

1 Title: **HIGH STOCKS, BUT SLOW RECOVERY, OF ECOSYSTEM CARBON IN**
2 **SOUTHERN OCEANIC TUSSOCK GRASSLANDS**

3 Running title: Taking stock of the world's densest grassland carbon store

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9 Keywords: Carbon, Falkland Islands, peat, *Poa flabellata*, restoration, tussock

10 Journal: Polar Biology

11 The final publication is available at Springer via DOI: 10.1007/s00300-017-2084-5

12 **ABSTRACT**

13 Peat-forming large tussock grasslands on oceanic and sub-Antarctic islands are
14 fundamentally understudied in terms of carbon (C) storage. Here we quantify both plant and
15 soil C and nitrogen (N) storage for the large-tussock grass *Poa flabellata* in the Falkland
16 Islands, at its most northerly range. In this study we adopt a spatially explicit sampling
17 approach to account for tussock and inter-tussock (between tussocks) areas for three habitats;
18 remnant stands (surviving clearance and overgrazing), restored stands (planted) and eroded
19 bare peat sites. We found that remnant stands of *P. flabellata* have above-ground C densities
20 of $49.8 \pm 9.7 \text{ Mg C ha}^{-1}$, equivalent to temperate and boreal forests. The majority of above-
21 ground C is stored within the pedestal, a compact accumulation of dead leaves, rhizomes and
22 roots. By surveying restored stands of increasing age we found that such C accrual may take
23 longer than two decades. Soil C stocks were horizontally and vertically spatially variable and
24 did not differ between habitat types. Plant and soil C and N stocks were strongly coupled
25 identifying the important role of N availability for C accrual in this system. Scaling-up our
26 results, planting tussock grass could accrue up to 0.9 million Mg C on a decadal timescale
27 across the islands, yet the impact of planting on soil C storage is likely to be more variable.
28 Our results highlight the local and regional importance of large tussock grasslands as dense C
29 stores and that land management and conservation of these communities needs to be more
30 carbon-conscious.

31

32 INTRODUCTION

33 Peat is composed of partially decomposed organic matter and represents one of the densest
34 forms of terrestrially stored carbon (C). Globally the majority of peatlands are found in the
35 cold to temperate wet northern latitudes as well as warm wet regions of central Indo-Asia
36 (Lottes and Ziegler 1994; Vitte 2000). Deviating from this distribution are peatlands of sub-
37 Antarctic and southern cool-temperate oceanic climates (Joosten 2010; HWSD 2015).
38 Coastal peat-forming plant communities in the southern hemisphere are fundamentally
39 understudied, notably those characterised by large tussock-forming grasses such as *Poa*
40 *flabellata* (South Atlantic Ocean), *Poa cookii* (South Indian Ocean), *Poa tennantiana* and
41 *Poa foliosa* (South Pacific Ocean). The rate of peat accumulation under these grasslands has
42 been suggested to be the fastest in the world, based on ¹⁴C-isotope aging of peat (Smith and
43 Clymo 1984; Smith and Prince 1985). Yet, the distribution of many of these coastal peat-
44 forming communities has declined significantly over the last century mainly through human
45 activity, directly via clearance (e.g. burning) or indirectly via the introduction of livestock
46 and rodents (Moen and Macalister 1994; Shaw et al. 2011). Due to limited records the extent
47 of habitat loss is often difficult to estimate. For example, on the Falkland Islands the land area
48 dominated by *P. flabellata* (tussac) has been estimated to have declined by 81% from 22,200
49 ha to 4,000-5,000 ha between pre-1840s and 1987 (Strange et al. 1988). Loss of these large
50 tussock grasslands potentially represents a loss of globally significant peat-forming plant
51 communities, yet to-date there has been no comprehensive quantification of densities of plant
52 and soil C stored within these grasslands.

53

54 Loss of tussock-forming plant communities is highly problematic for several reasons. For
55 example, following the loss of these plant communities, exposed peat becomes vulnerable to
56 high rates of water and wind driven erosion (Wilson et al. 1993; Selkirk and Saffigna 1999).
57 What is more, restoration of eroded areas, whether localised or landscape-scale, can be
58 difficult due to natural/environmental and socio-economic reasons. On uninhabited islands it
59 has been possible to encourage natural recolonisation by removing introduced species by, for
60 example, baiting rabbits on Macquarie Island in the southwest Pacific Ocean (Shaw et al.
61 2011) or culling reindeer (*Rangifer tarandus*) on South Georgia in the southern Atlantic
62 (GSGSSI 2014). However, removal of livestock from human inhabited regions is more
63 difficult due to the high economic and cultural value of these practices to local communities.

64 An alternative approach is to re-vegetate eroded areas either by planting grass tillers (living
65 shoots) or re-seeding with the eventual aim of establishing grazing restored stands.
66 Nonetheless, re-vegetation in remote locations has many challenges, including accessibility,
67 sufficient human labour (i.e. manually collecting seeds or tillers) and exclusion of grazers to
68 ensure plant establishment (Kerr 1994; Cris et al. 2001). Despite significant effort invested
69 into the establishment of restored stands, there has been no subsequent monitoring of the
70 impact of re-vegetating on ecosystem C storage. For instance, it is unknown whether in the
71 short-term restored stands negatively influence peatland C storage due to disturbance during
72 planting (Smith et al. 2014; Coralan and Fornara 2016) or if older restored stands are on a
73 trajectory to store equivalent quantities of C as remnant stands.

74

75 *Poa flabellata* is the most widespread large-tussock forming grass in the southern cool-
76 temperate oceanic climate and the sub-Antarctic region, naturally occurring across the Diego
77 Ramirez Islands, Falkland Islands, Gough Island, South Georgia and Tierra del Fuego (KEW
78 2015: Online Resource 1). *P. flabellata* is predominantly coastal (0-350 m a.s.l.) and forms
79 dense monocultures, typically with an un-vegetated inter-tussock area, unless the canopy is
80 interrupted either naturally (e.g. cliffs) or by large mammals (e.g. marine mammals or
81 livestock) (Moore 1968: Online Resource 1). *P. flabellata* forms a large tussock with an
82 aggregation of living tillers growing on top of a pedestal of accumulated dead leaves,
83 rhizomes and roots (Moore 1968; Broughton and McAdam 2005). Growing to heights of 3 to
84 4 m, estimates of total above-ground standing biomass of individual tussocks have been
85 reported up to 360 Mg ha⁻¹ (combined living and dead plant material) (Gunn 1976). *P.*
86 *flabellata* communities are also internationally important habitats for breeding colonies of sea
87 birds and mammals (Strange 1972; Smith and Prince 1985), but equally benefit from
88 allochthonous (marine-derived) nutrient inputs that enhance plant productivity (Bokhorst et
89 al. 2007) similar to other sub-Antarctic and oceanic large-tussock communities around the
90 world (Bergstrom et al. 2002; Ellis 2005). Nutrient enrichment, particularly forms of nitrogen
91 (N), is likely to enhance biomass production and therefore above-ground C storage for mature
92 stands and establishing restored stands.

93

94 Globally approximately 20% of *P. flabellata* is found in the Falkland Islands at the northern
95 limit of its distribution (FIG 2008). Across the Islands, *P. flabellata* communities exist as

96 three distinct habitats: old remnant stands that have survived historic and current human land
97 use; restored stands created through planting tillers; and bare soil with limited to non-existent
98 natural recolonisation (Strange et al. 1988). Thus the Falkland Islands represent an ideal
99 location in which to evaluate C storage in remnant stands and following restoration. In this
100 study, we conducted an island-wide survey of *P. flabellata* ecosystem (plant plus soil) C
101 storage across the Falkland Islands: (1) to describe the distribution of plant and soil C and N
102 storage in typical *P. flabellata* communities; (2) quantify plant and soil C and N stored within
103 different habitats (remnant, restored and eroded), including *P. flabellata* restored stands of
104 different ages; and (3) using the resulting data, up-scale our estimates of total ecosystem C
105 storage for remnant *P. flabellata* stands across the Falkland Islands for the historic habitat
106 range as well as the current distribution. By comparing different habitats of tussock
107 grasslands we aim to provide primary data on ecosystem C densities of this ecosystem in
108 different states of succession and development.

