for a complete description  
184 of the classes). Vegetation maps were produced from a multispectral Pléiades image acquired  
185 in February 2016 (2 m ground spatial resolution) that we analysed by performing a supervised  
186 classification with machine-learning algorithms. The supervised classification was based on  
187 botanical surveys conducted in December 2016 on training zones on *Île Australia*, *Île aux*  
188 *cochons* and *Île Mayes*, and used as references for the machine-learning algorithms.

189 Within each island, we selected in the field five sites among the preselected sites where  
190 an area covered with >90% of native plant species was close to an area covered with >90% of  
191 non-native plant species. The percent coverage of vegetation was estimated visually at that step.  
192 Then, we delineated a patch >150 m<sup>2</sup> within each of these areas and surveys were carried out  
193 within each patch. Distance between the two types of patch within a site ranged from 15 m to  
194 58 m. This resulted in 30 vegetation patches: 3 islands, 5 sites per island, 2 patches per site (one  
195 non-native, hereafter “non-native patch”, and one native, hereafter “native patch”) (Fig. 2).  
196 When selecting the sites, we controlled for abiotic conditions known to affect arthropods, such  
197 as the altitude, distance from the sea (Hullé and Vernon 2021), slope, dominant wind and sun  
198 exposures. All sites were at < 40 m altitude, > 50 m from the sea, with a slope <20%. Sun and  
199 dominant wind exposures differed between sites and islands but not between paired patches  
200 (Online Resource 2).

201 Note that the sampling conditions varied during the study. Harsh weather conditions  
202 were observed in *Île aux Cochons* where a hailstorm occurred during one day and in *Île Mayes*  
203 where low temperatures (4.4°C on average) and snowstorm occurred during three days.  
204 Conversely, sunny weather conditions were recorded throughout the sampling period in *Île*  
205 *Australia*.

206

## 207 PLANT SURVEYS AND TRAITS

208 A botanical survey was conducted within each of the 30 patches on the first day of the  
209 experiment (20<sup>th</sup> December 2017 on *Île aux Cochons*, 29<sup>th</sup> December 2017 on *Île Australia*, 9<sup>th</sup>  
210 January 2018 on *Île Mayes*). We used five quadrats of 0.50 m x 0.50 m haphazardly located  
211 within each patch. In each quadrat, we recorded the number of plant species and we estimated  
212 a percentage cover of the quadrat surface for each plant species. We calculated plant species  
213 diversity and mean cover of each plant species per patch over the five quadrats.

214 To characterize plant community features, seven plant traits reflecting important  
215 functions for plants (Diaz et al. 2016), and involved in plant-arthropod interactions (Carmona  
216 et al. 2011; Gardarin et al. 2018) were selected: plant height (PH) and plant width (PW), leaf  
217 length (LL) and leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), and  
218 leaf thickness (LT). In each island, 15-30 specimens of each plant species covering >10% of at  
219 least one vegetation patch were measured and one leaf per plant was sampled, excepting *A.*  
220 *selago* and *P. antiscorbutica* for which we only sampled a total of 2-5 leaves. Traits were  
221 measured following standard protocols (Cornelissen et al. 2003) and their values were averaged  
222 over the number of plant or leaf specimens per plant species and island.

223

## 224 ARTHROPOD SAMPLING

225 On the first or second day of the experiment, we sampled arthropods in the 30 patches (one  
226 trapping session) using two types of trap to accurately estimate arthropod diversity: pitfall traps  
227 and yellow pans (Southwood 1978). We placed five pitfall traps (7.5 cm diameter, 5 cm depth)  
228 and two yellow pans (20 cm diameter) per patch. Pitfall traps were placed haphazardly in the  
229 patch, while yellow pans were placed on the ground and located so that the distance was the  
230 highest between the native patch and the non-native patch within each site. Traps were filled  
231 with a preservative solution of water, a few drops of liquid soap and salt (10 gL<sup>-1</sup>). All traps  
232 within an island were set up on the same day and left in place for four trapping days. We stored  
233 all caught arthropods in the lab in a 70% ethanol solution. Macro-arthropods were identified to  
234 the lowest possible taxonomic level (usually species) following Hullé et al. (2018). We  
235 identified winged aphids to species level while we pooled all wingless aphids together.

236 We characterized macro-arthropods, i.e., insects and spiders, by calculating their  
237 taxonomic richness and abundance. For this purpose, we defined different groups of macro-  
238 arthropods according to their origin status and trophic group according to Hullé and Vernon  
239 (2021). To calculate taxa richness, we first pooled for each patch all macro-arthropods collected  
240 either in pitfall traps or in yellow pans. Then, we calculated native, non-native and total taxa  
241 richness, which included taxa with unknown native or non-native status. We also calculated  
242 taxa richness of three trophic groups: decomposers (taxa feeding on plant material and  
243 omnivorous taxa), herbivores and predators. For macro-arthropod abundances, we considered  
244 native macro-arthropods and performed separate analyses for pitfall traps and for yellow pans,  
245 pooling all individuals sampled in each patch. We also analysed the abundances of decomposers  
246 in yellow pans, herbivores in yellow pans and predators in pan traps by pooling all individuals  
247 sampled in each patch (see Badenhauer (2021) for a complete description of dataset). For  
248 micro-arthropods, we focussed on the abundances of Oribatida mites and Symphypleona  
249 springtails, which are generally epigaeic and tend to occur above or on the top of the ground



250 surface (Greenslade 2002). We analysed their abundances in pitfall traps by pooling all  
251 individuals sampled in each patch.

252

## 253 STATISTICAL ANALYSES

254 All statistical analyses were performed using the R statistical software (R Development Core  
255 Team 2020) version 4.0.3 and packages car (Fox and Weisberg 2019), emmeans (Lenth 2020),  
256 factoextra (Kassambara and Mundt 2020), FactoMineR (Le et al. 2008), FD (Laliberté and  
257 Legendre 2010; Laliberté et al. 2014) and lme4 (Bates et al. 2015).

258

### 259 *Characterization of plant functional community structure*

260 Two complementary components of the functional structure of plant communities were  
261 assessed, i.e., functional composition and functional diversity (Laliberté and Legendre 2010;  
262 Mouillot et al. 2013). Plant functional composition was estimated using the community  
263 weighted mean index calculated for each trait,  $CWM$ , and functional diversity using the multi-  
264 trait functional dispersion index,  $FDis$ . Both indices were calculated following Laliberté and  
265 Legendre (2010).

266  $CWM$  is the mean trait value of the community, weighted by the relative cover of each  
267 plant species. It reflects the trait values of the dominant species in the community. It was  
268 computed separately for the seven measured traits ( $CWM_{TRAIT}$ ):

$$269 \quad CWM_{TRAIT} = \sum_{j=1}^n p_j T_j$$

270 where  $n$  is the number of plant species in the vegetation patch,  $p_j$  is the relative cover of species  
271  $j$  in the patch (mean of species cover over the five quadrats per patch), and  $T_j$  is its mean trait  
272 value per island.

273 *FDis* is the mean distance in multidimensional trait space of individual species to the  
274 centroid of all species. It takes into account species abundances weighting distances of  
275 individual species by their relative abundances. Its minimum value is 0, when the community  
276 is composed of only one species. High *FDis* value in plant communities reflects a strong  
277 disparity in the distribution of traits. By providing a greater number of niches and microhabitats  
278 for arthropods, high *FDis* is expected to result in greater arthropod diversity (e.g., Deraison et  
279 al. 2015). It was computed as:

$$280 \quad FDis = \frac{\sum_{j=1}^n a_j z_j}{\sum_{j=1}^n a_j}$$

281 where  $n$  is the number of plant species in the vegetation patch,  $a_j$  is the cover of species  $j$  in the  
282 patch (mean of species cover over the five quadrats per patch),  $z_j$  is the distance of species  $j$  to  
283 the weighted centroid of the  $[x_{ij}]$  (trait  $\times$  species) matrix,  $c$ :

$$284 \quad c = [c_i] = \frac{\sum_{j=1}^n a_j x_{ij}}{\sum_{j=1}^n a_j}$$

285 We performed a principal component analysis (PCA) on the  $CWM_{TRAIT}$  of the seven  
286 selected traits to describe plant community features in the two types of patch and to evaluate  
287 how they correlated.

288 We used Linear Mixed Effects Models (LMM) fitted by log-likelihood criterion to test  
289 for the effect of the island and type of patch on plant species richness, the seven  $CWM_{TRAIT}$  and  
290 *FDis*. The interaction term between the type of patch and the island was included in the models  
291 since the effect of non-native plants may depend on the island and its invasion history. The site  
292 was included in the models as random effect to take into account for the effects of similar abiotic  
293 environmental conditions in the two patches per site. Models were simplified step by step by  
294 removing the interaction term and the main fixed effects if not significant ( $\alpha = 0.05$ ) using Wald  
295 Chi-square test,  $\chi^2$ . Parameters of the final models were estimated using restricted maximum  
296 likelihood (REML), and least-squares means were calculated. Predicted means were compared

297 using Tukey method and adequate contrasts. Model errors were inspected for normality,  
298 constant mean and variance. Model formula was:

$$299 \quad Y \sim (1|Site) + Island * Type\ of\ patch$$

300

### 301 *Effects of plant communities on arthropod communities*

302 The effects of plant communities on the richness and abundance of arthropods were analysed  
303 using LMM or Generalized Linear Mixed Effects Models (GLMM) depending on the  
304 distribution of the data and model errors, in order to satisfy the statistical assumptions of  
305 models. LMM was used for analysing i/ the taxa richness of macro-arthropods: native species,  
306 non-native taxa (sqrt-transformed), all taxa (sqrt-transformed), decomposers (sqrt-  
307 transformed), herbivores and predators; ii/ the abundances of macro-arthropods: decomposers  
308 (log-transformed), herbivores (log-transformed), predators (log-transformed); iii/ the  
309 abundance of Oribatida mites (log-transformed). GLMM with Poisson errors was used for  
310 analysing i/ the abundance of native macro-arthropods and ii/ the abundance of Symphypleona  
311 springtails.

