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22 **Spatial scale and specialisation affect how biogeography and functional traits predict long-**  
23 **term patterns of community turnover**

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32 **Running headline:** Biogeography & traits predict plant turnover

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## 47 **Summary**

- 48 1. Immigration, extirpation and persistence of individual populations of species are key  
49 processes determining community responses to environmental change. However, they are  
50 difficult to study over long time periods without corresponding historical and modern-day  
51 species occurrences.
- 52 2. We used historical and present-day plant species occurrence data from two different spatial  
53 scales (resolutions) to investigate plant community turnover during the 20th century in a  
54 Baltic Sea archipelago. Patterns of turnover were analysed in relation to plant functional  
55 traits relating to dispersal and competition/persistence, as well as biogeographical variables.
- 56 3. Turnover was largely driven by interactions between functional traits and measures of area,  
57 connectivity and distance to mainland. However, the combinations of traits and  
58 biogeographical variables that were most important for predicting immigration and  
59 extirpation differed between datasets, and between species associated with grassland  
60 management and the entire species pool.
- 61 4. Taller plants were more likely to persist regardless of scale and biogeography, reflecting the  
62 grazing abandonment which occurred in the study area. Interactions between dispersal traits  
63 and biogeography were related to immigrations when the entire species pool was  
64 considered. However, increased dispersal potential, together with a smaller island size and  
65 increasing distance to mainland combined to promote extirpations in management-  
66 associated species. A perennial life span and seed banking contributed to species persistence.  
67 At the larger spatial scale, trait-driven turnover was not mediated by the biogeographic  
68 context.
- 69 5. We showed that it is important to consider functional traits, biogeographical variables and  
70 their interactions when analysing community turnover over time. Furthermore, we found  
71 that the understanding of how combinations of traits and biogeography predict turnover

depends on the source and spatial scale of the available data, and the species pool analysed.

**Key-words:** Biodiversity, Extinction, Forest, Fourth-corner analysis, Fragmentation, Grassland, Historical ecology, Islands, Landscape, Specialist species.

## Introduction

Anthropogenic environmental change has far-reaching consequences for biodiversity on Earth.

Understanding how organisms and communities respond to changes in their environment over time is therefore central to many key questions in ecology (Sutherland *et al.* 2013). From local surveys to larger-scale biological records, historical species occurrence data can give important insights for the field of global environmental change through understanding how organisms and communities have responded to changes in the past (Vellend *et al.* 2013b; Powney & Isaac 2015).

Comparing local occurrences of plant species from two or more time periods allows the quantification of responses in biodiversity and community composition to environmental pressures such as agricultural abandonment, climate change, nitrogen deposition and urbanisation (Löfgren & Jerling 2002; Duprè *et al.* 2010; McCune & Vellend 2013; Savage & Vellend 2015). Despite the accepted view that biodiversity as a whole is threatened by human activity, results at local scales are generally mixed, leading a recent synthesis to report no net change in biodiversity over time (Vellend *et al.* 2013a; but see critique by Gonzalez *et al.* 2016). At larger, regional spatial scales, the distributional responses of plant species to environmental change are also highly variable (Doxford & Freckleton 2012).

Changes in plant biodiversity and distributions result from a combination of the three components of turnover: immigration, extirpation (local extinction) and persistence. The mechanisms driving

community turnover can be investigated by analysing functional traits of the individual species responding to change. For example, traits relating to competitiveness and the persistence of seeds and/or adult plants have responded well to land-use change at multiple spatial scales (Lindborg 2007; Saar *et al.* 2012; Powney *et al.* 2014). On the other hand, species adapted to long-distance dispersal have been found to be particularly prone to extirpation (Lindborg 2007; Johansson, Cousins & Eriksson 2010; Saar *et al.* 2012), as an ability to disperse long-distances is not sufficient for plants to persist at high levels of habitat fragmentation or degradation (Soons & Heil 2002; Teller, Miller & Shea 2015). Traits of immigrating species are less well-studied (but see McCune & Vellend 2015), and investigations have often focused on particular subgroups of species such as at-risk habitat specialists (Saar *et al.* 2012; Marini *et al.* 2012; Hemrová & Münzbergová 2015). Although concentrating on habitat specialists can yield valuable information for conservation management, considering the entire species pool -including colonising species- is important for understanding the system as a whole. Finally, plant species occurrences are strongly associated with landscape structure and configuration, following biogeography theory (Mayfield & Daily 2005; Aggemyr & Cousins 2012), and the plant functional traits at the community level are known to be affected by and interact with such spatial variables (Kimberley *et al.* 2014; Hemrová & Münzbergová 2015). Thus, it is important to consider how community turnover in response to environmental change is driven both by functional traits and biogeography.

