

Article (refereed) - postprint

Kimberley, Adam; Bullock, James M.; Cousins, Sara A.O.. 2019. **Unbalanced species losses and gains lead to non-linear trajectories as grasslands become forests.** *Journal of Vegetation Science*, 30 (6). 1089-1098.
<https://doi.org/10.1111/jvs.12812>

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1 Unbalanced species losses and gains lead to non-linear
2 trajectories as grasslands become forests

3 Running title: Community change in abandoned grasslands

4

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10 Funding information:

11 This work was funded by the Swedish Research Council (VR) to SAOC (Project code:

12 E0526301) and via CEH National Capability funding (project NEC06895) to JB

13 **Abstract**

14 **Questions**

15 Rates of plant community shifts after environmental changes depend on how quickly affected
16 species are gained and lost. Understanding how the balance between extinction and colonisation
17 varies over time, and how it is influenced by local and landscape factors, is essential to
18 understanding overall change trajectories. Investigating change requires data at several time-
19 steps over sufficient periods, and the paucity of such data represents an important knowledge
20 gap. We ask: 1. how variation over time in the rates of species' extinction and species'
21 colonization controls the trajectory of biodiversity change in abandoned semi-natural grasslands?
22 and 2. can landscape composition and habitat history modify change trajectories by acting
23 independently on groups within plant communities?

24 **Location**

25 Sweden, Stockholm Archipelago.

26

27 **Methods**

28 We use data on plant composition, management history and landscape context in former
29 grasslands, abandoned at different points since 1901, in a space-for-time analysis, comparing
30 rates of grassland species loss and forest species establishment and investigating resulting
31 biodiversity trajectories.

32 **Results**

33 Grassland species declined steeply in recently abandoned habitats before levelling off, while the
34 accumulation of forest species was linear, with no plateau reached even at the longest time since
35 abandonment. Hence, we observed a trough in biodiversity, with an initial decline in overall

36 species richness followed by a partial recovery. Only forest species gain was enhanced by nearby
37 habitat availability.

38 **Conclusions**

39 Information on community compositional changes over short time periods may be misleading
40 about the extent and even direction of ongoing biodiversity gains and losses. Moreover, the non-
41 linear changes observed suggest thresholds in time, after which succession to the forest
42 community accelerates and the ability to manage a return to the grassland community
43 diminishes. Accounting for the combined influence of landscape composition and history is key
44 to fully understanding community shifts over time.

45 **Keywords:** Biodiversity, Colonization, Extinction, Grassland abandonment, Succession, Land
46 use change, Time lag, Vegetation dynamics.

47 **Introduction**

48 Ongoing global land use changes are causing loss, fragmentation and degradation in quality of
49 many natural and semi-natural habitats (Foley et al. 2005). Such changes are generally expected
50 to result in significant biodiversity losses, as local conditions become unsuitable for many
51 species and important meta-population dynamics are disrupted (Newbold et al. 2015). Specialist
52 species, frequently limited to undisturbed or extensively managed habitats, are particularly
53 vulnerable due to the narrow range of conditions they can tolerate and their poor ability to rescue
54 threatened populations via dispersal (Ewers & Didham 2006; Lindborg et al. 2012). Despite this,
55 observed temporal trends in local biodiversity are often inconsistent, and heavily dependent on
56 the type of environmental change that occurs (Vellend et al. 2013; Vellend et al. 2017).

57 Long lived plants or those that regenerate clonally or via the soil seed bank are capable of
58 persisting as remnant populations following unfavourable change, even where their future local
59 extinction is likely (Eriksson 1996; Vellend et al. 2006; Plue & Cousins 2013). Similarly, poorly-
60 dispersing species take time to colonize new habitat, particularly where it is isolated from source
61 populations (Brunet 2007; Kimberley et al. 2014). The timescales over which species richness
62 change are therefore dependent on the relative magnitudes of these co-occurring “extinction
63 debts” and “colonization credits”, and the rates at which they are settled (Jackson & Sax 2010).
64 Where delayed colonisations and extinctions equilibrate over different periods, transient
65 “biodiversity deficits” or “biodiversity surpluses” (*sensu* Jackson and Sax, 2010) may develop,
66 leading to short term troughs or peaks in overall diversity. Furthermore, plant community
67 compositional change can become decoupled from changes in biodiversity, with changes in
68 species composition occurring more quickly than changes in absolute species richness
69 (Hillebrand et al. 2018). The full implications for species diversity are unlikely to become
70 apparent until after all delayed extinctions and colonisations are realised.

71 Despite the theory detailed above, knowledge of community change at long-term but fine-
72 grained temporal scales remains limited. In particular, differing trajectories followed by
73 concurrently declining and increasing species after human induced change have rarely been
74 examined in depth (McGill et al. 2015; Halley et al. 2017). Studies of trends in species diversity
75 are often over relatively short timescales, hindered by a lack of temporal resolution in data, or
76 generally focus upon a single set of declining or colonizing species, often within one particular
77 habitat type (e.g. Saar et al. 2012; Naaf & Kolk 2015; Lehtilä et al. 2016, Vellend et al, 2017, but
78 see e.g. Van Calster et al. 2008). Rates and even directions of compositional change can be
79 modified by aspects of habitat history and landscape configuration (Vellend 2003; Perring et al.

