

The recovery of plant community composition following passive restoration across spatial scales

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Keywords: biodiversity, chronosequence, old fields, regeneration, restoration, scale-dependence, succession

Word count (main text and figure captions): 6338

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Abstract

1. Human impacts have led to dramatic biodiversity change which can be highly scale-dependent across space and time. A primary means to manage these changes is via passive (here, the removal of disturbance) or active (management interventions) ecological restoration. The recovery of biodiversity, following the removal of disturbance is often incomplete relative to some kind of reference target. The magnitude of recovery of ecological systems following disturbance depend on the landscape matrix,

45 as well as the temporal and spatial scales at which biodiversity is
46 measured.

47 2. We measured the recovery of biodiversity and species composition over
48 27 years in 17 temperate grasslands abandoned after agriculture at
49 different points in time, collectively forming a chronosequence since
50 abandonment from one to eighty years. We compare these abandoned
51 sites with known agricultural land-use histories to never-disturbed sites as
52 relative benchmarks. We specifically measured aspects of diversity at the
53 local plot-scale (α -scale, 0.5m²) and site-scale (γ -scale, 10m²), as well as
54 the within-site heterogeneity (β -diversity) and among-site variation in
55 species composition (turnover and nestedness).

56 3. At our α -scale, sites recovering after agricultural abandonment only had
57 70% of the plant species richness (and ~30% of the evenness), compared
58 to never-ploughed sites. Within-site β -diversity recovered following
59 agricultural abandonment to around 90% after 80 years. This effect,
60 however, was not enough to lead to recovery at our γ -scale. Richness in
61 recovering sites was ~65% of that in remnant never-ploughed sites. The
62 presence of species characteristic of the never disturbed sites increased in
63 the recovering sites through time. Forb and legume cover declines in years
64 since abandonment, relative to graminoid cover across sites.

65 4. **Synthesis.** We found that, during the 80 years after agricultural
66 abandonment, old-fields did not recover to the level of biodiversity in
67 remnant never-ploughed sites at any scale. β -diversity recovered more
68 than α -scale or γ -scales. Plant species composition recovered, but not
69 completely, over time, and some species groups increased their cover
70 more than others. Patterns of ecological recovery in degraded ecosystems
71 across space and long time-scales can inform effective, targeted active
72 restoration interventions and perhaps, lead to better outcomes.

73

74 Introduction

75 The Anthropocene is characterised by dramatic impacts of people on the
76 biosphere, via a number of direct and indirect processes (e.g., land use, climate
77 change), often leading to altered numbers and types of species (i.e., biodiversity) in
78 those impacted ecosystems (Díaz et al., 2019; Newbold et al., 2015). While a primary
79 means to manage these changes is to reduce the extent and intensity of negative
80 drivers of biodiversity change (e.g., reduced destruction or degradation of natural
81 ecosystems), an increasingly important way to recover losses of biodiversity and the

82 ecosystem services it provides is via a cessation or reduction of the impacts and
83 restoration of those ecosystems (Jones et al., 2018). The United Nations has recently
84 announced 2021-2030 as the Decade on Ecosystem Restoration, with the goal of
85 restoring 350 million hectares of degraded land to achieve higher biodiversity and
86 ecosystem functions (UNEA, 2019).

87 Ecological restoration can take many forms. The Society for Ecological
88 Restoration (SER) recognises a 'restorative continuum' of interventions that can help
89 ecosystems recover to context-dependent benchmarks after disturbance (Gann et al.,
90 2019). This can range from passive restoration, or natural recovery, which is the
91 cessation of major disturbance (e.g., deforestation, agriculture) (Atkinson & Bonser,
92 2020; Chazdon et al., 2021) or reinstatement of disturbance and management regimes
93 (e.g., fire, grazing, mowing). Active, or assisted and reconstructive restoration,
94 includes the addition of interventions which might manipulate abiotic and biotic
95 factors including the reintroduction of desired biota (Atkinson & Bonser, 2020). Through
96 successional processes or the assistance of such processes, such as
97 recolonizations and extinctions, ecosystems can then recover on a trajectory towards
98 a desirable functioning state (Shackelford, Dudley, et al., 2021; Temperton et al., 2004).
99 However, this recovery is typically incomplete (Jones et al., 2018; Moreno-Mateos et al.,
100 2017; Rey Benayas et al., 2009). In addition, communities in restored/recovered
101 ecosystems are often composed of more generalist and alien species when
102 compared to reference sites (Kaul & Wilsey, 2021). The composition of recovering
103 sites at different time points can be tied to species life-history characteristics (Zirbel &
104 Brudvig, 2020), can have interactive inhibitory or facilitative effects for other species to
105 recolonise (Young et al., 2017), and can be influenced by the surrounding landscape,
106 history, and management (Funk, 2021; Grman et al., 2015; Guiden et al., 2021).

107 Despite frequent studies on how biodiversity responds to anthropogenic
108 impact and recovery (Murphy & Romanuk, 2014; Newbold et al., 2015), less attention
109 has been paid to how inference of restoration on biodiversity depends on the
110 ecological scale in which diversity is measured and observed (Catano et al., 2021;
111 Martin et al., 2005). Nevertheless, most measures of biodiversity inherently depend on
112 the spatial scale on which samples are taken (i.e., a 1m² quadrat compared to an
113 entire site), and on the temporal scales which are measured (i.e., a year or a
114 decade) (Matthews et al., 2021; Rosenzweig, 1995). As a result, scale can critically
115 influence the magnitude in which biodiversity changes are quantified, even when
116 sample effort is standardised (Chase et al., 2018; Chase & Knight, 2013; Field et al.,
117 2009; Hill & Hamer, 2004; Sax & Gaines, 2003).

118 While the scale-dependence of biodiversity responses to anthropogenic
119 activities are well known, the direction of scale dependence is less clear. Scale-
120 dependent biodiversity responses to anthropogenic activities are most often studied
121 in the context of changes to β -diversity, or the site differences in species composition
122 (Chase et al., 2019; Socolar et al., 2016). Often, anthropogenic activities are thought to
123 create a homogenising effect, reducing β -diversity (Gossner et al., 2016; Hautier et al.,
124 2018; Martin et al., 2005). When β diversity is reduced by an anthropogenic driver, this
125 can lead to cases where small to moderate effects of a driver at smaller scales (i.e.,
126 α -diversity) can become exacerbated at larger spatial scales. For example, (W. Li et
127 al., 2021) found that Mongolian semiarid grassland communities that were impacted
128 by grazing and mowing had fewer species in each locality (α -diversity) as
129 disturbance intensity increased. However, because more narrowly distributed
130 species were more strongly influenced by disturbance intensities than more

131 widespread species, β -diversity also decreased, and the effect at the larger (γ -
132 diversity) spatial scale was greater.

133 On the other hand, anthropogenic activities can lead to communities
134 becoming more different between sites (higher β -diversity), which can lead to cases
135 where relatively larger effects of a driver occur at smaller spatial scales (i.e., α -
136 diversity). These negative effects weaken as scale increases (i.e., γ -diversity). For
137 example, (Uchida et al., 2018) found that land abandonment in Japanese semi-natural
138 grasslands led to a reduction in small-scale species richness when compared to
139 intensive agriculture and traditional management practices, but this negative effect
140 sometimes dissipated as scale increased. Likewise, semi-natural grassland
141 communities in the Slovak Republic had lower α -diversity, but an increase in β -
142 diversity and γ -diversity in landscapes with a higher proportion of non-natural
143 habitats (Janišová et al., 2014). There are many underlying factors that can influence
144 the direction and magnitude of scale-dependence resulting from anthropogenic
145 drivers, with numerous examples supporting each (Chase et al. 2018, 2019).

