

## Compositional and functional indices for biodiversity monitoring

1 Running headline: Compositional and functional indices for biodiversity monitoring.

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3 **Using compositional and functional indices for biodiversity conservation monitoring of**  
4 **semi-natural grasslands**

5

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16 Temporal change.

17

18 **ABSTRACT**

19           Compositional indicators (i.e. indices that focus on the identity of species, genes or  
20 phylogeny) have been widely used to estimate and monitor biodiversity, however, their use in  
21 combination with species and/or community functional characteristics remains limited. Using  
22 large-scale, spatio-temporal data, we use both compositional and functional indices to  
23 investigate land-use change impacts on the vegetation of a semi-natural grassland ecosystem  
24 (Machair) for fourteen regions in Scotland, UK. Our study aimed to identify national- and  
25 regional-scale temporal vegetation patterns, and through use of simple compositional and  
26 functional indices (e.g. Competitor, Stress, Ruderal and Ellenberg scores) link observed  
27 changes to agricultural intensification and/or land-use abandonment. Using linear-mixed  
28 modelling and nonmetric multi-dimensional scaling, we showed significant national and  
29 regional-scale changes in species composition over time. Increases in diversity, particularly  
30 gains in Machair grassland, identified several regions that may have benefited from past  
31 government incentivised schemes to protect the Machair, but which may also be suffering from  
32 an extinction lag. Shifts in plant functional signatures (CSR & Ellenberg values) identified  
33 varying degrees of internal (competition) and external (land-use) factors, highlighting several  
34 regions where biodiversity change could be linked to reduced disturbance (i.e. lower grazing  
35 intensity) or greater disturbance (i.e. land-use intensification). Our results demonstrate the  
36 utility of simple compositional and functional indices for monitoring biodiversity of semi-  
37 natural grasslands and identifying land-use drivers of change across different spatial scales.

**38 1. INTRODUCTION**

39           Semi-natural grasslands (SNGs) constitute one of the most species-diverse communities  
40 in the World at small spatial-scales (Wilson et al. 2012). In Europe, the high level of  
41 biodiversity, characteristic of SNGs, is closely linked to century long associations with  
42 agricultural land-use (Eriksson et al. 2002; Poschlod and WallisDeVries 2002). However, for  
43 these tightly coupled social-ecological systems, cessation of traditional management (e.g.  
44 extensive grazing, hay making and rotational arable agriculture) in favour of land-use  
45 intensification or complete cessation of any form of management has become a widespread  
46 occurrence (refs). Typically linked to societal changes in response to economic factors, such  
47 land-use changes are considered the principal cause of habitat deterioration, fragmentation and  
48 biodiversity loss among European agricultural landscapes (Benton et al. 2003; Lindborg et al.  
49 2008). Therefore, given current and forecasted global biodiversity loss (Sala et al. 2000),  
50 appropriate design and implementation of conservation management for attempts to maintain  
51 and enhance these systems has global as well as local and regional importance.

52           However, there is a growing concern regarding the effectiveness of current monitoring  
53 frameworks for attempts to conserve and enhance biological diversity (Lindenmayer and  
54 Likens 2010), particularly of semi-natural landscapes (de Bello et al. 2010). For semi-natural  
55 grasslands, one part of the problem is likely to be the broad spatial grain common to many  
56 large-scale monitoring studies (e.g. The Countryside Survey of Great Britain; [http://](http://www.countrysidesurvey.org.uk/)  
57 [www.countrysidesurvey.org.uk/](http://www.countrysidesurvey.org.uk/)). European SNGs typically exhibit high spatial heterogeneity,  
58 usually as a result of spatially and temporally structured variation in agricultural management  
59 (Plieninger et al. 2006). Moreover, variation is intensified where land is apportioned to  
60 multiple landowners. Although such heterogeneity directly benefits the biodiversity of SNGs  
61 (Öster et al. 2007) and surrounding agricultural landscapes (Blitzer et al 2012), patterns of  
62 biodiversity change as a result of changing land-use (i.e. intensification vs abandonment)  
63 become extremely variable across relatively small spatial scales. As a result, management and

64 conservation policies designed and applied across large spatial extents may not always be  
65 appropriate (Fortin and Dale 2005), often failing to be successfully translated across highly  
66 heterogeneous landscapes (Stenseke 2006).

67 Another part of the problem is the complexity of biological diversity and the suite of  
68 indicators designed to measure its various facets. This issue was recently addressed by de Bello  
69 et al. (2010) who derived a framework to help standardise and converge the use of biotic  
70 indicators (i.e. direct measures of components of biodiversity) and biotic drivers (i.e. factors  
71 that govern local biodiversity) for monitoring biodiversity change, specific to semi-natural  
72 habitats. Biotic indices (e.g. species richness, Shannon diversity, Simpson diversity, see  
73 Magurran 2004) are commonly applied to measures of alpha diversity (*sensu* Whittaker 1960,  
74 1972) or a subset of alpha, targeted at indicator species (i.e. suites of species that commonly  
75 occur in a habitat under different environmental conditions – e.g. grazed or un-grazed,  
76 favourable or non-favourable conservation condition etc; see Rosenthal 2003; Wittig et al.  
77 2006). Such compositional measures are relatively easy to calculate and understand (Lamb et  
78 al. 2009) but they fail to provide information of potential abiotic or biotic drivers governing  
79 observed changes. On the other hand, direct measures of biotic drivers (e.g. pH, organic matter  
80 and nitrogen content), for which links with biodiversity have been well researched (Hartley et  
81 al. 2003; Pärtel et al 2004), are laborious and cost intensive, and therefore often unavailable.  
82 This is especially true for large-scale spatial temporal monitoring studies.