80 2018). Hence, long-term empirical data examining trends underlying general biodiversity
81 patterns, ideally across broad spatial scales, are essential to fully understand and predict plant
82 community changes following environmental change (Hillebrand et al. 2018).

83 In semi-natural grasslands the removal of regular, non-intensive disturbance with the
84 abandonment of traditional management methods results in substantial changes in plant
85 communities. Frequently succession to forest occurs, along with a shift towards species able to
86 compete for light or tolerate shade, and away from those adapted to disturbance (Poschlod et al.
87 2005; Vandewalle et al. 2014; Neuenkamp et al. 2016). Together with pressures of agricultural
88 intensification and habitat loss within the wider landscape, management abandonment has
89 contributed to a loss of vulnerable species across multiple taxa (Öckinger et al. 2006; Uchida &
90 Ushimaru 2014). Although this has negative consequences for some aspects of biodiversity,
91 succession on former semi-natural grasslands or former agricultural land might provide habitat
92 for species suited to deciduous forest, many of which are also threatened by habitat loss and
93 fragmentation in intensively managed landscapes (Kimberley et al. 2014; McCune & Vellend
94 2015).

95 There is some evidence that forest species accumulation occurs more quickly than grassland
96 specialist loss, leading to an increase in biodiversity, potentially preceding a later decline as the
97 extinction debts of grassland species are settled (Bagaria et al. 2015). However, the extent to
98 which this process applies generally and how it might be influenced by different local and
99 landscape scale factors is unclear. Although some plants are able to remain for some time
100 following grassland fragmentation or abandonment (Lindborg and Eriksson 2004, Vandewalle et
101 al. 2014), substantial grassland specialist extinctions have been detected over periods of less than
102 30 years (Pykälä et al. 2005; Deák et al. 2016; Neuenkamp et al. 2016). While the presence of

103 nearby intact grasslands may help slow population declines of grassland species (Evju et al.
104 2015; Hooftman et al. 2015), this may only be the case in very recently abandoned areas, where
105 light availability remains high enough for grassland species establishment (Bagaria et al. 2015;
106 Lindgren et al. 2018). Conversely, poorly-dispersing forest specialist species are slow to colonize
107 new habitat, particularly where it is isolated from source populations (De Frenne et al. 2011;
108 Brunet et al. 2011; Brunet et al. 2012; Naaf & Kolk 2015; Kimberley et al. 2016). Hence, in such
109 cases grassland species extinction would be expected to occur at a faster rate than forest species
110 colonization, although this difference may be less clear in areas with higher amounts of nearby
111 forest habitat. Trajectories of community compositional change are therefore likely to be
112 dependent on the balance between the suitability of both local environment and landscape
113 composition for winning and losing species, emphasizing the need to understand better the
114 factors that control the presence and magnitude of temporal lags (Hylander & Ehrlén 2013).

115 Here, we investigate temporal trends in species richness during forest succession on abandoned
116 semi-natural grasslands. Using land-cover information from several time points, in combination
117 with detailed plant survey data, we create a space-for-time analysis capturing the progression of
118 plant communities across multiple stages of succession over a period greater than 100 years.
119 From this we aim to assess how rates of forest species gain and grassland species loss differ, and
120 the extent to which present day and historical surrounding landscape influence the extinction and
121 colonization of species with differing habitat preferences, thus providing an insight into
122 biodiversity change in typical rural landscapes.

123 **Methods**

124 **Study area**

125 The study area comprises a 4323-hectare region on four islands within the Stockholm
126 archipelago, located in the Baltic Sea northeast of Stockholm, Sweden, within the boreo-nemoral
127 zone. The area has been subject to human activity for many hundreds of years, comprising
128 farming, low intensity grassland management and wood production. Mowing and grazing
129 practices were almost entirely abandoned in the mid-20th century, leading to a decline in the
130 areas of meadow (traditionally mown grasslands, often on wetter land) and outfield (marginal
131 land used for livestock grazing around houses and crop fields). Consequently, forest habitat now
132 dominates (mostly coniferous but with some deciduous or mixed areas, particularly on former
133 meadows or grazed outfield), along with arable land and built-up areas. Hence, the area
134 represents a typical modern agricultural/forest landscape, where the traditionally heterogeneous
135 landscape has become more homogeneous following land use change.