109

110 MATERIAL AND METHODS

111 SITE SELECTION

112 The study was carried out in the Falkland Islands, an archipelago with two main islands, East
113 and West, situated between 51°S and 53°S and 57°30' W and 61°30' W, between June and
114 September 2015. The Islands have a southern cool-temperate oceanic climate with mean
115 January and July temperatures of 9.4°C and 2.2°C respectively (1961-1990 average based on
116 data from the capital Stanley; see Jones et al. 2013), and an average annual precipitation of
117 640 mm, yet the majority of this falls during winter months with a soil moisture deficient
118 occurring in spring (October onwards; J.H. McAdam unpublished data). The Falklands are
119 particularly windy with average annual wind speeds of 8.5 m s⁻¹ (16.5 knots) and a high
120 frequency of severe gale force winds (Jones et al. 2013, 2015). Dominant soil types across the
121 Islands are fibric histosols and umbric leptosols (HWSD 2015), although this coarse
122 classification of soil types is currently under review (see IUCN 2015). Wildfires are a
123 component of the island ecology and are present throughout the palynological record (Barrow
124 1978), yet it is mainly human land use, namely livestock rearing, that has shaped vegetation
125 composition and structure over the last two centuries (see Munro 1924; Davies 1939).

126

127 Almost 95% of the land area is under extensive sheep and cattle grazing management with
128 Polwarth-Merino sheep as the dominant grazer, typically at low stocking densities between
129 0.5 - 0.9 sheep ha⁻¹ (FIG 2015). Historic overstocking and continuous open ranch livestock
130 grazing has altered the ecosystem so that it has become dominated by grazing tolerant small
131 tussock-forming grass, *Cortaderia pilosa* (whitegrass), and dwarf shrubs, *Empetrum rubrum*
132 (diddle-dee) and *Baccharis magellanica* (christmas bush) (Moore 1968; Broughton and
133 McAdam 2005). As livestock were introduced earlier to East Falkland than to West Falkland,
134 the former has had the largest loss of the estimated historic range of *P. flabellata*, particularly
135 across the northern and eastern coastlines in comparison to West Falkland and its outer
136 islands (Fig 1) (Strange et al. 1988). Given the historic land use of the islands, coastal tussock
137 communities are a mix of three distinct habitats: remnant stands (stands that have survived
138 historic clearance and overgrazing), restored stands (planted *P. flabellata* stands) and eroded
139 bare peat (without vegetation). In some areas, remnant stands have been able to persist near
140 to eroded areas due to natural barriers to livestock (e.g. cliffs), low stocking rates and/or
141 fencing (Strange et al. 1988). Due to our interest in sampling these different habitats, many of
142 our sampling sites were found on East Falkland and key outer islands where these three
143 distinct habitats occur in close proximity to each other (Fig A1).

144

145 TUSSOCK PLANT AND SOIL CARBON AND NITROGEN SAMPLING

146 Between June and September 2015 six farms across the Falkland Islands were surveyed for
147 total plant and soil C and N stocks with sites selected for similar characteristics (current or
148 former dominant species, i.e. *P. flabellata*, underlying soil type, elevation, slope, annual
149 rainfall and temperature) (Fig 1; Table 1). Within each farm three different habitats of *P.*
150 *flabellata* were sampled: remnant stands, restored stands and bare peat (herein referred to as
151 'eroded'). At a given site different habitats of *P. flabellata* peatlands were within 1 km of
152 each other, where possible, to minimise variation in underlying geology and climatic factors.
153 Local farmers and landowners with knowledge of the vegetation and grazing management
154 history aided identification of different habitats.

155

156 We selected successfully restored stands that ranged in ages from 2 to 23 years since
157 plantation. To minimise density effects on ecosystem C storage, sites restored by hand rather
158 than machinery were sampled to increase the likelihood of more random planting densities.

159 Furthermore, based on discussions with landowners and farmers, prior to sampling we
160 assumed that initial planting density would have a weak effect on overall restored habitat C
161 storage, because the original planted tillers typically die after 3 to 4 years and older stands
162 become composed of both planted tillers and their seed set (S. Poncet and B. Bernsten pers.
163 com.). Following guidance from landowners and farmers, areas within restored stands where
164 there had been secondary replanting were avoided.

165

166 In each of the 18 plots (six sites \times three habitats), the distribution of plant and soil C pools
167 was determined for three randomly selected tussock and inter-tussock areas (< 0.25 m apart)
168 inside the quadrat area marked out for mapping tussocks densities (see below). Across all
169 remnant and restored sites there was little to no inter-tussock vegetation, therefore all above-
170 ground C storage is solely that of *P. flabellata* tussocks. At the top of the tussock, 'shoot' C
171 or living tillers (including attached living roots and rhizomes) on the pedestal were sampled
172 by harvesting three tillers per remnant stand. Tillers were not removed from restored stands
173 so as not to hinder re-vegetation; instead shoot C densities from remnant stands were used to
174 estimate restored shoot C for nearby stands by adjusting for the area of restored tussocks (see
175 below). For both remnant and restored tussock, C stocks held within the pedestal composed
176 of dead leaves, rhizomes and roots were sampled using a Kubiëna tin ($7.5 \times 6.3 \times 3.8$ cm)
177 underneath the pedestal surface. Directly below the tussock and inter-tussock surface soil
178 samples (depth 15 cm) were collected using a 4.2 cm diameter bevel-ended corer. Deeper soil
179 samples were also collected between 40 and 60 cm below the surface using an open gouge
180 auger with a 2.7 cm diameter. The latter deeper region was selected based on a change in peat
181 characteristics in remnant stands from fibrous and semi-fibrous peat to humified peat (no
182 visible plant debris) and to contrast surface and deeper organic soil horizon for many eroded
183 sites (see Table 1). Maximum peat depth was determined at three random locations within
184 each plot by using the gauge. Three inter-tussock 5 g soil samples were collected to
185 determine $\text{pH}_{\text{H}_2\text{O}}$ via a pH meter (Mettler Toledo, MP 225, USA). On average the soil surface
186 of eroded sites was more acidic than remnant and restored sites (pH 3.69 compared to 4 and
187 4.05, respectively); yet pH did not relate to C and N stocks and was thus not included in the
188 analysis. After collection, all plant and soil material was stored at 4°C for a maximum of
189 three days before processing.

190

191 Prior to drying, and to enable us to estimate tiller above-ground biomass, the circumference
192 of each fresh turgid tussock tiller was measured and used to generate a measure of biomass
193 per unit area. All shoot material was oven-dried for 48 hrs at 80°C and weighed (± 0.01 g).
194 For each soil core, fresh soil was weighed wet and oven-dried for 48 hrs at 105°C to remove
195 all moisture and then reweighed. The difference in weight between fresh and oven-dried soil
196 (adjusted for stones) was used to determine field soil water content. Soil samples were sieved
197 (2 mm) to remove any stones, with the volume of stones measured using water displacement.
198 After drying, all plant and soil material was homogenized by blending and using a pestle and
199 mortar. Replicate plant and soil material within different habitats for each site was pooled
200 before chemical analysis. A standard 200 mg sub-sample of pooled samples was used to
201 determine carbon and nitrogen concentration on an elemental analyser (VarioCubeMax,
202 Germany).