312 First, we tested for the effects of the type of patch and plant *FDis* on the response  
313 variables mentioned above. We included in the models the island, the type of patch and their  
314 two-way interaction, and plant *FDis* as fixed effects. The site was included as random effect in  
315 all models. The model had the following structure:

$$316 \quad Y \sim (1|Site) + Island * Type\ of\ patch + FDis$$

317 Model simplification was conducted firstly by removing non-significant interaction  
318 term. Statistical assumptions were inspected, and model predictions and mean comparisons  
319 were performed as described above.

320 Second, we aimed to establish the relative importance of the functional composition of  
321 plant communities, namely *CWM<sub>TRAITs</sub>* and other components of plant community such as plant

322 species identity, in shaping arthropod communities. However, collinearity issues occurred when  
323 including the type of patch and single  $CWM_{TRAIT}$  in the same statistical models because  
324  $CWM_{TRAIT}$  and the type of patch were highly correlated (VIF values >2) (Zuur et al. 2010). For  
325 this reason and as an exploratory analysis, we have limited the analysis of the effects of  
326  $CWM_{TRAIT}$  on arthropods to a comparison of models including either the type of patch or single  
327  $CWM_{TRAIT}$ . As described above, we run LMM or GLMM to model macro-arthropod taxa  
328 richness and abundances, and micro-arthropod abundances. Model formula for the patch model  
329 was:

$$Y \sim (1|Site) + Island * Type\ of\ patch$$

331 Model formula for the  $CWM_{TRAIT}$  models was:

$$Y \sim (1|Site) + Island * CWM_{TRAIT}$$

333 After model simplification as described above, an information-theoretic approach (AIC-  
334 based approach corrected for small sample size;  $AICc$ ; Burnham and Anderson 2002) was used  
335 to compare for each  $CWM_{TRAIT}$  the simplified patch model and  $CWM_{TRAIT}$  model.  $AICc$   
336 difference (delta  $AICc$ ) between the two models was calculated. If  $|\text{delta } AICc| < 2$ , models were  
337 not significantly different, while if  $|\text{delta } AICc| > 2$  they differed, the best model being the one  
338 with the smallest  $AICc$ .

339

## 340 RESULTS

### 341 CHARACTERIZATION OF PLANT COMMUNITIES AT THE PATCH SCALE

342 Main native plant species in the patches were *A. magellanica*, *A. selago*, *F. contracta*, and *P.*  
343 *antiscorbutica* and main non-native species were *P. pratensis* generally associated with *T. gr.*  
344 *ruderalia*, and *T. erythrospermum*. Non-native plant species covered on average >95% in non-  
345 native patches (Fig. 3d, e, f) while native plant species covered ~ 90% in native patches (Fig.  
346 3a, b, c). Total plant species richness per patch did not vary between native and non-native

347 patches (LMM:  $p (>\chi^2_1) = 0.1484$ ). It was significantly lower (LMM:  $p (>\chi^2) = 0.0230$ ) on *Île*  
348 *Australia* (estimated mean  $\pm SE$ ,  $3.1 \pm 0.6$  plant species) and *Île Mayes* ( $3.4 \pm 0.6$ ) than on *Île*  
349 *aux Cochons* ( $5.3 \pm 0.8$ ). These differences between islands were due to differences in non-  
350 native plant species richness in the native patches, which was higher on *Île aux Cochons* than  
351 on *Île Mayes* than on *Île Australia* (LMM: Island:  $p (>\chi^2) = 0.0001$ ; Type of patch:  $p (>\chi^2) =$   
352  $0.0030$ ; Island  $\times$  type of patch:  $p (>\chi^2) = 0.0321$ ). Native plant species richness was the same in  
353 both types of patch and on the three islands (observed mean  $\pm SE = 1.9 \pm 0.3$ ). The functional  
354 dispersion *FDis* did not vary between the types of patch but between islands (Table 1).

355 The PCA performed on  $CWM_{TRAITS}$  showed that non-native and native patches formed  
356 distinct groups in the space of the two first PCA axes which accounted for 82.9% of the variance  
357 (Online Resource 3). The first PCA axis (60.1% of explained variance) mainly correlated to  
358 leaf dimensions, i.e., leaf length ( $CWM_{LL}$ ) ( $r = 0.96$ ) and leaf area ( $CWM_{LA}$ ) ( $r = 0.86$ ). The  
359 second PCA axis (22.8% of explained variance) correlated to leaf thickness ( $CWM_{LT}$ ) ( $r =$   
360  $0.79$ ).

361 All  $CWM_{TRAIT}$  values differed significantly between native and non-native patches  
362 (Table 1). Native patches were characterized by low-stature plants, thick and small leaves, small  
363 SLA, and large LDMC. Non-native patches were characterized by large stature plants (+33%  
364  $CWM_{PH}$ ; +36%  $CWM_{PW}$ ), thinner leaves (-45%  $CWM_{LT}$ ) with larger dimensions (+103%  $CWM_{LL}$ ;  
365 +80%  $CWM_{LA}$ ), larger SLA (+38%  $CWM_{SLA}$ ) and smaller LDMC (-15%  $CWM_{LDMC}$ ). All  
366  $CWM_{TRAIT}$  values but  $CWM_{SLA}$  also differed between islands (Table 1).

367

## 368 EFFECTS OF PLANT COMMUNITIES ON MACRO-ARTHROPOD COMMUNITIES

369 Overall, we collected nine native macro-arthropod species, 16 non-native taxa (among which  
370 13 species), and four taxa not classifiable as native vs non-native species (*Smittia* sp., *Ixodes*  
371 spp., Siphonaptera, Thysanoptera). Among macro-arthropods, 785 of the collected individuals

372 belonged to native species (560 in pitfall traps, 225 in yellow pans), 49 224 to non-native taxa  
373 and 108 specimens were not classifiable (70 *Smittia* sp., 36 Siphonaptera, one *Ixodes* spp., one  
374 Thysanoptera). One non-native taxa was numerically dominant, i.e., the aphids which  
375 represented >90% of the total counts whatever the type of patch and island (see Badenhäusser  
376 (2021) for a complete description of dataset).

377

### 378 *Macro-arthropod diversity and native macro-arthropod abundance*

379 The same native macro-arthropod species with very few exceptions were collected in native  
380 and non-native patches within each island. They belonged to three trophic groups, i.e.,  
381 decomposers, herbivores and predators. Taxa richness of native macro-arthropods was low and  
382 differed between islands (estimated means  $\pm$  SE, *Île Australia*:  $3.5 \pm 0.4$ ; *Île aux Cochons*:  $2.7$   
383  $\pm 0.4$ ; *Île Mayes*:  $1.9 \pm 0.4$ ) (Table 2). The type of patch had no effect on the taxa richness of  
384 native macro-arthropods but plant *FDis* had a positive significant effect (Table 2) (LMM:  
385 Parameter estimate  $\pm$  SE,  $6.31 \pm 3.11$ ) suggesting that a wide variety of food niches or micro-  
386 habitats was favorable to native macro-arthropods. Taxa richness of non-native macro-  
387 arthropods was roughly twice the taxa richness of native macro-arthropods and differed  
388 between islands (*Île Australia*:  $7.6 \pm 0.7$ ; *Île aux Cochons*:  $5.1 \pm 0.6$ ; *Île Mayes*:  $4.3 \pm 0.5$ )  
389 (Table 2). The type of patch and *FDis* had no effect on the taxa richness of non-native macro-  
390 arthropods (Table 2). Total macro-arthropod richness per patch was the same in native and non-  
391 native patches on *Île Australia* (native patches:  $11.9 \pm 1.3$ ; non-native patches:  $13.7 \pm 1.3$ ) and  
392 *Île aux Cochons* (native patches:  $9.2 \pm 1.0$ ; non-native patches:  $7.6 \pm 1.0$ ) (Table 2). On *Île*  
393 *Mayes*, it was significantly lower in native patches ( $5.2 \pm 0.8$ ) relative to non-native patches  
394 ( $8.2 \pm 1.0$ ) (Table 2). *FDis* had a positive significant effect on total richness (Table 2).

395 The native spiders, *Neomaso antarcticus* and *Myro kerguelensis*, represented ~90% of  
396 the abundances of native macro-arthropods collected in pitfall traps whatever the type of patch

397 and the island, and >50% in yellow pans. Native macro-arthropod abundances in pitfall traps  
398 were significantly lower in native patches relative to non-native patches and differed between  
399 islands (Table 2, Fig. 4a). In addition, they increased significantly with *FDis* (Table 2) (GLMM:  
400 Parameter estimate  $\pm$  *SE*,  $2.46 \pm 1.09$ ). The island, type of patch, and *FDis* had no significant  
401 effect on the abundances of native macro-arthropods collected in yellow pans (GLMM: Island:  
402  $p$  ( $>\chi^2$ ) = 0.0966; Type of patch:  $p$  ( $>\chi^2$ ) = 0.9381; Island  $\times$  Type of patch:  $p$  ( $>\chi^2$ ) = 0.2201;  
403 *FDis*:  $p$  ( $>\chi^2$ ) = 0.1413).

404 Results of the comparison between the patch model and *CWM<sub>TRAITS</sub>* models showed that  
405 *CWM<sub>PW</sub>* and *CWM<sub>LA</sub>* models were better than the patch model in explaining the taxa richness  
406 of native macro-arthropods (Online Resource 4). In these models, *CWM<sub>PW</sub>* and *CWM<sub>LA</sub>* had  
407 opposite effects depending on the island (Online Resource 4). No *CWM<sub>TRAIT</sub>* model was selected  
408 as the best model relative to the patch model in explaining the non-native and total taxa richness,  
409 and the abundance of native species (Online Resource 4).