136 **Landscape data**

137 We used economic maps from 1901 (“*Häradsekonomiska kartan*”), in combination with black
138 and white aerial ortho-rectified photographs dating from 1942 to identify areas of past grassland
139 habitat. The economic maps contain information on major land use (the locations of open water,
140 arable fields, meadows and outfield land (Swedish “*Utmark*”; a combined class representing
141 forest and grazed non-arable land)), in addition to major settlements and roads. Land that was
142 categorised as meadow in 1901 was manually digitized and classified as meadow grassland.
143 Land mapped as “outfield” in 1901 and where no trees were present in the 1942 aerial
144 photographs was also digitized and classified as grazed grassland. Non-arable areas that were
145 open in 1942 are highly likely to have been subject to grazing activity in 1901. These digitized
146 grasslands were used as potential plant survey sampling sites (.

147 A series of subsequent aerial photographs was used to determine the point at which former
148 grasslands became encroached by forest (i.e. an unbroken canopy was present over the whole
149 area). This series included the 1942 images, in addition to others from 1960, 1995 (also black
150 and white), 2008 and 2015 (colour infra-red). To ensure consistency of data collection the point
151 of forest encroachment was assumed to have occurred midway between the latest date an open
152 area was observed and the earliest showing a closed canopy. This time point was subsequently
153 used in all analyses as an estimate of the age of wooded habitat on former managed grassland
154 areas.

155 We used several spatial variables to investigate the influence of the surrounding landscape on
156 plant species composition. The presence of nearby open habitat enables grassland species to
157 rescue threatened populations through dispersal (Eriksson 1996; Evju et al. 2015), while
158 proximity to a dispersal source is important for colonization of new habitat areas by forest
159 specialists (Vellend 2003; Brunet 2007; Paal et al. 2017). Hence, we extracted the amount of
160 both present day open and forest habitat within a 200 m radius of sampling plots from a
161 manually digitized layer, created by classifying land as open, forest or built-up based on the 2015
162 aerial photographs. Since many grassland species display a stronger association with past
163 landscape configuration than from the present day (Lindborg & Eriksson 2004; Otsu et al. 2017),
164 the amount of open and forest habitat present in 1901 was also estimated for the same areas, by
165 summing the meadow and grazed grassland areas identified from the historical maps
166 (Supplementary material Appendix S1).

167 **Plant species data**

168 In July and August 2016, all plant species were inventoried in 130 plots of 5 x 5 m. These were
169 placed randomly within a random selection of grasslands as classified in 1901. Exact numbers in

170 each category varied according to their frequency in the landscape (open in 2016 = 31,
171 abandoned 2008-2016 = 2, abandoned 1995-2008 = 13, abandoned 1960-1995 = 34, abandoned
172 1945-1960 = 33, abandoned 1901-1945 = 17). Seventy-six of these plots were located in former
173 meadow habitat and fifty-four in former grazed outfield locations.

174 **Statistical analyses**

175 We tested for nested patterns within plant communities across sampling sites. Nestedness
176 analyses allow for the identification of consistent shifts in both species richness and composition
177 across communities. They are therefore an effective tool for observing ordered extinction and
178 colonization events (Ulrich et al. 2009; Sasaki et al. 2012). The degree of nestedness was
179 investigated using the NODF (nestedness based on overlap and decreasing fill) metric (Almeida-
180 Neto et al. 2008). NODF uses the extent to which row and column sums decrease from left to
181 right and top to bottom across a maximally packed community presence-absence matrix (i.e.
182 sorted by species frequency of occurrence and plot species richness), with perfect nestedness
183 occurring where all species found in less species-rich sites are also present in all more species
184 rich communities (Sasaki et al. 2012).

185 Here, three separate analyses were performed. The first included the full plant occurrence
186 dataset, to investigate trends in overall species richness. Additionally, two subsets of the full
187 dataset were created, based on species' preferences for either deciduous forest (species found
188 mainly in closed forest and species found in forest openings or edges) or open land (occurring
189 mainly or solely in open habitats) according to Heinken *et al.* (2019). These were considered
190 forest and grassland specialist communities respectively. Generalist species, capable of surviving
191 in both forest and open habitats and therefore equally likely to exist across former grasslands of
192 all ages, were excluded from both forest and grassland species datasets to prevent noise

193 dampening the signal observed in more specialized species (see Supplementary material
194 Appendix S2 for species categorizations).

195 Nestedness was determined by testing for a significant difference between the observed NODF
196 value and the mean NODF of 999 simulated random communities using the function *oecosimu* in
197 the R package *vegan* (Almeida-Neto *et al.* 2008, Oksanen *et al.* 2017). The default “r00” method
198 was applied, with a one-tailed significance test (with the null hypothesis that the nestedness
199 statistic of the overall community was not greater than the average randomly simulated
200 community). The plot ranks of individual sampling plots (overall community plot rank order,
201 grassland community plot rank order and forest community plot rank order) were then used as
202 response variables in subsequent statistical models. These ranks, ranging from 1 to 130, are
203 derived from the position of each plot in the maximally packed nested matrix. Plant communities
204 in plots of higher absolute rank value are considered nested subsets of the communities in plots
205 with lower absolute rank value. Hence, we were able to explicitly establish whether the response
206 variable used represents ordered extinctions/colonizations over time as forests age and extinction
207 debts and colonization credits created by forest encroachment are gradually settled, rather than a
208 temporal turnover of distinct communities. Raw rankings generated were reversed to provide a
209 more intuitive variable, whereby a low value represents a small number of species present within
210 a plot and a high value represents a large number of species present.