146 Spatial scale can influence our understanding of how biodiversity recovers
147 following cessation of major disturbance. For example, small-scale (α) diversity
148 usually does not fully recover to pre-disturbance levels even under active restoration
149 (Isbell et al., 2019; Moreno-Mateos et al., 2017; Rey Benayas et al., 2009). What is less
150 clear, however, is how β and γ -diversity respond during recovery. If β -diversity is not
151 influenced by the removal of disturbance and does not increase through time, the
152 incomplete recovery of diversity following restoration would be equivalent at both α
153 (within-plot) and γ (site) scales. If β -diversity is reduced by removal of disturbance
154 (i.e., via homogenization) and does not recover during restoration, the incomplete
155 recovery of α diversity would be exacerbated at larger (γ) scales. Finally, if β -

156 diversity increases following removal of the disturbance, incomplete recovery of α
157 diversity could be accompanied by a more complete recovery of diversity at larger
158 spatial scales. To date, few studies have examined the influence of recovery and
159 restoration on the scale-dependence of biodiversity and β -diversity in particular, and
160 those that have measured β -diversity do so in a number of different, often non-
161 comparable, ways. There is some evidence that β -diversity and γ -diversity recover
162 even less than α -diversity (Martin et al., 2005; Passy & Blanchet, 2007; Polley et al., 2005;
163 Wilsey et al., 2005). In a meta-analysis of grassland studies, however, (Catano et al.,
164 2017) showed that the effects of disturbance can lead to homogenization (lower β -
165 diversity) or differentiation (higher β -diversity) depending on the effects of
166 disturbance on stochastic factors and dispersal rates. Furthermore, β -diversity can
167 be enhanced in restoration, for example, when restoration actively targets β -diversity
168 via larger species pools (Grman & Brudvig, 2014).

169 While there is evidence of deficits of α , β and γ -diversity in passively
170 recovering and actively restored ecosystems, and in grassland systems in particular
171 (Martin et al., 2005; Polley et al., 2005; Sluis, 2002), it remains unclear how long these
172 potential deficits manifest on the landscape. Grasslands are one of the most
173 endangered and least protected biomes globally (Hoekstra et al., 2004), and are
174 experiencing extreme levels of land use change locally and regionally (Carbutt et al.,
175 2017; Roch & Jaeger, 2014). There are few old growth and continuous tracts of
176 grassland left (Nerlekar & Veldman, 2020; Scholtz & Twidwell, 2022). Here, we take
177 advantage of long-term surveys of vegetation in remnant savannah prairies and
178 recovering grasslands at the Cedar Creek Ecosystem Science Reserve in Minnesota
179 (USA). Isbell et al. (2019) used data from remnant prairies and a 37-year survey of
180 old-fields with different amounts of time since agricultural abandonment (ranging

181 from 1 to 91 years) to examine how α -scale (within-plot) species richness, species
182 diversity, evenness and productivity recovered (measured in 0.3 m² plots). They
183 found that even after more than 91 years since abandonment of agriculture, species
184 richness only recovered to 75% of its value in the reference site that was never-
185 ploughed. However, because species richness is a scale-dependent metric, it is
186 unclear how larger scale diversity recovered. Using the same system, and some, but
187 not all of the same sampling as Isbell et al. (2019), and taking different spatial scales
188 explicitly into account, we asked the following: (1) how do larger scale measures of
189 diversity (i.e., β and γ -diversity) vary through time across the chronosequence
190 following agricultural abandonment and how do they compare to the smaller scale
191 (α) measures? (2) How do measures of diversity other than species richness, such
192 as those that incorporate evenness, respond at the α , β and γ -scales? (3) How has
193 species composition, as a different component of recovery compared to measures of
194 richness and diversity, responded through time? (4) How has the cover of species
195 with different growth forms and life histories responded through time?

196

197

198 **Methods**

199 **Study system**

200 Cedar Creek Ecosystem Science Reserve, hereafter referred to simply as
201 Cedar Creek, is a 2,200-hectare long-term ecological science reserve (LTER) run by
202 the University of Minnesota (USA) in cooperation with the Minnesota Academy of
203 Science located 50 km north of Minneapolis. Cedar Creek lies on a glacial outwash
204 sand plain, between deciduous forest to the east and prairie to the west, forming a

205 mosaic of oak savanna, prairie, upland deciduous forest, lowland marshes and
206 swamps (Inouye et al., 1987). Soils are largely outwash sediments of fine and medium
207 sands, poor in nitrogen, which was further depleted by agricultural practices in old
208 field sites (Inouye et al., 1987).

209 Agricultural land use in this area began after 1900, but aerial photography
210 suggests some areas were never cleared (MHAPO, 2015; Pierce, 1954). As a result,
211 there are now a series of agricultural sites (old-fields) abandoned at different times
212 during the last century under passive recovery, as well as never-ploughed remnant
213 prairies and savannas scattered across the reserve (Fig. S1, Table S1). Secondary
214 succession in the abandoned old-fields is significantly limited by nitrogen (Tilman,
215 1987), and dispersal limitation (Tilman, 1994). While fire does play a key role in
216 maintaining prairies and savannas, succession does not consistently lead to
217 afforestation in the absence of fire (Clark et al., 2019). The natural history of Cedar
218 Creek is described in more detail in (Inouye et al., 1987).

219

220 **Study design and sampling**

221 We analysed vegetation from several sites that were part of long-term
222 research at the Cedar Creek Ecosystem Science Reserve (Fig. S1). Specifically, we
223 used data from otherwise comparable sites that could be categorised into two states
224 (see Table S1 for details): (1) Never-ploughed sites, which included 18 upland oak
225 savannas (plots of “Experiment 133”); (2) recovery sites that included 17 old-fields
226 which were ploughed and used for agriculture, but were abandoned so that natural
227 succession and recovery of the vegetation could be followed (“Experiment 014”).
228 Old-fields were abandoned between 1927 and 2015 (Clark et al., 2019). Each field
229 was measured approximately 6 times, with ~5-6 year measurement intervals from

230 1983- 2010 (27 years). At the start of the surveys, old-fields ranged from 1 year
231 since agricultural abandonment to 48 years (Table S1). All sampled sites were
232 located on well-drained upland sands (Inouye et al., 1987).

233 For surveys in both experiments, plants were estimated using percent cover
234 classes (“Experiment 133”) and species-level percent cover (“Experiment 14”) in
235 0.5 m² plots (1m x 0.5m). Cover classes are based on a modified Domin scale (1 =
236 1%, 2 = 2-5%, 3 = 6-25%, 4 = 26-50%, 5 = 51-75%, and 6 = 76-100%). Cover in both
237 studies could exceed 100%. In Experiment 133 (never-ploughed fields), four parallel
238 50 m long transects were laid out within fire management block units within each
239 field, 25 m apart, and 6 plots were placed every 10m along each transect, for a total
240 of 24 plots in fields in most years. In Experiment 14 (old fields), four permanent
241 parallel 40m long transects were laid in each field, 25 m apart, and 25 plots were
242 placed every 1.5 m along each transect, totalling 100 plots per field.

243 We did not include plots from the never-ploughed sites that had also never
244 been burned. This is because fire is a natural disturbance that maintains these
245 systems, and woody encroachment ensues when there is human-induced fire
246 suppression (Clark et al., 2019). Within the old-fields, we kept all plots surveyed in
247 years before the first year of burning, or those that have not been burned to
248 represent site recovery after abandonment before fire. We also did not include sites
249 that contained many trees (Clark et al., 2019). Because sample effort was not equal
250 between all of the sites in some years (e.g., 1999, 2011), we selected sites and years
251 that had a minimum of 24 samples, and used 20 randomly selected survey plots
252 from each site (site E14 was sub-sampled to match the minimum number of samples
253 in site E133). We took the midpoint of each cover class (“Experiment 133”) to
254 quantify percent cover of species, so that the summed cover of all species could

255 exceed 100%. Species cover relative to each plot's summed cover was quantified as
256 a proportion.