410

#### 411 *Diversity and abundance of trophic groups*

412 Herbivores represented >95% of the counts whatever the island and type of patch  
413 (Online Resource 5). This group was mainly composed of four aphid species among which  
414 *Myzus ascalonicus* was dominant (>95% of winged aphids), and one thrips species *Apterothrips*  
415 *apteris*. Four native species represented other herbivores, which were very few (47 individuals  
416 in total). Singular fit occurred in LMM conducted on herbivore richness, which was not  
417 analysed. Herbivore abundance was similar or higher depending on the island in non-native  
418 patches relative to native (Table 2; Fig. 4b). Plant *FDis* had strong effects on herbivore  
419 abundance, which increased with increasing *FDis* (Table 2) (LMM: Parameter estimate  $\pm$  *SE*,  
420  $11.22 \pm 3.58$ ). In addition, *CWM<sub>LL</sub>* and *CWM<sub>SLA</sub>* models explained significantly more variability  
421 in herbivore abundance relative to the patch model (Online Resource 4). Herbivore abundance

422 increased with increasing  $CWM_{LL}$  and  $CWM_{SLA}$  whose single effects were selected in the  
423 simplified models (Online Resource 4).

424 Decomposers (feeding on plant material and omnivorous pooled) represented ~1% of  
425 the macro-arthropods (Online Resource 5). This group was the richest with 13 taxa, among  
426 which the sciarid *Lycoriella sativae* represented half of the counts. Decomposer taxa richness  
427 was the same in both types of patch on *Île Australia* (estimated means  $\pm SE$ , native patches:  $4.4$   
428  $\pm 0.8$ , non-native patches:  $5.1 \pm 0.9$ ), and *Île aux cochons* (native patches:  $3.2 \pm 0.7$ , non-native  
429 patches:  $2.4 \pm 0.6$ ). It was higher in non-native patches relative to native patches on *Île Mayes*  
430 (native patches:  $1.7 \pm 0.5$ , non-native patches:  $3.0 \pm 0.7$ ) (Table 2). The same results were  
431 observed for decomposer abundance (Table 2, Fig. 4c).  $FDis$  had no effect on decomposer taxa  
432 richness and abundance (Table 2).  $CWM_{LA}$  and  $CWM_{LDMC}$  models better modeled decomposer  
433 taxa richness than the patch model, and the effects of  $CWM_{LA}$  and  $CWM_{LDMC}$  differed between  
434 islands (Online Resource 4).

435 Predators represented 2.6% of the macro-arthropods collected in pitfall traps (Online  
436 Resource 5). Predator trophic group was composed of two native spider species, *N. antarcticus*,  
437 *M. kerguelensis*, and two non-native species, the spider *Tenuiphantes tenuis*, and the carabid  
438 beetle, *Merizodus soledadinus* (only 2.0% of the predators). Predator richness was the same in  
439 native and non-native patches on *Île Australia* (native patches:  $3.0 \pm 0.3$ ; non-native patches:  
440  $3.4 \pm 0.3$ ) and on *Île Mayes* (native patches:  $2.2 \pm 0.3$ ; non-native patches:  $2.6 \pm 0.3$ ). On *Île*  
441 *aux Cochons* it was higher in native patches ( $3.2 \pm 0.3$ ) than in non-native patches ( $2.6 \pm 0.3$ )  
442 (Table 2). Predators were significantly more abundant in non-native patches relative to native  
443 ones on *Île Australia* and *Île Mayes* (Table 2, Fig. 4d). On *Île aux Cochons*, they were as  
444 numerous in both types of patch (Table 2, Fig. 4d). Neither  $FDis$  nor  $CWM_{TRAITS}$  had any effect  
445 on predator richness and abundance (Table 2, Online Resource 4).

446



## 447 EFFECTS OF PLANT COMMUNITIES ON MICRO-ARTHROPOD COMMUNITIES

448 Overall, 9845 micro-arthropods were collected in pitfall traps among which 9001 Oribatida  
449 mites and 844 Symphypleona springtails. Oribatida mites represented >80% of micro-  
450 arthropods on the three islands. Native patches had higher Oribatida mite (Fig. 5a) and  
451 Symphypleona springtail (Fig. 5b) abundances relative to non-native patches whatever the  
452 island (Table 2). *FDis* had a strong negative effect on Symphypleona springtails (GLMM:  
453 Parameter estimate  $\pm$  SE,  $-7.25 \pm 1.00$ ) while it had no effect on Oribatida mites (Table 2).  
454 Results of the comparison between the patch model and *CWM<sub>TRAITS</sub>* models showed that  
455 *CWM<sub>PW</sub>* model was better than the patch model in explaining Symphypleona abundance, which  
456 decreased with increasing *CWM<sub>PW</sub>* whatever the island (Online Resource 4).

457

## 458 DISCUSSION

459 Our study shows opposite effects of non-native plants on macro-arthropods and micro-  
460 arthropods. Despite strong differences in the functional composition of plant communities, we  
461 didn't demonstrate any negative effect of non-native plants on native macro-arthropods. In fact,  
462 macro-arthropod diversity and abundance were similar or higher in non-native plant  
463 communities whatever their native or non-native status, and their trophic group. Conversely,  
464 micro-arthropods, i.e., Symphypleona springtails and Oribatida mites, abundances were higher  
465 in native plant communities relative to non-native. Finally, we found that plant functional  
466 diversity was similar in native and non-native plant communities, and benefited native macro-  
467 arthropods while it had a null or negative effect on micro-arthropods.

468

## 469 FUNCTIONAL STRUCTURE OF NATIVE AND NON-NATIVE PLANT COMMUNITIES

470 Trait-based indices, i.e., *CWM<sub>TRAITS</sub>* and *FDis*, were used to characterize the functional  
471 composition and diversity of native and non-native patches. Traits associated with leaf structure

472 and quality were expected to be involved in trophic plant-arthropod interactions, and those with  
473 plant stature in non-trophic interactions through their effects on arthropod habitats (Lavorel et  
474 al. 2013; Gardarin et al. 2018). All  $CWM_{TRAITS}$  differed between the two types of patch,  
475 reflecting the very high cover of respectively native and non-native plant species in the patches  
476 and trait differences between dominant native and non-native species. Dominant native plant  
477 species, i.e., *A. magellanica* and *F. contracta*, had low stature and leaf dimensions, low SLA  
478 and high LDMC, indicating low relative growth rate, low nutrient content and slow resource  
479 capture. They contrasted with dominant non-native species, i.e., *P. pratensis* and *T. gr.*  
480 *ruderalia* whose large stature and leaf dimensions, large SLA and low LDMC, correspond to  
481 fast-growth rate, high nutrient content and good light competitor (Diaz et al. 2016). Other  
482 studies also observed these characteristics in native and non-native plant communities  
483 (Ordonez et al. 2010; Gross et al. 2013). We also found that  $FDIs$  did not differ between native  
484 and non-native patches. This reflects the fact that native and non-native species did not mix or  
485 mixed very little within the patches. It also reflects similar range of trait disparity between the  
486 two dominant species within each type of patch, i.e., between a grass species (*F. contracta* in  
487 native patches and *P. pratensis* in non-native patches) and an herb species (*A. magellanica* in  
488 native patches and *T. gr ruderalia* in non-native patches).

489

#### 490 NON-NATIVE PLANTS HAVE NO NEGATIVE EFFECT ON NATIVE MACRO- 491 ARTHROPODS

492 Plant  $FDIs$  significantly contributed to explaining the effect of plants on native macro-  
493 arthropods, which benefited as expected from a greater diversity of plant resources and micro-  
494 habitats in both native and non-native vegetation. Differences in the composition of native and  
495 non-native vegetation, did not lead to negative effects on native macro-arthropods. Although  
496 this result does not match the general expectation (review in Spafford et al. 2013), it is

497 interesting to note that it is in agreement with the only published comparative study on the effect  
498 of non-native plants on invertebrates at the community scale, and in the context of sub-Antarctic  
499 islands (Gremmen et al. 1998). In this study, which focussed on soil fauna communities, native  
500 macro-invertebrate abundance was similar or higher in vegetation dominated by the non-native  
501 grass *Agrostis stolonifera* compared to vegetation dominated by *A. magellanica*. Obviously,  
502 non-native plants would have had a negative impact on specialist native macro-arthropods  
503 feeding on some particular native plant species. However, highly specialist native macro-  
504 arthropods were scarce in our study, probably because we focussed on herbaceous habitats,  
505 while specialist species were more likely to be found in fellfield habitats (Hullé and Vernon  
506 2021). Two hypotheses may explain the lack of negative effects of non-native plants on native  
507 macro-arthropods. First, the spatial scale of our paired sampling design, i.e., the short distances  
508 separating native and non-native patches could result in native macro-arthropod communities  
509 being composed of the same species in both types of patch. Indeed, the mosaic landscape and  
510 entangled patterns of native and non-native plant communities observed on the islands studied  
511 (Fig. 2) may allow between-patch movements of individuals either actively walking, or flying,  
512 depending on species dispersal abilities, or passively carried by wind from and to nearby areas  
513 (Schooley and Wiens 2003). At the scale of the patch, higher abundances of some macro-  
514 arthropod species in non-native patches may be related to better local conditions provided by  
515 the non-native plants. Similar small-scale distribution patterns in arthropods depending on plant  
516 species within the vegetation mosaic have been described (e.g., Coulson et al. 2003). A second  
517 hypothesis is that interactions between non-native and native macro-arthropods play a greater  
518 role than plant-arthropod interactions in shaping native macro-arthropods. Indeed, an important  
519 feature of macro-arthropod communities was that non-native species outnumbered native in  
520 both types of vegetation, as already highlighted on Kerguelen archipelago (Frenot et al. 2005).  
521 For instance, the predatory beetle *M. soledadinus* had a strong impact on native invertebrates

522 e.g., the flies *Anatalanta aptera* and *C. moseleyi*, resulting in their local extinction on some  
523 coastal habitats of the Kerguelen Islands (Lebouvier et al. 2020). In our surveys, *M. soledadinus*  
524 were few and could not have any impact on native arthropods. Dominant non-native taxa in our  
525 study were the aphids, which are sap-feeders and the thrips *A. apteris*, which feeds on the  
526 content of leaf cells (Karban and Strass 1994). By occupying previously vacant or unsaturated  
527 ecological niche (Russel et al. 2017; Houghton et al. 2019), they probably don't compete with  
528 native species. Since data is missing from locations on Kerguelen Islands that do not host non-  
529 native invertebrates (Hullé and Vernon 2021) against which to compare the diversity and  
530 abundance observed in our surveys, it is difficult to conclude on this hypothesis.