83 To overcome these limitations, one approach is to use biotic indicators as surrogates for  
84 biotic drivers, particularly those that focus on the functional characteristics of species and  
85 ecological communities (i.e. functional indicators *sensu* de Bello et al. 2010). It is well  
86 understood that plant functional characteristics, pre-adapted to the local environment, provide  
87 distinct signatures to drivers of change that are not always easily measurable, and which often  
88 relate well to land-use processes (Pakeman 2004; Quetier et al. 2007; Lewis et al. 2013). For  
89 example: the Competitor-Stress-Ruderal (CSR) classification of plant functional types (Grime

1974) is frequently used to describe variation in vegetation through its functional composition (Cerabolini et al. 2010; Bornhofen et al. 2011). Among SNGs, shifts in CSR functional strategies can be observed. Land-use abandonment leads to size asymmetric competition for light (Mason et al 2011; Laliberte et al 2013), resulting in competitive displacement of grazing tolerant specialists (Tilman and Lehman 2001). Alternatively, declines in stress tolerant plant species should be observed with soil nutrient enrichment brought through land-use intensification (Maskell et al. 2010). Similarly, Ellenberg indicator values for plants (Ellenberg 1988), which define species habitat preferences and distribution, provide clear linkages between plant species occurrences and the environment, proving valuable for detecting changes in species compositions as a result of changes in land-use management. For example: Ellenberg N scores prove to be good correlates of mineralisable nitrogen (Rowe et al. 2011) and grassland productivity (Wagner et al. 2007).

Understanding the nature of vegetation change over time in this way can be paramount to the appropriate design of nature conservation practices, policies and land management across local, regional and national scales for all terrestrial habitats, not least SNGs. Coupled with monitoring indicator species, functional classifications such as plant CSR strategies, and/or Ellenberg values can prove extremely useful for highlighting the effects of land-use impacts.

In this study we demonstrate the potential utility of simple functional indicators as proxies of biodiversity drivers in indentifying temporal shifts in land use patterns among SNGs. Using archived biological records and revisitation data, valuable for quantifying long-term patterns of vegetation change (e.g. McCollin et al. 2000; Bennie et al. 2006; McGovern et al. 2011), we quantify national- and regional-scale temporal shifts in plant species diversity and composition for an internationally important SNG (machair). Through utilising simple land-use measures and functional indicators, surrogates for abiotic/biotic drivers, we link changes in the vegetation to changes in land-use, and identify regions where machair SNGs are subject to

116 land-use intensification and those that are subject to management declines over the last three  
117 decades. We highlight regions of potential conservation concern and discuss how simple  
118 environmental surrogates can be a useful, cost effective measure for multi-scale biodiversity  
119 monitoring.

120

## 121 **2. METHODS**

### 122 **2.1 Study Area**

123 We used the grassland vegetation of the Scottish Machair as a case study (Fig. 1).  
124 Confined globally to the northwestern fringes of Europe, sampled were 14 regions,  
125 encompassing almost the entire national resource of Scottish machair, i.e. over two thirds of  
126 the World's total machair extent (ca. 30,000ha; Dargie 2000). Machair SNGs make a good  
127 study system as their high floristic diversity and conservation value is tightly coupled to  
128 century-long associations with human settlement (Gilbertson et al. 1996) and land-use  
129 practices (Supporting Information S1), and presents a clear example of how SNGs are  
130 threatened through agricultural and socio-economic change (Pakeman et al. 2012).

131

### 132 **2.2 Floristic Data**

133 Species compositional data were collated from two sample periods. Baseline data was  
134 taken from the Scottish Coastal Survey (1975-1977; Shaw et al. 1983). The temporal aspect  
135 was completed through a partial re-survey between 2009 and 2010 of regions known to include  
136 machair communities, i.e. all transient communities from seaward embryo dunes to inland sand  
137 affected peatlands, including machair grasslands (Angus 2006; Supporting Information S2).  
138 Re-survey methodology followed closely that of the original survey (for details see Shaw et al.  
139 1983), estimating cover of all higher plants and measuring environmental proxies for land-use  
140 management within 5 m x 5 m plots.

141 Data specific to the focal community (i.e. machair grassland) was abstracted from the  
142 temporal dataset. Only those plots with a National Vegetation Classification (NVC)  
143 representative of machair grassland (Angus 2006; Table S1) were analysed. The resulting  
144 matrix (Matrix 1) comprised 321 species from 853 plots, from two sample periods. Matrix 1  
145 was used to quantify biodiversity change. To reduce noise within the dataset (see Gauch 1982)  
146 Matrix 1 was further constrained, removing species present in less than 5 plots. This species  
147 data matrix (Matrix 2) comprised 213 species from 853 plots, from two sample periods and  
148 was used to quantify compositional change. A schematic representation of how the data was  
149 handled prior to analyses is provided in Supporting Information (Fig. S1).