211 Subsequent models were fit using the *gamm* function in the package *mgcv* in R (Wood, 2006).
212 Generalized additive mixed models (GAMMs) use penalized regression splines to model smooth
213 terms where the exact shape of the relationship between predictor and response is not known *a*
214 *priori*. Time since forest encroachment was included as a smooth term, to allow potential non-
215 linear effects of time since change to be identified. The maximum degrees of freedom for the

216 smooth term was limited to six, due to the number of unique values obtainable from the aerial
217 photographs. The significance of the smooth term in the GAMM indicates the importance of
218 time since grassland abandonment in determining the nested plot rank, while the estimated
219 degrees of freedom indicates the shape of the relationship between time since change and
220 community composition (Wood, 2011).

221 Three GAMMs were fit using the three plot rank orders (overall and for forest specialists and
222 grassland species) as response variables. All models included time since grassland abandonment,
223 habitat class in 1901 (meadow or outfield) and amount of surrounding open habitat in 1901 as
224 explanatory variables (surrounding forest habitat in 1901 was too closely correlated with
225 surrounding forest in 2015 to be included). The model of forest species plot rank also contained
226 the area of surrounding forest habitat in 2015 as an additional predictor, while the model for
227 grassland species contained the surrounding open land area in 2015. These two landscape
228 variables were non-independent (land occupied by forest cannot also be occupied by open
229 habitats) and therefore they were not included within the same model. For the overall species
230 richness model, since it was hypothesized *a priori* that the amount of surrounding suitable
231 habitat would have a stronger effect on forest species colonization than grassland species
232 extinction, the amount of forest habitat was used. It should be noted however that higher levels
233 of forest habitat also mean lower levels of open habitat when interpreting these results. To
234 account for possible spatial autocorrelation occurring where multiple sampling points occurred
235 within the same former grassland patch, 1901 grassland patch identity was included as a random
236 intercept.

237 **Results**

238 Overall, forest and grassland communities all showed significant nested patterns (Table 1).

239 Communities within the least species rich sites (overall and in terms of both forest and grassland
240 species) can therefore be considered more nested subsets of the species present in more species
241 rich areas than would be expected under a random distribution.

242 In all models, the plot rank order of communities within the nested matrix was significantly
243 related to time since forest encroachment (Table 2, Figure 1). As expected, the number of forest
244 specialists within sampling plots increased with time since grassland abandonment. The increase
245 was modelled with an estimated degree of freedom of one in the GAMM, suggesting a linear
246 relationship over the age gradient (Figure 1b). There was no evidence of levelling off, even in the
247 oldest woodland habitats. Conversely, the relationship between grassland species and time since
248 woody encroachment was non-linear (Figure 1c, Table 2). A large reduction in grassland species
249 plot rank was observed with increasing time since abandonment. However, the steepness of the
250 decline reduced and then leveled off in former grasslands that had been abandoned for more than
251 20 years. Overall plot rank order followed a concave relationship, falling initially with increasing
252 age while increasing gradually again in the oldest plots, although the plot ranks of the oldest
253 abandoned grasslands were still lower than those that remained open.

254 Former meadow habitats differed in overall plot rank from former grazed outfields, with former
255 outfields significantly more species rich. The lack of a similar effect of grassland management
256 history on either forest or grassland communities suggests that this is related to the number of
257 generalist species able to colonize these sites. Meadows are often sited on moister, more
258 productive land, potentially providing environmental conditions suited to a narrower range of
259 species.

260 A larger area of forest surrounding a vegetation plot in 2015 had a positive effect on forest plot
261 rank, indicating that forest specialist species accumulated faster where there was more forest
262 habitat nearby. Surrounding forest area also had a significant positive effect on overall plot rank.
263 Conversely, the amount of open habitat in 2015 had no effect on the number of grassland species
264 present in sampled plots. The amount of surrounding grassland in 1901 also had no significant
265 effect in any of the models tested.