531

#### 532 THE ABUNDANCE OF MACRO-ARTHROPODS OF DIFFERENT TROPHIC GROUPS IS 533 HIGHER IN NON-NATIVE VEGETATION

534 Non-native plants also had no negative effect on macro-arthropods belonging to different  
535 trophic groups, i.e., herbivores, decomposers and predators whose diversity and abundance  
536 were similar or higher in non-native patches. The aphid *M. ascalonicus* and the thrips *A. apteris*  
537 much dominated among herbivores. Both species being polyphagous, they were able to feed on  
538 native and non-native species such as *A. magellanica* and *T. gr ruderalia* (Karban and Strauss  
539 1994; Hullé et al. 2003). Plant *FDis* had an important contribution to explaining the abundance  
540 of macro-herbivores, which benefited as expected from diversified resources (Carmona et al.  
541 2011; Moretti et al. 2013). This result highlights that the traits we selected were involved in  
542 herbivore-plant interactions, as also suggested by the strong positive effects of  $CWM_{SLA}$  and  
543  $CWM_{LL}$  on herbivore abundance. Decomposers mainly comprised omnivorous taxa, which feed  
544 mostly on carcasses or faeces of mammals and seabirds. Their weak trophic link with plants  
545 might explain their moderate response to native and non-native vegetation, as well as to plant  
546 *FDis*. Predator diversity and abundance were not impacted by plant *FDis*. Predators, i.e., three

547 spiders, were more abundant in non-native patches relative to native, perhaps partly due to  
548 differences in prey availability, which is an important factor driving spider dynamics (Pearson  
549 2009). Indeed, these species have a very large diet consisting mainly of small insects (larvae,  
550 adults) (Ysnel and Ledoux 1988), whose abundances were higher on non-native patches. This  
551 result may contribute to explain higher abundances of native macro-arthropods in non-native  
552 patches since the native spiders, *N. antarcticus* and *M. kerguelensis*, represented ~90% of their  
553 abundance.

554

#### 555 THE ABUNDANCE OF MICRO-ARTHROPODS IS LOWER IN NON-NATIVE 556 VEGETATION

557 Non-native plants had negative effects on the abundance of both Oribatida mites and  
558 Symphypleona springtails. This result was also observed at *Marion Island* where  
559 Symphypleona springtails and one dominant Oribatida species had higher abundances on the  
560 native plant species *A. magellanica* than on the non-native *A. stolonifera* (Gremmen et al. 1998).  
561 Several studies conducted in the sub-Antarctic islands, concluded that both mites and springtails  
562 were mainly controlled by abiotic factors, in particular plant or soil moisture and temperature  
563 (Travé 1981; McGeoch et al. 2006). Local plant community can have indirect effects on micro-  
564 arthropods through the effects of plant traits on local abiotic conditions, which in turn may  
565 affect micro-arthropods. For instance, such mechanisms were suggested to explain springtail  
566 responses to different plant functional groups (Eisenhauer et al. 2011). In this study, lower  
567 densities of springtails in the legume group were explained by higher plant biomass production,  
568 which, by depleting soil water content, directly affected springtails; it also depleted nutrients in  
569 the soil, which in turn negatively affected fungal growth, i.e., the amount of food available to  
570 springtails. Interestingly, *FDis* had a strong negative effect on Symphypleona springtails and  
571 no effect on Oribatida mites. These finding echoes that of Milcu et al. (2013) who found the

572 same results, and suggested that the negative effect of *FD* on springtail abundance was mediated  
573 by its negative effect on root biomass. In contrast to macro-arthropods, micro-arthropods are  
574 less mobile and therefore they might not be able to reach the native patches such as macro-  
575 arthropods can do to find more resources. Further investigations on the relationship between  
576 plants, soil micro-arthropods and their main food resources, i.e., soil microbes, could allow  
577 understanding the mechanisms generating the results we observed. Indeed, we may hypothesize  
578 that the negative effects of non-native plants on Oribatida mites and Symphypleona springtails  
579 resulted at least partly from changes in the microbial networks in links to changes in plant  
580 communities (Boeddinghaus et al. 2019; Karimi et al. 2019).

581

## 582 **CONCLUSION**

583 Our study contributes to document the under-explored question of the interactions between  
584 plants and arthropods, in the context of biological invasions in the sub-Antarctic islands. This  
585 is particularly true for micro-arthropods, where the drivers of community assemblages, inter-  
586 specific interactions, species feeding preferences and ecology are largely unknown (Houghton  
587 et al. 2019). Our results point out the importance of conducting studies at different spatial scales  
588 and repeated over time, which could allow understanding the mechanisms by which non-native  
589 plants change native communities and modify the dynamics of both plant and arthropod  
590 communities. This would also make it possible to assess the long-term consequences for species  
591 conservation and ecosystem functioning. Indeed, by changing abundances of macro-arthropods  
592 belonging to different trophic groups and by depleting micro-arthropods, which are essential  
593 for nutrient cycling and primary production in terrestrial ecosystems, our findings suggest that  
594 non-native plant species may alter trophic interactions and whole ecosystem functioning in sub-  
595 Antarctic islands.

596

597 **ACKNOWLEDGMENTS**

598 The authors thank Peter Convey and two anonymous referees for helpful comments on an  
599 earlier version of the manuscript. The authors thank M. Lebouvier and G. Le Provost for useful  
600 comments on an earlier version of the manuscript. The authors thank all the contributors  
601 involved in the long-term plant and arthropod monitoring carried out within the framework of  
602 the programme 136 (IPEV). This research was supported by the ‘Institut Polaire Français Paul-  
603 Emile Victor’ (IPEV, programme 136), the CNRS (Zone-Atelier de Recherches sur  
604 l’Environnement Antarctique et Subantarctique).

605

606 **REFERENCES**

607 Badenhausser I (2021) Do non-native plants affect terrestrial arthropods in the sub-Antarctic  
608 Kerguelen Islands?

609 <https://data.inrae.fr/dataset.xhtml?persistentId=doi:10.15454/DPILL6>

610 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using  
611 lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>

612 Boeddinghaus RS, Marhan S, Berner D, Boch S, Fischer M, Hölzel N, Kattge J, Klaus VH,  
613 Kleinebecker T, Oelmann Y, Prati D, Schäfer D, Schöning I, Schrupp M, Sorkau E,  
614 Kandeler E, Manning P. (2019) Plant functional trait shift explain concurrent changes  
615 in the structure and function of grassland soil microbial communities. *J Ecol*  
616 107:2197–2210. <https://doi.org/10.1111/1365-2745.13182>

617 Burnham KP, Anderson DR (2002) Multimodel inference: understanding AIC and BIC in  
618 model selection. *Sociol Method Res* 33:261–304

619 Carmona D, Lajeunesse M, Johnson M (2011) Plant traits that predict resistance to herbivores.  
620 *Funct Ecol* 25:358–367. <https://doi.org/10.1111/j.1365-2435.2010.01794.x>

621 Chapuis JL, Le Roux V, Asseline J, Lefèvre L, Kerleau F (2001) Eradication of rabbits  
622 (*Oryctolagus cuniculus*) by poisoning on three islands of the subantarctic Kerguelen  
623 Archipelago. *Wildl Res* 28:323–331. <https://doi.org/10.1071/WR00042>

624 Chapuis JL, Frenot Y, Lebouvier M (2002) Une gamme d'îles de référence, un atout majeur  
625 pour l'évaluation de programmes de restauration dans l'archipel de Kerguelen. *Rev Ecol*  
626 (Terre Vie) 9:121–130

627 Chown SL, Convey P (2016) Antarctic Entomology. *Annu Rev Entomol* 61:119–137.  
628 <https://doi.org/10.1146/annurev-ento-010715-023537>

629 Chown SL, Gremmem NJM, Gaston KJ (1998) Ecological biogeography of southern islands:  
630 species-area relationships, human impacts and conservation. *Am Nat* 152:562–575.  
631 <https://doi.org/10.1086/286190>

632 Collins GE, Hogg ID, Convey P, Sancho LG, Cowan DA, Lyons WB, Adams BJ, Wall DH,  
633 Green TGA (2020) Genetic diversity of soil invertebrates corroborates timing estimates  
634 for past collapses of the West Antarctic Ice Sheet. *Proc Natl Acad Sci USA* 117:22293–  
635 22302. <https://doi.org/10.1073/pnas.2007925117>

636 Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege  
637 H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of  
638 protocols for standardised and easy measurement of plant functional traits worldwide.  
639 *Aust J Bot* 51:335–380. <https://doi.org/10.1071/BT02124>

640 Coulson SJ, Hodkinson ID, Webb NR (2003) Microscale distribution pattern in high Arctic soil  
641 microarthropod communities: the influence of plant species within the vegetation  
642 mosaic. *Ecography* 26:801–809. <https://doi.org/10.1111/j.0906-7590.2003.03646.x>



643 Crafford JE, Scholtz CH (1986) Impact of *Embryonopsis halticella* Eaton larvae (Lepidoptera:  
644 Yponomeutidae) feeding in Marion Island tussock grassland. *Polar Biol* 6:191–196

645 Deharveng L, Travé J (1981) Ecologie des Oribates (Acariens) et des Collemboles (Insectes)  
646 de Kerguelen. *CNFRA* 48:109–140

647 Deraison H, Badenhauer I, Loeuille N, Scherber C, Gross N (2015) Functional trait diversity  
648 across trophic levels determines herbivore impact on plant community biomass. *Ecol*  
649 *Lett* 18:1346–1355. <https://doi.org/10.1111/ele12529>

650 Díaz S, Kattge J, Cornelissen JH, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C,  
651 Prentice IC, Garnier E, Bönisch G, Westoby M, Poorter H, Reich PB, Moles AT, Dickie  
652 J, Gillison AN, Zanne AE, Chave J, Wright SJ, Sheremet'ev SN, Jactel H, Baraloto C,  
653 Cerabolini B, Pierce S, Shipley B, Kirkup D, Casanoves F, Joswig JS, Günther A,  
654 Falczuk V, Rüger N, Mahecha MD, Gorné LD. (2016) The global spectrum of plant  
655 form and function. *Nature*. <https://doi.org/10.1038/nature16489>

656 Dunn AM, Hatcher MJ (2015) Parasites and biological invasions: parallels, interactions, and  
657 control. *Trends Parasitol*. <https://doi.org/10.1016/j.pt.2014.12.003>

658 Eisenhauer N, Sabais ACW, Scheu S (2011) Collembola species composition and diversity  
659 effects on ecosystem functioning vary with plant functional group identity. *Soil Biol*  
660 *Biochem* 43:1697–1704. <https://doi.org/10.1016/j.soilbio.2011.04.015>

661 Fourcy D, Chapuis JL, Lebouvier M, Robin M (2018) Combining satellite datasets to track  
662 changes in the vegetation of Kerguelen. POLAR2018 Abstract proceedings - Open  
663 Science Conference, 19-23 June 2018 Davos, Switzerland. Polar2018 SCAR/IASC  
664 Open Science Conference, Davos (CH).

