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Historical, local and landscape factors determine the success of grassland restoration for arthropods

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Abstract

In Europe, extensively managed grasslands have undergone large-scale declines due to intensive agriculture and abandonment. Their restoration supports arthropod biodiversity within farming systems. We investigated limiting factors for arthropod establishment during grassland restoration across a chronosequence of 52 restoration sites established by either natural regenerating or direct seeding. Our study covered 363 arthropod species of 10 orders, including detritivores, herbivores, predators and pollinators. These were sampled using pitfall traps, suction sampling and transect walks. The similarity of plant communities on restoration sites to target species rich grasslands was positively correlated with the similarity of the arthropod communities to these same grasslands. There was evidence that restoration sites located in landscapes suffering from historic large-scale loss of species rich grassland (1930 to 2015) had lower success in replicating the composition of arthropod communities and supported the lowest levels of species richness. The age of the restoration site was a predictor of restoration success for some trophic levels. For example, predator species richness was greatest in the oldest restoration sites. However, this was only the case were sites were either of large size or located in landscapes with the lowest historic loss of species rich grassland. Impacts of within site management also affected arthropod communities. The annual frequency of cutting negatively affected detritivores species richness, and selected against traits including herbivore monophagy. Overall arthropod species richness was positively correlated with sward height. These results emphasise the relative importance of the success with which the floral community is replicated, as well as landscape and management factors, during grassland restoration. This has implications for future agri-environmental schemes. In particular, achieving high quality within-site management that maximises establishment of the plant communities needs to be the initial focus of any restoration program.

Key-words: arable recreation; calcareous grassland; ex-arable land; functional traits; arthropods; extinction debt; trait-environment correlations, trophic levels.

1. Introduction

Species-rich grasslands provide crucial breeding and foraging habitat for a diverse range of arthropods (Batáry *et al.*, 2007; Knop *et al.*, 2011; Woodcock *et al.*, 2012b; Habel *et al.*, 2019). Across much of Europe these have undergone wide-scale degradation and conversion to other habitat types, so that between 1960 to 2013 there has been a 47% reduction in their area across Europe (van Swaay, 2002; Ridding *et al.*, 2015). This has contributed to wide scale negative impacts on arthropod diversity (Habel *et al.*, 2019). Species loss may also occur as a result of historic patterns of land use change, potentially resulting in extinction debts (Kuussaari *et al.*, 2009; Löffler *et al.*, 2020). To help rectify this issue several government policies across Europe have recommended the restoration of well-connected landscapes through the re-establishment of high quality grasslands (e.g. Lawton *et al.*, 2010). In Europe, agri-environmental schemes provide financial support to farmers to recreate these lost habitats, although this is expensive, time-consuming and characterised by considerable variability in its success (Knop *et al.*, 2011; Török *et al.*, 2011; Czerwiński *et al.*, 2018). Elucidation of the factors that limit the successful restoration of these grasslands will allow policy makers and land managers to maximise biodiversity gains in the context of limited land and financial resources.

There is a strong link between host-plant establishment and the colonisation of phytophagous arthropods during grassland restoration, particularly for herbivores (Woodcock *et al.*, 2010; Knop *et al.*, 2011; Littlewood *et al.*, 2012; Woodcock *et al.*, 2012b; Konig and Krauss, 2019). For grassland plant species this is often achieved through the introduction of plant propagules (e.g. seeds) followed by management, such as cutting or grazing, to control competitive interactions

between species (Török *et al.*, 2011; Czerwiński *et al.*, 2018). In the case of plants, the introduction of propagules into the restoration site can be achieved using equipment and skills typically available to land managers or farmers, i.e. the spreading of commercially available seed mixes onto a prepared seed bed (Török *et al.*, 2011; Czerwiński *et al.*, 2018). However, overcoming dispersal limitation in arthropods can be more complicated, as comparable methods rely on either unusual techniques or equipment. As such, this can make these approaches prohibitively expensive as well as potentially damaging donor site. For example, turf translocation to move arthropods from one site to another can require the extracting of tonnes of soil and as such may both damage donor sites and require specialised digging equipment (Morris *et al.*, 1994). For this reason, dispersal ability is likely to be a key limiting factor for many arthropods during grassland restoration (Woodcock *et al.*, 2010; Knop *et al.*, 2011; Konig and Krauss, 2019). Landscape structure, and in particular the proximity of source populations of specialist arthropods, has been suggested to play a significant role in the success of grassland restoration (Woodcock *et al.*, 2010; Knop *et al.*, 2011; Littlewood *et al.*, 2012). Other functional or behavioural characteristics of species (referred to hereafter as traits) may also affect establishment success and subsequent persistence, for example, traits affecting the ability of species to fly such as wing size polymorphisms (Knop *et al.*, 2011; Woodcock *et al.*, 2012b; Sydenham *et al.*, 2017; Konig and Krauss, 2019). Understanding species traits that predict establishment during restoration could play an important role in identifying new approaches to maximise restoration success, such as targeting site location to areas close to existing grasslands (e.g. for dispersal traits) or the need to alter management practices to benefit particular functional groups (e.g. cutting for herbivores) (van Klink *et al.*, 2019).

We investigated how complex, multi-trophic communities of arthropods, including detritivores, herbivores, pollinators and predators, respond to the process of grassland restoration. We focus on calcareous grasslands, a rare and speciose habitat in N.W. Europe (van Swaay, 2002). We quantified arthropod communities present on 52 ex-arable restoration sites in S. England, ranging in age from 1 to 30 years, as well as five pristine examples of species rich calcareous

grasslands in the same landscapes that act as reference communities with which to asses restoration success. In the context of this paper, restoration success is defined as the degree of similarity (as measured using the Jaccard's similarity index – see below) between the communities of restored sites and those of these target species rich grasslands. By studying arthropod assemblages we explored how environmental conditions, both within the restoration sites and surrounding them, affected species establishment. We predicted that: 1) The extent to which plant communities resembled target species rich grasslands would be positively correlated with arthropods species richness and the similarity of those arthropod communities to the same target grasslands; 2) The overall similarity of the arthropod communities to target species rich grasslands will be positively correlated with the proximity of these same restoration sites to these high quality sites; 3) Older restoration sites will have the highest levels of species richness as they have had longer time periods over which to accumulate colonising species.