257

258 **Calculating Within-Site Metrics of Diversity**

259 We examined how biodiversity recovered across scales by calculating and
260 comparing multiple metrics of diversity at multiple scales between the never-
261 ploughed and recovery treatments. We estimated diversity at two spatial scales: (i)
262 the α -scale, which was the diversity in a given 0.5m² plot in a given treatment and
263 year, and (ii) the γ -scale, which here we define as the total diversity in 20 0.5m² of
264 combined plots within a site and year. Note, here we simply use α and γ -diversity to
265 denote smaller and larger scales, and make no assumptions whether these scales
266 correlate with any local or regional coexistence mechanisms. Finally, from these α
267 and γ estimates, we calculate (iii) Whittaker's multiplicative β -diversity ($\beta = \gamma/\alpha$,
268 (Whittaker, 1972) to quantify plot-to-plot variation, or the heterogeneity of plots within
269 sites at each time point. While the sampling approach was not designed to sample
270 the range of variation in the whole site, the amount and the equal number of samples
271 across sites allows an estimation of this variation. Additionally, we extrapolated
272 expected species richness from the γ -scale across 50 samples (Chao et al., 2014).

273 At each observed spatial scale, we estimated two metrics of diversity: (i)
274 species richness, which was simply the total number of species observed in a given
275 α -plot or γ - site, and (ii) an estimate of diversity that more heavily weights common
276 species, the probability of interspecific encounter (PIE). The PIE is the probability
277 that two species sampled randomly from a community are of a different species
278 (Hulbert, 1971), and higher values represent more even communities. For analyses,
279 we transformed the PIE into an effective number of species (ENS_{PIE}), that has the

280 same number of units as species richness using the proportion of each species (Jost,
281 2006); this is equivalent to Simpson's inverse diversity index (Simpson, 1949; Williams,
282 1964). By comparing results of species richness versus ENS_{PIE} , we can evaluate
283 whether differences are more strongly influenced by rare species only (in which case
284 species richness results should be different from ENS_{PIE} results), or by both rare and
285 common species (in which case, results from both metrics would be more similar)
286 (Smith & Wilson, 1996). At all scales, we standardized the cover to sum 100%. At the
287 α -scale, we summed cover across all species, and at the γ -scale, we summed
288 across all species and plots. We used this relative proportion to calculate ENS_{PIE} at
289 all scales.

290

291

292 **Species composition**

293 The measures of biodiversity (species richness and ENS_{PIE}) explored here
294 across scales (α , β , γ) allow us to compare numbers and types of species from plots
295 within a given site status (i.e., never-ploughed versus ploughed sites). They do not,
296 however, allow us to quantify the difference in species composition between the
297 sites. For example, many highly specialised prairie and savanna plants rarely
298 establish in the early phase of old-field recovery, which instead is dominated by
299 weedy species that are less frequently found in pristine sites (Inouye et al., 1987).

300 To quantify the difference in species composition between never-ploughed
301 sites and recovering sites, we calculated Jaccard's dissimilarity index indicating the
302 dissimilarity in species composition between site status (ranging from 0 to 1). We
303 partitioned the difference between the turnover and nestedness components of
304 Jaccard's index (Baselga, 2009; Baselga & Orme, 2012). These metrics are known to

305 be sensitive to pre-existing differences in alpha-diversity (Vellend et al., 2007).

306 Through the careful design of our approach, we avoid these issues.

307 We used a checklist approach to identify species present within old-fields and
308 across fields that have never been ploughed. First, we compiled a checklist of all
309 species present across all never-ploughed sites within every time point measured
310 (1984, 1990, 1995, 2000, 2005, 2010) to determine the 'regional' species pool for the
311 never-ploughed sites within each year, resulting in one 'regional checklist' for every
312 year. This never-ploughed regional checklist represents a temporally accurate
313 relative restoration reference target. Next, we compiled a checklist of all species
314 present within every old-field site and time point measured (1983, 1989, 1994, 1997,
315 2002, 2006), resulting in a checklist for every old field site and every year. If a
316 species was present across multiple plots within a site, it was only represented once
317 in the never-ploughed or old-field checklist with a presence of 1. We then compared
318 species present in the checklist of every old-field site within each year to the regional
319 checklist across all never-ploughed sites at the closest calendar year and nearest
320 comparable time-point measured (eg. 1983 compared to 1984) as a single pairwise
321 comparison (Marion et al., 2017). This quantifies the site-level compositional change of
322 each old-field since agricultural abandonment relative to the total species present
323 within all never-ploughed sites at the most comparable time-point as a consistent
324 comparison benchmark. If species from the checklist of never-ploughed sites were
325 recolonizing old-fields over time, we expect nestedness to increase in each old-field
326 as years since agricultural abandonment progress. If species colonising old-field
327 sites since abandonment are different from that of never-ploughed sites, then we
328 would expect the turnover component to increase across time.

329 Lastly, to quantify changes in relative cover after years since agricultural
330 abandonment, we calculated the relative cover of species broad growth form groups
331 (graminoids, forbs, and legumes) and their origin (native, exotic) for every plot
332 measured in every year.

333 We used the R Environment for Statistics and Computing (R Core Development
334 Team, 2019) for all data preparation, manipulation, quantification of diversity metrics,
335 statistical analysis and graphic visualisation of results. To quantify diversity metrics
336 (e.g., α , β , γ species richness) we used tidyverse (Wickham et al., 2019) and vegan
337 (e.g., α , β , γ ENS_{PIE}) packages (Oksanen et al., 2019). For dissimilarity and its partition
338 into turnover and nestedness, we used the beta.part package (Baselga & Orme, 2012;
339 Oksanen et al., 2019). We used the iNEXT package (Chao et al., 2014; Hsieh, T.C. et al.,
340 2020) to interpolate and extrapolate (up to 50 samples) species richness across
341 scales based on average observed samples across each site status and year since
342 agricultural abandonment (Fig. S2, S3).

343

344 **Statistical analysis**

345 We quantified field status (old-field vs never-ploughed) effects on biodiversity
346 using hierarchical linear models (Discrete analysis) with site status (i.e., old-field or
347 never-ploughed) as a categorical fixed effect. We modelled site and calendar year as
348 random effects, and allowed random intercepts to vary (Supplementary Information
349 Table S2, Fig. S4-S9 for all model details).

350 The effect of years of agricultural abandonment on the recovery of old-fields
351 compared to the never-ploughed sites at each scale of diversity were quantified
352 using hierarchical linear models (continuous analysis). Year since agricultural
353 abandonment was modelled as a continuous fixed effect and was log-transformed.

354 We found logarithmic trends to be the most parsimonious for statistical models
355 looking at diversity (e.g. α , β , γ , richness and ENS_{PIE}) as a function of years since
356 abandonment, similar to previous work (Isbell et al., 2019). At both spatial scales, we
357 quantified each log-transformed diversity component in old-fields as the percentage
358 compared to the mean of the never-ploughed sites at that same metric and scale.
359 We allowed random intercepts and slopes to vary for years since agricultural
360 abandonment, and for categorical calendar year, assuming variation between each
361 site, the year it was abandoned and the calendar year sampling started
362 (Supplementary Information for all model details). For the α -scale, we modelled plot
363 nested within transect, nested within site as random effects and for β and γ -scales,
364 site as a random effect. We plotted log-transformed trends on a linear scale, which is
365 why the visualisation of the overall trends have some curvature.