665 [https://www.polar2018.org/uploads/2/4/6/0/24605948/polar2018\\_abstractproceedings.](https://www.polar2018.org/uploads/2/4/6/0/24605948/polar2018_abstractproceedings.pdf)  
666 pdf

667 Fox J, Weisberg S (2019) An {R} Companion to Applied Regression, Third Edition. Thousand  
668 Oaks CA: Sage. URL: <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>

669 Frenot Y, Gloaguen JC, Massé L, Lebouvier M (2001) Human activities, ecosystem disturbance  
670 and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. *Biol*  
671 *Conserv* 101:33–50. [https://doi.org/10.1016/S0006-3207\(01\)00052-0](https://doi.org/10.1016/S0006-3207(01)00052-0)

672 Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicki M, Bergstrom DM (2005)  
673 Biological invasions in the Antarctic: extent, impacts and implications. *Biol Rev* 80:45–  
674 72. <https://doi.org/10.1017/S1464793104006542>

675 Gardarin A, Plantegenest M, Bischoff A, Valantin-Morison M (2018) Understanding plant-  
676 arthropod interactions in multitrophic communities to improve conservation biological  
677 control: useful traits and metrics. *J Pest Sci* 91:943–955.  
678 <https://doi.org/10.1007/s10340-018-0958-0>

679 Greenslade P (2002) Assessing the risk of exotic Collembola invading subantarctic islands:  
680 prioritising quarantine management. *Pedobiologia* 46:338–344.  
681 <https://doi.org/10.1078/0031-4056-00141>

682 Greenslade P, Convey P (2012) Exotic Collembola on subantarctic islands: pathways, origins  
683 and biology. *Biol Invasions* 14:405–417. <https://doi.org/10.1007/s10530-011-0086-8>

684 Gremmen NJM, Chown SL, Marshall DJ (1998) Impact of the introduced grass *Agrostis*  
685 *stolonifera* on vegetation and soil fauna communities at Marion Island, sub-Antarctic.  
686 *Biol Conserv* 85:223–231

- 687 Gressitt JL (1970) Subantarctic entomology and biogeography. *Pac Insects Monogr* 23:295–374
- 688 Gross N, Börger L, Duncan RP, Hulme PE (2013) Functional differences between alien and  
689 native species: do biotic interactions determine the functional structure of highly  
690 invaded grasslands? *Funct Ecol* 27:1262–1271. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2435.12120)  
691 2435.12120
- 692 Houghton M, Terauds A, Merritt D, Driessen M, Shaw J (2019) The impacts of non-native  
693 species on the invertebrates of Southern ocean islands. *J Insect Conserv* 23:435–452.  
694 <https://doi.org/10.1007/s10841-019-00147-9>
- 695 Hullé M, Vernon P (2021) The terrestrial macro-invertebrates of the sub-Antarctic Îles  
696 Kerguelen and Île de la Possession. Iste-Wiley, London
- 697 Hullé M, Pannetier D, Simon JC, Vernon P, Frenot Y (2003) Aphids of sub-Antarctic Îles  
698 Crozet and Kerguelen: species diversity, host range and spatial distribution. *Antarct Sci*.  
699 <https://doi.org/10.1017/S0954102003001184>
- 700 Hullé M, Buchard C, Georges R, Vernon P (2018) Guide d'identification des invertébrés des  
701 Îles sub-Antarctiques Kerguelen et Crozet. 2<sup>nd</sup> edn. Université Rennes 1.  
702 <https://doi.org/10.15454/1.5375302767618145E12>
- 703 Joern A, Laws AN (2013) Ecological mechanisms underlying arthropod species diversity in  
704 grasslands. *Annu Rev Entomol* 58:19–36. [https://doi.org/10.1146/annurev-ento-](https://doi.org/10.1146/annurev-ento-120811-153540)  
705 120811-153540
- 706 Karban R, Strauss SY (1994) Colonization of new host-plant individuals by locally adapted  
707 thrips. *Ecography* 17:82–87. <https://doi.org/10.1111/j.1600-0587.1994.tb00079.x>

708 Karimi B, Dequiedt S, Terrat S, Jolivet C, Arrouays D, Wincker P, Cruad C, Bispo A,  
709 Chemidlin Prévost-Bouré N, Ranjard L (2019) Biogeography of Soil Bacterial  
710 Networks along a Gradient of Cropping Intensity. *Sci Rep* 9:3812.  
711 <https://doi.org/10.1038/s41598-019-40422-y>

712 Kassambara A, Mundt F (2020) factoextra: Extract and Visualize the Results of Multivariate  
713 Data Analyses. R package version 1.0.7.  
714 <http://www.sthda.com/english/rpkgs/factoextra>

715 Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity  
716 from multiple traits. *Ecology* 91:299-305. <https://doi.org/10.1890/08-2244.1>

717 Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple  
718 traits, and other tools for functional ecology. R package version 1.0-12

719 Lavorel S (2013) A novel framework for linking functional diversity of plants with other trophic  
720 levels for the quantification of ecosystem services. *J Veg Sci* 24:942–948.  
721 <https://doi.org/10.1111/jvs.12083>

722 Le S, Josse J, Husson F (2008) FactoMineR: An R Package for Multivariate Analysis. *J Stat*  
723 *Softw* 25:1–18. <https://doi.org/10.18637/jss.v025.i01>

724 Lebouvier M, Laparie M, Hullé M, Marais A, Cozic Y, Lalouette L, Vernon P, Candresse T,  
725 Frenot Y, Renault D (2011) The significance of the sub-Antarctic Kerguelen Islands for  
726 the assessment of the vulnerability of native communities to climate change, alien insect  
727 invasion and plant viruses. *Biol Invasions* 13:1195–1208.  
728 <https://doi.org/10.1007/s10530-011-9946-5>

729 Lebouvier M, Lambret P, Garnier A, Convey P, Frenot Y, Vernon P, Renault D (2020) Spotlight  
730 on the invasion of a carabid beetle on an oceanic island over a 105-year period. *Sci Rep*  
731 10:17103. <https://doi.org/10.1038/s41598-020-72754-5>

732 Lenth RV (2020) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package  
733 version 1.5.3. <https://CRAN.R-project.org/package=emmeans>

734 Le Provost G, Gross N, Börger L, Deraison H, Roncoroni M, Badenhausser I (2017) Trait-  
735 matching and mass effect determine the functional response of herbivore community  
736 to land use intensification. *Funct Ecol* 31:1600–1611. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2435.12849)  
737 2435.12849

738 McGeoch MA, Le Roux PC, Hugo EA, Chown SL (2006) Species and community responses  
739 to short-term climate manipulation: Microarthropods in the sub-Antarctic. *Austral Ecol*  
740 31:719–731. <https://doi.org/10.1111/j.1442-9993.2006.01614.x>

741 McGeoch MA, Shaw JD, Terauds A, Lee JE, Chown SL (2015) Monitoring biological invasion  
742 across the broader Antarctic: A baseline and indicator framework. *Glob Environ Change*  
743 32:108–125. <https://doi.org/10.1016/j.gloenvcha.2014.12.012>

744 Milcu A, Allan E, Roscher C, Jenkins T, Meyer ST, Flynn D, Bessler H, Buscot F, Engels C,  
745 Gubsch M, König S, Lipowsky A, Loranger J, Renker C, Scherber C, Schmid B,  
746 Thebault E, Wubet T, Weisser WW, Scheu S, Eisenhauer N (2013) Functionally and  
747 phylogenetically diverse plant communities key to soil biota. *Ecology* 94:1878–1885.  
748 <https://doi.org/10.1890/12-1936.1>

749 Moretti M, de Bello F, Ibanez S, Fontana S, Pezzatti G, Dziock F, Rixen C, Lavorel S (2013)  
750 Linking traits between plants and invertebrate herbivores to track functional effects of  
751 land-use changes. *J Veg Sci* 24:949–962. <https://doi.org/10.1111/jvs.12022>

752 Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional  
753 approach reveals community responses to disturbance. *Trends Ecol Evol* 28:167–177.  
754 <https://doi.org/10.1016/j.tree.2012.10.004>

755 Ordonez A, Wright IJ, Olff H (2010) Functional differences between native and alien species:  
756 a global-scale comparison. *Funct Ecol* 24:1353–1361. <https://doi.org/10.1111/j.1365-2435.2010.01739.x>

758 Pearson DE (2009) Invasive plant architecture alters trophic interactions by changing predator  
759 abundance and behaviour. *Oecologia* 159:549–558. <https://doi.org/10.1007/s00442-008-1241-5>

761 Perterra LR, Aragon P, Shaw JD (2017) Global thermal niche models of two European grasses  
762 shows high invasion risks in Antarctica. *Glob Chang Biol* 23:2863–2873.  
763 <https://doi.org/10.1111/gcb.13596>

764 R Development Core Team (2020) R: A language and environment for statistical computing. R  
765 Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>