203

204 SPATIALLY HETEROGENEOUS TUSSOCK STOCKS

205 To upscale above-ground C and N stocks we adopted an approach to account for the spatially
206 heterogeneous distribution of grass tussock structures by mapping all the tussocks within a
207 quadrat (see Smith et al. 2014). For both remnant and restored *P. flabellata* stands a 10 m \times 2
208 m quadrat area was marked out following random cardinal directions. Detailed records were
209 made of all individual tussocks structures within the area. Records included total number of
210 alive and dead tussocks within a quadrat, circumference of each tussock and corresponding
211 height of pedestal from the ground surface to the base of the living tillers. From these
212 measurements the surface area of each tussock was calculated (surface area = circumference²
213 $\times (4/\pi)$). Measured parameters from 214 living tussocks ranging in size from 0.004 m² to
214 5.4 m² were used in this study. The height of each pedestal was then multiplied by tussock
215 area to provide an estimate of the pedestal volume. Total biomass for each quadrat was then
216 calculated for all tussocks, first by summing shoot area and pedestal volume and multiplying
217 it by their biomass densities. Shoot and pedestal biomass was then multiplied by respective C
218 and N concentrations and storage was expressed as mega-grams C and N Mg ha⁻¹.

219 Separate tussock and inter-tussock total organic soil C stocks were calculated for both surface
220 soil horizon (depth 15 cm) and a deeper horizon (depth 50 \pm 10 cm). Surface soil C stocks
221 represent the mean bulk density of three replicate cores, while deeper soil cores were derived
222 from a gouge auger sample for both tussock and inter-tussock at each habitat. In order to

223 compare surface and deeper horizons, soil depth and bulk density within the core and auger
224 were extrapolated to a standard 15 cm depth and estimated C and N stocks adjusted
225 accordingly. A volume-based measure of soil C and N storage was calculated from soil bulk
226 density (without stones >1 mm), core volume and C and N concentration and scaled to C and
227 N Mg ha⁻¹.

228

229 ECOSYSTEM AND ISLAND-WIDE CARBON STORAGE

230 Total ecosystem C and N were calculated by combining both tussock and inter-tussock plant
231 and soil pools. For each quadrat, average plant plus soil tussock and inter-tussock C and N
232 storage was adjusted for the relative area of these structures. We estimated C and N storage to
233 a total depth of 50 cm. The upper half of the profile (0-25 cm) was estimated by extrapolating
234 C densities derived from the surface soil core, while the lower half (25-50 cm) was
235 extrapolated from the deeper auger soil core. A 25 cm cut-off was used as this is where
236 deeper soil C densities start to significantly differ from surface soil for most grasslands (see
237 Ward et al. 2016). We acknowledge that deeper peat and mineral horizons are likely to
238 contain significant quantities of C and N; however, peat profiles deeper than 50 cm were not
239 consistent across sites or habitats. Total peat depth was only marginally significantly different
240 between habitats (ANOVA; $F_{2,27}=3.2$, $p=0.056$, square root transformed) where remnant
241 stands were deeper than eroded sites, but neither habitat differed in depth in comparison to
242 restored stands (see Table 1).

243 To scale up ecosystem C stored in remnant *P. flabellata* stands across the whole of the
244 Falkland Islands, we generated an estimated total land area dominated by *P. flabellata* using
245 data from a series of island-wide field surveys conducted between 1983 and 2013 (data from
246 South Atlantic Research Institute, <http://south-atlantic-research.org/ims-gis>). These surveys
247 covered 531 of the 776 islands of the Falkland Islands, or approximately 68.4% of all islands
248 belonging to the island group. The shortfall in the number of islands is likely to reflect
249 smaller islands of less than 1 ha area and inland islands being omitted from the majority of
250 the surveys. As part of these surveys *P. flabellata* area was estimated *in situ* either on foot or
251 viewed from a boat and assessed as either (1) percentage area of an island dominated by *P.*
252 *flabellata* or (2) estimated total area in hectares covered by *P. flabellata*. For islands where
253 only percentage area dominated by *P. flabellata* was provided, the area in hectares was
254 estimated by using the total area of the island using geospatial software qGIS (2.4.0-Chugiak,

255 2014). For islands visited multiple times across the different surveys, we have used the most
256 recent estimate of vegetation area. From these surveys, the total *P. flabellata* dominated land
257 area on outer islands was 5,663 ha, whilst land area dominated by *P. flabellata* remaining on
258 the two main islands was estimated at 65 ha (Strange et al. 1987). Based on these surveys, the
259 current remnant *P. flabellata* land cover was estimated to be 5,728 ha in total across the
260 Falkland Islands. Total above-ground, total soil C (combined 15 cm and 50 cm estimates) and
261 ecosystem C (plant plus soil) for remnant stands was scaled-up to the current land area of *P.*
262 *flabellata* and for the estimated area pre-1840s area of 22,200 ha (Strange et al. 1987).

263

264 STATISTICAL ANALYSIS

265 Total above-ground C and N storage (shoot plus pedestal), surface soil (15 cm), deep soil (50
266 cm) and total ecosystem storage were analysed using separate linear mixed effect models
267 with residual maximum likelihood estimates (REML) via the *lme4* and *nlme* package (version
268 3.2.2, R Development Core Team 2014; Bates and Maechler 2010). The fixed effect for total
269 above-ground stocks and ecosystem storage was habitat (remnant, restored, eroded) and
270 covariates were pedestal to shoot biomass ratio and average tussock size. In order to explore
271 the effects of spatial heterogeneity, for surface and deep soil C and N stocks the fixed effect
272 was whether the sample was a tussock or inter-tussock. All models included farm as random
273 factor, thus accounting for the grouping of different habitats. For each factor, we presented
274 results of the best model retained based on minimum Akaike's Information Criterion (AIC)
275 and factor significance was assessed by removing it from the best model and performing
276 likelihood ratio deletion tests (LRTs) (Pinheiro and Bates 2000). Statistical significance of
277 the different habitats was obtained through formulating contrast statements between habitats
278 within the same model structure (see Hothorn et al. 2008; Cichini et al. 2011). Soil C and N
279 concentrations were tested using the same method as outlined above. As only above-ground
280 biomass was collected from remnant stands, shoot and pedestal chemical concentrations were
281 analysed using ANOVAs. Similarly for restored stands only, above-ground and soil C and N
282 stocks were analysed separately using an ANOVA in relation to restored stand age only. We
283 did not include other factors in the restored stand only model due to significant positive co-
284 linearity between restored stand age, tussock size and density. All means are presented with
285 standard errors (mean \pm SE).

286

287 **RESULTS**

288 ABOVE-GROUND *POA FLABELLATA* CARBON AND NITROGEN STORAGE

289 *Poa flabellata* pedestals, structures comprising accumulated dead leaves, rhizomes and roots,
290 were the largest above-ground C pool (Fig 2). On average across the islands, pedestals in
291 remnant stands contained 37.8 ± 9.6 Mg C ha⁻¹ and in restored stands 2.4 ± 1.2 Mg C ha⁻¹,
292 approximately 72% and 25% of the total above-ground C stock, respectively. A higher
293 pedestal to shoot biomass ratio correlated strongly with greater total above-ground C storage
294 (Table 2; Fig 3a). However, the importance of well-developed pedestals for total above-
295 ground C stocks was more significant for remnant stands than restored stands. When
296 analysing restored stands separately, the pedestal to shoot ratio did not correlate with total
297 above-ground C (ANOVA; $F_{1,4} = 0.22$, $p = 0.661$). Furthermore, plant material was more
298 compact in pedestals from remnant stands, with a bulk density of 0.15 ± 0.06 g cm⁻³,
299 compared to restored stands 0.07 ± 0.06 g cm⁻³.

300

301 Total above-ground (shoot plus pedestal) carbon stocks were significantly greater in remnant
302 stands 49.8 ± 9.7 Mg C ha⁻¹ than in restored stands 6.7 ± 3.1 Mg C ha⁻¹ (Table 2; Fig 2). Older
303 restored stands were larger stores of above-ground C (ANOVA; $F_{1,4} = 23.9$, $p = 0.008$), had
304 higher densities of tussock (youngest to oldest: 0.2 to 1.75 m⁻²) and contained larger
305 individual tussock size (0.07 to 0.33 m²) in comparison to younger restored stands (Fig 3b).
306 Based on this analysis, accrual of restored above-ground C and associated tussock parameters
307 appeared to take over a decade and a significant difference was only detectable due to the two
308 oldest sites survey. Older restored stands were similar in density and size to remnant stands;
309 yet the oldest restored stands surveyed only stored half the total above-ground C of the
310 smallest remnant stand C stocks. Combined for both remnant and restored stands there was
311 no relationship between above-ground C storage, tussock density and size for remnant stands
312 (Table 2).