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In this study, we examine plant community turnover during a 100-year period in an archipelago system in the Baltic Sea. During the 20th century, widespread grazing abandonment has led to a shift from (semi-)open grassland to closed forest in the area, which combined with isostatic land uplift has caused substantial community turnover (Aggemyr & Cousins 2012). We use two independent datasets covering approximately the same time period at different spatial resolutions to investigate how functional traits and biogeographical variables predict turnover, and how this is

122 affected by spatial scale and habitat specialisation. We hypothesise that turnover reflects the  
123 prevailing change in land use, benefiting relatively taller and more competitive species. We also  
124 expect that species adapted to long-distance dispersal will have experienced relatively more  
125 extirpation due to the high degree of land-use change (see Table 1 for detailed expectations based  
126 on previous results in the literature). Biogeographical variables are predicted to mediate and  
127 reinforce the trait-driven changes, with larger patch sizes and proximity to species sources  
128 promoting immigration and persistence. Finally, we expect that differences in species identity and  
129 rates of turnover relating to spatial scale and habitat specialisation might cause different  
130 combinations of traits and biogeography to affect turnover between the two datasets and between a  
131 subset of species associated with grassland management and the entire species pool.

**Table 1.** Expectations regarding how plant functional traits and biogeographical variables predict plant community turnover following 20<sup>th</sup> century agricultural abandonment in a Baltic sea archipelago. Immigration is when species were absent from the historical inventory and present in the recent inventory on a particular island or grid square. Extirpation/persistence is when species were present in the historical inventory and absent/present in the recent inventory,

	Immigration		Extirpation (invert operator for persistence)	
Traits				
Dispersal traits				
Seed mass	-	Species with small, numerous seeds and those with appendages should be more capable of the long-distance dispersal required to immigrate into new areas [1-2].	-	Species adapted to dispersal have been found to perform badly in fragmented landscapes and following habitat degradation [2-4].
Seed morphology	+		+	
Seed number	+		+	
Persistence traits				
Leaf area	+	Shade tolerance predicts colonisation following afforestation [5].	-	A lack of shade tolerance is regularly associated with extirpation following abandonment [4,6,7].
Life span	+	Perennial species more likely to colonise following afforestation [5].	-	A perennial life span found to delay extirpations following habitat degradation [3,8].
Plant height	+	Abandonment favours the colonisation of taller species [7].	-	Smaller plants are more likely to go extinct following abandonment [3,4,7].
Seed-bank persistence		No expectation	-	Grassland plant communities are able to form persistent seed banks and facilitate persistence in fragmented landscapes [8, 10,11]. However, seed-banking was related to extirpation in abandoned coppices [6].
Biogeography				
Area	+	Larger areas are able to support more species, and therefore there should be a higher chance that species will immigrate [5,11,12].	-	Larger areas are able to support more species, and therefore a higher chance that species will persist [11,12].
Connectivity	+	Proximity of nearby or mainland population should facilitate immigration [13-14].	-	Populations further from other nearby populations or the mainland are less likely to be replaced following extirpation (rescue effect) [11].
Distance to mainland	-		+	