2. Materials and methods

2.1. Study sites

In 2014, we established a chronosequence of 52 arable restoration sites on former arable fields located on calcareous soils in Southern England (Fig. 1). Sites were selected to maximise variation in age (1-30 years) as well as area (1.0 – 22.8 ha; Appendix Fig. A1). There was no systematic bias in site area with the age of the restoration site (years 1-10 - μ =8.7ha, SE ± 1.41; years 11-20 μ=8.04, SE ± 0.97; >20 years μ = 11.2, SE ± 2.50). The method of restoration differed between sites, ranging from natural regeneration, the use of simple grass dominated seed mixes, to reseeding using complex grass and forb seed mixes including the application of local provenance seeds within green hay. We focus on site age as opposed to establishment restoration method as our predictor in subsequent analyses. However, we directly test to see if restoration methods was a better predictor

than site age where this was found to be a significant predictor for the response variables in questions (see statistics section). While we do not directly look at the role of establishing management in the main analyses, we captured the outcomes of these practices in terms of the success with which the floral communities established. This was done by sampling five examples of high-quality species rich grasslands (34 -341 ha), located in the same geographical area of the surveyed sites, were monitored and provided a basis for assessing restoration success for both the plants and arthropods (Fig 1). These high quality National Nature Reserves grasslands were chosen through consultation with the regulatory body responsible for the delivery of grassland restoration schemes (Natural England) and represented examples of what they hoped grassland restoration could achieve. Preferentially sites of large area were chosen as targets to minimise edge effects that may have led to the historic loss of species over time (Tscharntke *et al.*, 2002). Appendix Table A1 provides details on a comparison between the target species rich grasslands and the restored grasslands in terms of management, plant community and arthropod species richness. In subsequent analyses (described below), we use these five pristine grasslands to create an idealised target to act as a reference for assessing restoration success. As such we are able to compare the similarity of individual target grasslands to this idealised overall community. The presence of low intensity sheep grazing (0.5-1.5 livestock unit per hectare) and the frequency of cutting management was recorded for each site. These represented long-term management practices that are consistent across years. No sites received artificial fertiliser.

2.2. Arthropod monitoring

It was not possible to identify all species found within the grasslands for reasons of both taxonomic intractability and resource limitations. A sub-set of taxa were chosen on the basis of their numerical abundance within grasslands, their trophic level with its association with key ecosystem processes (e.g. detritivore, herbivores, predators and pollinators as a special case of herbivory), as well as

145 dispersal ability and cultural significance (e.g. butterflies). Table 1 summarises these criteria used to
146 select arthropod groups for subsequent identification. The following groups were identified to
147 species: bees (Apoidea), ants (Formicidae), butterflies (including Zygaenidae moths), hoverflies
148 (Syrphidae), beetles (selected families of Carabidae, Coccinellidae, Staphylinnidae, Curculionidae,
149 Apionidae, Chrysomelidae and Elateridae), plant/leaf hoppers (Auchenorrhyncha), true bugs
150 (Heteroptera), spiders (Araneae), woodlice (Isopoda) and millipedes (Diplopoda). Bees and
151 hoverflies were identified while alive during transect walks, as such it was necessary to apply generic
152 level classifications were applied in some cases (e.g. *Neoascia spp*., *Cheilosia spp*., *Hylaeus spp*. and
153 *Lasioglossum spp*.). This taxonomic resolution still provides important trait information. Juveniles
154 were excluded from the analysis.

155 Arthropods were sampled using pollinator transects, pitfall traps and suction sampling. Each
156 technique was suited to different functional and taxonomic groups. Pollinator transects were used
157 to sample butterflies, bees and hoverflies. At each site a single 2 × 100 m fixed transect was
158 established and walked at a constant speed on three occasions from July to August 2014. On each
159 occasion transects were walked twice (i.e. two transect walks were undertaken on the same day). All
160 pollinator transects were performed between 10.00 and 16.00 hours when weather conditions met
161 standards laid out by Pollard and Yates (1993). Suction sampling collected sward active arthropods
162 using a Vortis suction sampler (Berkard Ltd, UK). Sampling occurred on two occasions at each site in
163 June and July 2014. Following Brook *et al.* (2008) each sample was composed of 55 separate suctions
164 (10 seconds) separated at 1 m intervals along a transect - equivalent to a total of 2.10 m^2 per site
165 combined over both sampling dates. Pitfall trapping was used to compliment the suction sampling
166 by collecting surface active taxa, including the ground beetles, woodlice, ants and millipedes. At each
167 site five pitfall traps (7 cm diameter) were set at 5 m intervals along a transect of 20 m in length.
168 Traps were filled with a 50% solution of ethylene glycol and unscented detergent and were left out
169 for a four-week period from June to mid-July 2014, with traps collected at two weekly intervals. A
170 single pitfall trap was lost from only one site due to animal activity.

171 All subsequent analysis were based on aggregated data across all three sampling methods
172 and collection dates. This produced a single abundance value for each species for each site. We use
173 the *Chao1* index to estimate species richness to account for differential sampling effort between the
174 different methods as well as to account for sample completeness. This method estimates species
175 richness from the asymptote of a species accumulation curves (Chao and Chun-Huo, 2016). Species
176 richness was calculated both overall and separately for each of the arthropod trophic groups of
177 detritivores, herbivores, predators and pollinators.

178

179 *2.3. Arthropods functional traits*

180 To provide broad information on the functional characteristics of individual species traits were
181 derived from a range of sources (e.g. Cowley *et al.*, 2001; Webb and Lott, 2006; Bommarco *et al.*,
182 2010; Woodcock *et al.*, 2012a; Woodcock *et al.*, 2012b). We classified all arthropods as: 1)
183 **Grassland specialist**: This habitat association trait was derived largely from autecological data (ISIS
184 database SAT codes F111, F112, F211: Webb and Lott, 2006); 2) **Low dispersal ability**: We focus here
185 only on those species that could be identified from published studies (Cowley *et al.*, 2001) and wing
186 development (Southwood and Leston, 1959; Waloff, 1973; Woodcock *et al.*, 2010) to have poor
187 dispersal ability. Note flightless species were generally considered to be poor dispersers, although
188 ballooning spiders were an exception. This low dispersal trait defines those species most likely to be
189 negatively affected by aspects of fragmentation or isolation (van Swaay, 2002; Woodcock *et al.*,
190 2010; Löffler *et al.*, 2020); 3) **Body mass**: this key trait has direct impact on a wide range of species
191 characteristics ranging from energetic requirements, reproductive potential and dispersal ability
192 (Konig and Krauss, 2019); 4) **Overall trophic level**: species were classified as detritivores, herbivores
193 (distinguishing between mono-, oligo- and polyphagous), predators and pollinators. Species could
194 belong to more than one trophic level, so that hoverflies could be pollinators (as adults) and
195 predatory (as larvae).