150

### 151 **2.3 Environmental Variables**

152 Environmental proxies for land-use management included measures of past and present  
153 management, current grazing intensity, presence/absence of grazing animals and categorical  
154 measures of sward height for grasses and herbs (Table 1). Methods on how grazing pressure  
155 levels and past cultivation were determined are detailed in Supporting Information (S3).

156

### 157 **2.4 Statistical Analysis**

158 All statistical analyses were carried out using the R statistical software (Version 2.15.0,  
159 R Development Core Team 2012). Where necessary, data were transformed to meet  
160 assumptions of normality and homogeneity of variance.

161

#### 162 *2.4.1 Quantifying temporal change in biodiversity*

163 Two biotic diversity indices: i) richness (i.e. the count of all species per 5m x 5m plot)  
164 and ii) the reciprocal of the Simpson's index ( $1/D$ ) were calculated from Matrix 1. Paired  $t$ -  
165 tests, and General Linear Mixed Models (GLMM) with a poisson link function, were used to

166 identify statistically significant national- and regional-scale shifts respectively. The GLMM  
167 (M1) took the following structure:

168  $(response \sim year/region, random = land-owner/plot)$  (M1)

169 Where, 'year' and 'region' were nested fixed factors, and land-owner and individual plots  
170 formed nested random factors accounting for the expected spatial and temporal auto-  
171 correlation.

172 These analyses were extended to investigate subsets of species, indicative of different  
173 vegetation conditions of the machairs taken from published guidance for conservation  
174 monitoring (Joint Nature Conservation Committee 2004; Table S2). Selected were four species  
175 indicator groups, indicative of good and poor quality machair grassland, fallow areas  
176 (indicative of continuous rotational arable agriculture) and active cultivation. Statistically  
177 significant shifts in mean species richness was tested using GLMM with a poisson link  
178 function. Similarly, temporal change in relative abundance was also investigated using linear  
179 mixed models with a residual maximum likelihood (REML) estimating procedure. Model  
180 structures equalled M1.

181

#### 182 *2.4.2 Quantifying temporal change in species composition*

183 Non-metric Multi-Dimensional Scaling (NMDS; Legendre and Legendre 1998) of plots  
184 in two-dimensional ordination space was applied to Matrix 2, following the procedure  
185 recommended by Minchin (1987). The scores of the resulting NMDS axes were subsequently  
186 used as numeric values representing community composition in consecutive analyses (Kahmen  
187 et al. 2005). The Bray-Curtis (Bray and Curtis 1957) dissimilarity index was used for the  
188 computation of NMDS. Species contributing most to the overall Bray-Curtis measured  
189 temporal dissimilarity were identified through similarity percentage analyses (SIMPER; Clarke  
190 1993). NMDS was performed using the function 'metaMDS' within the *vegan* package  
191 (Oksanen et al. 2013).



192 Temporal change in species compositions was measured by calculating the paired  
 193 distance between NMDS site scores for each plot for each survey year, in two-dimensional  
 194 ordination space. The statistical significance of these shifts provides a reliable indication of  
 195 species compositional change: paired t-test (national-scale) and linear-mixed modelling with  
 196 REML (M1; regional-scale).

197

#### 198 *2.4.3 Linking environmental surrogates to biodiversity and compositional change*

199 Environmental surrogates, proxies for land-use change (Table 1), and measured  
 200 functional indicators were projected onto the NMDS ordination, linking national and regional  
 201 compositional change with changing land-use parameters. Significant national and regional  
 202 shifts between survey years for the two functional classifications: CSR and Ellenberg scores  
 203 were tested using paired t-test (national-scale) and linear-mixed modelling with REML (M1;  
 204 regional-scale). Species abundances' (Matrix 2) were summarised as compositions of these  
 205 functional classifications (McGovern et al. 2011), acting as environmental surrogates for  
 206 various land-use changes. CSR scores of Grime (1974), derived using a spreadsheet based tool,  
 207 described in Hunt et al. (2004) and freely downloadable, were used to provide an indication of  
 208 external factors likely to alter plant growth (e.g. stress through lack of plant available resources  
 209 and disturbance). Similarly, Ellenberg indicator values, cover weighted and adjusted for British  
 210 plants, taken from Hill et al. (1999), were used to reflect plant species preferences in terms of  
 211 nutrient level (EbN), acidity (EbR), moisture (EbW), light (EbL) and salinity (EbS).

212 Land-use disturbance surrogates (Table 1) were examined to see how well they  
 213 explained the temporal compositional shifts. Between year differences in land-use measures  
 214 were regressed against between year differences in NMDS scores through further GLMMs:

215  $(response \sim Land-use, random = land-owner/plot)$  (M2)

216

### 217 **3. RESULTS**

**218 3.1. Biodiversity change**

219 National gains in biodiversity, measured through both mean species richness (SR) and  
220 Simpson's diversity (Sim) were significant (Table 2). Regional-scale analyses identified  
221 significant gains in SR and Sim for two regions (Colonsay and Tiree), and significant declines  
222 in SR and Sim for three regions (Benbecula, Harris and Monachs. Significant gains in SR  
223 coupled with significant declines in Sim were observed for two regions (Barra and S.Uist).