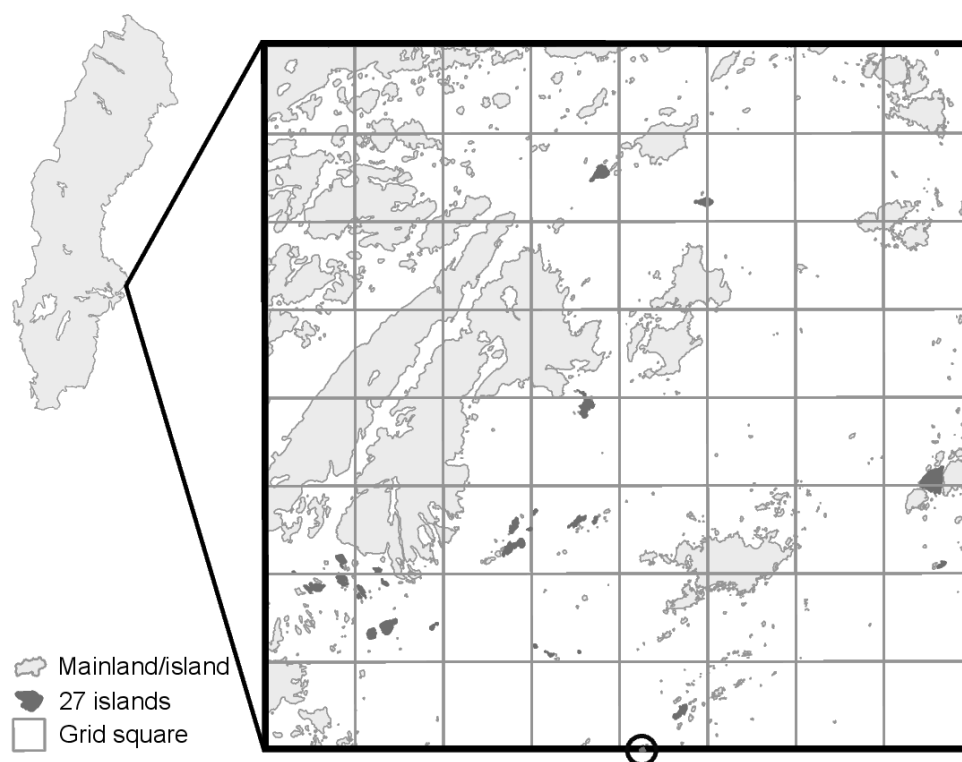
[1] Auffret *et al.* 2012; [2] Soons & Heil 2002; [3] Johansson *et al.* 2010; [4] Saar *et al.* 2012; [5] McCune & Vellend 2015; [6] Kopecký *et al.* 2013; [7] Walker *et al.* 2009; [8] Lindborg 2007; [9] Thomson *et al.* 2011; [10] Auffret & Cousins 2011; [11] Piessens *et al.* 2004; [12] Aggemyr & Cousins; [13] Mayfield & Daily 2005; [14] Brudvig *et al.* 2009.

## 148 **Materials and methods**

### 149 *Study area*

150 This study is based on data collected from a 400 km<sup>2</sup> area in the northern Stockholm archipelago  
151 (midpoint 59°35'7 N, 18°60' E; Fig. 1). The area has a long history of human influence based  
152 around farming and fishing, with livestock grazing occurring on all but the smallest islands. In the  
153 1950s, agriculture was largely abandoned (Aggemyr & Cousins 2012). Forest (mostly coniferous)  
154 now covers 73% of terrestrial areas, with the whole study area containing only 23 patches of  
155 valuable grassland registered on the Swedish government's database (TUVa database –  
156 <http://www.jordbruksverket.se/tuva>).

157



159 **Figure 1.** Map over the 400 km<sup>2</sup> area of the Stockholm archipelago used in this study, showing 27  
160 islands surveyed in 1908 and 2008, and the 2.5 × 2.5 km grid squares used for plant-atlas dataset.  
161 Circle shows location of one island on the very edge of the grid.



162 *Species occurrence data*

163 27 Islands

164 We resurveyed island-level plant occurrences on 27 small islands, 0.003-0.33 km<sup>2</sup> in area  
165 (mean±SD: 0.06±0.07). This area of the archipelago was first inventoried between 1884 and 1908  
166 by J.W. Hamnér (1909), who surveyed plant species occurrences on a total of 48 islands in the study  
167 area. Based on a study of the original documents, Hamnér's inventories were judged to be  
168 sufficiently comprehensive on 27 of these islands. Spending an equal time per unit area, Aggemyr  
169 and Cousins (2012) carefully recorded presence of all plant species on each island. We are confident  
170 that the island inventories are comprehensive and comparable in both 1908 and 2008. A total of 382  
171 species were counted across all islands and both time steps (Aggemyr & Cousins 2012).