266 **Discussion**

267 Our results show that rates of species' extinction and colonisation vary both separately and over
268 time within habitats following land use change, with important consequences for how shifts in
269 community composition progress. Such differences in rates of species turnover for different
270 species groups have previously been predicted, however they have seldom been observed due to
271 difficulties in obtaining local scale data at sufficient temporal resolution (Jackson & Sax 2010;
272 McGill et al. 2015). Here, using a detailed space-for-time substitution in recently abandoned
273 grasslands, we show that substantial early losses of grassland species are not initially offset by a
274 corresponding increase in forest species. Over time however, the rate of grassland species loss
275 slows, with a continuing gradual increase in forest specialists contributing to a partial recovery in
276 overall biodiversity at later successional stages. Since forest specialist colonization credits still
277 appeared to remain, species richness might be expected to continue to increase for some time
278 (Naaf & Kolk 2015). Hence, grassland abandonment and slow forest succession has possibly led
279 here to a short-term trough in biodiversity, likely to diminish (to some degree) once future
280 colonisations are complete. Eventually, a relatively modest impact on total species numbers may
281 be observed at the local scale once communities have equilibrated, despite a substantial shift in
282 community composition (Hillebrand et al. 2018). This suggests the presence of a point following

283 grassland abandonment, before which community shifts are dominated by the initial loss of open
284 species, and after which ongoing change becomes dominated by forest specialist colonisation.
285 Once this point has been crossed, the lack of remnant populations means that any attempt to
286 restore the grassland community will rely largely on colonisation from other sites, or from the
287 soil seed bank.

288 The non-linear changes seen here suggest that long-term trends may differ substantially from
289 short-term patterns observed between any two intermediate points (Ewers et al. 2013). Hence, it
290 is likely to be difficult to understand and predict eventual biodiversity change from changes
291 which have occurred over a short period. Similarly, trends in abandoned grasslands which are at
292 different stages of succession may appear inconsistent unless their varying history is properly
293 accounted for. Understanding the factors that control the balance between co-occurring
294 extinction and colonization is therefore vital in predicting future shifts in biodiversity and
295 community composition within changing landscapes. In particular, if colonisation and/or
296 extinction are affected by landscape habitat configuration, this may mean processes such as
297 habitat fragmentation or loss of dispersal vectors can fundamentally change successional
298 trajectories (Bullock et al. 2002). Although the amount of nearby forest habitat had a positive
299 effect on forest species colonization, we saw no effect of open habitat amount (past or present)
300 on grassland specialists. This is contrary to other studies, which have found relationships
301 between historical landscape composition and present day grassland species occurrence (Helm et
302 al. 2006; Auffret et al. 2018). The difference is likely due to the relative lack of remaining semi-
303 natural grassland within the study area. The likelihood of threatened species being rescued by
304 immigration from neighbouring populations declines with increasing isolation and decreasing
305 habitat amount (Evju et al. 2015; Hooftman et al. 2015), and grassland species are often heavily

306 reliant on grazing livestock to disperse seeds (Plue & Cousins 2018). Hence the complete loss of
307 landscape-scale grazing and grassland management in the study area used here is likely to have
308 drastically reduced species' resilience to changes in habitat availability (Kuussaari et al. 2009;
309 Eriksson & Cousins 2014; Neuenkamp et al. 2016). This may have contributed to a more rapid
310 loss of vulnerable species and a relatively brief period before extinction debts were fully paid.

311 Semi-natural grasslands are a key biodiversity refuge within European landscapes. Their long
312 continuity of low-intensity mowing or livestock grazing, without significant application of
313 artificial fertilizers, means that they act as a habitat for many rare and specialised plant species
314 (Wilson et al. 2012; Eriksson & Cousins 2014). The loss of grassland species observed here is
315 therefore of conservation concern. Grassland specialists initially declined steeply, suggesting that
316 local management abandonment leads to a relatively fast rate of extinction (Kahmen & Poschlod
317 2004; Öckinger et al. 2006; Uchida & Ushimaru 2014; Neuenkamp et al. 2016). This is in
318 contrast to grasslands that are still regularly grazed or mown but which have been subjected to
319 similar landscape fragmentation, where extinction debts lasting up to 100 years have been
320 identified (Krauss et al. 2010; Cousins & Vanhoenacker 2011), although this may depend on the
321 magnitude and rate of fragmentation, since other studies have found no evidence of extinction
322 debts (Adriaens et al. 2006). However, despite general declines overall, abandoned grasslands
323 (especially those wooded for 20 years or less) retained a proportion of the grassland specialist
324 species found in open areas, with a number of species persisting even in forest habitat older than
325 60 years.

326 One explanation for the inferred delayed loss of grassland species is the continued presence of
327 remnant populations of persistent plants that are doomed to eventual local extinction in areas that
328 have recently become unsuitable (Eriksson 1996; Jonason et al. 2014). Plants forming remnant

329 populations in abandoned semi-natural grasslands tend to be long lived and capable of clonal
330 reproduction, rather than able to tolerate increased shading and competition from woody species
331 (Johansson et al. 2011). The response of grassland species to afforestation is complex however,
332 and depends on the rate of successional change and on the degree of specialization of affected
333 species (Lehtilä *et al.* 2016). In some cases persistence in abandoned grasslands might also be
334 related to a greater ability to tolerate the changed environment (Kahmen & Poschlod 2004;
335 Falster et al. 2017). A gradual change across a successional gradient might result in slow
336 (apparently delayed) changes in plant species composition, yet species might be lost rapidly if
337 and when individual environmental thresholds are crossed. The reverse may be true for the slow
338 colonization of forest specialist species. Those that are more able to tolerate an early
339 successional environment or take advantage of modified abiotic conditions may arrive more
340 quickly, with stricter specialists arriving at a later date (Baeten et al. 2010). Both persistence and
341 greater environmental tolerance are likely to result in an eventual shift in community
342 composition, but the mechanisms responsible for the continued existence of remnant populations
343 and apparent extinction debts and colonization credits may vary (Hylander & Ehrlén 2013). In
344 fact, the environmental limitations constraining species establishment can vary even at a species
345 level over relatively short timescales (Baeten & Verheyen 2017).