366 We quantified the year of abandonment effects on the turnover and
367 nestedness components of Jaccard's dissimilarity using two univariate hierarchical
368 linear models (dissimilarity analysis). We modelled the year since abandonment as a
369 continuous fixed effect and site as a random effect. We allowed random intercepts
370 and slopes to vary for years since agricultural abandonment, for every old field and
371 for calendar year, assuming there was variation in each site and each year of
372 sampling

373 We quantified the effect of years since agricultural abandonment on the
374 relative cover of growth forms (graminoid, forb, legume) and their origin (native and
375 introduced) using a univariate hierarchical linear model. We modelled the year since
376 abandonment as a continuous fixed effect (log-transformed), including growth form
377 and origin and their 3-way-interaction as categorical fixed effects. We log-
378 transformed relative percent cover and allowed random intercepts and slopes to vary

379 for all fixed effects across every site, and year. We plotted log responses on a linear
380 scale.

381 For Bayesian inference and estimates of uncertainty, we fit models using the
382 Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter et al., 2017), and coded
383 using the brms package (Bürkner, 2018). We fit all models with four chains, differing
384 iterations, and differing assumed distributions (See Supplementary Information for all
385 model details). We used weakly regularising priors and visual inspection of the HMC
386 chains showed excellent convergence.

387

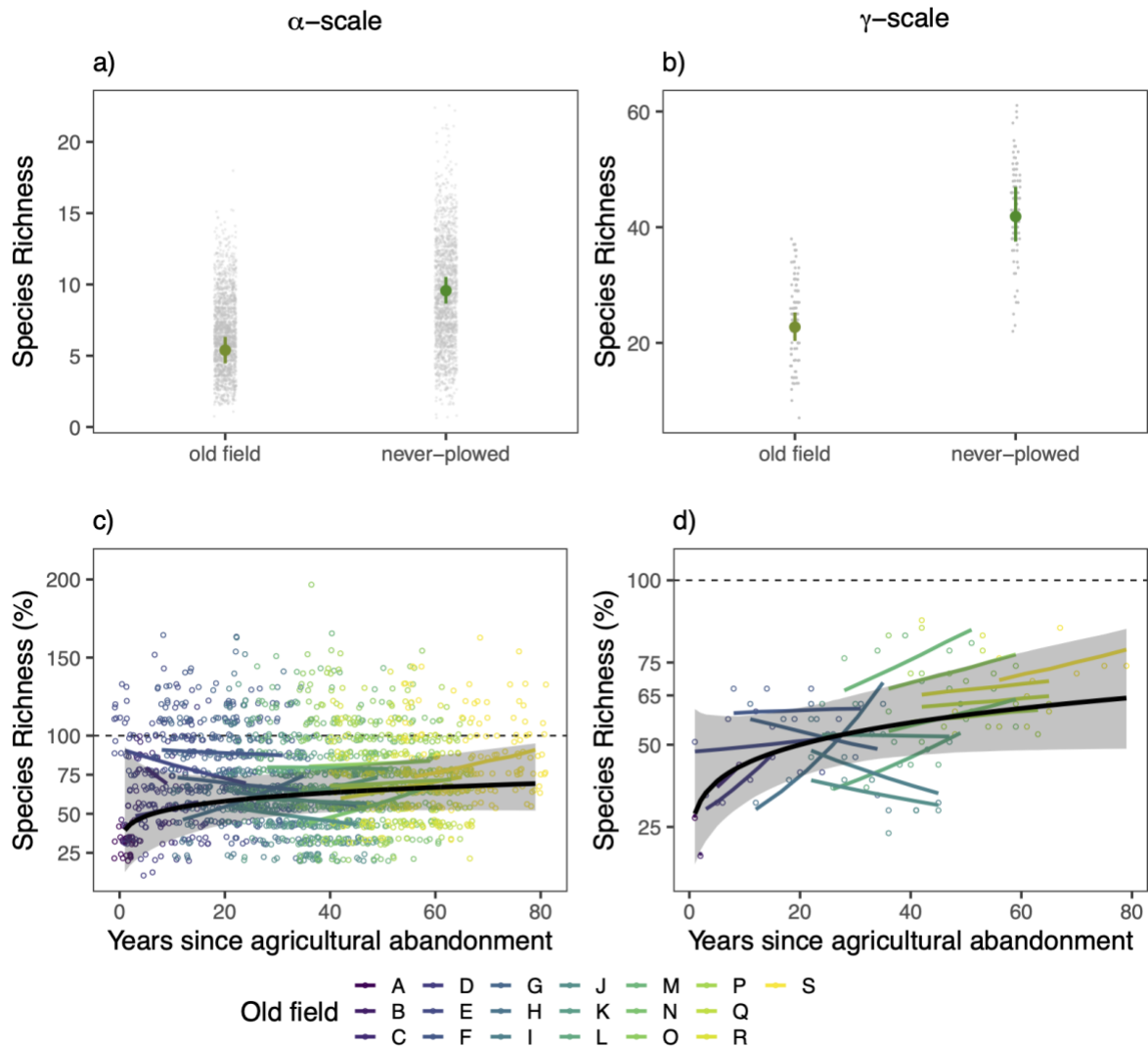
388 **Results**

389 **α -scale and γ -scale species richness**

390 For the discrete analysis (Figs 1 a, b), we found that, old-field plots had on
391 average 59% of species richness (5.65, 95% credible interval: 4.66 to 6.56) found in
392 never-ploughed sites (9.59, CI: 8.70 to 10.51, Fig. 1a) at the α -scale (0.5 m²) and
393 approximately 55% fewer species (23.6, 21.2 to 26.1) than never-ploughed sites
394 (42.6, 38.6 to 47.1, Fig. 1b) at the γ -scale (the combination of 20 plots and thus
395 10m²). We found a similar difference between old-fields and never-ploughed sites
396 when we extrapolated species richness estimates based on incidence-based species
397 accumulation to 50 samples (Figs S2, S3).

398 In the continuous analysis (Figs 1 c, d), richness weakly increased across
399 years since agricultural abandonment at the α -scale, but with high uncertainty
400 (Slope: 0.13, 95% credible interval: -0.17 to 0.53, Fig. 1c). After ~80 years since
401 abandonment, α -scale species richness in old-fields was about 70% of that found in
402 never-ploughed sites. At the γ -scale, grassland species richness increased across

403 years since agricultural abandonment (Fig. 1d), but again with high uncertainty
 404 (Slope: 0.13, CI: -0.11 to 0.40). γ -scale richness in old-fields was about 65% of that
 405 found in never-ploughed sites after 80 years.



406

407 **Figure 1: α -scale and γ -scale species richness.** a) α -scale and b) γ -scale
 408 species richness as a function of site status. Small points show data models were fit
 409 to; large points are the conditional effects of site status and the lines show the 95%
 410 credible intervals of conditional effects. c) α -scale and d) γ -scale species richness as
 411 a function of 'years since agricultural abandonment'. Black dashed line represents
 412 the mean diversity metric of all never-ploughed sites (18 sites). The thick black line
 413 represents the average effect of years since agricultural abandonment on species
 414 richness across all old-fields. The grey shading around the black line represents the
 415 95% credible interval of that effect estimate. Each colored line represents the

416 average predicted values for each site. Each open point represents an old-field plot
417 (α -scale) or a site (γ -scale) calculated as the percentage of richness, compared to
418 never-ploughed sites. Y-axes vary for clarity.