172

173 Indicator species analysis (Dufrêne & Legendre 1997; R package: *labdsv*, function: *indval*; Roberts  
174 2013) was used to identify plant species associated with grassland management in 1908 (n = 48).

175 *Management-associated species* were defined as those species with a significantly (p = 0.05) higher  
176 relative frequency in 1908 on the 12 islands which had relatively intensive grassland management  
177 compared to the 15 otherwise-similar islands with only low-intensity forest grazing, using detailed  
178 land-use maps from 1906 (Aggemyr & Cousins 2012). This subgroup includes a mixture of species  
179 traditionally associated with open, intensively managed grassland (*grassland specialists*; Krauss *et*  
180 *al.* 2010), together with those more associated with low-intensity management in woodland  
181 (*ancient forest species*; Hermy *et al.* 1999), as well as many intermediate species (see Supporting  
182 Information Appendix S1). It is not our intention to assign any additional conservation value to  
183 these species, or to discuss the appropriateness of each species' inclusion in the subgroup.

184

185 Plant atlas

186 To compare our own resurvey with one at another spatial scale and resolution, we used the regional

187 plant atlas covering the study area (Upplands Flora; Jonsell 2010), which presents plant species  
188 occurrences in  $2.5 \times 2.5$  km grid squares based on systematic inventories carried out between 1991  
189 and 2005. The grid squares also include occurrences of 454 rare to frequent plant species (the rarest  
190 and most-common were not mapped; Sundberg 2014) found in the region by Almquist (1929) based  
191 on fieldwork from the 1910s and 1920s. Our study area was covered by 64 of these grid squares, of  
192 which 48 contained species observations (see Fig. 1). These 48 grid squares contain a mean $\pm$ SD of  
193  $1.44 \pm 1.45$  km<sup>2</sup> land area, and  $21.6 \pm 16.0$  islands are represented in each square. Three-hundred and  
194 twenty five of the 454 species were present in these grid squares. Almquist made detailed  
195 distribution maps for a selection of species (albeit a large selection), and the modern-day plant atlas  
196 is a result of extensive inventories. Therefore, we are confident that the grid-square occurrence data  
197 are accurate and comparable between time-steps.

198

#### 199 Data preparation

200 Species names from both the 27 island and the plant-atlas data were checked and changed to match  
201 the nomenclature of Karlsson (1997) and each other. A total of 102 species were shared across the  
202 two spatial scales of the data. Although this overlap appears to be quite low, many common (and  
203 rare) species not covered by Almquist's inventories will have been observed in our own inventories,  
204 and the larger area covered by the plant-atlas data increases the number of species in the total  
205 species pool. The complete present-day species list from the relevant grid squares (excluding  
206 records from the small area of the Swedish mainland) was also acquired and changed to match the  
207 list of the 27 island data, finding that 363 (95%) of the 382 species from the 27 island inventories  
208 were also recorded in the modern plant atlas. Reasons for missing species might include lack of  
209 detection in the plant-atlas inventories and the inventories being carried out up to 17 years apart.

210

211 To be conservative with regard to eventual false absences or occasional species misidentification

212 and thus avoid the issue of pseudo-turnover, only species which were recorded on at least three  
213 islands (27 islands data) or three grid squares (plant-atlas data) across both time steps were retained  
214 for analysis. For clarity, if a species was recorded on the same island/grid square in both time-steps  
215 it counted as two records. Cryptogams were removed as they do not exhibit the dispersal (seed)  
216 traits tested. This resulted in 256 species (67% of those recorded) in the 27-island dataset, including  
217 46 management-associated species, and 246 species (76%) in the plant-atlas dataset.