196

197 *2.4. Plant community sampling*

198 Ten 1 × 1 m quadrats were used to quantify percentage cover of all vascular plant species. All
199 vegetation assessments were undertaken in the same area as arthropod sampling. Plant surveys
200 were undertaken in June – July 2014, before any sward cut. An average measure of sward height was
201 derived to describe the structural condition of the sward at the time of arthropod sampling. This was
202 assessed using a drop disks, a circle of plywood (diameter 30 cm and 150 g) dropped down a
203 measuring ruler through a hole in its centre onto the vegetation (Stewart *et al.*, 2001). Drop disk
204 measurements were repeated at 20 locations separated by 1 m and recorded on three occasions
205 concurrent with arthropod sampling. An average measure of sward height was derived for each site.

206

207 *2.5. Community metrics of restoration success*

208 While species richness is widely used as an indicator of the success of conservation measures (e.g.
209 Krebs, 1999; Poyry *et al.*, 2009; Powney *et al.*, 2019), it fails to capture faunal similarity between
210 restoration and target communities (Woodcock *et al.*, 2010). This is an important aspect of
211 restoration where management is actively trying to replicate a particular habitat type and the
212 species it contains. To account for this, we calculated Jaccard's similarity between the 52 restored
213 sites and an averaged community taken across all five target high quality species-rich grasslands.
214 This similarity measure was derived at the level of the whole community only. Jaccard's similarity is
215 a binary similarity index that compares species presence and absence and scales between 0 (totally
216 dissimilar sharing no common species) and 1 (identical, sharing all the same species with no non-
217 common species). By averaging across the five target sites, we produced a single community that
218 included all arthropod species found within the target sites. This approach was used to account for
219 underlying site differences that may have affected community composition. Note, target high quality

species rich grasslands ranged in Jaccard's similarity to the overall target from 0.49 to 0.63 out of a maximum similarity score of 1. In comparison, restoration sites ranged in their similarity to this overall target from 0.06 to 0.47. Jaccard's similarity is defined as:

$$J = \frac{A}{A + B + C}$$

Where: *A*= number of species common to both the restoration site and overall target community; *B* = number of species found only in the restored site; *C* = number of species found only in the overall target community (Krebs, 1999). To provide a covariate in subsequent analyses Jaccard's similarity was derived in the same manner for the plant communities.

2.6. Landscape metrics

Quantification of landscape structure was undertaken using the 2015 UK Land Cover Map (LCM) at a resolution of 25 m pixels (Rowland *et al.*, 2017). We derived the proximity of species rich grassland surrounding each restoration site. This index represents the average of the area of species rich grassland patches surrounding a restoration site, divided by the square of the edge-to-edge distance between the two (McGarigal *et al.*, 2012). This proximity index increases as patches of species rich grassland surrounding the restoration site become increasingly close and contiguous. Proximity was limited to include only grassland patches within 1000 m of the study site and ranged for the grassland restoration sites from 0 to 5.54 (μ = 1.9, SE ± 0.19). We also defined historical change in the percentage cover of species rich grassland by comparing the 2015 land cover to that recorded in 1930 as part of the land utilisation survey of Great Britain (Stamp, 1931). This was used to quantify the potential impact of extinction debts that may have progressively reduced local species pools (Kuussaari *et al.*, 2009). This was defined for a 2 km radius around each study site.

243 *2.7. Statistical analysis*

244 We used generalised linear models to assess the response of arthropod similarity ($J'_{Arthropods}$) to the
245 target sites and arthropod *Chao1* species richness (overall, and separately for detritivores,
246 herbivores, pollinators and predators) to a range of explanatory environmental variables assessed
247 simultaneously using generalised linear models. Models included all eight fixed effects and pairwise
248 interaction terms of the following explanatory covariates: 1) site area (ln transformed); 2) site age
249 (years); 3) the similarity of the floral community to the target high quality grassland community
250 (J'_{Plants}); 4) local management effect of the number of sward cuts per year, vegetation height (ln
251 transformed) and the presence or absence of sheep grazing; 5) landscape metrics describing
252 Proximity to species rich grassland (ln transformed) and the change in percentage cover of species
253 rich grassland from 1930-2015. Log transformation of some covariates was used to normalise that
254 data. Response variables were not significantly intercorrelated (Appendix Table A2). For each
255 response variable a saturated generalised linear model was fitted with all eight fixed effects and
256 pairwise interaction terms. Stepwise deletion of least significant effect was used to sequentially
257 remove individual terms in the model until all remaining terms were significant at $\alpha = 0.05$.
258 Jaccard's similarity and the continuous *Chao1* measure of species richness were modelled using a
259 Gaussian distribution and identity link function. This analysis was restricted to the grassland
260 restoration sites only. Standard residual plots were used to check model assumptions including
261 variable independence (largest VIF < 3.0, Zuur *et al.*, 2010). Although we tested for the presence of
262 spatial autocorrelation using Morran's I in no case did we find evidence of this. A potential problem
263 with the data was that there have been historical trends in advice for how to restore grasslands. As
264 a result establishment management has changed to some extent over time, for example older sites
265 are often (but not exclusively) natural regeneration. Although we focus on site age as a core metric
266 of interest during the main analysis, where this was found to have a significant effect on the
267 response variable, we re-run these models substituting age with establishment management. These
268 two models are then compared using AIC values to determine whether establishment management

269 represented a better predictor of the response variable in question. All analysis were undertaken
270 within in R version 3.6.1 (Team, 2019).

271 A fourth-corner analyses were performed to assess how environmental factors acted to filter
272 species occurrence across all grasslands in response to their unique functional trait characteristics
273 (Legendre *et al.*, 1997). To achieve this the fourth-corner analysis links matrices of sites ×
274 environmental drivers (*R*), sites × arthropod species (*L*), and species × functional traits (*Q*). The site ×
275 species matrix was binary describing only species presence of absence. The analysis used the same
276 environmental variables as applied in the general linear models to filter all species traits. This
277 analysis allows for direct hypothesis testing, as it provides sequential tests of individual environment
278 – trait associations after combining the three *R*, *L* and *Q* matrices. A randomization approach (49999
279 permutations) was used to test the significance of each associations while correcting for type I errors
280 with the False Discovery Rate (FDR) procedure (Legendre *et al.*, 1997). The fourth-corner analysis
281 was undertaken in R version 3.6.1 (Team, 2019) using the package ade4 (Dray and Dufour, 2007).