224 Analyses of species subsets indicative of different vegetative states identified  
225 significant national gains in richness and cover of machair grassland specialists, and a  
226 significant national decline in relative abundance of species indicative of arable agriculture  
227 (Fig. 2). Regional-scale analyses differentiated between regions in favourable condition, where  
228 significant temporal gains in machair specialists occurred (Barra, Coll, Colonsay, Islay, S. Uist  
229 and Tiree), and those of conservation concern where significant temporal declines in richness  
230 and cover of species indicative of good quality machair grassland occurred (Benbecula,  
231 Monachs and Shetland; Fig.2). Significant declines in the number of species indicative of  
232 arable and rotational arable agriculture occurred among 5 regions (Barra, Harris, Monachs,  
233 North Coast and North Uist), with significant declines in cover for 7 regions (Barra,  
234 Benbecula, Islay, Monachs, North Uist, Shetland and South Uist).

235

**236 3.2 Compositional change**

237 The NMDS ordination showed clear shifts in species composition between survey years  
238 (Fig. 3). This was supported by statistically significant temporal shifts in ordination scores at  
239 both national- and regional-scales (Fig 4). Projection of environmental proxies identified a  
240 positive shift along NMDS Axis 1 to indicate plant compositional change towards shorter  
241 grassy and herbaceous swards. In addition, functional classifications Ellenberg Water and  
242 Ellenberg Reaction were positively ranked with NMDS Axis 1 indicative of communities'  
243 subject to higher saturation and more acidic substrate. Regional scale analyses identified five

244 regions to display significant positive shifts (Coll, Colonsay, Islay, S.Uist and Tiree) and one  
245 region to display a significant negative shift (Benbecula) along NMDS Axis 1 (Fig. 4).

246 Proxies for land-use disturbance, e.g. vegetation sward heights, evidence of livestock  
247 and cultivation, as well as stress tolerant species, were all strong correlates with NMDS Axis 2  
248 (Fig. 3). Patterns indicate communities positively ranked with Axis 2 to have associations with  
249 cultivation practice, be it, past or present, and or low intensity rotational arable agriculture or  
250 larger-scale farming. Higher Ellenberg N values were also positively ranked with Axis 2. Only  
251 one region (Shetland) was found to positively and significantly shift along Axis 2 (Fig 4).

252 An opposite trend, where communities were negatively ranked with Axis 2 displayed  
253 strong associations with proxies for disturbance through grazing (i.e. shorter vegetation sward  
254 heights, heavy and moderate gazing, presence of sheep and species with higher stress tolerance  
255 (Figs 3). Significant negative shifts along this Axis were recorded for 2 regions (Barra and  
256 Coll; Fig. 4).

257

### 258 **3.3. Linking environmental surrogates to temporal change**

259 Significant national and regional shifts were indentified among the functional  
260 indicators. At the national-scale, a significant increase in functionally competitive species ( $p <$   
261  $0.001$ ) with a concomitant significant decline in ruderal species ( $p = 0.005$ ) was observed (Fig.  
262 5i). Eight regions mirrored this national trend, while only two (Barra and North Uist) were  
263 found to have statistically significant gains and declines in competitor and ruderal species  
264 respectively (Fig. 5i). Patterns not borne at the national-scale were revealed at the regional  
265 level. Three of the four regions (Barra, Monachs and North Uist) displaying significant  
266 declines in ruderal species were met by significant increases in stress tolerators. The opposing  
267 pattern where ruderals increased and stress tolerators declined was observed for five regions,  
268 with statistically significant change identified for two (Islay and Shetland). All significant  
269 changes in competitors were positive.

270 Significant national and regional shifts in Ellenberg values were also observed (Fig.  
271 5ii). At the national-scale community composition shifted significantly towards species  
272 favouring acidic substrate (EbR,  $p < 0.001$ ) and mineralisable nitrogen (EbN,  $p = 0.008$ ), while  
273 species favouring moist soil conditions significantly declined (EbW,  $p < 0.001$ ). At the  
274 regional-scale, significant changes were observed among 11 of the 14 regions surveyed (Fig.  
275 5ii). Significant regional trends for EbR, EbN and EbW were consistent with the national  
276 changes observed, the only exception being a significant declines in species favouring  
277 mineralisable nitrogen for one region (Lewis). A general decline was observed in light  
278 competitive species (EbL), with the exception of one region (Monachs) where EbL  
279 significantly increased ( $p < 0.001$ ). Significant shifts among salt tolerant species (EbS) varied  
280 across regions, significantly increasing (Harris, Monachs and Sanday), and significantly  
281 declining (Lewis, North Coast and Tiree).

282 Temporal change in measured land-use proxies indicative of arable agriculture  
283 (RecCult & OldCult) displayed a significant positive relationship with temporal compositional  
284 change measured as the change in NMDS scores for both Axis 1 and 2 (Table 3). Change in  
285 vegetation height classifications for graminoids over 50cm tall significantly and negatively  
286 related to compositional changes measured as the change in NMDS scores for Axis 1.  
287 Temporal change in the herb layers classifications i.e. Hrb<20 & Hrb>50 were also shown to  
288 have a significant positive relationship with species compositional change for Axis 1 and Axis  
289 2 respectively (Table 3).