346 Space-for-time analyses must be interpreted carefully, to avoid the possibility of wrongly
347 attributing observed patterns to temporal factors rather than other, underlying environmental
348 differences (Johnson & Miyanishi, 2008). However such comparisons are highly valuable tools
349 in investigating long term trends where genuine time series data is difficult or impossible to
350 obtain. Chronosequences are particularly applicable where, as here, the analysis addresses highly
351 comparable sites (in terms of history, climate and environment) which are converging over time,

352 using multiple aspects of community composition and with data from several intermediate time
353 steps (Walker et al. 2010). Time since forest encroachment was used as a proxy for time since
354 grassland abandonment, but this is likely an underestimate due to the lag before canopy cover
355 fully develops (Hudjetz et al. 2014). The exact periods over which changes are occurring may
356 therefore be somewhat longer. Additionally, even remaining open land may have previously lost
357 species due to reductions in habitat at the landscape scale (Hooftman et al. 2015). Comparison
358 with the state of grasslands prior to these losses likely would have revealed an additional step of
359 species decline.

360 The rate of grassland species loss following management abandonment highlights the importance
361 of continued management to maintain grassland species diversity, and suggests that longer
362 abandoned grasslands are likely to be less viable as targets for grassland restoration efforts
363 (Öckinger et al. 2006; Waldén & Lindborg 2016; Otsu et al. 2017; Waldén et al. 2017).

364 Similarly, since forest species accumulation continued in former grasslands that had been
365 wooded for over 60 years, offsetting the loss of older forest areas with newly created or restored
366 habitat is likely to take a long time to pay off. This is likely to be particularly true where forest
367 habitat is less abundant within the landscape, meaning unoccupied newly created areas are
368 isolated from potential source populations (Brunet et al. 2011; Naaf & Kolk 2015). Maintaining
369 existing semi-natural grasslands and forests of long continuity is therefore vital to preserving
370 specialist plant species (Peterken 2000; Verheyen & Hermy 2004; Johansson et al. 2008).

371 Time since change is a key factor determining how changes in community composition progress.
372 Our results show that overall changes in plant communities in successional grasslands comprise
373 parallel changes across forest species and open land species, which vary independently in rate
374 both over time and depending upon the composition of the surrounding landscape. Untangling

375 the separate responses of declining and increasing species as communities adjust to
376 environmental and landscape change over the long-term is vital to help to understand the
377 ecological mechanisms driving extinction debts and colonization credits, and therefore
378 biodiversity responses to ongoing global change drivers.

379 **Acknowledgements**

380 The authors would like to acknowledge the fieldwork carried out by Evelina Lindgren and
381 Anneli Nilsson. Swedish maps and aerial photographs ©Lantmäteriet.

382 **Author contributions**

383 All authors were responsible for the conception of ideas and the methodological design. AK
384 analysed the data, AK led the writing of the manuscript and all authors contributed critically to
385 the drafts and gave final approval for publication

386 **Data accessibility**

387 All landscape summaries and species composition data used in this study are archived at
388 <https://doi.org/10.5281/zenodo.3406339>

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573

574 **Table 1. Nestedness based on overlap and decreasing fill metrics for 130 observed plant**
575 **communities in grasslands abandoned at different times, the mean of 999 random**
576 **simulated communities, and the result of a one-tailed significance test between these two**
577 **values to test the nestedness of observed communities, presented for the overall, forest**
578 **specialist and grassland specialist species communities.**

| Community | Observed NODF | Mean sim NODF | P value |
|----------------------|----------------------|----------------------|----------------|
| Overall | 18.099 | 9.141 | <0.001 |
| Forest specialist | 38.029 | 11.965 | <0.001 |
| Grassland specialist | 15.263 | 6.109 | <0.001 |