282

283 **3. Results**

284 Overall 24,955 individuals (N) representing 363 species (SR) from 53 families of arthropods were
285 collected from the arable restoration (N = 20,475, SR = 347) and target grassland sites (N = 4480, SR
286 = 159). This included detritivores (N = 5,659, SR = 30), herbivores (N = 9,575, SR = 198), and
287 predators (N = 10,038, SR = 138), with many species occupying multiple feeding relationships, e.g.
288 omnivores. There were also 78 species of pollinators, split between the bees (N = 1,891, SR = 31),
289 hoverflies (N = 1,163, SR =22), butterflies and day flying moths (N = 2,389, SR = 25). For the
290 herbivores, monophagous (N = 1,367, SR = 19), oligophagous (N = 3,596, SR = 104) and polyphagous
291 species (N = 4,621, SR = 75) were found. There was considerable range in the success with which the
292 floral communities were restored, with J'_{Plants} ranging from 0.06 to 0.47. Site age was not correlated

293 with the similarity of the restoration sites to target grassland floral communities (J'_{Plants}; $F_{1,51} = 0.12$,
294 $p>0.05$).
295

296 *3.1. Overall arthropod community*

297 Overall arthropod species richness (*Chao1*) was positively correlated with J'_{Plants} ($F_{1,49} = 8.62$,
298 $p=0.001$, Fig 2a) and the percentage landscape loss of species rich grasslands from 1930 to 2015
299 ($F_{1,49} = 8.96$, $p < 0.001$, Fig. 3a). Note, in the case of this latter correlation this counterintuitively
300 means that species richness was lowest in those sites located in landscapes with the greatest historic
301 loss of species rich grassland. There were no other significant single or pairwise interaction effects
302 identified as predictors of overall arthropod species richness. Jaccard's arthropod similarity was
303 strongly positively correlated with J'_{Plants} ($F_{1,48} = 53.4$, $p < 0.001$, Fig 2b). Jaccard's similarity of the
304 arthropod communities was also positively correlated with both the percentage loss of species rich
305 grasslands from the surrounding landscape ($F_{1,48}= 6.53$, $p = 0.01$, Fig. 3b) as well as sward height ($F_{1,48}$
306 $= 16.5$, $p < 0.001$, Fig. 3c). No other single or pairwise interaction effects had a significant effect on
307 arthropod Jaccard's similarity.

308

309 *3.2. Detritivores*

310 Detritivore species richness (*Chao1*) was positively correlated with J'_{Plants} ($F_{1,48} = 4.56$, $p =$
311 0.04, Fig 2c). However, detritivore species richness was negatively correlated with both the age of
312 the restoration sites ($F_{1,48} = 4.53$, $p = 0.04$, Fig 2d) and the annual number of sward cuts ($F_{1,48} = 4.94$,
313 $p = 0.03$, Fig 2e). No other single or pairwise interaction effects had a significant effect on detritivore
314 species richness. As there was a tendency for establishment management to change over time this
315 analysis was repeated substituting site age for establishment management, defined as either natural
316 regeneration, sown with a grass only or sown with a floristically diverse seed mix. The original

317 model that included site age was a superior fit to the data based on AIC (GLM with age: AIC = 245.7;
318 GLM with establishment management: AIC = 255.0)

319

320 *3.3. Herbivores including pollinators.*

321 Overall herbivore species richness (*Chao1*) was positively correlated J'_{Plants}, but only as part
322 of an interaction with sheep grazing ($F_{1,47}$ = 10.3, p = 0.002). Where sites were grazed by sheep
323 there was an overall positive correlation with J'_{Plants} (Fig. 2d), however, where sites were not sheep
324 grazed the slope of this relationship did not differ significantly from zero (t_{47} = -0.67, p = 0.50).
325 Herbivore species richness was also positively correlated with the percentage loss in species rich
326 grasslands cover from the landscape ($F_{1,47}$ = 7.17, p = 0.01, Fig. 3f). No other single or pairwise
327 interaction effects had a significant effect on herbivore species richness.

328 Pollinators were considered separately as a special case of herbivory. Pollinator species
329 richness (Chao1) was affected by a significant interaction between sward height and the percentage
330 loss in species rich grasslands cover ($F_{1,48}$ = 15.3, p < 0.001). This suggested a complex pattern,
331 whereby pollinator species richness was highest both in areas of low sward height in landscapes with
332 little historic loss of species rich grassland, but also comparably high for tall swards situated in
333 landscapes where the loss of species rich grassland had been the greatest (Fig 4a). No other single
334 or pairwise interaction effects had a significant effect on pollinator species richness.

335

336 *3.5. Predators*

337 Predator species richness (*Chao1*) was found to show a significant correlations with the age
338 of the restoration, site area and the loss of species rich grassland from the landscape, but only as
339 part of pairwise interacting terms. The first of these was a significant interaction between site age

340 and area ($F_{1,46}$=2.43, p=0.02). This relationship suggested that the oldest restoration sites with the
341 largest area would support the highest predator species richness (Fig. 4b). The second significant
342 interaction was seen with the age of the restoration site and the landscape scale loss of species rich
343 grassland ($F_{1,46}$=12.7, p<0.001). This suggested that older sites would again support the highest
344 predator species richness, but only where those sites were located in landscape that had shown low
345 levels of historic loss of species rich grasslands (Fig. 4c). No other single or pairwise interaction
346 effects had a significant effect on predator species richness. As described above, we repeated this
347 analysis substituting site age for original establishment management. The original model with age
348 was a superior fit to the model using establishment method (GLM with age: AIC=395.1; GLM with
349 establishment management: AIC=416.6).

350

351 3.*6. Environmental filtering of species by their traits*

352 A forth corner analysis was used to assess how environmental factors acted to filter
353 arthropod species occurrence across all grasslands in response to their unique functional trait
354 characteristics. J'_{Plants} acted to positively filter for species traits of monophagous herbivory
355 (obs.=0.11, Std.obs.=5.49, adj-p<0.01), pollination (obs.=0.10, Std.obs.=3.38, adj-p<0.02), body mass
356 (obs.=0.07, Std.obs.=3.06, adj-p<0.02) and grassland specialism (obs.=0.12, Std.obs.=4.40, adj-
357 p<0.01) (Appendix Fig. A2 and Table A3). Increased J'_{Plants} negatively filtered against predatory
358 species traits (obs.=-0.10, Std.obs.=-4.73, adj-p<0.01). The age of the grassland acted to positively
359 filter for species traits associated with monophagous herbivory (obs.=0.07 Std.obs=3.38, adj-p<0.05),
360 grassland specialism (obs.=0.12, Std.obs.=4.29, adj-p<0.05) and body size (obs.=0.07, Std.obs.=3.65,
361 adj-p<0.05). The area of the restored sites also acted to positively filter for species traits associated
362 with grassland specialism (obs.=0.09, Std.obs.=3.05, adj-p<0.05) and body size (obs.=0.07,
363 Std.obs.=3.40, adj-p<0.05). Cutting frequency negatively filtered against monophagous herbivory
364 (obs.=-0.05, Std.obs.=-0.8, adj-p<0.03), pollination (obs.=-0.08, Std.obs.=-2.82, adj-p<0.03) and

grassland specialism (obs.=-0.78, Std.obs.=-2.76, adj-p<0.03). Neither sward height, sheep grazing, proximity to species rich grasslands or the historic loss of species rich grasslands from the landscape (1930-2015) were found to filter individual species traits (p>0.05; Table A3).