290

## 291 **4. DISCUSSION**

### 292 **4.1. Biodiversity change: linking shifts to species indicator groups**

293 The biodiversity value of semi-natural grasslands is well understood to be promoted by  
294 low-intensity land-use management (Eriksson et al. 2002; Poschlod and WallisDeVries 2002).  
295 For machair grasslands, century-long associations with human land-use (Gilbertson et al. 1996)

296 have resulted in these habitats developing in tandem, with a constant disturbance regime that  
297 can now be considered a ‘natural part’ of the local habitat conditions. Given this tight historical  
298 coupling between the biodiversity value and land-use practices, temporal changes in  
299 biodiversity are likely to be linked to changes in the form, frequency and intensity of land-use  
300 disturbances. In this study, we report significant national and regional temporal changes in  
301 plant species diversity of Scottish machair grasslands. For many regions biodiversity  
302 significantly increased, coupled with increases in richness and relative abundance of machair  
303 grassland specialists. These positive changes in diversity were, for many regions linked to  
304 concomitant gains in plant species indicative of rotational arable agriculture. Collectively these  
305 species can be viewed as favourable machair species, i.e. species that belong to the habitat  
306 specific species pool. A high proportion of these species can suggest a community to be more  
307 complete, relative to the species pool (Pärtel et al. 2013). Results suggest for those regions  
308 where biodiversity in favourable species increased, land-use management may be more in-line  
309 with biodiversity conservation objectives, and therefore be regions of conservation importance.  
310 Conversely, declines in favourable species, reported among regions where overall biodiversity  
311 declined, highlights regions that may benefit from biodiversity restoration.

312         It is possible for positive changes to have been borne, in part by the adoption of  
313 traditional management funded by the Environmentally Sensitive Areas (ESA) scheme.  
314 Introduced to Scotland, in 1987, ESA schemes provided financial incentives to land managers  
315 to undertake environmentally friendly practices to maintain and enhance biodiversity,  
316 landscape and historic values of designated habitats. Although the schemes have since been  
317 superseded, for several regions where they were implemented, species richness increased (Fig.  
318 6). The pattern suggests that financially incentivised, low intensity management may have  
319 either; directly or indirectly begun a process of widespread maintenance and enhancement of  
320 the machair.

321           There is however an exception to this pattern as more northern ESA designated areas  
322 (Benbecula, North Uist and Shetland), displayed significant declines in favourable species.  
323 This raises debate over the appropriateness of preservation policies that specifically aim to  
324 preserve traditional management by making them financially attractive. In the EU, such  
325 policies are implemented through the Common Agricultural Policy (CAP, European  
326 Commission for Agriculture and Rural Development 2010), and their application is widely  
327 unquestioned. However, there are concerns that such artificial ties between people and the  
328 landscape will only lead to a decoupling between ecosystems and social systems (Fischer et al.  
329 2012). Over time, naturally beneficial feedbacks between nature management and society are  
330 forgotten, and where monetary incentives cease so do the environmentally beneficial land-use  
331 practices. Biodiversity declines reported in this study for regions once designated as ESAs may  
332 then have rapidly reverted towards more economic, yet environmentally insensitive land-use  
333 practices.

334           Biodiversity gains alone may not necessarily be enough to conclude current land-use  
335 trends to be inline with biodiversity conservation objectives. Many regions where favourable  
336 species increased, species not belonging to the machair species pool (i.e. non-favourable  
337 species) increased. This pattern was significant for three regions (Coll, Islay and Tiree), for  
338 which species indicative of poor quality machair and active cultivation also increased. Results  
339 suggest, for these regions arable cultivation may have intensified supporting the finding of  
340 Lewis et al. (2013), where declines in functional richness were subsequently linked to land-use  
341 intensification.

342           Changes in the frequency and or intensity of disturbances can result in a relaxation in  
343 the competitive interactions among plant communities, permitting successful invasions of  
344 species from the regional species pool (Mayfield et al. 2010). Where disturbances are  
345 intensified, invaders commonly possess ruderality or opportunistic life strategy traits, and often  
346 do not belong to the invading habitat species pool. Equally, many extant species, particularly

347 long-lived plants will possess high inertia to environmental change, capable of persisting in a  
348 community as remnant populations long after changes have occurred (Diamond 1972; Eriksson  
349 1996; Helm et al. 2006; Lindborg 2007). Therefore, at the regional-scale, invasions may not  
350 result in an immediate loss of favourable species from the habitat-specific species pool. The  
351 result is a colonization credit persisting of non-favourable species and a potential extinction  
352 debt (i.e. extant species expected to go extinct because threshold conditions for their  
353 persistence are no longer satisfied; Tilman et al. 1994) persisting of favourable species.  
354 Extinction debt has significant implications for conservation and restoration of threatened  
355 grassland habitats and species (Helm et al. 2006; Cousins 2009). Machair regions where  
356 biodiversity declines are not evident, but do show evidence of increased non-favourable  
357 species linked to land-use intensification should therefore be of high restoration importance,  
358 and warrant further investigations before desired parts of diversity are lost.