767 Russel JC, Meyer JY, Holmes ND, Pagad S (2017) Invasive alien species on islands: impacts,  
768 distribution, interactions and management. *Environ Conserv* 44:359–370.  
769 <https://doi.org/10.1017/S0376892917000297>

770 Schaffers AP, Raemakers IP, Sykora KV, Ter Braak CJF (2008) Arthropod assemblages are  
771 best predicted by plant species composition. *Ecology* 89:782–794.  
772 <https://doi.org/10.1890/07-0361.1>

773 Schooley RL, Wiens JA (2003) Finding habitat patches and directional connectivity. *Oikos*  
774 102:559–570. <https://doi.org/10.1034/j.1600-0706.2003.12490.x>

775 Shaw JD, Spear D, Greve M, Chown SL (2010) Taxonomic homogenization and differentiation  
776 across Southern Ocean Islands differ among insects and vascular plants. *J Biogeogr*  
777 37:217–228. <https://doi.org/10.1111/j.1365-2699.2009.02204.x>

778 Southwood TRE (1978) *Ecological methods, with particular reference to the study of insect*  
779 *populations*. Chapman and Hall, London

780 Spafford RD, Lortie CJ, Butterfield BJ (2013) A systematic review of arthropod community  
781 diversity in association with invasive plants. *Neobiota* 16:81–102.  
782 <https://doi.org/10.3897/neobiota.16.4190>

783 Travé J (1981) Structure des peuplements de microarthropodes à Kerguelen. Essai de synthèse.  
784 Colloque sur les écosystèmes terrestres subantarctiques, CNFRA 51:73–80

785 Tréhen P, Vernon P, Delettre Y, Frenot Y (1986) Organisation et dynamique des peuplements  
786 diptérologiques à Kerguelen. Mise en évidence de modifications liées à l'insularité.  
787 CNFRA 58:241–253

788 Vernon P, Vannier G, Tréhen P (1998) A comparative approach to the entomological diversity  
789 of polar regions. *Acta Oecol* 19:303–308. [https://doi.org/10.1016/S1146-](https://doi.org/10.1016/S1146-609X(98)80034-9)  
790 [609X\(98\)80034-9](https://doi.org/10.1016/S1146-609X(98)80034-9)

791 Voisin JF, Chapelin-Viscardi JD, Ponel P, Rapp M (2017) Les Coléoptères de la province de  
792 Kerguelen (îles subantarctiques de l'océan Indien). *Faune de France 99*, Fédération  
793 Française des Sociétés de Sciences Naturelles, Paris

794 Ysnel F, Ledoux JC (1988) Données sur le cycle biologique de quelques araignées des terres  
795 australes françaises (Kerguelen, Crozet). *Bulletin de la Société Scientifique de Bretagne*  
796 59:209–221

797 Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common  
798 statistical problems. *Methods Ecol Evol* 1:3–14. [https://doi.org/10.1111/j.2041-](https://doi.org/10.1111/j.2041-210X.2009.00001.x)  
799 [210X.2009.00001.x](https://doi.org/10.1111/j.2041-210X.2009.00001.x)

800



801 **Table 1.** Effect of island, type of plant patch (native or non-native) and their two-way interaction on the plant community functional diversity  
802 ( $FD_{is}$ ) and the community-weighted means of plant traits ( $CWM_{TRAIT}$ ).  $CWM_{PH}$  = plant height,  $CWM_{PW}$  = plant width,  $CWM_{LL}$  = leaf length,  $CWM_{LA}$   
803 = leaf area,  $CWM_{LT}$  = leaf thickness,  $CWM_{SLA}$  = specific leaf area,  $CWM_{LDMC}$  = leaf dry matter content. Values and significance of Type II Wald  
804 Chi-square tests,  $\chi^2$ , realized on fixed effects tested in LMM models (Island:  $\chi^2_2$  Type of patch:  $\chi^2_1$ , Island  $\times$  Type of patch:  $\chi^2_2$ ). Significant fixed  
805 effects are in bold. We also show predicted means  $\pm$  standard errors ( $\alpha = 0.05$ ) of  $FD_{is}$  and  $CWM_{TRAIT}$ 's for each island  $\times$  type of patch combination.  
806

Variable	Fixed factor	$\chi^2$	$p (>\chi^2)$	<i>Île Australia</i>		<i>Île aux cochons</i>		<i>Île Mayes</i>	
				Native patch	Non-native patch	Native patch	Non-native patch	Native patch	Non-native patch
$FD_{is}$	Island	9.16	<b>0.0103</b>						
	Type of patch	1.47	0.2258	0.081 $\pm$ 0.023	0.081 $\pm$ 0.023	0.158 $\pm$ 0.023	0.158 $\pm$ 0.023	0.155 $\pm$ 0.023	0.155 $\pm$ 0.023
	Island $\times$ Type of patch	1.28	0.5255						
$CWM_{PH}$ (cm)	Island	235.34	< <b>0.0001</b>						
	Type of patch	117.88	< <b>0.0001</b>	16.8 $\pm$ 0.9	23.9 $\pm$ 0.9	21.5 $\pm$ 0.9	25.2 $\pm$ 0.9	25.3 $\pm$ 0.9	35.5 $\pm$ 0.9
	Island $\times$ Type of patch	34.62	< <b>0.0001</b>						
$CWM_{PW}$ (cm)	Island	6.36	<b>0.0416</b>						
	Type of patch	10.18	<b>0.0014</b>	15.4 $\pm$ 1.8	20.7 $\pm$ 1.8	11.7 $\pm$ 1.8	17.1 $\pm$ 1.8	16.8 $\pm$ 1.8	22.2 $\pm$ 1.8
	Island $\times$ Type of patch	0.58	0.7479						

$CWM_{LL}$ (cm)	Island	12.30	<b>0.0021</b>						
	Type of patch	92.30	< <b>0.0001</b>	$7.3 \pm 1.0$	$16.0 \pm 1.6$	$8.9 \pm 1.2$	$18.4 \pm 1.7$	$12.3 \pm 1.4$	$23.1 \pm 1.9$
	Island $\times$ Type of patch	1.83	0.3997						
$CWM_{LA}$ (cm <sup>2</sup> )	Island	6.45	<b>0.0396</b>						
	Type of patch	9.78	<b>0.0017</b>	$16.8 \pm 6.4$	$31.9 \pm 8.8$	$12.7 \pm 5.6$	$26.1 \pm 8.0$	$34.0 \pm 9.1$	$54.3 \pm 11.5$
	Island $\times$ Type of patch	1.33	0.5131						
$CWM_{LT}$ (mm)	Island	14.36	<b>0.0008</b>						
	Type of patch	224.60	< <b>0.0001</b>	$0.69 \pm 0.03$	$0.38 \pm 0.02$	$0.60 \pm 0.03$	$0.33 \pm 0.02$	$0.74 \pm 0.04$	$0.41 \pm 0.02$
	Island $\times$ Type of patch	5.5	<b>0.0638</b>						
$CWM_{SLA}$ (cm <sup>2</sup> g <sup>-1</sup> )	Island	2.70	0.2589						
	Type of patch	82.4	< <b>0.0001</b>	$139.0 \pm 4.5$	$192.0 \pm 4.5$	$139.0 \pm 4.5$	$192.0 \pm 4.5$	$139.0 \pm 4.5$	$192.0 \pm 4.5$
	Island $\times$ Type of patch	0.18	0.9142						
$CWM_{LDMC}$	Island	12.02	<b>0.0024</b>						
	Type of patch	7.04	<b>0.0079</b>	$0.255 \pm 0.015$	$0.224 \pm 0.015$	$0.287 \pm 0.015$	$0.256 \pm 0.015$	$0.225 \pm 0.015$	$0.194 \pm 0.015$
	Island $\times$ Type of patch	1.40	0.4945						

807

808

809 **Table 2.** Effect of island, type of patch (native or non-native), their two-way interaction and plant community *FDis* on macro-arthropod taxa  
810 richness and abundance, and micro-arthropod abundance. Taxa richness was calculated pooling pitfall traps and yellow pans. Taxa abundance was  
811 calculated using pitfall trap data (macro-arthropods: native species, predators; micro-arthropods) or yellow pan data (macro-arthropods: herbivores,  
812 decomposers). Values and significance of Type II Wald Chi-square tests,  $\chi^2$ , realized on all fixed effects tested in GLMM (native macro-arthropod  
813 abundance, Symphypleona abundance) or LMM (all other models). Significant fixed effects in the simplified models are in bold.

Arthropod taxa and metrics	Island		Type of patch		Island $\times$ Type of patch		<i>FDis</i>	
	$\chi^2$	$p (>\chi^2)$	$\chi^2$	$p (>\chi^2)$	$\chi^2$	$p (>\chi^2)$	$\chi^2$	$p (>\chi^2)$
Macro-arthropod richness								
Native species	11.58	<b>0.0030</b>	0.36	0.5456	5.63	0.0597	5.63	<b>0.0175</b>
Non-native taxa	17.76	<b>0.0001</b>	1.03	0.3103	4.45	0.1081	1.29	0.2560
All taxa	24.99	<b>&lt;0.0001</b>	5.24	<b>0.0220</b>	16.52	<b>0.0003</b>	8.91	<b>0.0028</b>
Decomposers	10.98	<b>0.0041</b>	0.61	0.4337	9.60	<b>0.0082</b>	3.01	0.0824
Predators	4.11	0.1281	0.52	0.4702	8.52	<b>0.0141</b>	1.07	0.3000
Macro-arthropod abundance								
Native species	19.38	<b>&lt;0.0001</b>	29.98	<b>&lt;0.0001</b>	5.17	0.0751	2.53	<b>0.1113</b>
Herbivores	0.65	0.7206	25.55	<b>&lt;0.0001</b>	11.93	<b>0.0025</b>	13.03	<b>0.0003</b>
Decomposers	12.28	<b>0.0021</b>	1.29	0.2549	7.32	<b>0.0256</b>	0.11	0.7387
Predators	21.17	<b>&lt;0.0001</b>	11.08	<b>0.0009</b>	6.78	<b>0.0337</b>	1.51	0.2184
Micro-arthropod abundance								
Oribatida mites	4.09	0.1294	5.57	<b>0.0183</b>	0.75	0.6870	0.039	0.8423