4. Discussion

In this this study we show that the restoration of grassland arthropod communities was highly dependent on the success with which restoration was able to replicate floral communities typical of target pristine grasslands (prediction 1). This was true for both overall species richness and the similarity of the arthropod community to those same grasslands. We found that the historic loss of species rich grassland from landscapes surrounding the restoration sites negatively impacted on arthropod restoration success. Both arthropod species richness and arthropod similarity to the target grasslands were greatest in those landscapes with the lowest historical declines in species rich grassland (prediction 2). The age of the restoration site was an important predictor of arthropod restoration success (prediction 3). However, its role in predicting restoration success was complicated, characterised by both negative correlations and complex interactions with sward height and the loss of species rich grasslands from the landscape. We discuss the evidence for why these effects may have occurred across a diverse range arthropod species.

4.1. The importance of replicating the floral communities for arthropods

The success with which the floral communities were replicated was the most important factor in predicting the success with which arthropod communities established, eliciting consistent correlations with overall arthropod similarity to the target grasslands, as well as with species richness across a range of trophic groups. The success with which the floral communities were replicated also acted to filter for pollination, body mass, monophagy and grassland specialism traits.

This suggested that successful restoration of the plant communities represents a minimum requirement for the arthropods. This was true in terms of not only the occurrence of host plants, but also potentially the availability of specific plant structures, such as seed heads or flowers, upon which individual trophic groups depend (van Swaay, 2002; Littlewood *et al.*, 2012). Indeed, the results strongly suggest that a minimum requirement for arthropod grassland restoration was to adequately establish suitable host plants, as well as provide plants that support important structural refuges such as tussock grasses. There was also an indirect indication that the floral composition of leaf litter may affect community structure of detritivores (Vos *et al.*, 2013). Management practices used to establish grassland communities over the last 30 years have evolved, moving from a greater (but not exclusive) reliance on natural regeneration to reseeding into soils chosen for their low fertility (Török *et al.*, 2011; Littlewood *et al.*, 2012; Czerwiński *et al.*, 2018). While we found no evidence that establishment management practices were a better predictor of restoration success than the age of the restoration site, this does not mean that such management is not an important determinant of floral community establishment (Crofts and Jefferson, 1999; Czerwiński *et al.*, 2018). Indeed the increased prevalence of modern evidence based strategies to enhance the establishment of plant species, including practices such as green hay spreading that introduce native provenance seeds (e.g. Czerwiński *et al.*, 2018), could dramatically improve the quality of grassland restoration for arthropods in the future (Littlewood *et al.*, 2012; Woodcock *et al.*, 2012b).

4.2.The role of sward management

Sward height was a simple measure of sward structure recorded at the time of arthropod sampling and directly affected by both cutting and grazing management (Stewart *et al.*, 2001). Sward height was found to be a positive predictor of arthropod restoration success in terms of the overall similarity to the target communities. For many arthropods, sward structure interacts with floral community composition to determine what species persist. For example, many phytophagous

414 insects require the presence of the correct host-plants together with the correct phenological
415 structure, such as flowers or seed head, for larval development (van Swaay, 2002; Woodcock *et al.*,
416 2012b). Similarly, for predatory taxa the structure of the sward is associated with the presence of
417 prey, key refuges and hunting locations (Littlewood *et al.*, 2012). Positive correlations between both
418 overall arthropod species richness and sward height emphasise the importance of managing sward
419 structure during grassland restoration.

420 While increased sward height at the time of sampling typically had a beneficial effect for the
421 arthropod communities, its destruction by frequent cutting had a negative effect. Cutting frequency
422 negatively filtered against a range of arthropod species traits, including monophagous herbivory,
423 pollination and grassland specialism, in addition it was negatively correlated with detritivore species
424 richness. This may reflects the catastrophic nature of cutting for most grassland arthropods,
425 particularly when compared to the more gradual process of grazing (Humbert *et al.*, 2009).
426 However, in the case of the detritivores the direct removal of cut hay may well have reduced the
427 availability of detrital vegetation on which they could feed (Vos *et al.*, 2013). It should be noted that
428 very frequent cutting (more than once a year) only occurs in very young restoration sites where it is
429 used to reduce the cover of competitively dominant plants (Crofts and Jefferson, 1999; van Swaay,
430 2002). While this is a sensible long-term management practice, it may be linked with short-term
431 negative effects on the arthropod communities (Humbert *et al.*, 2009).

432

433 *4.3. Site age and area*

434 The colonisation by arthropods into newly created habitats is normally considered to be
435 limited by the availability of source populations in the surrounding landscape interacting with an
436 individual species mobility (Woodcock *et al.*, 2010; Knop *et al.*, 2011; Sydenham *et al.*, 2017;
437 Breitenmoser *et al.*, 2020). Restoration success is therefore normally predicted to increase over

time, simply because it provides a greater window of opportunity for species to reach a newly created site (Grimbacher and Catterall, 2007). Indeed, previous research suggested that it takes 13 - 20 years for beetle and butterfly communities to maximise their similarity to target species rich grasslands during restoration (Woodcock *et al.*, 2012a; Woodcock *et al.*, 2012b). In agreement with these previous studies, grassland specialist arthropods and monophagous herbivores were both associated with older grasslands. This was also the case for species with larger body mass, although this linked principally to the occurrence of grassland specialist butterflies in older sites. The impact of site age on overall patterns in species richness was often more complex. In the case of predators the importance of site age for maximising species richness was conditional on other environmental factors. Here the oldest restoration sites supported the highest species richness, but only where those sites were large in area or located in landscapes characterised by the lowest historic loss of species rich grassland. In the case of the interaction between site age and area it may be that larger sites are more likely to maintaining minimum adequate populations allowing greater retention of colonising species over time (Krauss *et al.*, 2003; Littlewood *et al.*, 2012). Similarly, landscape that have lost little of their historic cover of species rich grassland may be more likely to have source populations available to colonise the sites, with the colonisation of accumulating disproportionately over time (Grimbacher and Catterall, 2007). However, with the exception of the predators, the importance of site age was lower than expected for most measures of species richness. In the case of detritivore species richness, site age even had a negative effect. It is possible that this may be due to the absence of a relationship between the success of floral restoration and the age of the restoration sites. If this is the case a colonisation event would only lead to species persistence where important within-site resources on which they depend had established (WallisDeVries and Ens, 2010; Littlewood *et al.*, 2012; Woodcock *et al.*, 2012b).