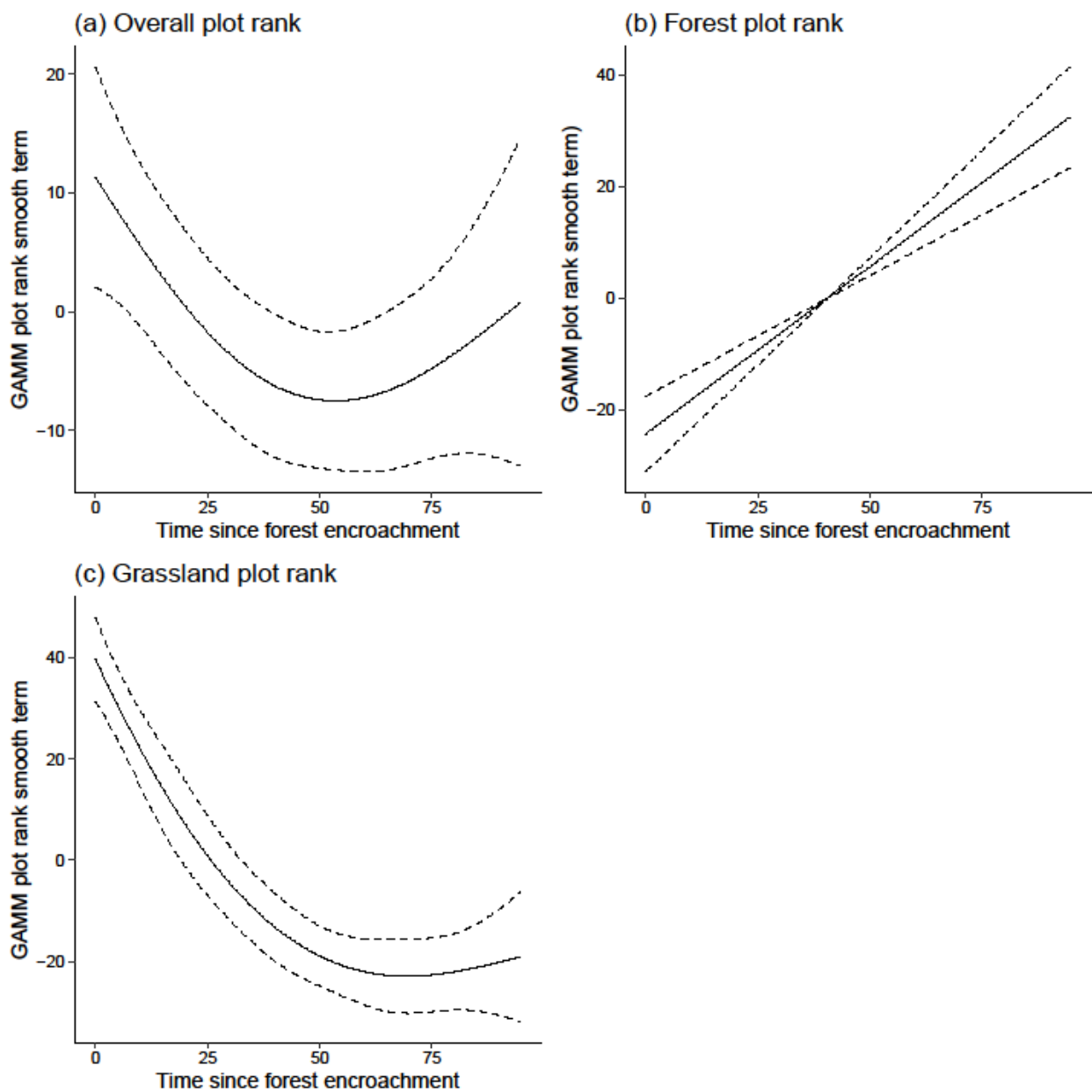
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580

581 **Table 2. Results from GAMM models of nestedness plot ranks versus time since**
582 **abandonment and landscape variables, for overall plant communities, forest specialist**
583 **plant communities and grassland specialist plant communities. Estimated degrees of**
584 **freedom are shown for smooth terms and indicate the shape of the modelled relationship**
585 **between the richness of separate communities and time since forest encroachment.**
586 **Adjusted R squared values are for the entire model, as output from GAMM in mgcv.**
587 **Significant terms (at the 0.05 level) are shown in bold.**

| Model | Predictor | Est. df | Parameter estimate | P value | Adjusted R² |
|----------------------|--------------------------------------|--------------------|-------------------------------|--------------------|-----------------------------------|
| Overall plot rank | Intercept | | 31.414 | | |
| | 1901 Class | | 15.783 | 0.042 | |
| | Surrounding forest (2015) | | 2.545 | 0.039 | |
| | Surrounding open (1901) | | 2.424 | 0.256 | |
| | Time since encroachment | 1.932 | | 0.037 | 0.096 |
| Forest plot rank | Intercept | | 39.703 | | |
| | 1901 Class | | 10.923 | 0.083 | |

| | | | | |
|-----------|---------------------------|--------------|------------------|--------------|
| | Surrounding forest | 2.248 | 0.027 | |
| | (2015) | | | |
| | Surrounding open | 1.138 | 0.518 | |
| | (1901) | | | |
| | Time since | 1.00 | <0.001 | 0.365 |
| | encroachment | | | |
| Grassland | Intercept | 71.875 | | |
| plot rank | | | | |
| | 1901 Class | 0.175 | 0.975 | |
| | Surrounding open | 0.374 | 0.760 | |
| | (2015) | | | |
| | Surrounding open | -2.017 | 0.207 | |
| | (1901) | | | |
| | Time since | 2.778 | <0.001 | 0.449 |
| | encroachment | | | |