814

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Symphyleona springtails	12.58	<b>0.0019</b>	79.63	<b>&lt;0.0001</b>	2.83	0.2423	41.35	<b>&lt;0.0001</b>
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815 **FIGURE CAPTIONS**

816 **Fig. 1** Map of Kerguelen Islands and location of Kerguelen Islands in the Southern Indian  
817 Ocean

818

819 **Fig. 2** Vegetation maps, based on Pléiades 1A PMS satellite image acquired in 2016, in 1 km<sup>2</sup>  
820 areas around the sampled patches, and location of the sampled patches (centroids) within native  
821 and non-native areas. Native patches are in white and non-native patches in black and white.  
822 Vegetation was classified in 10 classes: Steppe dominated by non-native Poaceae; Tall grassland  
823 of non-native Poaceae; Mixed herbfield of native and non-native species; Tall herbfield of  
824 *Acæna magellanica* (ACAMA); Tundra of *Azorella selago* (AZOSE), *A. magellanica* and  
825 *Festuca contracta* (FESCO); Native herbfield of *A. selago*, *A. magellanica* and *Pringlea*  
826 *antiscorbutica* (PRIAN); Open cushion-carpet of *A. selago*; Mire; Steppe dominated by native  
827 Poaceae; Fellfield. See Online Resource 1 for a detailed description of the classes. Maps  
828 highlight spatial patterns of vegetation, contrasting vegetation dominated by native plant  
829 species (in green) and vegetation dominated by non-native plants species (in yellow and pink)

830

831 **Fig. 3** Mean plant species cover over the five quadrats per patch, in native and non-native  
832 patches in the islands studied: *Île Australia* (a) native patches (d) non-native patches, *Île aux*  
833 *Cochons* (b) native patches (e) non-native patches, *Île Mayes* (c) native patches (f) non-native  
834 patches). Native plant species: *Acaena magellanica* (ACAMA), *Azorella selago* (AZOSE),  
835 *Deschampsia antarctica* (DESAN), *Festuca contracta* (FESCO), *Galium antarcticum*  
836 (GALAN), *Ranunculus biternatus* (RANBI), *Pringlea antiscorbutica* (PRIAN); Non-native  
837 plant species: *Cerastium fontanum* (CERFO), *Cerastium glomeratum* (CERGL), *Poa annua*  
838 (POAAN), *Poa pratensis* (POAPR), *Sagina procumbens* (SAGPR), *Stellaria alsine* (STEAL),

839 *Stellaria media* (STEME), *Taraxacum erythrospermum* (TARER), *Taraxacum gr. ruderalia*  
840 (TAROF), *Vulpia bromoides* (VULBR)

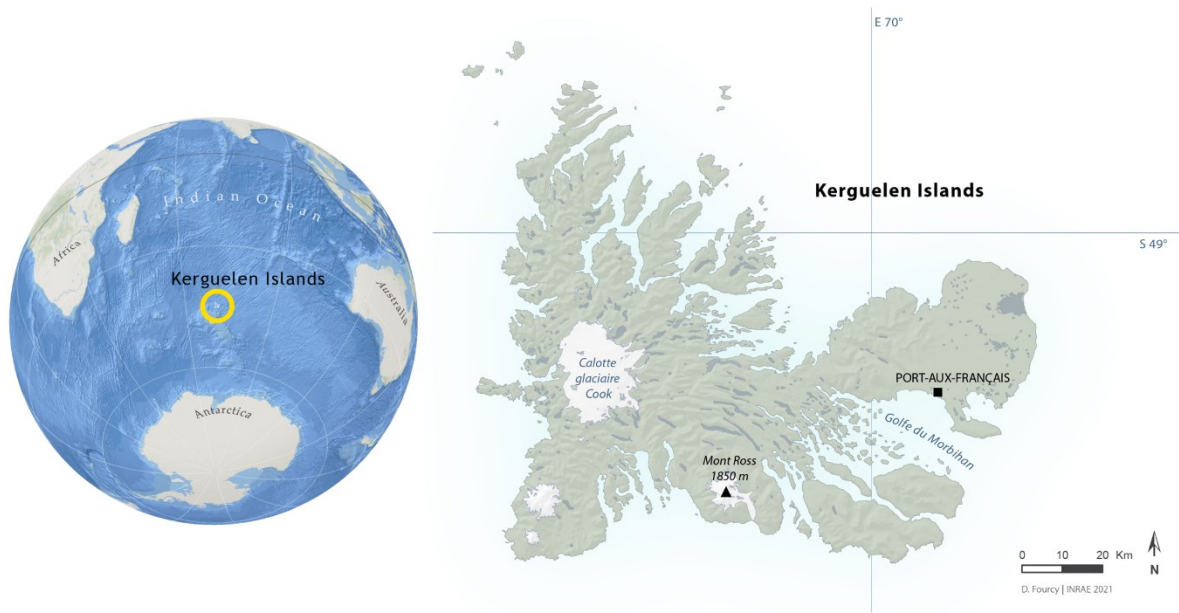
841

842 **Fig. 4** Model predictions  $\pm SE$  of the effect of the type of patch (native in green, non-native in  
843 red) on macro-arthropod abundance: (a) native species (pitfall traps) (see Table 2 for GLMM  
844 results), (b) herbivores (yellow pan counts), (c) decomposers (yellow pan counts) and (d)  
845 predators (pitfall trap counts) (see Table 2 for LMM results). Predictions are on a log scale.  
846 Shown are the results of the comparison between native and non-native patches (additive effect:  
847  $p$  is the  $p$ -value of Chi-square test,  $\chi^2$  in LMM or GLMM; interactive effect with the island:  $p$   
848 is the  $p$ -value for comparing the estimates of native vs non-native patches within each island  
849 with Tukey's method and paired contrasts)

850

851 **Fig. 5** Model predictions  $\pm SE$  of the effect of the type of patch (native in green, non-native in  
852 red) on micro-arthropod abundance: (a) Oribatida mites (pitfall trap) (see Table 2 for LMM  
853 results), and (b) Symphypleona springtails (pitfall traps) (see Table 2 for GLMM results).  
854 Predictions are on a log scale. Shown are the results of the comparison between native and non-  
855 native patches (additive effect:  $p$  is the  $p$ -value of Chi-square test,  $\chi^2$  in LMM or GLMM)