4.2. Landscape

Assuming minimum standards of site quality can be achieved during restoration, actively locating restoration sites in landscapes with high percentage cover of exiting species rich grassland has been proposed as method to facilitate arthropods colonisation (Snyder and Hendrix, 2008; Woodcock *et al.*, 2010; Knop *et al.*, 2011; Littlewood *et al.*, 2012). Such landscape scale targeting of restoration sites has appeal to both conservationists and policy makers as it may increasing the average success achieved with the same management effort and cost (Benayas *et al.*, 2009). In some respects, we found little evidence in support of this idea, as the proximity of patches of species rich grassland to the restoration sites was not correlated with any measure of arthropod restoration success. However, the historic loss of species rich grassland from 1930 to 2015 in the landscapes surrounding restoration sites did affect arthropod restoration success. These positive correlations point to poorer arthropod restoration success in landscapes characterised by the greatest historic loss of species rich grassland. This was seen for both overall similarity of the arthropods to the target species rich grasslands, as well as overall and herbivore species richness. This may be associated with reduced species pools in the local landscape following the loss of this high quality grassland. Such lost grassland would have previously supported species that may have otherwise colonised restoration sites (Kuussaari *et al.*, 2009; Woodcock *et al.*, 2010; Littlewood *et al.*, 2012; Löffler *et al.*, 2020). This is likely to have included many species typical of species rich grasslands, such as butterflies (Kuussaari *et al.*, 2009; Löffler *et al.*, 2020).

An unexpected finding was a complex relationship between pollinator species richness and the loss of species rich grassland as it interacted with sward height. Pollinator species richness was highest both in areas of low and high historic loss of species rich grassland, but only where the sward height was respectively either short or tall. This may suggest that species colonising from existing patches of species rich grasslands had a preference for the floral communities associated with short swards. It also seems that there is an equivalent pollinator assemblage associated with landscapes suffering large scale historic loss of species grasslands that showed a preference for taller swards.

There is some evidence for this dichotomy with specialist pollinator often being more sensitive to land use change than generalist ones (Redhead *et al.*, 2018; Powney *et al.*, 2019; Löffler *et al.*, 2020).

5. Conclusions

The restoration of species-rich grassland can play an important role in supporting local arthropod biodiversity (Lawton *et al.*, 2010; Habel *et al.*, 2019). This is one of a small number of studies supporting this evidence base by incorporating information across taxonomically diverse and multi-trophic arthropod communities. We identify that common environmental factors exist that can potentially be manipulated to control the outcomes of habitat restoration. In particular, the results emphasise the importance of successfully establishing floral communities typical of the target species rich grasslands as a necessary requisite to restore the arthropod species. Similarly, landscape context appears to play an important role, although in an unexpected way, with sites located in areas where there has been a high historic loss of species rich grassland being the least likely to fail. This may have important implications for agri-environmental policy as it may be more cost effective to target restoration into such landscapes. However, such an approach may have the undesirable effect of leaving some regions already denuded of biodiversity in a poor ecological state due to lack of improvement.

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Supporting Information

On acceptance of the manuscript species, trait and environmental data for the restoration and target grasslands become open access though the NERC Environmental Data Informatics Centre (doi.org/10.5285/78408af3-452f-41af-95f3-ffc13b05c232).

Appendix Fig. A1. Establishment dates for the 52 arable restoration sites.

Appendix Fig. A2. Fourth-corner plot.

Appendix Table A1. Summary comparison of differences between restored grasslands and target species rich grasslands.

Appendix Table A2. Pearson's correlation coefficients between covariates.

Appendix Table A3. Fourth-corner test statistics.

654 **Table 1**. Taxonomic groups identified to species within the 52 restoration and five species rich
655 grasslands used as a target for assessing restoration. These groups were chosen based on their
656 numerical dominance in grasslands, trophic level (including its relevance to the delivery of key
657 ecosystem processes), low dispersal ability and cultural significance. We consider pollination to be a
658 special case of herbivory due to its importance in the provision of this key ecosystem service. This
659 table focuses on species found within this study.

660

	Numerical dominance	**Key trophic role**	**Species with low dispersal ability**	**Cultural significance**
Bees	*Low*	*Pollination*	*None*	*High*
Ants	*Moderate*	*Predation*	*None*	*Low*
Butterflies	*Low*	*Pollination, Herbivory*	*Yes – e.g. some Lycaenidae.*	*High*
Hoverflies	*Low*	*Pollination, herbivory and predation.*	*None*	*Low*
Beetles	*High*	*Detritivores, herbivores and predators*	*Yes – including flightless species.*	*Low*
Plant/leaf hoppers	*High*	*Herbivores*	*None*	*Low*
True bugs	*Moderate*	*Herbivores and predators*	*None*	*Low*
Spiders	*High*	*Predators*	*Yes – including non-ballooning species*	*Low*
Woodlice	*Moderate*	*Detritivores*	*Yes - all flightless*	*Low*
Millipedes	*Low*	*Detritivores*	*Yes - all flightless*	*Low*

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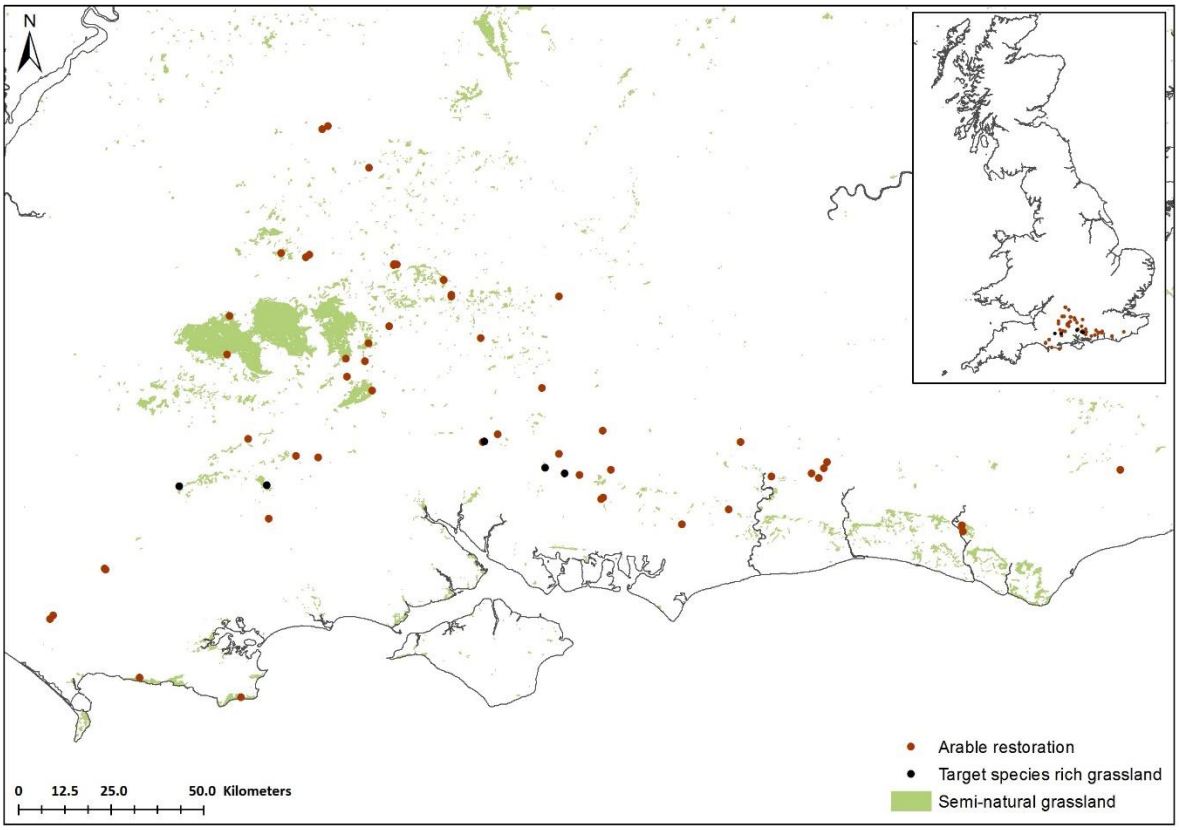
Figure captions