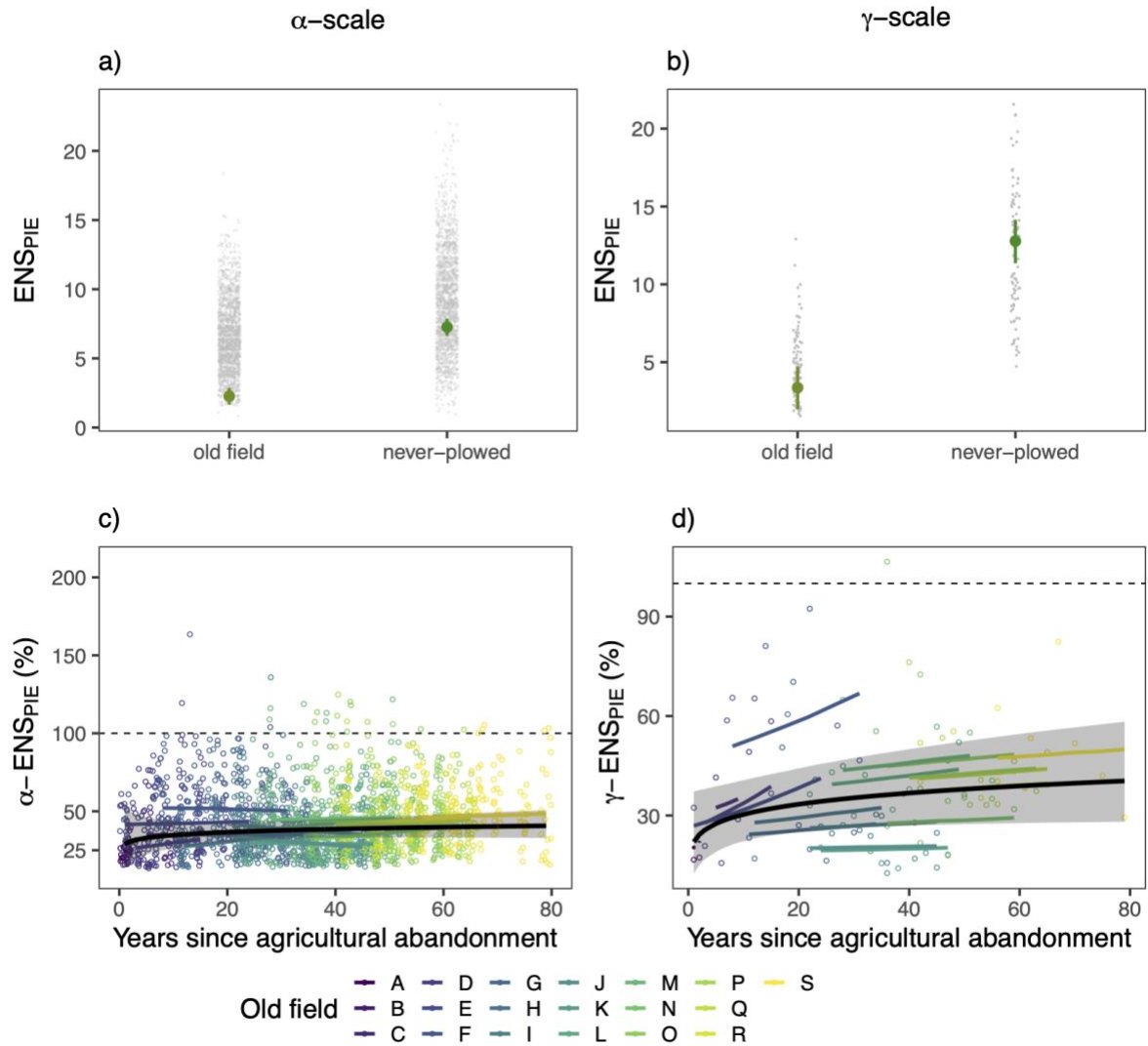
419

420 **α -scale and γ -scale ENS_{PIE}**

421 In discrete analysis (top row) at the α -scale, old-field sites overall had
422 approximately 31% of ENS_{PIE} (2.27, 1.66 to 2.89) (relative abundance was less
423 even) found in never-ploughed sites (7.21, 6.62 to 7.82, Fig. 2a). At the γ -scale, old-
424 field sites had approximately 28% (3.53, 2.14 to 4.88) fewer species equivalents than
425 in never-ploughed sites (12.61, 11.27 to 14.02, Fig. 2b).

426 At the α -scale, ENS_{PIE} does not increase strongly across years since
427 agricultural abandonment (Slope: 0.07, 95% Credible Intervals: -0.14 to 0.37, Fig.
428 2c). After ~ 80 years, α -scale plots within old-fields have less than 50% ENS_{PIE} than
429 those that were never disturbed. At the γ -scale, ENS_{PIE} weakly increases across
430 years since agricultural abandonment with high uncertainty (Slope: 0.15, CI: -0.08 to
431 0.36, Fig. 2d), and had less than 50% ENS_{PIE} than the never-ploughed sites after 80
432 years.

433



434

435 **Figure 2: α -scale and γ -scale ENSPIE** a) α -scale and b) γ -scale ENSPIE as a function
 436 of site status. Small points show data models were fit to; large points are the
 437 conditional effects of site status and the lines show the 95% credible intervals of
 438 conditional effects. c) α -scale and d) γ -scale species evenness as a function of
 439 'years since agricultural abandonment'. Black dashed line represents the mean
 440 diversity metric of all never-ploughed sites (18 sites). The thick black line represents
 441 the mean fitted line of years since agricultural abandonment on species richness
 442 across all old-fields. The grey shading around the black line represents the 95%
 443 credible interval of that mean effect estimate. Each colored line represents the
 444 average predicted values for each site. Each open point represents an old-field plot
 445 (α -scale) or a site (γ -scale) calculated as the percentage of evenness, compared to
 446 never-ploughed sites. Y-axes vary for clarity.