218

#### 219 *Functional traits*

220 Seven traits relating to plant species competition, persistence and dispersal ability were extracted  
221 from the LEDA traitbase (Kleyer *et al.* 2008). Competition/persistence traits were: seed bank  
222 persistence (persistent or transient), life span (perennial or annual, including biennial), leaf area  
223 ( $\text{mm}^2$ ) and plant height (m). Dispersal traits were: seed mass (mg), seed morphology (long-distance  
224 dispersal: presence of hook, balloon-appendage, fleshy fruit or other appendage; short-distance  
225 dispersal: no appendage) and seed number (per shoot). For the numerical traits, the geometric mean  
226 of all records for each species was calculated to reduce the influence of extreme values present in  
227 the database. These data were then complemented by values from other sources. Plant life span was  
228 extracted for all remaining species from Mossberg and Stenberg (2003), while other trait values  
229 were extracted (in the following order) from data from the projects VISTA (Garnier *et al.* 2007) and  
230 COCONUT (EU project SSPI-CT-2006-044346; Marini *et al.* 2012), as well as the databases  
231 Biolflor (Kühn, Durka & Klotz 2004) and Ecoflora (Fitter & Peat 1994). Finally, remaining gaps in  
232 the trait data (none for life span, 6-14% for other traits) were filled using Multivariate Imputation by  
233 Chained Equations using the package *mice* in the statistical environment R 3.1 (van Buuren &  
234 Groothuis-Oudshoorn 2011; R Development Core Team 2015), a method recommended by  
235 Taugourdeau *et al.* (2014).

236

## 237 *Biogeographical variables*

238 We calculated three spatial variables related to the biogeography of the study area. For the 27  
239 islands we considered island area, distance to mainland (including the two much larger islands in  
240 the study area; Aggemyr & Cousins 2012) and connectivity. We used the following connectivity  
241 measure ( $C$ ):

$$242 \quad C_i = \sum_{j \neq i} W_{A_j} W_{d_j} A_j \text{ where } W_{A_j} = \frac{A_j}{\sum_{l \neq i} A_l} \text{ and } W_{d_j} = k \frac{d_{ij}^{-r}}{r}$$

243

244

245 Where  $A_j$  is the area of island  $j$  and  $A_l$  is the area of all islands within buffer radius  $r$ ,  $d_{ij}$  is the  
246 Euclidean distance between island  $i$  and  $j$ ,  $k$  is a constant set to 0.01 to assign less weight to islands  
247 further away from the focal island. Higher values of  $C$  indicate more landscape connectivity. We  
248 used a buffer radius of 200 m, as this was previously identified as the distance which best explained  
249 the absolute turnover of plant species on the 27 islands between 1908 and 2008 (Aggemyr &  
250 Cousins 2012). For the plant-atlas data, we used the total area of land within each grid square, the  
251 distance from the centre of the square to the mainland (mainland proper) and the number of islands  
252 represented within the square. The dominance of forest cover today, together with the scarcity of  
253 valuable grasslands (none present on the 27 islands), indicates uniform abandonment of grazing  
254 between the two surveys. Therefore, the possibility of earlier and higher magnitude abandonment  
255 on smaller grasslands further from the mainland is unlikely to confound the purely spatial effects of  
256 the above variables in our analysis of community turnover. The data analysed in this study are  
257 available from the figshare repository (Auffret *et al.* 2016).

258

## 259 *Data analysis*

260 The interaction of environmental variables and functional traits has recently been shown to be well-  
261 represented by the trait:environment interaction terms of generalized linear models (GLM; Jamil *et*

262 *al.* 2013; Brown *et al.* 2014). Our analytical approach involved relating species traits and  
263 environmental (in our case biogeographical) variables to the different components of turnover,  
264 using immigration (absent in historical and present in present-day inventories) and  
265 extirpation/persistence (present in historical and absent/present in present-day inventories) as our  
266 binary response variables for each species on each island (27-island data) or each grid square (plant-  
267 atlas data).

268

269 Collinearity between our quantitative functional traits was tested using Spearman's correlation test.  
270 Correlations (range 0.16-0.36) were comfortably below accepted thresholds (Dormann *et al.* 2013),  
271 and therefore all traits were retained for analysis. See Appendix S1 for all correlations, along with  
272 comparisons of trait ranges between management-associated species and the entire species pool. All  
273 quantitative explanatory variables were then zero-mean scaled, before our three matrices (binary  
274 response, traits and biogeography) were vectorised into one long matrix for incorporation into  
275 generalized linear mixed models. Vectorising the three matrices allowed us to subsequently remove  
276 NA values in the response field (for example in the immigration analysis where a species was  
277 already present on a specific island in the historical dataset), which would have caused problems  
278 had the analysis been run using separate matrices.