Fig. 1. Distribution of the 52 arable restoration sites (blue circles) and the five target species-rich grasslands located in National Nature Reserves (green circles).

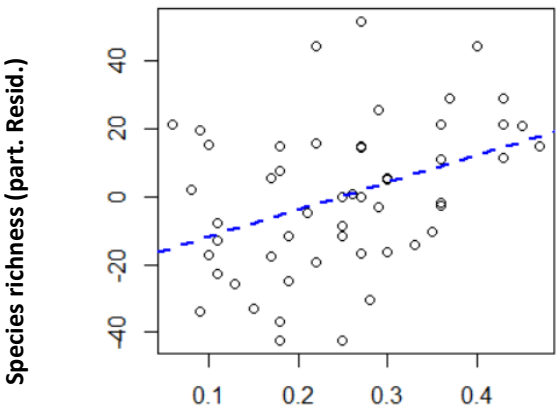
Fig. 2. Response of arthropod communities to the success with which the restoration sites replicated target floral communities typical of high quality species rich grasslands measured using Jaccard's similarity. All graphs represent partial residual plots (component + residual) to account for other significant independent covariates in GLM models explaining responses in either Jaccard's similarity of the arthropod communities to the target grasslands or measures of species richness as estimated with the Chao1index. We show only sheep grazed restoration sites (Fig 2c) as these were the only ones to show a significant correlation between herbivore species richness and floral similarity to the target.

Fig. 3. Response of arthropod community Jaccard's similarity to the target grasslands or measures of species richness (Chao1 index) to individual significant responses to either sward height, landscape scale loss of species rich grassland from 1930-2015 and annual number of sward cuts. All graphs represent partial residual plots (component + residual) to account for other significant independent covariates in GLM models. Note, as cutting management may occur less than annually it is expressed in these cases as a fraction, e.g. biennial cutting has an annual frequency of 0.5.

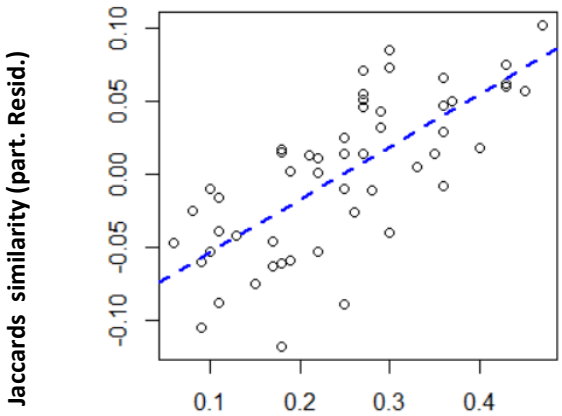
Fig. 4. Response of arthropod species richness (Chao1 index) to significant interaction with either the number of years the restoration site has been in existence (Age), the area of the restoration site (Ha), or the landscape scale loss of species rich grassland from 1930-2015. All graphs present predicted model values to show the pattern of the trend between the interactions.


N
0 12.5 25.0 50.0 Kilometers
Arable restoration
Target species rich grassland
Semi-natural grassland

a) Overall arthropod species richness

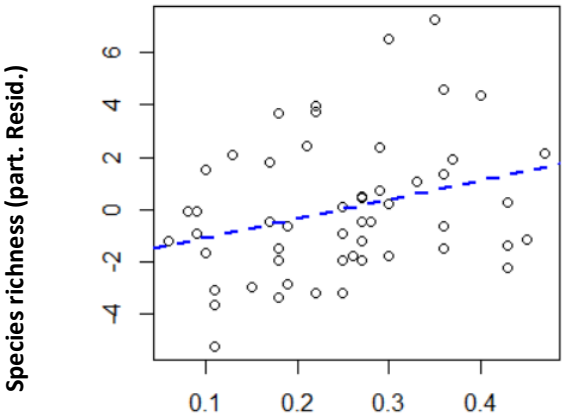


b) Overall arthropod similarity to target

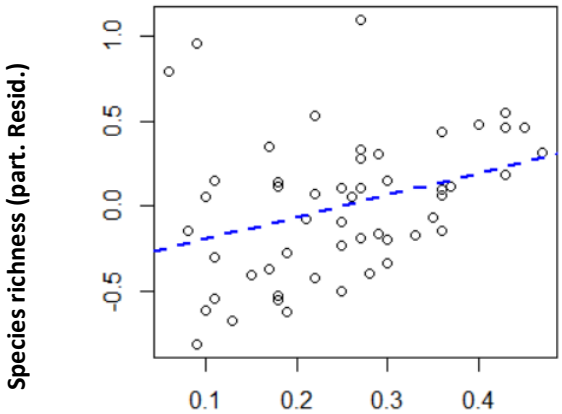


Floral similarity to target grassland (Jaccards index)

c) Detritivore species richness (Chao1)