359

#### 360 **4.2. Compositional change: Linking shifts to environmental surrogates**

361 For grassland communities, functional characteristics of plant species can help to  
362 distinguish between different land-use disturbances (Garnier et al. 2007, Pakeman 2011) and  
363 land-use changes (Lavorel and Garnier 2002; Lewis et al. 2013). In this study we use very  
364 simple functional classifications that differentiate between competitors, ruderals, stress  
365 tolerators (Grime 1974), as well as heliophyte, helophyte, halophyte, nitrophilous, ericaceous  
366 and calcicole species (Ellenberg 1988). Projection of these environmental surrogates on the  
367 NMDS ordination, coupled with the simple proxy measures of disturbance, provides an  
368 indication of land-use drivers of plant compositional change. We found significant national and  
369 regional compositional changes, measured as shifts in Bray Curtis dissimilarity (Bray and  
370 Curtis 1957) between survey years, suggesting a change in species community dynamics over  
371 time. Positive changes along NMDS Axis 1 scores, for which was the most common  
372 significant pattern among regions, could be linked to gains in ruderal species. As mentioned

373 earlier, invasion of ruderals is often a result of a decline in competitive interactions, usually  
374 attributable to some form of disturbance. Three regions (Coll, Islay and Tiree), where positive  
375 shifts along NMDS Axis 1 were identified, are also those regions identified in the biodiversity-  
376 change analyses to have likely suffered from agricultural intensification since the original  
377 survey. Although not clear from the NMDS ordination, regression of change in land-use  
378 proxies with change in ordination scores confirm arable cultivation practices to significantly  
379 drive compositional change along NMDS Axis 1, and therefore subsequently linked to  
380 significant compositional turnover of Scottish machair grasslands.

381 Correlates with NMDS Axis 2 were shown to be environmental surrogates linked to  
382 proxies of disturbances. Livestock grazing was negatively ranked, while cultivation and  
383 fertilisation practices were positively ranked. Land-use intensification through agricultural  
384 intensification, particularly in conjunction with nitrogen deposition typically results in  
385 compositional and taxonomic turnover among species assemblages, as environmental  
386 conditions change to favour more competitive, fast growing species that locally displace slow  
387 growing stress tolerators (Ordonez et al. 2009; Maskel et al. 2010). This pattern was evident  
388 for one region (Shetland) that displayed a significant positive shift along NMDS Axis 2, a  
389 significant decrease in stress tolerator species in favour of competitors and a significant gain in  
390 Ellenberg N, indicative of an increase in fertility. The national increase in Ellenberg N, is  
391 consistent with other long-term studies which report nation-wide gains in fertility values  
392 among semi-natural vegetation types across much of the UK (McCollin et al 2000; Smart et al.  
393 2005). Experimental studies on calcareous grasslands have found N deposition to lead to shifts  
394 in species composition, with increases in rank grasses and loss of forbs and bryophytes  
395 (Morecroft et al., 1994; Lee and Caporn, 1998; Johnson et al. 1999). However, regional gains  
396 in Ellenberg N in this study were often shown with gains in competitive species without  
397 biodiversity loss. It may be regions are experiencing a relaxation period between land-use  
398 changes and stable equilibriums (Diamond 1972), whereby local extinctions are likely for those



399 species with lower soil nitrogen preferences (Sarr et al 2012). However, it may equally be due  
400 to interacting effects of multiple land-use practices, arable agriculture and livestock grazing,  
401 whereby grazers prevent potential dominants taking advantage of the increases in fertility.

402 Increased fertility among semi-natural grasslands therefore present concerns for  
403 biodiversity conservation, particularly where land-use disturbances through traditional farming  
404 practices are in decline. Declines in active management, particularly in grazing intensity,  
405 typically result in increased dominance of competitor species and decline in ruderal species as  
406 competition for space, light and nutrients increase (Pakeman 2004). For many European  
407 countries, cessation in active management is recognised as the major threat to semi-natural  
408 grasslands (Levin 2012). Evidence of management declines were certainly prominent in our  
409 study, illustrating where shifts in functional indicators suggest reduced disturbance, these  
410 regions were mostly those with significant declines in biodiversity. This highlights the negative  
411 impact declines in active management and disturbance intensity have upon the conservation  
412 value of semi-natural grasslands. For the machairs of Scotland, it appears a complete de-  
413 coupling between the land and land-users to have a more immediate impact on biodiversity  
414 value, than land-use intensification, stressing the importance of maintaining strong linkages  
415 between nature and societies. Therefore, among landscapes with historic land-use traditions a  
416 vital goal of conservation policy should be to help reconnect people with nature, fostering  
417 socio-economic development while maintaining biodiversity (Fischer et al. 2012).

418

### 419 **4.3. Value of biotic indicators and environmental surrogates for biodiversity monitoring**

420 Given high temporal variability in land-use changes, and the ability of many species to  
421 persist long after disturbances have occurred, biodiversity indices alones reveal little  
422 information on whether current land-uses are in-line with conservation efforts. Interpretation of  
423 results becomes more spurious where sample efforts are small and temporal lags are large.  
424 However, introducing simple environmental surrogates as an additional component to

425 traditional diversity indices and select target species, help significantly for attributing land-use  
426 drivers to observed patterns of change. Although rare, good quality temporal datasets can  
427 provide documented evidence of vegetation composition prior to major global change impacts,  
428 and are consistently proven for quantifying long-term patterns of vegetation change (McCollin  
429 et al. 2000; Smart et al. 2005; Bennie et al. 2006). Given the extensive sampling effort in this  
430 study non-representative samples should not have undue influence, however we do  
431 acknowledge that caution should be expressed in the interpretation from only two snapshots in  
432 time, particularly with large temporal lags between surveys.