447

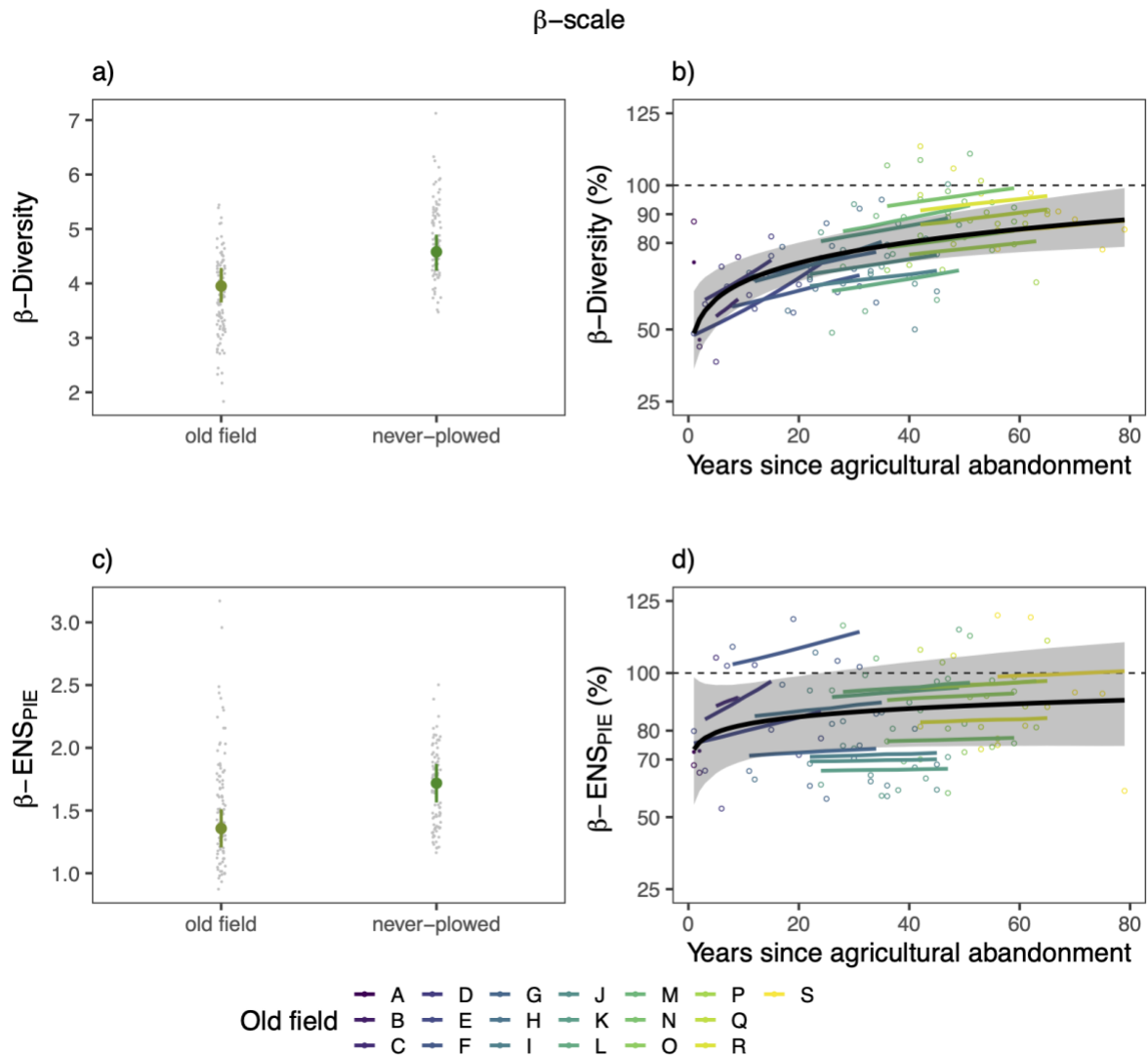
448

449 **β -diversity**

450 In the discrete analysis, β -diversity ($\beta = \gamma/\alpha$, Whittaker, 1972) values were
451 82% (3.50, 95% Credible Interval: 3.25 to 3.77) of that found in never-ploughed sites
452 (4.28, 4.02 to 4.53, Fig. 3a). In the continuous analysis, β -diversity values increased
453 notably across years since agricultural abandonment (Slope: 0.15, CI: 0.09 to 0.22),
454 and recovered up to 90% of the heterogeneity of that compared to never-ploughed
455 sites (Fig. 3b).

456 In the discrete analysis, β -ENS_{PIE} values were 82% (1.31, CI: 1.15 to 1.46) of
457 that found in never-ploughed sites (1.59, CI: 1.45 to 1.75, Fig. 3c). In the continuous
458 analysis, β -ENS_{PIE} did not increase across years since agricultural abandonment
459 (Slope: 0.10, CI: 0.02 to 0.19, Fig. 3d), and recovered to about 95% of that
460 compared to never-ploughed sites.

461



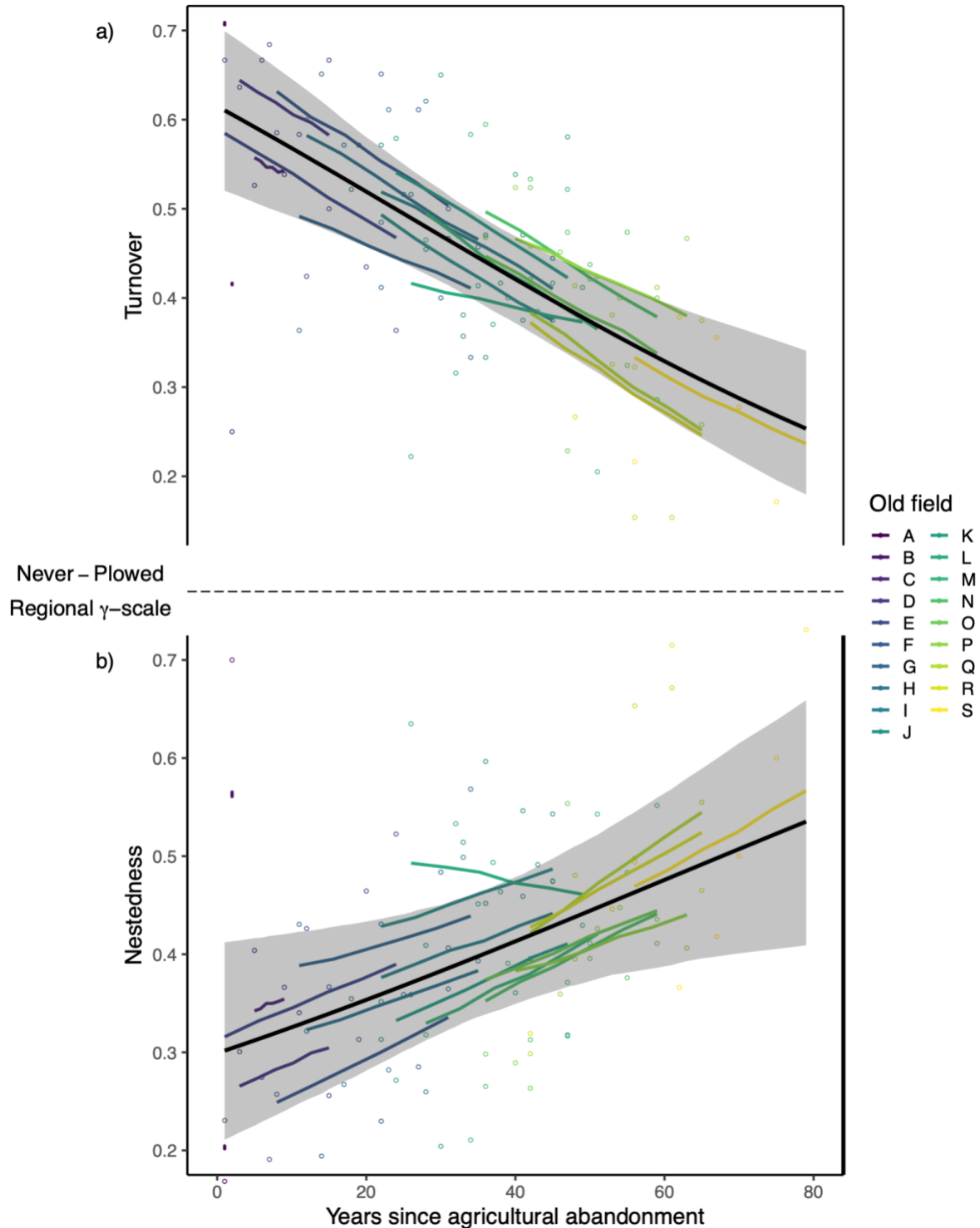
462

463 **Figure 3:** Whittaker's β -Diversity (a, b) and β -ENS_{PIE} (c, d). a) & c) as a function of
 464 site status and b) & d) as a function of 'years since agricultural abandonment'. In a)
 465 and c) small points show data models were fit to; large points are the conditional
 466 effects of site status and the lines show the 95% credible intervals of conditional
 467 effects. In b) and d) the thin black dashed line represents the mean diversity metric
 468 of all never-ploughed sites (18 sites). The thick black line represents the fitted mean
 469 line of years since agricultural abandonment on each diversity metric across all old-
 470 fields. The grey shading around the black line represents the 95% credible interval of
 471 that mean effect estimate. Each colored line represents the average predicted values
 472 for each site. Each open point represents an old-field calculated as the percentage of
 473 β -diversity, or β -ENS_{PIE} compared to the overall average of never-ploughed sites.
 474 Each colored line shows the slope of each site across years since agricultural
 475 abandonment. Y-axes vary for clarity.