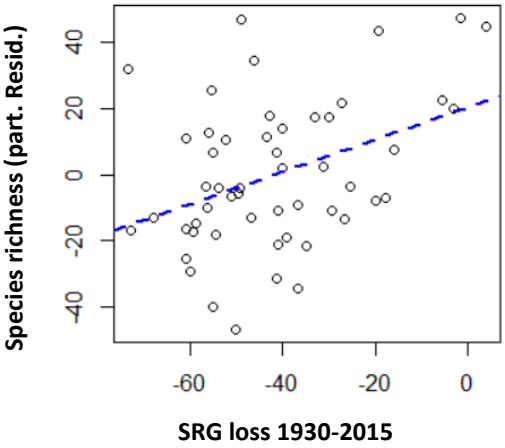


Herbivore species richness (Chao1)

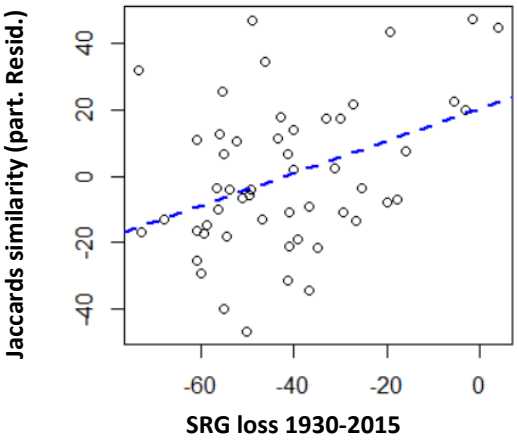


Floral similarity to target grassland (Jaccards index)

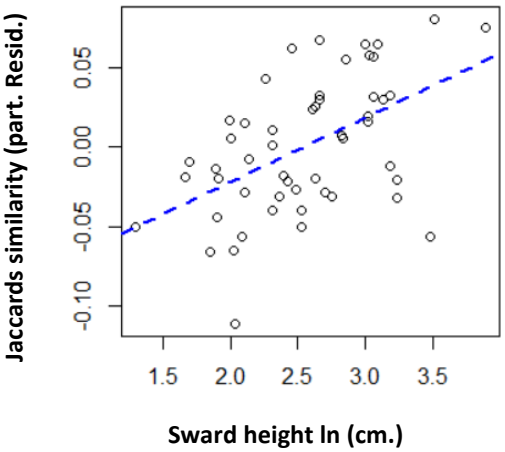
a) Overall species richness (Chao1)



b) Overall arthropod similarity to target



c) Overall arthropod similarity to target



d) Detritivore species richness (Chao1)

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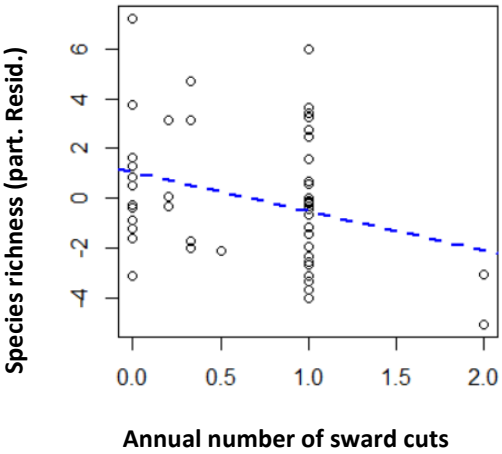
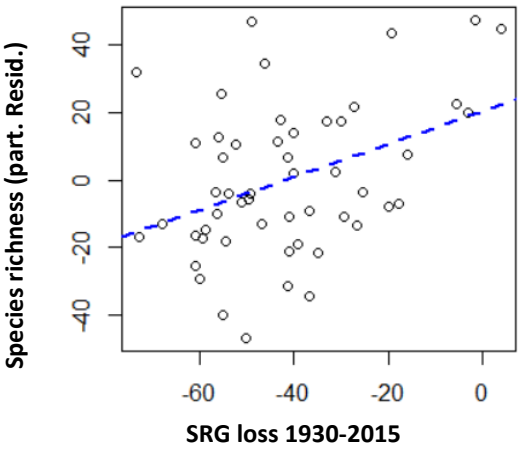
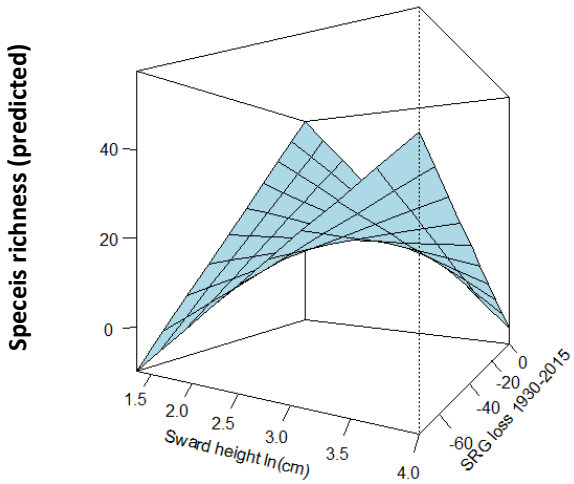


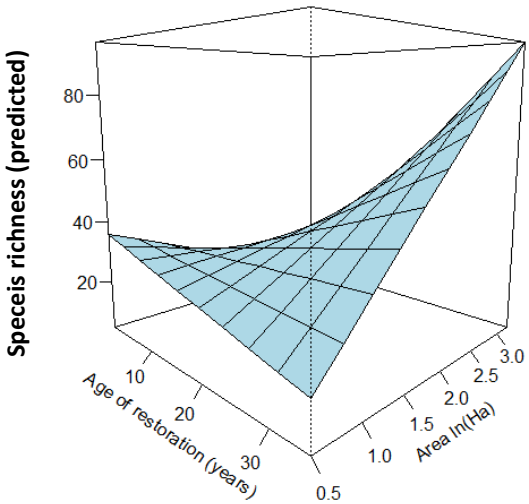
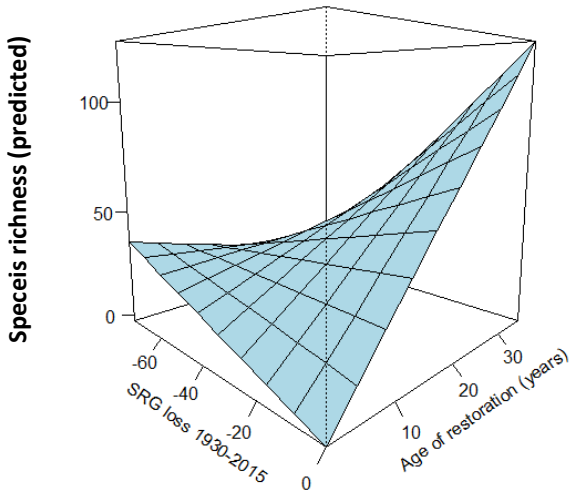
d) Herbivore species richness (Chao1)



a) Pollinator species richness (Chao1)



b) Predator species richness (Chao1)



c) Predator species richness (Chao1)