313 Above-ground N pools were similarly distributed as C pools, with pedestals as the largest
314 store. For both remnant stands and restored stands pedestal to shoot ratio correlated positively
315 to total above-ground N stocks (Table 2; Fig 2; restored stands only, ANOVA: $F_{1,4} = 9.85$,
316 $p = 0.035$). Unlike C stocks, there was no significant difference in above-ground N stocks
317 between habitats likely due to the low replications within the study, although stands with
318 larger tussocks, namely old restored stands and remnant stands, had on average greater N

319 above-ground stores (Table 2). Pedestal and shoot C and N concentrations were unrelated to
320 each other across plant and soil pools, apart from a weak positive correlation between shoot
321 N and pedestal C concentration (remnant stands only, ANOVA: $F_{1,4}=5.26$, $p=0.084$). Above-
322 ground C and N concentrations were unrelated to habitat, pedestal to shoot ratio or average
323 tussock size (data not shown).

324

325 BELOW-GROUND *POA FLABELLATA* CARBON AND NITROGEN STORAGE

326 Surface soil was the densest C store in the *P. flabellata* ecosystem, containing on average
327 three times as much C as above-ground stocks for remnant stands and 83 times as much as
328 restored stands (Fig 2). Soil organic C was spatially and vertically heterogeneous in
329 distribution with significant differences between inter-tussock and tussock stocks for remnant
330 stands (Table 2) but not for restored stands (restored stands only, ANOVA: $F_{1,25}=2.85$,
331 $p=0.107$). Surface soil (15 cm) C stocks were 29% greater in the inter-tussock than
332 underneath tussock, yet spatial distribution was reversed deeper down the soil profile (50
333 cm), where soil C underneath tussocks was 40% greater than in inter-tussocks. Soil C
334 densities were more consistent through the soil profile underneath tussocks for remnant
335 stands, declining only by 14% for tussocks compared to 89% for inter-tussocks. Changes in
336 soil C densities were related to soil bulk density. Tussock soil bulk densities declined from
337 the surface to deeper horizons from 0.19 to 0.14 g cm³, whereas for inter-tussocks soil bulk
338 densities reduced from 0.25 to 0.12 g cm³ in remnant stands. Surface soil bulk densities were
339 significantly lower underneath tussocks than in the inter-tussock area (linear mixed model;
340 $X_2=5.489$, $d.f.=1$, $p=0.019$), yet there was no difference in the deeper horizon. Total soil N
341 stocks showed a similar spatial and vertical heterogeneity with tussock and inter-tussock as
342 soil C stocks (Fig 2; Table 2). Surface soil from remnant stands was wetter than restored or
343 eroded habitats, with 270% water per oven-dry weight soil compared to 176 and 216% water
344 per oven-dry soil weight, respectively (linear mixed model; $X_2=14.479$, $d.f.=1$, $p<0.001$).
345 Soil water content was lower beneath tussocks compared to inter-tussocks, but this difference
346 was non-significant. Deeper soil was wetter, averaging 331% water per oven-dry soil weight
347 across all samples, yet there was no difference in deep soil water content between habitats or
348 in relation to tussock structure.

349

350 HABITAT CARBON AND NITROGEN SOIL AND ECOSYSTEM STOCKS

351 There was no difference in surface soil (15 cm) or deeper (50 cm) soil C and N stocks
352 between remnant stands, restored stands and eroded peat (Fig 2; Table 2). Equally there were
353 no differences between habitats in ecosystem C and N stocks when accounting for the relative
354 tussock and inter-tussock area (Table 2). Furthermore, C and N storage were not related to
355 restored stand age (data not shown). Nevertheless, soil surface properties differed between
356 habitats: remnant stands had lighter fibrous peat with a lower bulk density compared to the
357 denser horizons of eroded sites ($z_{30}=2.38$, $p=0.045$) and restored stands ($z_{30}=3.63$, $p<0.001$).
358 Surface soil C concentrations were significantly higher for remnant stands compared to
359 eroded bare peat sites ($z_{30}=2.69$, $p=0.019$), but not greater than for restored stands ($z_{30}=1.80$,
360 $p=0.169$). Bulk density and C concentration for deeper soil horizons across habitats did not
361 differ (data not shown).

362

363 Ecosystem C and N stocks were unrelated to habitat, but positively correlated with larger
364 average tussock sizes (Table 2). Up-scaling ecosystem C storage to an archipelago-wide
365 scale, current storage in the Falkland Islands is approximately 2.32 million Mg C compared
366 to a historic (pre-1840s) storage potential of up to 9.02 million Mg C (Table 3). Given the
367 limited difference between habitats, increasing the current range of *P. flabellata* is unlikely to
368 have consistent effects on soil C storage. Nevertheless, restoring above-ground storage across
369 the historic land cover, *P. flabellata* could accrue up to 0.81 million Mg C over several
370 decades.

371

372 **DISCUSSION**

373 This study highlights that large tussock-forming grasslands distributed across southern
374 oceanic and sub-Antarctic islands are locally and regionally important plant and soil carbon
375 stores. Building upon former studies that have sampled individual tussocks (Gunn 1976) and
376 by accounting for the spatial distribution of tussock structures, we have provided a realistic
377 quantification of ecosystem C storage. Tussock above-ground C is stored in pedestals similar
378 to other semi-arid grasslands accruing organic matter in hummocks or mounds (Burke et al.
379 1998, 1999), yet these pedestals are one of densest grassland C stores in the world. Results
380 from this study across restored stands of increasing ages demonstrate that the formation and
381 accrual of C in pedestals can take several decades. Tussock structures equally related to the
382 soil C stocks with horizontal and vertical variations in soil C storage. Surprisingly, we found

383 little difference in soil C storage between habitats, potentially highlighting the role of crusts,
384 or hardened desiccated peat on the peat surface that inhibit erosion (Campbell et al. 2002;
385 Warburton 2003) and that may enable unvegetated deep peat deposits to persist on the
386 Falkland Islands. Nevertheless, differences in the quality of the peat surface between eroded
387 and remnant tussock stands suggest that a historic loss of vegetation has led to a loss of
388 fibrous surface peat. On an island-wide scale, we predict that planting tussocks can increase
389 above-ground C stocks over several decades, while changes to total soil C storage in the
390 initial few decades are likely to be variable.

391

392 Writing on the natural history on Beauchêne Island, Smith and Prince (1985) noted '*the*
393 *tussac [P. flabellata] ecosystem is closely comparable with a forest of evergreen trees*'. In
394 this study, we have calculated that *P. flabellata* grasslands can store equivalent densities of
395 living and dead above-ground C (31 - 93 Mg C ha⁻¹) as broadleaf deciduous and boreal
396 forests found in temperate (32 - 233 Mg C ha⁻¹) or cold (28 - 99 Mg C ha⁻¹) climates (Dixon
397 et al. 1994; Lal 2005; Fang et al. 2006; Keith et al. 2009; Thurner et al. 2014). In large
398 tussock communities, above-ground C is concentrated in the form of compact dead leaves,
399 rhizomes and roots. In addition to this study showing that pedestal C is accrued on a decadal
400 timescale, radiocarbon dating has shown that pedestals are long-term C stores with an
401 average age of 290 ± 40 years (Smith and Prince 1985), indicating that *P. flabellata* above-
402 ground C pools can persist longer than many soil C fractions (Schmidt et al. 2011). In
403 addition, soil C fractions of smaller tussock-forming communities in the southern hemisphere
404 have predicted turnover times of 100 to 400 years (Tate et al. 1995). However, pedestal
405 formation depends on both plant growth and decomposition rates, which are both in turn
406 underpinned by climatic factors and nutrient availability. Spanning both cool-temperate
407 oceanic and sub-Antarctic climates, rates of pedestal formation and development for *P.*
408 *flabellata* could vary across this temperature gradient. Yet, related sub-Antarctic species on
409 Macquarie Island show weak temperature plasticity in growth rates (Medek et al. 2007) and
410 studies of seasonal carbohydrate cycling suggest a potentially similar weak growth response
411 from *P. flabellata* (Gunn and Walton 1985). Instead, variations in soil moisture and nutrient
412 availability may be drivers for differences in growth and pedestal formations for this species
413 (Smith 1985). Further research is needed across the entire distribution of *P. flabellata* to
414 understand the biogeochemical processes that allow these dense C pedestals to persist above-
415 ground. From an above-ground C perspective, large tussock grasslands of southern oceanic

416 and sub-Antarctic islands are a unique system and differ from the traditional view of
417 grassland above-ground C stocks as small and temporary composed of highly decomposable
418 leaf and herbaceous material.