279

280 Separate analyses were carried out for immigration and extirpation/persistence for the management-  
281 associated species in the 27-island dataset, all species in the 27-island dataset and all species in the  
282 plant-atlas dataset. In each case, a full model was first created using the function *glmer* in the R  
283 package *lme4* (Bates *et al.* 2014). This model contained all traits, all biogeographical variables and  
284 their interactions as fixed terms. Sites were included as random terms to account for inherent  
285 differences between sites, and species-dependent random terms for each biogeographical variable  
286 were included to account for species-specific environmental associations. See Jamil *et al.* (2013) for

287 further details on model construction and the statistical motivation. Terms were then dropped  
288 individually from this model using the function *drop1*. All terms whose removal did not result in a  
289 significant ( $p=0.05$ ) increase in Akaike Information Criterion (AIC) in the resulting model as  
290 determined by Chi-square likelihood-ratio tests were dropped. This process was repeated until only  
291 terms which contributed to a lower AIC score remained in the resulting model, plus any single  
292 terms which were included in a significant interaction term. The explanatory power of each of the  
293 final models was then estimated by calculating their marginal and conditional  $R^2$ , which represent  
294 the proportion of variance explained by fixed factors alone and the proportion explained by both the  
295 fixed and random factors, respectively (Nakagawa & Schielzeth 2013).

296

## 297 **Results**

298 Land-use change during the 20th century resulted in a great deal of plant species turnover in our  
299 study area. The 256 species analysed from the 27-island dataset revealed 1414 immigration events,  
300 632 extirpation events and 781 incidences where a species was recorded on the same island in both  
301 inventories. Forty-one new species immigrated to the islands between 1908 and 2008, whereas 30  
302 were extirpated and 185 were persistent. All of the 30 extirpated species are present elsewhere in  
303 the study area according to the modern-day plant atlas. For the plant atlas data, there were 1891  
304 immigration events, 820 extirpations and 1581 incidences of persistence. Ten species were  
305 extirpated from the study area, 13 immigrated and 223 persisted.

306

307 Our analysis showed that combinations of, and interactions between biogeographical variables and  
308 functional traits relating to species persistence and dispersal predicted patterns of turnover during  
309 the 20th century (Table 2; Appendix S2). However, the variables included in the final models  
310 depended on the scale of analysis. Turnover of management-associated species on the 27 islands  
311 was generally predicted by biogeographical variables and their interactions with relatively few

312 traits, whereas several traits explained turnover in all species. At the plant-atlas level, final models  
313 included no significant biogeographic terms and turnover was associated only with  
314 competition/persistence traits.

315

316 Only biogeographical variables explained immigration of the management-associated subgroup of  
317 species, with immigration being more likely on larger islands and those closer to the mainland.  
318 Management-associated species with smaller seeds were more likely to be extirpated on smaller  
319 islands, as were those producing more numerous seeds on islands further from the mainland. Taller  
320 management-associated species were generally less likely to become extirpated from an island.  
321 When all species in the 27-islands were analysed, immigration was related to a range of functional  
322 traits and biogeographical variables. Long-lived and relatively taller species were more likely to  
323 immigrate to islands with a higher connectivity, but larger-leaved species were less likely to  
324 colonise such islands. Species producing heavier seeds were less likely to immigrate to islands  
325 further from the mainland. Long-lived and taller plants were less likely to be extirpated, as were  
326 seed-banking species on larger islands. At the plant-atlas scale, both immigration to and persistence  
327 within a grid-square were more likely for long-lived species, with taller species also less likely to be  
328 extirpated.

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**Table 2.** Components of the final models explaining immigration and extirpation/persistence of plant species in an area of the Stockholm archipelago during the 20th century at different scales. Coefficients of significant variables are shown in bold. Predictions can be found in Table 1, and full model summaries are provided in Supporting Information Appendix 2.