476

477 **Community Composition**

478 Dissimilarity due to turnover in old-fields compared to the never-ploughed
479 region decreased across years since abandonment (Slope: -0.02, 95% Credible
480 Interval: -0.03 to -0.01) (Fig. 4). That is, old-fields were colonised with species that
481 were unique to old-field sites, when first abandoned, and this decreased over time.
482 Dissimilarity due to nestedness in old-fields compared to never-ploughed sites
483 increased across years since abandonment (Slope: 0.01, CI: 0.001 to 0.02) (Fig. 4).
484 In other words, old-fields were increasingly colonised by species characteristic of the
485 never-ploughed sites over time since abandonment, but never fully converged. In
486 total, we found 63 species that occurred only in never-ploughed sites, never in any
487 old-fields. Conversely, we found 34 species that occur only in old fields, and never in
488 never-ploughed sites.



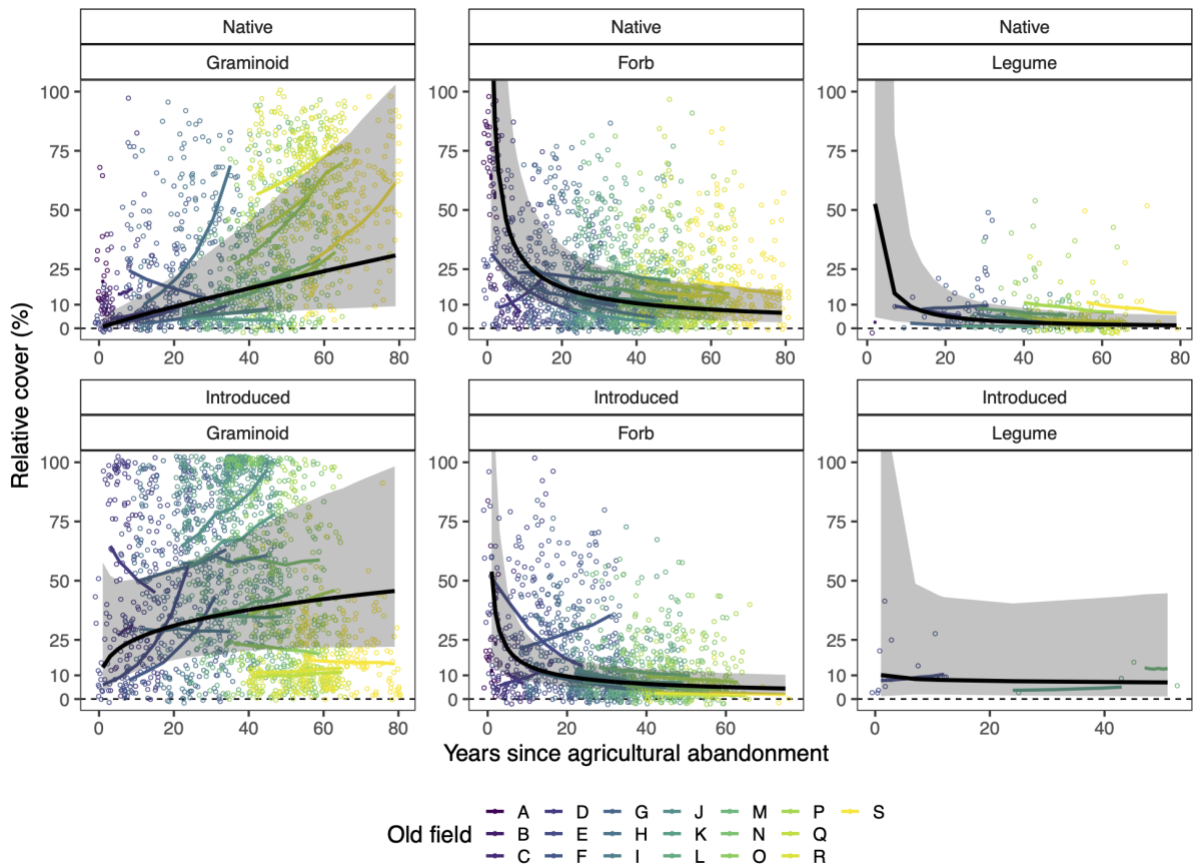
489

490 **Figure 4:** a) Spatial turnover and b) spatial nestedness components of
491 Jaccard's dissimilarity index as a function of 'years since agricultural abandonment'.
492 Each old-field at each time point was compared to the regional- γ species pool of all
493 never-ploughed sites. The black dashed line represents a value of zero (0). The thick
494 black line represents the average effect of years since agricultural abandonment on

495 components across all old-fields compared to never-ploughed sites. The grey
496 shading around the black line represents the 95% credible interval of that effect
497 estimate. Each open point represents an old-field at a time since agricultural
498 abandonment compared to the never-ploughed region. Each colored line shows the
499 predicted slope of each old-field across years since agricultural abandonment.
500

501 **Growth Form and Origin Cover**

502 Relative cover of growth form groups (graminoid, forb, legume) of differing
503 origins (i.e., native and introduced) found in never-ploughed fields changed as a
504 function of years since agricultural abandonment in old fields (Fig. 5). Native
505 graminoid cover increased during years since agricultural abandonment in many
506 sites, but the credible intervals overlap zero (Slope: 0.15, CI: -0.50 to 0.85). Both
507 native forbs (-0.70, CI: -1.15 to -0.27) and native legumes (-1.34, CI: -2.36 to -0.36)
508 decreased. Introduced graminoid cover increased in many sites since abandonment
509 but again the credible intervals overlap zero (0.29, CI: -0.12 to 0.67). Both introduced
510 forbs decreased (-0.57, CI: -0.98 to -0.20) and introduced legumes decreased (-0.10,
511 CI: -0.86 to 0.56).



512

513 **Figure 5:** Relative cover of native a) graminoids b) forbs and c) legumes, and
 514 introduced d) graminoids e) forbs and f) legumes, characteristic of never-ploughed
 515 sites as a function of 'years since agricultural abandonment'. The thick black line
 516 represents the average effect of years since agricultural abandonment on species
 517 growth form and origin groups across all old-fields. The grey shading around the
 518 black line represents the 95% credible interval of that effect estimate. Each open
 519 point represents the relative cover of each respective growth form and origin in an
 520 old-field plot at a time since agricultural abandonment. Each colored line shows the
 521 predicted slope of each old-field across years since agricultural abandonment for
 522 each growth form and origin.

523

524 Discussion

525 A major tenet in disturbance ecology has been that, given enough time,
526 removal of major anthropogenic disturbances such as agriculture will allow
527 biodiversity to recover (Moreno-Mateos et al., 2017). At the same time, accruing
528 evidence suggests that, in the absence of active restoration interventions (and even
529 in their presence), this recovery can take an exceedingly long time and is often
530 incomplete (Buisson et al., 2018; Isbell et al., 2013; Nerlekar & Veldman, 2020). For
531 example, using many of the same sites as in the present study (see Supplementary
532 Table 1 for details), Isbell et al. (2019) showed that α -scale (0.3m²) species richness
533 had recovered to only ~75% of that of the never-ploughed sites even after 91 years
534 of recovery. Not surprisingly, we found similar results in our α -scale (0.5 m²)
535 analyses, where within-plot species richness increased slightly through time, but
536 remained ~70% lower than never-ploughed plots, even after 80 years of recovery
537 (Fig. 1c). While passive recovery is a nice option given resource constraints, it
538 carries with it some hidden costs, such as incomplete recovery (Zahawi et al., 2014).
539 Here, we examine the scale-dependent dynamics of this passive recovery over long-
540 time scales. Given that active restoration is more expensive upfront, is not silver-
541 bullet solution (Bekessy et al., 2010), nor is yet predictable (Brudvig & Catano,
542 2021), perhaps understanding scale-dependent dynamics of passive recovery better
543 can help point to actionable improvements for restoration.