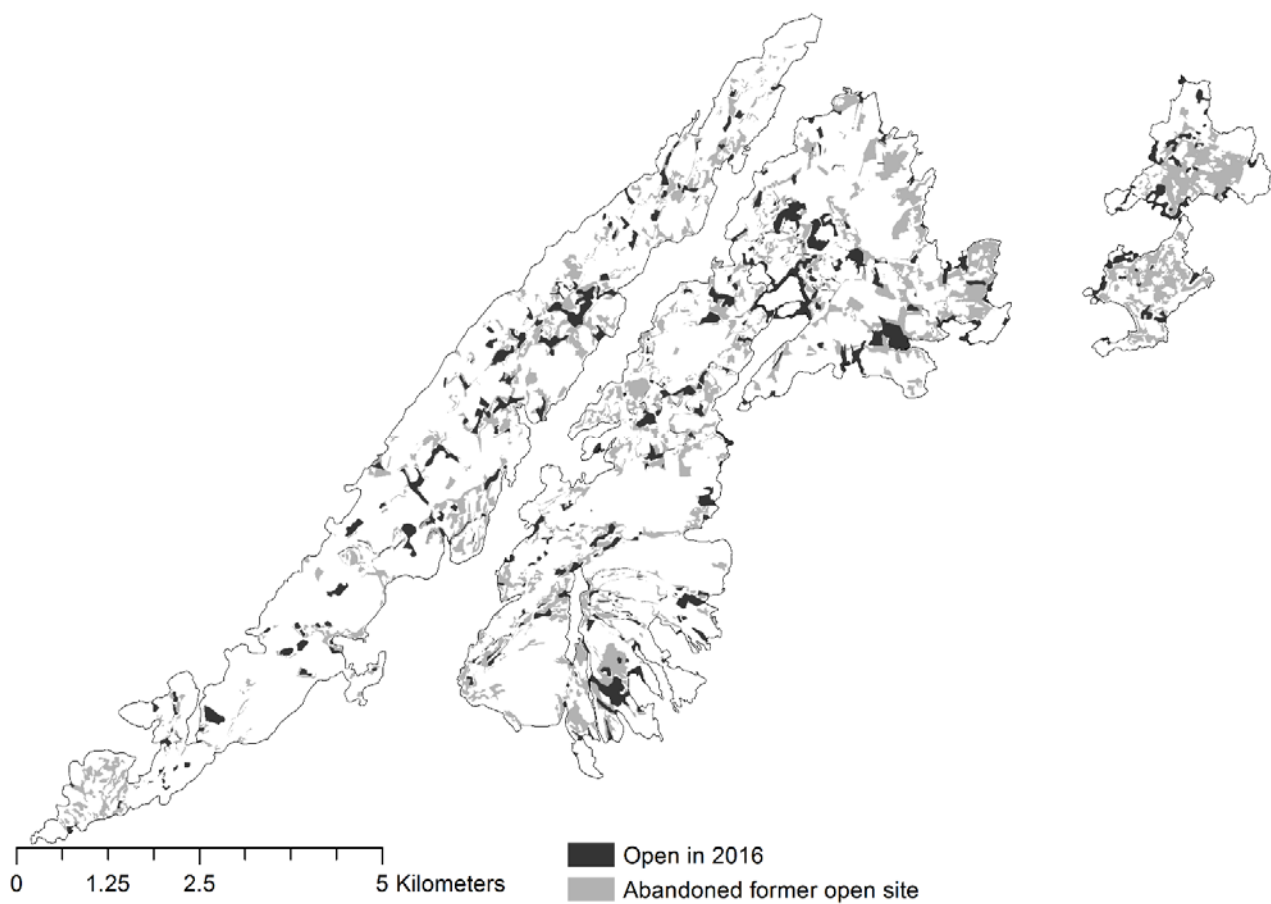
590

591 **Figure 1. Modelled relationship between species diversity and time since forest**
 592 **encroachment in abandoned grasslands. Solid lines show the fitted partial response of plot**
 593 **rank to time since forest encroachment, scaled and centred on zero and with all other**
 594 **covariates held constant. Dashed lines represent 95% confidence bands. GAMM models**

595 **shown for (a) overall plant communities, (b) forest specialist plant communities and (c)**
596 **grassland specialist communities.**

597 **Supporting Information to the paper Kimberley, A. et al. Unbalanced species losses and**
598 **gains lead to non-linear trajectories as grasslands become forests. Journal of Vegetation**
599 **Science.**

600 **Appendix S1: Map showing the islands included in the study and the locations of remaining**
601 **and former open grasslands.**



602