Biogeography		Traits		Interactions		R2GLMM		Matched predictions?
		Persistence	Dispersal			Marginal	Conditional	
<i>Islands</i>								
<i>Management-associated species</i>								
	Immigration	Area +1.68 Dist. mainland -0.38				0.25	0.76	Yes
	Extirpation	Area -0.93 Dist. mainland -0.97	Plant height -1.55	Seed mass -4.35 Seed number 9.67	Area:Seed mass -4.61 Dist. mainland:Plant height -1.54 Dist. mainland:Seed number 11.62	0.19	0.6	Yes
<i>All species</i>								
	Immigration	Area +0.87 Connectivity -0.46 Dist. mainland -0.83	Leaf area +0.21 Long-lived +0.78 Plant height +0.53	Seed mass -0.9	Dist. mainland:Seed mass -0.75 Connectivity:Leaf area -0.11 Connectivity:Long-lived +0.58 Connectivity:Plant height +0.32	0.24	0.68	Mixed
	Extirpation	Area +0.26 Connectivity +0.94	Long-lived -1.58 Plant height -0.52 Seed bank -0.08		Area:Seed bank -0.52 Connectivity:Long-lived -1.04	0.06	0.64	Yes
<i>Plant atlas</i>								
<i>All species</i>								
	Immigration		Long-lived +0.83			0.01	0.58	Yes
	Extirpation	Land area +0.004	Long-lived -1.51 Plant height -1.18		Land area:Plant height +0.39	0.21	0.61	Yes

## 342 **Discussion**

343 We have found that plant functional traits related to dispersal ability and persistence are significant  
344 predictors of species turnover over the past century. In many cases, interactions of these traits with  
345 biogeographical variables were important in explaining immigration, persistence and extirpation in  
346 our study area. Many of our results matched our individual expectations, such as more competitive  
347 species benefiting from grassland abandonment and the general positive effects of increased habitat  
348 area, proximity to a species source and connectivity (Tables 1 and 2). However, the identification of  
349 the interactions between functional traits and biogeography is an important finding. Importantly,  
350 different predictors were associated with different responses when comparing trends across spatial  
351 scales in the same region, and when considering the whole species pool and a subgroup of  
352 management-associated species. Biogeographical variables contributed to island-level turnover  
353 independent of association to grassland management, but interactions with functional traits were not  
354 important for explaining patterns of turnover at larger spatial scales.

355

### 356 *Traits and biogeography*

357 The plant functional traits and biogeographical variables which helped to explain turnover during  
358 the 20th century reflect the type of environmental change which occurred in the study area, as well  
359 as the nature of the island system studied (Table 1 and 2). Ability to persist in the established  
360 vegetation and in the seed bank were both helpful in preventing extirpations. At the island level, the  
361 persistence provided by a perennial life span tended ( $p=0.08$ ) to be strengthened by increased  
362 connectivity. Long-lived species have previously been associated with persistence following  
363 grassland abandonment (Lindborg 2007; Saar *et al.* 2012), but as long-lived adult plants can only  
364 temporarily survive in unsuitable environments (Honnay & Bossuyt 2005), it is understandable that  
365 populations on better-connected habitat patches are more likely to be 'rescued' (Piessens *et al.*  
366 2004). On larger islands, seed banking contributed to species persistence, supporting previous work

367 identifying its potential role in buffering changes in land use and configuration (Lindborg 2007;  
368 Auffret & Cousins 2011). It is likely that persistent seed banks are present on all islands, but that on  
369 larger islands there is logically a higher chance of natural or anthropogenic disturbance, leading to  
370 the manifestation of seed-banking species in the established vegetation. The persistence of taller  
371 species at the expense of their shorter neighbours is another common phenomenon (Walker, Preston  
372 & Boon 2009; Saar *et al.* 2012; Kopecký, Hédli & Szabó 2013), being pervasive across our study  
373 landscape and showing no significant interactions with biogeography. On the other hand,  
374 immigration was promoted by the interaction of performance-related traits and landscape  
375 connectivity, trends which have previously been identified separately (Brudvig *et al.* 2009; Van  
376 Kleunen, Weber & Fischer 2010).

377  
378 Increased dispersal potential, together with a smaller island size and increasing distance to mainland  
379 combined to promote extirpations in management-associated species (Table 2). This provides  
380 empirical support to modelling studies suggesting that species apparently adapted to long-distance  
381 dispersal can be disproportionately affected by high levels of habitat loss, due to the low probability  
382 of propagules arriving in suitable habitat (Teller *et al.* 2015; Martin & Fahrig 2016). In our study  
383 area, dispersal potential was clearly strongly affected by the high levels of habitat loss and cessation  
384 of rotational grazing (Soons & Heil 2002; Auffret *et al.* 2012). As expected, immigration was partly  
385 limited by both dispersal potential and biogeography (Ehrlén & Eriksson 2000; Aggemyr & Cousins  
386 2012; McCune & Vellend 2015). Our results indicate that it is often the interaction of functional  
387 traits and biogeography that best predicted plant community turnover together, rather than  
388 independently. Therefore, considering biogeographical variables together with functional traits can  
389 provide valuable insights for understanding ecological responses to environmental change.