544 Importantly, coexistence and diversity are highly scale-dependent patterns
545 and it is less clear how larger-scale patterns of diversity recover. Anthropogenic
546 disturbances are known to often influence β -diversity in grassland ecosystems, both
547 positively and negatively (Catano et al., 2017; Eskelinen & Harrison, 2015; Martin et al.,
548 2005; Polley et al., 2005). As a result, we would either expect exacerbated effects of

549 that driver and recovery at larger spatial scales (if β -diversity is lower) or enhanced
550 effects of that driver and recovery at larger spatial scales (if β -diversity is higher). We
551 found that β -diversity was indeed lower than in never-ploughed sites following
552 agricultural abandonment, and while this diversity showed signs of recovery over
553 time, it remained lower overall than in the never-ploughed sites. Complementary
554 results have been found in successional sites that showed heterogeneity among
555 plots increasing, and across sites decreasing, as succession progressed (S. Li et al.,
556 2016). Other studies found that fire treatments increased in α -diversity, while β -
557 diversity remained unchanged (Joner et al., 2021).

558 Given the lower β -diversity in recovering compared to never-ploughed sites
559 (Fig 3a), we might expect that the magnitude of the deficit of species richness in
560 recovered relative to never-ploughed sites might increase with spatial scale. This
561 was true for the absolute number of species; the deficit in recovering relative to
562 never-ploughed sites was ~4 species at the α -scale (Fig. 1a), but ~19 species at the
563 γ -scale (Fig. 1b). But it was not true for the ratio of the deficit; the deficit of species
564 richness was 59% at the α scale (Fig. 1a), with a similar recovery deficit of 55% at
565 the γ -scale (Fig. 1b). In addition, there was little evidence that the deficit in species
566 richness declined through time over the course of the observations, consistent with
567 comparable findings and speculations on the slow recovery of secondary grasslands
568 (Nerlekar & Veldman, 2020).

569 Although we cannot explicitly discern the mechanism underlying the continued
570 deficit of species richness at α and γ -scales in these recovering old-fields, we
571 suspect dispersal limitation between sites might play a key role. Several previous
572 studies at Cedar Creek have shown that seed additions can lead to significantly
573 increased levels of species richness (Fargione et al., 2011; Ladouceur et al., 2020;

574 Symstad, 2000; Tilman, 1997). Even seeds added to a never-ploughed prairie-savanna
575 led to a doubling of α plant diversity that persisted for 13 years or longer (Catford et
576 al., 2019; Tilman, 1997). For example, the γ -diversity of Field H recovers rapidly (Fig.
577 1d), and is located right next to field N which has been recovering after
578 abandonment for 35 years more than field H (Fig. S1, Table S1). This is evidence for
579 spatially-dependent dispersal limitation. This is also consistent with our results
580 comparing the nestedness and turnover components of compositional dissimilarity,
581 which indicated that species composition in the old-fields was becoming more similar
582 to the never-ploughed sites over time (Fig. 4), likely through species gains (Foster &
583 Tilman, 2000). It is also possible that the soils in recovering sites have been
584 significantly altered by added fertilisers so that environmental filters also play a role
585 in limiting recovery (Seabloom et al., 2020).

586 By comparing the results of how species richness recovered following
587 agricultural abandonment to those of ENS_{PIE} , a diversity metric that strongly weights
588 the most common species, we can see how patterns of recovery are influenced by
589 more common versus rare species. In this case, ENS_{PIE} following agricultural
590 abandonment recovered to only ~31% of that observed in the never-ploughed sites
591 at the α -scale (Fig. 2a). Compared to the ~59% recovery of species richness at the
592 α -scale (Fig. 1a), this suggests that much of the recovery was among species that
593 are relatively common in the community and that there is less recovery of community
594 evenness. At the site scale, ENS_{PIE} in old-fields recovered to 28% of that in never
595 disturbed sites (Fig. 2b), compared to the 55% recovery of species richness at the
596 site scale (Fig. 1b). The higher recovery of species richness than ENS_{PIE} is also
597 consistent with previous studies (Martin et al., 2005; Sluis, 2002; Wilsey et al., 2005),

598 suggesting that rarer species drive a lot of the passive recovery in abandoned old-
599 fields.

600 Despite the fact that measurements of species diversity (richness and
601 evenness) only partially recovered across scales even after nearly a century of
602 agricultural abandonment, species composition has consistently recovered through
603 time (Fig. 4). Early in the time series, recovering old-fields were colonised by species
604 not typically found in never-ploughed sites. Grass cover characteristic of never-
605 ploughed fields, both native and exotic, increased in old fields through time, and forb
606 cover declined, suggesting that some growth forms may predictably recolonise (Clark
607 et al., 2019), and increase their cover more readily than others (Fig. 5). Similar
608 studies in other systems that have observed that perhaps species that are the
609 slowest to recover on their own are less-effective dispersers (Fensham et al., 2016).
610 Finally, we predict that without intervention, recovery to 95% of reference sites may
611 take much longer, but this time to recovery may be different for each scale (Fig.
612 S10). Given that successional recovery has been found to be most successful in
613 colder, more humid systems (Prach & Walker, 2019), passive recovery, and even
614 active restoration in more arid and hot systems is expected to be more difficult
615 (Shackelford, Paterno, et al., 2021).

616 Here, to actively assist recovery, the control of invasive grasses, combined
617 with direct seeding of native forbs, and management actions (e.g., fire, soil
618 restoration) may be a favourable action to accelerate the recovery of diversity.
619 Additionally, focusing restoration treatments on specific native grass and forb
620 species that have not recovered may help to prioritise resources and actions through
621 time. Combined with appropriate management actions (Guiden et al., 2021), and
622 targeted support for trophic relationships (Heelemann et al., 2012; Ladouceur et al.,

623 2022), restoration can also have cascading effects for passively supporting the
624 recovery of the fauna community structure and function (Pearson et al., 2022).

625 Overall, our results show that analyses of multiple metrics across scales more
626 fully reveals how ecological communities recover following disturbance in space and
627 time. To accelerate or assist this recovery, active intervention via restoration may be
628 considered a viable option. Understanding how biodiversity recovers on its own after
629 disturbance across space and time can help us to better assist this recovery and
630 restore systems more effectively and predictably into the future.

631

632 **Acknowledgements**

633 We thank the staff, researchers, students, and interns who have worked for more than three
634 decades to maintain the old field surveys and experiments at Cedar Creek. Data collection
635 was supported by the NSF LTER program, including DEB- 8114302, DEB- 8811884, DEB-
636 9411972, DEB-0080382, DEB-0620652, and DEB-1234162, and by the Cedar Creek
637 Ecosystem Science Reserve and the University of Minnesota. We gratefully acknowledge
638 the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-
639 Leipzig, funded by the German Research Foundation (DFG–FZT 118, 202548816). We
640 thank Christian Krause and the UFZ administrative and support staff of the High-
641 Performance Computing Cluster EVE, a joint effort of the Helmholtz Centre for
642 Environmental Research (UFZ) and iDiv, for access to, and support associated with, EVE.
643 EL thanks the Alexander von Humboldt Foundation. Authors declare no conflict of interest.

644

645 **Author Contributions**

646 EL, JMC and FI conceived the idea. FI and ATC contributed ideas and suggestions
647 for data selection, preparation, analysis and interpretation. GDT, PBR and ATC
648 provided data. EL conducted data analysis. JMC & WSH contributed ideas to
649 analyses. EL & JMC wrote the manuscript. EL, FI, ATC, WSH, PBR, GDT and JMC
650 contributed to the shaping of the manuscript, and made edits and suggestions
651 leading to the final version.

652

653 **Data Availability**

654 Data is archived at Cedar Creek Ecosystem Science LTER Reserve Data Catalogue:
655 <https://www.cedarcreek.umn.edu/research/data> . Data summaries at different scales
656 needed to reproduce results will be archived at a data repository like DRYAD or
657 FigShare. Code will be archived at <https://github.com/emma-ladouceur> and
658 assigned a DOI through Zenodo.

659

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