419

420 Primary data on peat depth, bulk density and carbon content are often lacking from remote
421 peatlands in arctic and tropical systems (Page et al. 2011), yet such data on remote oceanic
422 and sub-Antarctic islands is even scarcer. In this study our calculations of soil C stocks to a
423 depth of 50 cm for *P. flabellata* grasslands at 356 Mg C ha⁻¹ are in line with global averages
424 for histosols at 425 Mg C ha⁻¹ (Batjes et al. 1996). However, soil C storage in the temperate
425 ecosystem on the Falkland Islands is denser than in its counterpart peatlands in the northern
426 hemisphere (190 - 270 Mg C ha⁻¹ at an equivalent depth) (Garnett et al. 2000; Ostle et al.
427 2009). At the same time, soil C storage may be greater for large tussock grassland
428 communities in colder climates, i.e. islands within the sub-Antarctic. For instance, *P.*
429 *flabellata* communities on Beauchêne Island, the most southerly island of the Falklands
430 Islands, had a maximum peat depth of 13 m deep (Smith and Cylmo 1984; Smith and Prince
431 1985), whilst the deepest profiles in this study were 3.7 m. Equally noteworthy is the role of
432 soil depth in influencing our estimates of both total soil and ecosystem C storage as well as
433 the role of potential differences between habitat types. In this study, we restricted our
434 estimate of total soil C to a depth of 50 cm, yet two-thirds of our sites had deeper peat
435 profiles (Table 1). A recent survey of deep grassland soil C found a 54% increase in
436 estimated total soil C sampling to a depth of 1 m compared to 60 cm (Ward et al. 2016).
437 Typically eroded and restored habitats had shallower peat profiles than remnant habitats, yet
438 overall peat depth did not significantly differ between habitats in this study. Nonetheless,
439 given the latter, remnant habitats could store more soil C than restored or eroded habitats
440 when accounting for deeper soil C (i.e. below 50 cm). On the other hand, unvegetated and
441 recently planted *P. flabellata* habitats can retain deep peat profiles as found in some of our
442 sites, and such deposits may persist due to variations in topography, wind exposure and
443 proximity to seabird and marine mammal colonies. Despite this study providing useful
444 primary peatland data on remote oceanic islands, further work that accounts for deeper peat
445 underneath such large-tussock forming communities is needed in order to improve our
446 estimates of soil and ecosystem C stocks.

447

448 Due to limited resources in remote locations, it is often necessary to prioritise conservation
449 strategies (McCauley et al. 2013). On the Falkland Islands, both the restoration and protection
450 of *P. flabellata* have challenges (FIG 2008). For example, anecdotal evidence suggests that
451 restored stands have had a low success rate on the Islands (Kerr 1994). At the same time,
452 opportunities exist. As our study shows, ecosystem C storage is strongly coupled with N and
453 larger tussocks store more N, even to the extent that a weak correlation between pedestal C
454 and shoot N indicates potential soil mineralisation within pedestals. Thus, the importance of
455 N for large tussocks could be utilised by establishing restored stands near seabird and marine
456 mammal colonies (Smith and Cylmo 1984). For remnant stands, many farmers still graze
457 cattle on *P. flabellata* during the winter months. In other tussock grassland systems, livestock
458 grazing has been shown to reduce tussock densities and consequently plant and soil C storage
459 after several decades (Burrow et al. 2012), yet grazing may have only a limited impact when
460 it is seasonal and/or undertaken at low-stocking densities (Smith et al. 2014). Although our
461 results found little relationship between tussock density and C storage in remnant stands, for
462 restored stands above-ground C was positively related to tussock density, suggesting that
463 more work is required to determine when to graze established restored stands. Overall, in
464 terms of C storage, this study supports greater protection or, at the minimum, appropriate
465 management of remnant stands to store C, because accruing equivalent quantities of C in
466 restored stands may take decades to centuries.

467

468 Grassland communities on oceanic and sub-Antarctic islands have been shaped by human
469 land use and management. Many of these islands are internationally important biodiversity
470 hotspots; yet, as this study shows, these islands are also globally important C stores. To verify
471 our findings, more primary soil C data is required for related large tussock-forming species
472 on other islands and such studies will need to adopt a spatially heterogeneous sampling
473 approach. Internationally, the offsetting of CO₂ emissions has focused strongly on planting
474 forests and improving forest practices, yet such methods are not appropriate on naturally tree-
475 less islands. Instead, protecting, appropriately managing or planting large-tussock grass
476 provides an option for island communities in the southern hemisphere to store equivalent
477 quantities of C on a decadal timescale.

478

479

480 **Acknowledgements**

481 We are grateful to the farmers and landowners involved in this work and particularly the
482 valuable insights and support from Ben Bernsten, Sally Poncet, Dion Poncet and Juliette
483 Hennequin. Arwyn Edwards and Richard Hill provided analytical assistance to determine C
484 and N concentrations. We would like to thank constructive inputs on earlier versions of
485 manuscript from Rodney G. Burton, James D.M. Speed and Anne Jungblut. SWS was funded
486 by Darwin Plus Initiative Project (DPLUS023) via Department of Environment, Food and
487 Rural Affairs, UK and Shackleton Scholarship Fund (2015/2016).

488 **References**

- 489 Aldiss DT, Edwards EJ (1999) The geology of the Falkland Islands. British Geological
490 Survey Technical Report WC/99/10
- 491 Bates DM, Maechler M (2010). lme4: Linear mixed-effects models using “Eigen” and S4.
492 <https://cran.r-project.org/web/packages/lme4/index.html>. Accessed 20 July 2016
- 493 Batjes NH (1996) Total carbon and nitrogen in soils of the world. *Eur J Soil Science* 47:151-
494 163
- 495 Barrow CJ (1978) Postglacial Pollen Diagrams from South Georgia (Sub-Antarctic) and West
496 Falkland Island (South Atlantic). *J Biogeogr* 5:251-274
- 497 Bergstrom DM, Stewart GR, Selkirk PM, Schmidt S (2001) ^{15}N natural abundance of fossil
498 peat reflects the influence of animal-derived nitrogen on vegetation. *Oecologia* 130:309-314
- 499 Bokhorst S, Husikes A, Convey P, Aerts R 2007 External nutrient inputs into terrestrial
500 ecosystems of the Falkland Islands and the Maritime Antarctic region. *Polar Biol* 30:1315-
501 1321
- 502 Broughton DA, McAdam JH (2005) A checklist of the native vascular flora of the Falkland
503 Islands (Islas Malvinas): New information on the species present, their ecology, status and
504 distribution. *J Tor Bot Soc* 132:115-148
- 505 Burke IC, Lauenroth, WK, Vinton MA, Hook PB, Kelly RH, Epstein HE, Aguiar MR,
506 Robles MD, Aguilera MO, Murphy KL, Gill RA (1998) Plant-soil interactions in temperate
507 grasslands. *Bio- geochemistry* 42:121–143

508 Burke IC, Lauenroth WK, Riggle R, Brannen P, Madigan B, Beard S (1999) Spatial
509 variability of soil properties in the shortgrass steppe: the relative importance of topography,
510 grazing, microsite, and plant species in controlling spatial patterns. *Ecosystems*
511 2:422–438