433         This study clearly demonstrates the value of simple biotic indicators and environmental  
434 surrogates for use in biodiversity monitoring assessments, demonstrated here across a large  
435 national extent of semi-natural grasslands. In this study we used very simple indices and  
436 functional indicators, which allowed us to differentiate between possible regions and infer with  
437 some confidence the likely land-use changes driving species compositional and biodiversity  
438 patterns. Our approach shows that functional indicators need not be overly complex,  
439 particularly for assessing broad-scale regional change. Functional traits measures that are  
440 nowadays also easily accessible are exceptional useful for gaining in depth knowledge of land-  
441 use impacts on the composition and biodiversity of plant assemblages, and can also be used to  
442 identify community assemble processes (refs). Nevertheless, high variability in terms of land-  
443 use practices, land-use change and species compositions within single regions complicate the  
444 generalisations that can be made. Therefore, we argue that broad functional classifiers to be  
445 equally proficient in identifying patterns and process of change at broader spatial scales, and  
446 are a useful tool for identifying regions of conservation concern that may warrant more  
447 detailed, finer-scaled investigations.

448         Scale therefore is an extremely important factor when making interpretations from  
449 biodiversity monitoring studies. Many pattern and trends identified at regional-scales were not  
450 apparent at the national scales, as contrasting divergent and convergent trends between

451 geographic regions counteract, revealing little or no national pattern. Regional results from this  
452 study are still generalisations, and are unlikely to reflect entire grassland assemblages within a  
453 predefined geographic boundary. Nevertheless, our results clearly show the value to analysing  
454 national data at smaller geographic scales.

455

## 456 **5. Conclusions**

457 This study clearly demonstrates the value of simple biotic indicators and environmental  
458 surrogates for use in biodiversity monitoring assessments, demonstrated here across a large  
459 national extent of semi-natural grasslands. We used very simple indices and functional  
460 indicators, which allowed us to differentiate between possible regions and infer with some  
461 confidence the likely land-use changes driving species compositional and biodiversity patterns  
462 of Scottish semi-natural coastal grasslands. Our approach highlights that functional indicators  
463 need not be overly complex, particularly for assessing broad-scale regional change. Functional  
464 traits measures that are nowadays relatively easily to obtain, are also exceptionally useful for  
465 providing an in-depth understanding of land-use impacts on the composition of vegetation  
466 (Pakeman et al., 2009; Lewis et al., 2014), as well as insights into the community assembly  
467 processes that govern plant assemblages (e.g. Mouchet et al., 2010). Nevertheless, high  
468 variability in terms of land-use practices, land-use change and species compositions within  
469 single regions complicate the generalisations that can be made. Simple, broad functional  
470 classifiers, as used here, can therefore be equally proficient in identifying patterns and process  
471 of change at broader spatial scales, and are a useful tool for identifying areas of conservation  
472 concern that may warrant more detailed, finer-scaled investigations.

473

474 Spatial extent is therefore an extremely important factor when making interpretations  
475 from biodiversity monitoring studies. In this study, many patterns and trends identified at the  
476 regional scale were not apparent at the larger national scale, as contrasting divergent and  
477 convergent trends between geographic regions counteracted, resulting in little or no national  
478 pattern. Regional results from this study are still generalisations, and are unlikely to reflect  
479 entire grassland assemblages within a pre-defined geographic boundary. Nevertheless, our  
480 results clearly showed the value of analysing

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484

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486

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489 Habitats and Ecosystems”) for financial support.

490

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683

684 **Table 1:** Description of land-use proxies measured for each 5m x 5m plot.

Disturbance Proxy	Data description	Environmental Variable	Abbreviation
Animal signs	Plot level presence or absence of dung from 5 herbivore species	Cattle Sheep Rabbits	N/A N/A N/A
Grazing pressure	Intensity of herbivore grazing pressure	None Light Moderate Heavy	NoGrz LghtGrz ModGrz HvyGrz
Vegetation structure	Indication of vegetation height and structure for each plot (0,1,2,3 = no, sparse, intermediate and full cover respectively)	Grasses < 20cm Grasses 20-50cm Grasses > 50cm Herbs < 20cm Herbs 20-50cm Herbs > 50cm	Gra20 Gra2050 Gra50 Hrb20 Hrb2050 Hrb50
Cultivation	Plot level presence or absence of a suite of cultivation factors, from no cultivation to current standing crop	No Cultivation Standing Crop Recent Cultivation (past 3 years) Old Cultivation (4 or more years)	NoCult StdCrp RecCult OldCult

685

686

687 **Table 2.** National and regional Mean ( $\bar{X}$ ) temporal shift in the species diversity of machair  
 688 grassland between 1976 and 2010 measured through i. richness (species count) and ii. Inverse  
 689 Simpson index. Significance tested through paired t tests (national) and general liner mixed  
 690 model with poisson function (regional). ‘\*\*\*’  $p \leq 0.001$ , ‘\*\*’  $p \leq 0.01$ , ‘\*’  $p \leq 0.05$ .