390

391 *Scale and specialisation*

392 Many of our results regarding how community turnover is related to functional traits and  
393 biogeography matched our expectations based on the literature and the nature of environmental  
394 change that took place in our study area. However, we showed that like changes in biodiversity (Sax  
395 & Gaines 2003; Hannus & Von Numers 2010; Cousins & Vanhoenacker 2011), the biogeographical  
396 variables and traits driving turnover depend on spatial scale and specialisation. Importantly, the  
397 association of greater dispersal ability with extirpation was only apparent for management-  
398 associated species, while dispersal ability was not significantly related to immigration or  
399 extirpation/persistence at the plant atlas scale. Processes of immigration and extirpation  
400 understandably take longer at larger compared to smaller spatial scales, as sampling units of a larger  
401 size require larger average dispersal distances for immigration, and the disappearance of more  
402 populations is required for extirpation. Therefore, groups of at-risk species may share traits which  
403 contribute to negative trends over time, but are not identified when considering the whole species  
404 pool, or when analyses are carried out at a large spatial grain. While general habitat and niche-  
405 related traits appear important in understanding broad-scale changes over time (e.g. Powney *et al.*  
406 2014), we have shown that specific plant traits related to dispersal and persistence drive turnover at  
407 smaller scales and for specific species, which could later translate into larger-scale patterns in  
408 distributions over time.

409

410 Although considering the responses of a sub-group of species of interest can yield useful  
411 information for conservation purposes, differences between the whole species pool and this sub-  
412 group might not always be purely driven by the species' habitat specialisation. We found that fewer  
413 functional traits explained turnover in management-associated species, but those patterns that were  
414 found were in general agreement with results for the whole species pool (Table 2). It could be that  
415 differences were to some extent driven by the smaller number of species, the resulting fewer  
416 turnover events and differences in the ranges and fractions of the quantitative and categorical traits,

417 respectively (Appendix S1). The possibility that some differences between models could be due to  
418 management-associated species being merely a small subgroup of the species pool warrants further  
419 investigation, and we recommend that future studies interested in habitat specialists also consider  
420 responses of the whole species pool.

421

422 Finally, despite our efforts in both data collection and preparation to ensure that our datasets were  
423 compatible and comparable, the use of different datasets to examine ecological changes in time and  
424 space can affect results and their interpretations. Thus, the variation in trait and environment signals  
425 across spatial scales may not always be purely related to scale, but can also be affected by methods  
426 associated with data collection through differences regarding the number, identity and expertise of  
427 observers, the timing, duration and sampling effort of fieldwork.

428

429

#### 430 *Concluding remarks*

431 Our study provides further evidence that historical data are a very useful resource for understanding  
432 ecological responses to environmental change. We show that it is important to consider both  
433 functional traits and the biogeographic context when investigating turnover, and that traits relating  
434 to both species dispersal and persistence can play important roles in determining species responses.  
435 Our results also highlight that different signals can emerge depending on the spatial resolution of  
436 available data, as well as habitat associations of the species investigated. This has consequences for  
437 the interpretation of previous and future studies investigating community turnover over time.

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453

## 454 **Supporting information**

### 455 **Appendix S1.**

456 **Table A1.** Species associated with grassland management in 1908 for 27 islands in the  
457 Stockholm archipelago

458 **Table A2.** Results of Spearman's correlation tests between quantitative traits.

459 **Figure A3.** Comparison of ranges of quantitative plant functional traits between the species  
460 pool and management-associated species.

461 **Figure A4.** Comparison of relative fractions of qualitative plant functional traits between the  
462 species pool and management-associated species.

463

### 464 **Appendix S2. Output summaries of the final GLMM models.**

465

466

467   **Data accessibility**

468   The data used in this study have been deposited to figshare (Auffret et al. 2016)

469

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