512 Burrow L, Peltzer D, Lynn I, Clayton R (2012) Ecosystem carbon and grazing reduction on
513 high country lands. Landcare Research, New Zealand

514 Campbell DR, Lavoie C, Rochefort L (2002) Wind erosion and surface stability in abandoned
515 milled peatlands. *Can J Soil Sci* 82:85-95

516 Carolan R, Fornara DA (2016) Soil carbon cycling and storage along a chronosequence of re-
517 seeded grasslands: Do soil carbon stocks increase with grassland age? *Agr Ecosyst Environ*
518 218:126-132

519 Cichini K, Schwienbacher E, Marcante S, Seeber GUH, Erschbamer B (2011) Colonization
520 of experimentally created gaps along alpine successional gradient. *Plant Ecol* 212:1613-1627

521 Cris R, Buckmaster S, Bain C, Bonn A (eds) (2011) UK Peatland Restoration –
522 Demonstrating Success. IUCN UK National Committee Peatland Programme, Edinburgh

523 Davies W (1939) The grasslands of the Falkland Islands. Government printers, Stanley

524 Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon
525 pools and flux of global forest ecosystems. *Science* 263:185-191

526 Ellis JC (2005) Marine birds on land: a review of plant biomass, species richness and
527 community composition in seabird colonies. *Plant Ecol* 181:227-241

528 Fang J, Brown S, Tang Y, Nabuurs G-J, Wang X, Shen H (2006) Overestimated biomass
529 carbon pools of the northern mid- and high latitude forests. *Climatic Change* 74:355-368

530 Falkland Islands Government (FIG) (2008) Falkland Islands Biodiversity Strategy 2008-
531 2009. Falkland Islands Government, Stanley

532 Falkland Island Government (FIG) (2015) Farming statistics.
533 <http://www.fig.gov.fk/agriculture/index.php/publications/farming-stastics>. Accessed 25 April
534 2016

535 Garnett MH, Ineson P, Stevenson AC (2000) Effects of burning and grazing on carbon
536 sequestration in ta Pennine blanket bog, UK. *The Holocene* 10:729–736

537 Government of South Georgia and the South Sandwich Islands (GSGSSI) (2014) Reindeer
538 eradication project: End of Phase 2 report.
539 [http://www.gov.gs/docsarchive/Environment/Invasive%20Species/SG%20reindeer%20erradi](http://www.gov.gs/docsarchive/Environment/Invasive%20Species/SG%20reindeer%20eradication%20phase%20%20report_FINAL.pdf)
540 [cation%20phase%20%20report_FINAL.pdf](http://www.gov.gs/docsarchive/Environment/Invasive%20Species/SG%20reindeer%20eradication%20phase%20%20report_FINAL.pdf). Accessed 20 July 2016

541 Gunn TC (1976) The autecology of *Poa flabellata* (Lam.) Hook. Ph.D. thesis, University of
542 Manchester

543 Gunn TC, Walton DWH (1985) Storage carbohydrate production and overwintering strategy
544 in a winter-green tussock grass on South Georgia (Sub Antarctic). *Polar Biol* 4:237-242

545 Harmonized world soil database v 1.2 (HWSD).
546 <http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/>. Accessed
547 15 September 2015

548 Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models.
549 *Biometrical J* 50:346-363

550 International Union for Conservation of Nature UK Peatland Programme (IUCN).
551 <http://www.iucn-uk-peatlandprogramme.org/falklands-update2015>. Accessed 28 July 2016

552 Joosten H (2010) The Global Peatland CO₂ Picture: Peatland status and drainage related
553 emissions in all countries of the world. Wetlands International, Ede

554 Jones PD, Harpham C, Lister DH (2013) Construction of high spatial resolution climate
555 scenarios for the Falkland Islands and southern Patagonia. United Kingdom Falkland Islands
556 Trust. [http://www.ukfit.org/wp-content/uploads/2014/08/FALKLANDS-CLIMATE-](http://www.ukfit.org/wp-content/uploads/2014/08/FALKLANDS-CLIMATE-CHANGE_report_08-10-2013.pdf)
557 [CHANGE_report_08-10-2013.pdf](http://www.ukfit.org/wp-content/uploads/2014/08/FALKLANDS-CLIMATE-CHANGE_report_08-10-2013.pdf). Accessed 25 April 2016

558 Jones PD, Harpham C, Lister D (2015) Long-term trends in gale days and storminess for the
559 Falkland Islands. *Int J Climatol* 36:1413–1427

560 Keith H, Mackay BG, Lindenmayer DB (2009) Re-evaluation of forest biomass carbon
561 stocks and lessons from the world’s most carbon-dense forests. *P Natl Acad Sci USA*
562 28:11635-11640

563 Kerr JA (ed) (1994) Proceedings of the first farmers' forum on tussac grass and sand grass
564 planting in the Falkland Islands. Farmers' Association and Department of Agriculture,
565 Stanley

566 Kew Royal Botanic Gardens (KEW) (2015) World checklist of selected plant families.
567 http://apps.kew.org/wesp/namedetail.do?name_id=435918. Accessed 27 August 2015

568 Lal R (2005) Forest soils and carbon sequestration. *Forest Ecol Manag* 220:242-258

569 Lottes AL, Ziegler AM (1994) World peat occurrence and the seasonality of climate and
570 vegetation. *Palaeogeogr Palaeoclimatol* 106:23-37

571 McCauley DJ, Power EA, Bird DW, McInturff A, Dunbar RB, Durham WH, Micheli F,
572 Young HS (2013) Conservation at the end of the world. *Biol Conserv* 165:139-145

573 Medek DE, Ball MC, Schortemeyer M (2007) Relative contributions of leaf area ratio and net
574 assimilation rate to change in growth rate depend on growth temperature: comparative
575 analysis of subantarctic and alpine grasses. *New Phytol* 175:290-300

576 Moen J, Macalister H (1994) Continued range expansion of introduced reindeer on South
577 Georgia. *Polar Biol* 14:459-462

578 Moore DM (1968) Vascular plant flora of the Falkland Islands. British Antarctic Survey
579 Reports No. 60. British Antarctic Survey, London

580 Munro H (1924) Report of an investigation into the conditions and practice of sheep farming
581 on the Falkland Islands. Government printers, Stanley

582 Ostle NJ, Levy PE, Evans CD, Smith P (2009) UK land use and soil carbon sequestration.
583 *Land Use Policy* 26:S274-S283

584 Page SE, Rieley JO, Banks CJ (2011) Global and regional importance of tropical peatland
585 carbon pool. *Glob Change Biol* 17:798-818

586 Pinheiro JC, Bates DM (2000) *Mixed Effects Models in S and S-PLUS*. Springer, New York

587 Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M,
588 Kögel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore
589 SE (2011) Persistence of soil organic matter as an ecosystem property. *Nature* 478:49-56

590 Selkirk JM, Saffigna, LJ (1999) Wind and water erosion of a peat and sand area on
591 subantarctic Macquarie Island. *Arct Antarct Alp Res* 31:412-420

592 Shaw J, Terauds A, Bergstrom D (2011) Rapid commencement of ecosystem recovery
593 following aerial baiting on sub-Antarctic Macquarie Islands. *Ecological Management &*
594 *Restoration* 12:241-244

595 Smith, P (2014) Do grasslands act as a perpetual sink for carbon? *Glob Change Biol* 20:2708-
596 2711

597 Smith RIL, Cylmo RS (1984) An extraordinary peat-forming community on the Falkland
598 Islands. *Nature* 309:617-620

599 Smith RIL (1985) Growth and production of *Poa flabellata* in relation to soil nutrient status
600 and exposure at South Georgia. In: Siegfried WR, Condy PR, Laws RM (eds) *Antarctic*
601 *Nutrient Cycles and Food Webs*. Springer, Berlin, pp 221-228