	Species Richness			1/Simpsons		
	$\bar{X}$	z	sig	$\bar{X}$	z	sig
National	2.32	7.60	***	-0.25	2.17	*
Barra	4.21	4.31	***	-2.33	-4.28	***
Benbecula	-3.36	-1.99	*	-1.71	-1.97	*
Coll	10.07	12.51	***	0.67	1.72	
Colonsay	14.70	7.39	***	2.68	2.75	**
Harris	-5.13	-3.60	***	-2.44	-3.12	**
Islay	8.89	8.47	***	0.22	0.40	
Lewis	-2.15	-2.59	**	0.40	1.02	
Monach	-3.06	-2.87	**	-1.46	-2.97	**
North Coast	-1.02	-1.33		1.15	3.44	***
North Uist	-0.35	-0.68		-1.30	-5.16	***
Sanday	0.04	0.04		0.17	0.38	
Shetland	-3.29	-2.97	**	-1.08	-1.89	
South Uist	4.98	7.40	***	-0.93	-2.85	**
Tiree	10.23	13.96	***	1.96	5.34	***

701

702 **Table 3.** Significance of change in land-use disturbance proxies in explaining temporal  
 703 compositional change as measured by the NMDS analyses (Figure 3). Significance tested  
 704 through general liner mixed model. ‘\*\*\*\*’  $p \leq 0.001$ , ‘\*\*\*’  $p \leq 0.01$ , ‘\*’  $p \leq 0.05$ .

Land-Use	NMDS AXIS 1		NMDS AXIS 2			
NoGrz	0.05	0.66	0.02	0.42		
LightGrz	0.05	0.76	0.03	0.77	707	
ModGrz	0.03	0.37	0.03	0.57		
HvyGrz	0.05	0.66	0.06	1.28	708	
RecCult	0.48	5.69	***	0.28	4.97	***
OldCult	0.17	3.02	**	0.11	3.11	709
StndCrp	0.10	0.68		0.08	0.83	
Gra20	-0.02	-1.08	<0.01	<0.01		710
Gra2050	-0.01	-0.65		-0.01	-1.13	
Gra50	-0.06	-3.23	***	-0.01	-1.17	711
Hrb20	0.04	2.16	*	0.01	0.86	
Hrb2050	0.03	1.65		<0.01	0.35	712
Hrb50	0.06	1.67		0.05	2.31	*
Cattle	<0.01	0.03		0.02	1.07	713
Sheep	0.01	0.30		-0.02	-1.00	
Rabbit	0.01	0.38		-0.01	-0.50	714

715

716 **Fig. 1.** Distribution of original and resurveyed study sites across Scotland. For site details see  
 717 Appendix A.

718  
 719 **Fig. 2.** Mean richness and % cover change for species groups indicative of different conditions  
 720 and land-use states of machair grasslands: Cult = species indicative of cultivated land; Fallow  
 721 = species indicative of rotational arable machair i.e. fallow grasslands; Machair = species  
 722 indicative of machair grasslands; Poor = species indicative of degraded machair grasslands.  
 723 Mean differences are presented with standard error bars of the mean. Shaded bars represent  
 724 statistically significant change ( $p < 0.05$ ) tested using General Linear Mixed Models (GLMM;  
 725 Richness) and linear-mixed modelling with residual maximum likelihood (REML;  
 726 Abundance).

727  
 728 **Fig. 3.** NMDS ordination of machair grassland communities across Scotland, computed using  
 729 the Bray Curtis dissimilarity. Figures i-ii: Displayed are the convex hulls for each survey  
 730 (dashed and solid lines refer to the original and resurvey respectively). (i) Projected  
 731 environmental proxies for land-use  $p < 0.001$  (see Table 1). (ii) Projected functional signatures:  
 732 Ellenberg and CSR scores. (iii) Displayed as text are species with a significant statistical  
 733 relationship ( $p < 0.001$ ) and a goodness of fit ( $r^2 \geq 0.05$ ) along Axis 1 and or Axis 2. Species  
 734 are represented by the following letter codes: Aa *Ammophila arenaria*, As *Agrostis stolonifera*,  
 735 Bry Bryophytes, Cf *Carex flacca*, Cn *Carex nigra*, Cp *Cardamine pratensis*, Er *Elymus repens*,  
 736 Gp *Galium palustre*, Gv *Galium verum*, Hv, *Hydrocotyle vulgaris*, Lp *Lolium perenne*, Pa  
 737 *Potentilla anserina*, Pv *Prunella vulgaris*, Rr *Ranunculus repens*, Sp *Succisa pratensis*, Tp  
 738 *Thymus polytrichus*, Tr *Trifolium repens*. Non-significant species are represented by ‘•’.

739  
 740 **Fig. 4.** National and regional shifts in NMDS ordination axes scores for computed using Bray  
 741 Curtis in two dimensional ordination space. Displayed are kernel densities for NMDS axis 1



742 and axis 2. Dashed and solid lines refer to the original and resurvey respectively. Shaded  
743 density graphs (green = original survey & purple = resurvey) represent statistically significant  
744 shifts between survey years ( $p < 0.05$ ) tested using nested linear mixed models with residual  
745 maximum likelihood (REML).

746

747 **Fig. 5.** National and regional cover-weighted functional classification values (i. CSR & ii.  
748 Ellenberg) for the surveyed machair grasslands of Scotland. Mean plot scores are presented  
749 with standard error bars of the mean. Grey bars represent statistically significant change  
750 between survey years ( $p < 0.05$ ) tested using nested linear mixed models with residual  
751 maximum likelihood (REML).

752

753 **Fig. 6.** Patterns between regional species richness gains and loses since 1976 and those regions  
754 once designated as an Environmentally Sensitive Area (ESA).