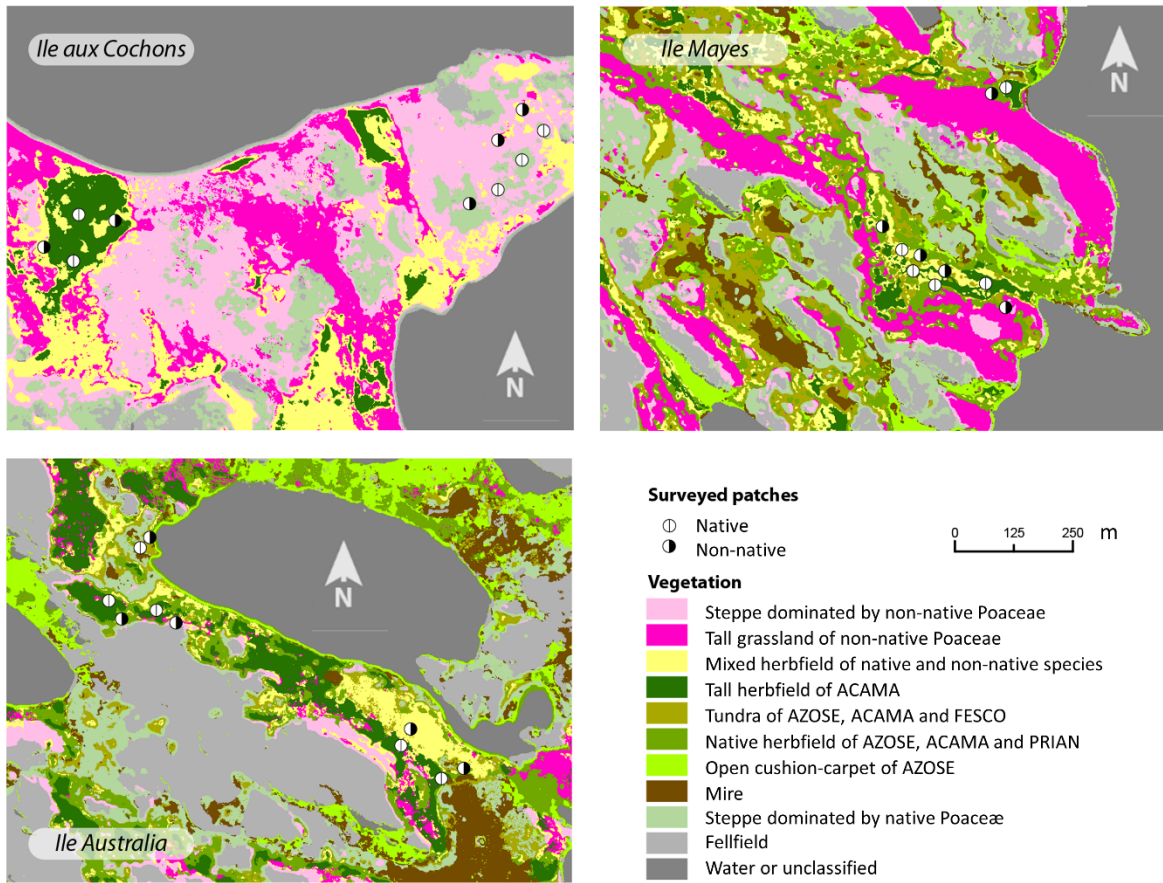
856



857

858 Fig. 1

859

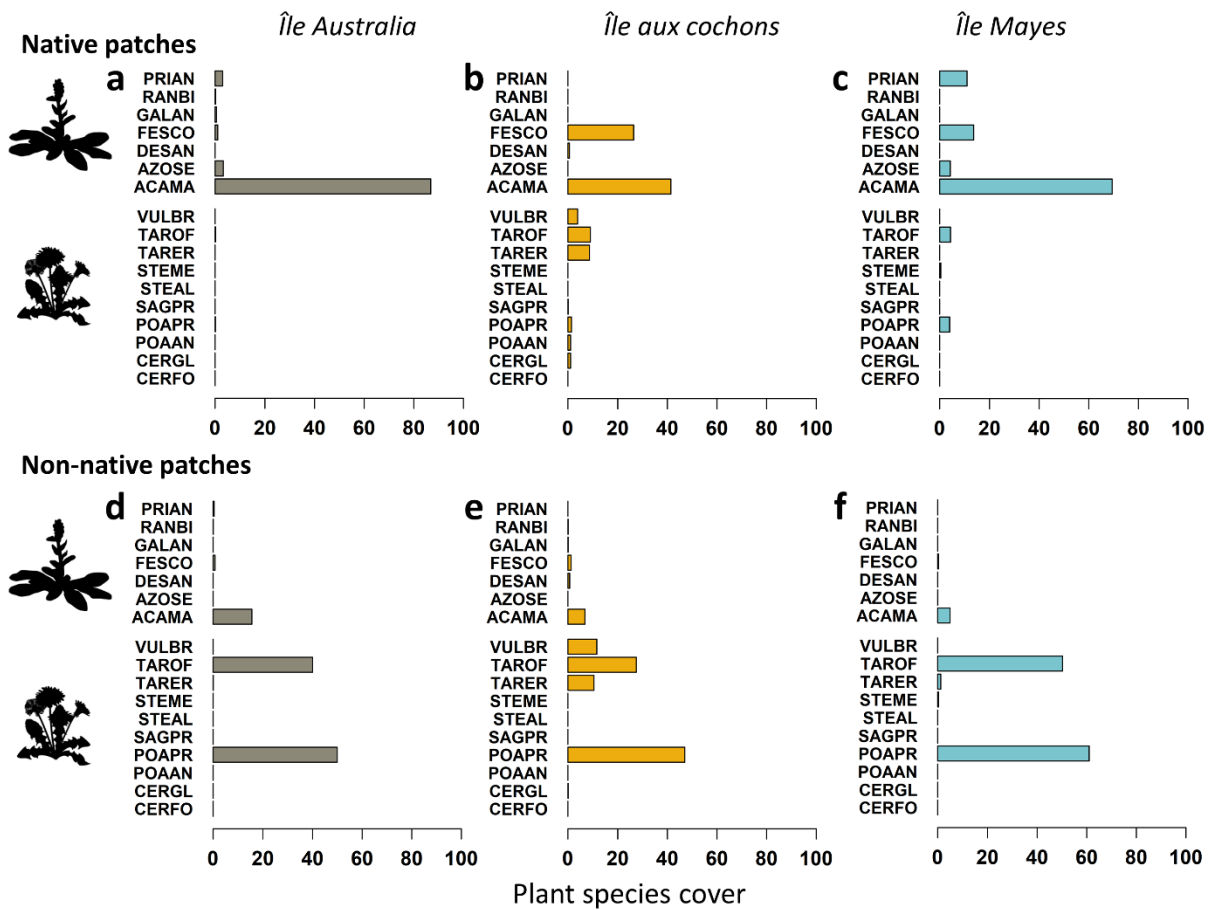


860

861 Fig. 2

862

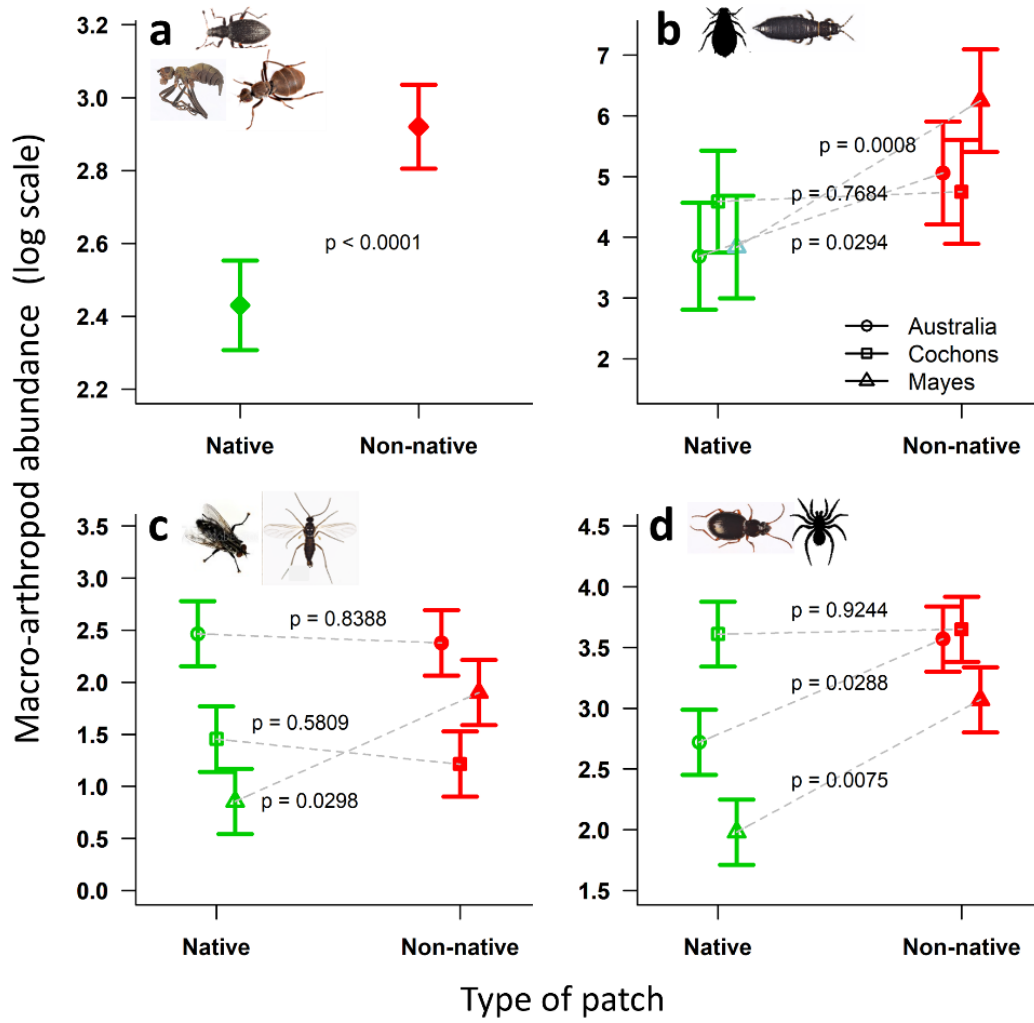




863

864 Fig. 3

865

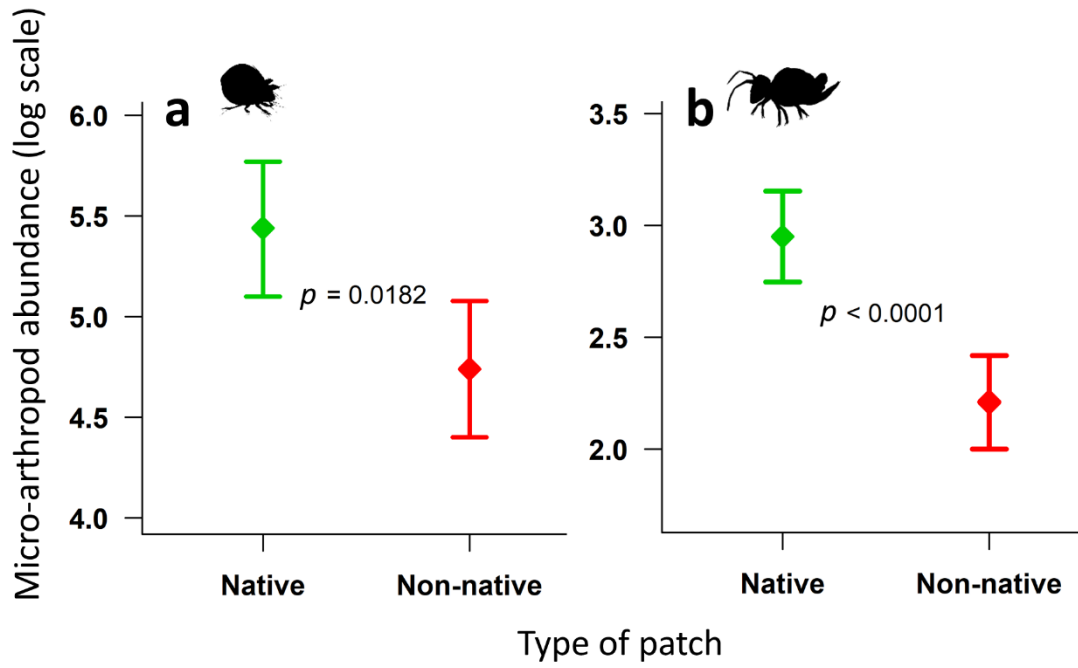


866

867 Fig. 4

868

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870

871 Fig. 5

872

873 **Supplementary Information**

874 Additional Supporting information may be found in the online version of this article:

875 **Online resource 1.** Description of vegetation categories used to map vegetation on the three  
876 islands studied

877 **Online resource 2.** Physical description of the surveyed vegetation patches

878 **Online resource 3.** PCA results conducted on  $CWM_{TRAITs}$  (community-weighted means of  
879 plant trait) calculated on native and non-native vegetation patches. PH = plant height, PW=plant  
880 width, LL=leaf length, LA=leaf area, LDMC=leaf dry matter content, SLA=specific leaf area,  
881 LT=leaf thickness

882 **Online resource 4.** Results and model outputs of the comparison between patch model and  
883 single  $CWM_{TRAIT}$  models

884 **Online resource 5.** Cumulated counts of three macro-arthropod trophic groups: herbivores,  
885 decomposers and predators, collected in pitfall traps and in yellow pans, on the three islands  
886 studied (*Île Australia* in grey, *Île aux Cochons* on yellow, *Île Mayes* in blue) in non-native (in  
887 red) and native patches (in green)