602 Smith RIL, Prince PA (1985) The natural history of Beauchêne Island. *Biol J Linn Soc*
603 24:233-283

604 Smith SW, Vandenberghe C, Hastings A, Johnson D, Pakeman RJ, van der Wal R, Woodin
605 SJ (2014) Optimizing carbon storage within a spatially heterogeneous upland grassland
606 through sheep grazing management. *Ecosystems* 17:418-429

607 Strange IJ (1972) Wildlife in the Falklands. *Oryx* 11:241-257

608 Strange IJ, Parry CJ, Parry MC, Wood RW (1988) *Tussac grass in the Falklands*. Falkland
609 Islands Foundation, Brighton

610 Tate KR, Parshotam A, Ross DJ (1995) Soil carbon storage and turnover in temperate forests
611 and grassland – a New Zealand perspective. *J Biogeogr* 22: 695-700

612 Thunder M, Beer C, Santoro M, Carvalhais N, Wutzler T, Schepaschenko D, Shvidenko A,
613 Kompter E, Ahrens B, Levck SR, Schmullius C (2014) Carbon stock and density of northern
614 boreal and temperate forests. *Global Ecol Biogeogr* 23:297-310

- 615 Vitt DH (2000) Peatlands: ecosystems dominated by bryophytes. In: Shaw AJ, Goffinet B
616 (eds) Bryophyte biology. Cambridge University Press, Cambridge, pp 312-343
- 617 Warburton J (2003) Wind-splash erosion of bare peat on UK upland moorlands. *Catena*
618 52:191-207
- 619 Ward SE, Smart SM, Quirk H, Tallowin JRBB, Mortimer SR, Shield RS, Wilby A, Bardgett
620 RD (2016) Legacy effects of grassland management on soil carbon to depth. *Glob Change*
621 *Biol* 22:2929-2938
- 622 Wilson P, Clark R, McAdam JH, Cooper EA (1993) Soil erosion in the Falkland Islands: an
623 assessment. *Appl Geogr* 13:329-352

TABLES

Table 1. *Poa flabellata* carbon and nitrogen stock survey locations (WGS84), habitat type (remnant, restored, eroded), farm/landowner, restored stand age, maximum peat depth, lithology and geology (Aldiss and Edwards 1999), altitude, annual temperature and annual rainfall (Jones et al. 2013).

Site number	Longitude	Latitude	Habitat	Farm/landowner	Restored stand age (yrs)	Max. peat depth (cm)	Lithology and geology	Elevation (m)	Mean annual temperature (°C)	Annual precipitation (mm)
1	-58.6910	-51.3278	Remnant	Elephant Beach		65	Quartzite and sandstone	8.5	6.6	601
2	-58.7406	-51.3188	Restored		10	66	<i>Port Stephens formation</i>	10.6	6.7	591
3	-58.7229	-51.3254	Eroded			26		7.6	6.7	570
4	-57.7861	-51.7016	Remnant	Surf Bay/		365	Quartzite and sandstone	7.6	6.2	578
5	-57.7817	-51.6961	Restored	Cape Pembroke	5	21	<i>Port Stanley formation</i>	6.4	6.2	555
6	-57.7652	-51.6905	Eroded			295		13.1	6.6	637
7	-58.9667	-51.2358	Remnant	Cape Dolphin		85	Quartzite and sandstone	15.2	6.8	615
8	-58.9068	-51.2782	Restored		4	45	<i>Albermale member</i>	23.9	6.7	610
9	-58.9079	-51.2775	Eroded			14		25.4	6.8	615
10	-58.8546	-52.2161	Remnant	Bleaker Island		236	Sandstone and mudstone	5.0	6.3	448
11	-58.8409	-52.2106	Restored		15	35	<i>Bay of Harbours formation</i>	18.4	6.2	491
12	-58.8432	-52.2099	Eroded			26		17.6	6.3	480
13	-59.0730	-52.4208	Remnant	Sea Lion Island		285	Sandstone and mudstone	8.9	6.3	402
14	-59.0728	-52.4239	Restored		2	200	<i>Brenton Loch formation</i>	14.1	6.3	413
15	-59.0730	-52.4208	Eroded			250		7.3	6.3	420
16	-61.2052	-51.8325	Remnant	Beaver Island		276	Quartzite and sandstone	4.4	7.2	406
17	-61.2780	-51.8663	Restored		23	372	<i>Port Stephens formation</i>	8.9	7.2	428
18	-61.2036	-51.8230	Eroded			28		15.4	7.2	431

Table 2. Differences in carbon and nitrogen pools in relation to habitat type (remnant, restored, eroded), tussock vs. inter-tussock, pedestal to shoot ratio and average tussock size.

Carbon pools	Land form			Tussock vs. inter-tussock			Pedestal to shoot ratio			Tussock size		
	X ²	d.f.	P	X ²	d.f.	P	X ²	d.f.	P	X ²	d.f.	P
Shoot and pedestal	3.92	5	0.048	-	-	-	11.79	5	<0.001	-	-	-
Soil (surface)	-	-	-	4.99	4	0.026	-	-	-	-	-	-
Soil (deep)	-	-	-	7.23	4	0.007	-	-	-	-	-	-
Ecosystem	-	-	-	-	-	-	-	-	-	7.94	4	0.005
Nitrogen pools	X ²	d.f.	P	X ²	d.f.	P	X ²	d.f.	P	X ²	d.f.	P
	Shoot and pedestal	-	-	-	-	-	-	8.13	5	0.004	13.09	5
Soil (surface)	-	-	-	5.25	4	0.022	-	-	-	-	-	-
Soil (deep)	-	-	-	12.25	4	<0.001	-	-	-	-	-	-
Ecosystem	-	-	-	-	-	-	-	-	-	8.47	4	0.004

Table 3. Total above-ground, soil (0 - 50 cm depth) and ecosystem *Poa flabellata* carbon storage for the current (2013) and historic (pre-1840s) land cover across the Falkland Islands. Stocks are presented in millions of Megagrams (m Mg).

Carbon pool	C densities (Mg ha ⁻¹)	Current C storage (m Mg)	Historic C storage (m Mg)
Total above-ground	49.76	0.28	1.10
Total soil (50 cm depth)	356.55	2.04	7.92
Ecosystem	406.31	2.32	9.02

FIGURES

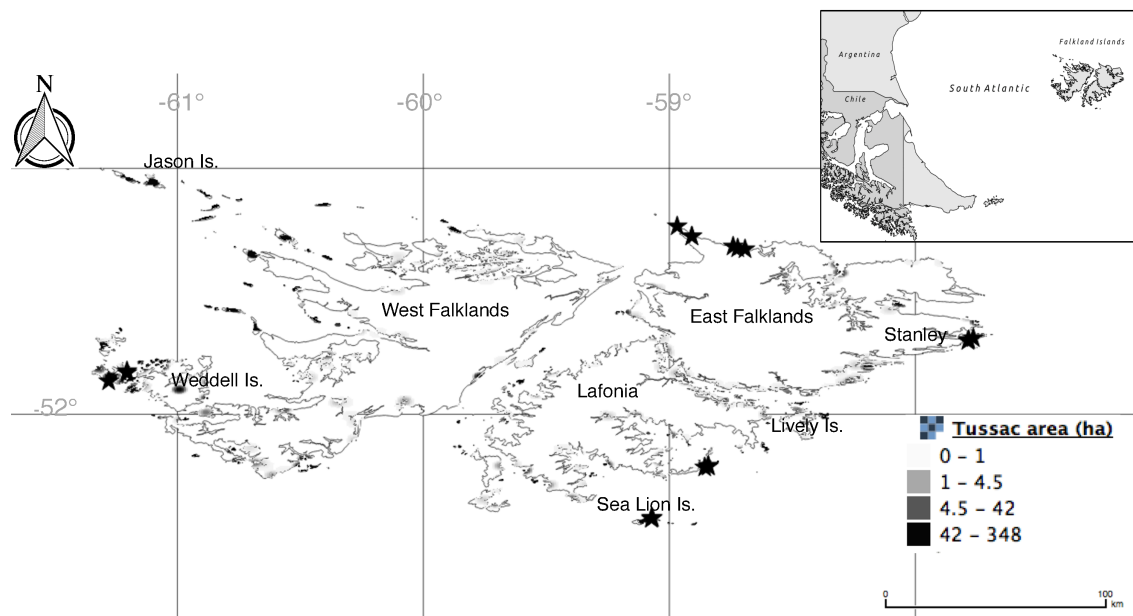


Figure 1. Surveyed locations across the Falkland Islands shown as black stars ($n = 18$) in relation to estimated densities (stands ha^{-1}) of remnant *Poa flabellata* stands (2008 - 2013).

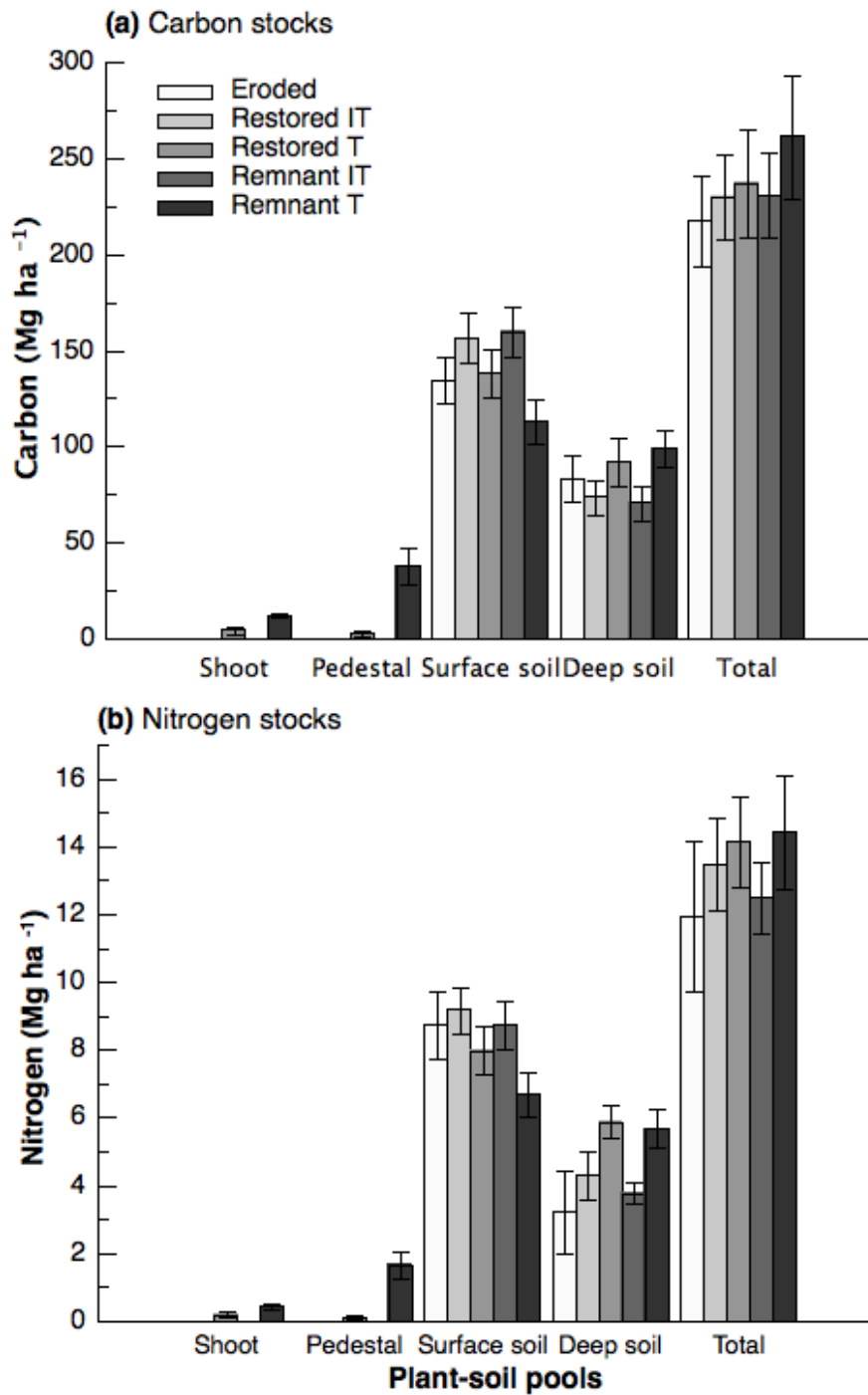


Figure 2. Plant and soil (a) carbon (C) and (b) nitrogen (N) pools (Mg ha^{-1}) above-ground and below-ground averaged for different habitats of *Poa flabellata* (eroded, restored, remnant) and for tussock (T) and inter-tussock (IT) areas. Surface soil (0 - 15 cm) and deep soil (40 - 60 cm) C and N pools have both been adjusted to a standard 15 cm depth. Standard error bars are ± 1 SE.

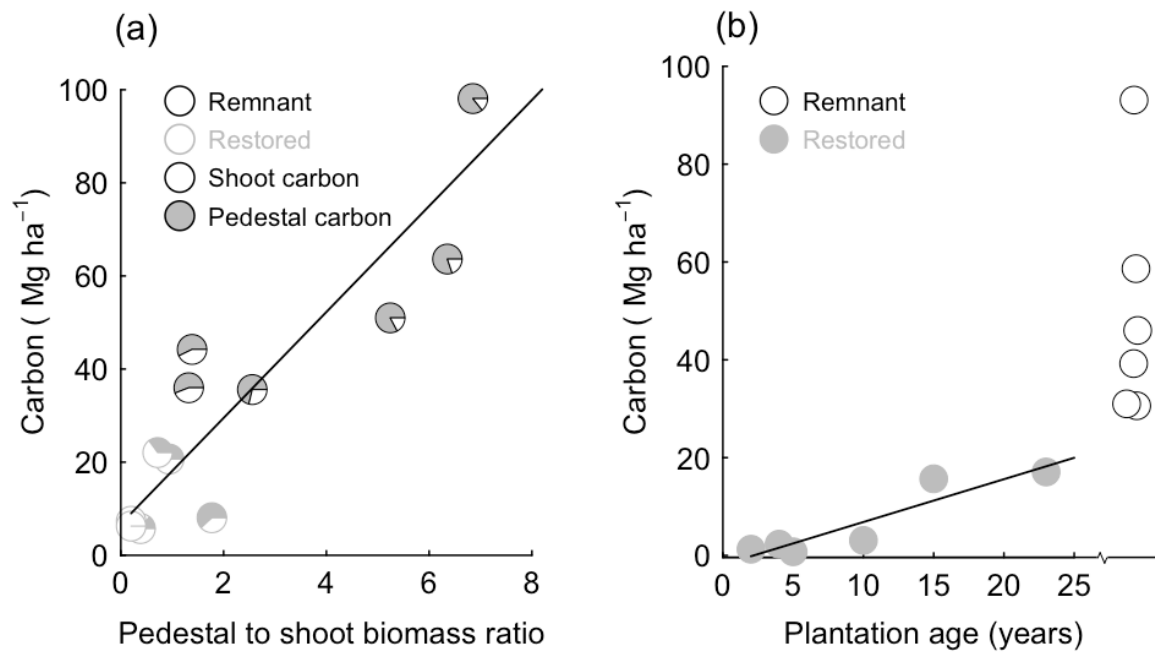


Figure 3. Total above-ground carbon storage for remnant (black bordered) and restored stands (grey bordered) *Poa flabellata* stands in relation to **(a)** shoot to pedestal ratio and **(b)** plantation age. For pedestal to shoot ratio, symbols show the proportion carbon retained in shoot (white) and pedestal (grey) with the solid black fitted line from the linear mixed model. Ages for remnant stands were unknown and solid back line is the fitted linear model ($y = -1.9 + 0.88x$, $r^2 = 0.82$) for restored stands only ($n = 6$).