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

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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, $0.5m^2$) and site-scale (γ-scale, $10m^2$), 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

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, Dudney, 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 1m^2 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 m^2 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

Methods

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 m^2 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

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 $0.5m^2$ plot in a given treatment and

263   year, and (ii) the γ-scale, which here we define as the total diversity in 20 $0.5m^2$ 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 (β = γ/α,

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
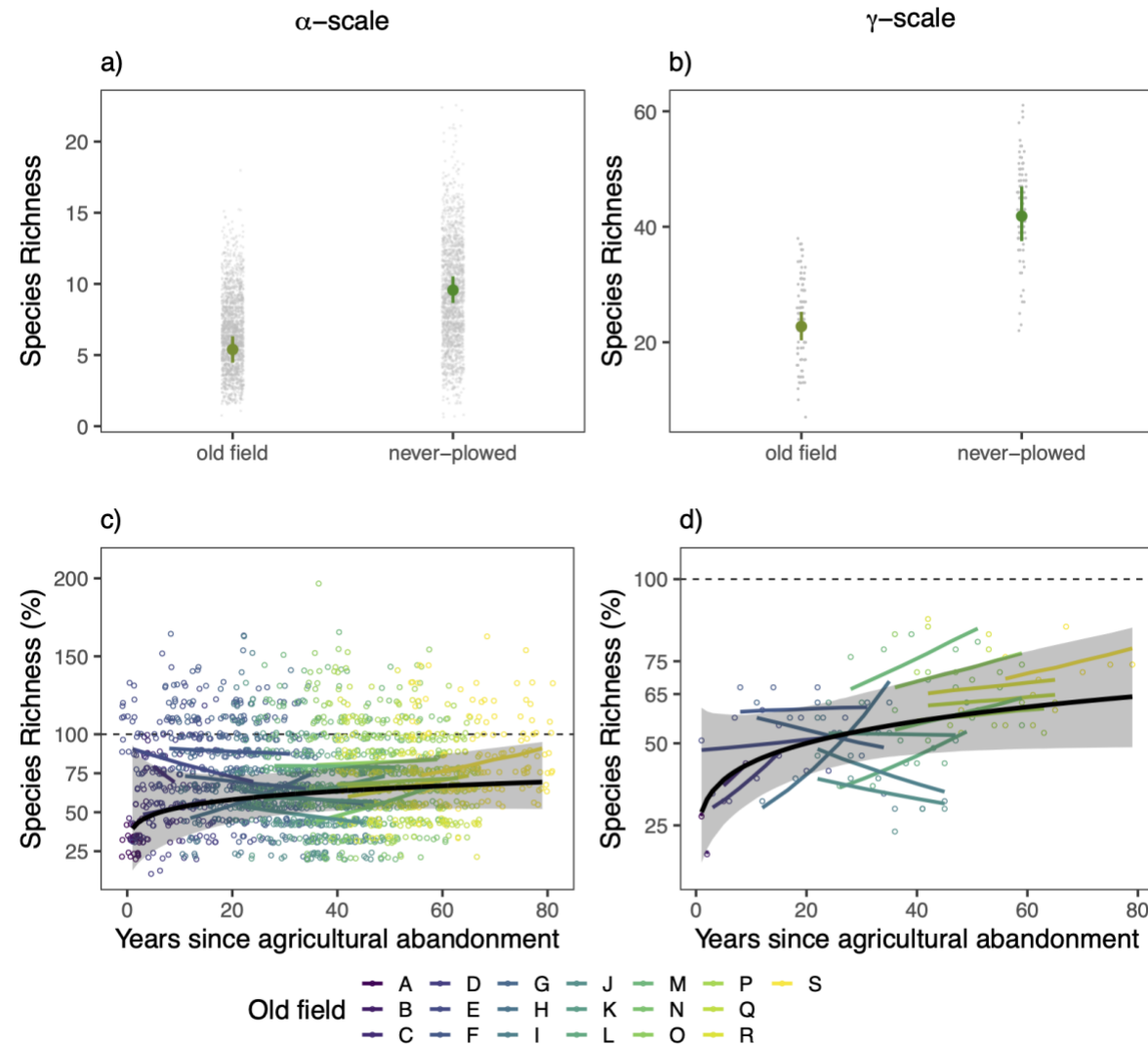
386   chains showed excellent convergence.

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 m^2) 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   10m^2). 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
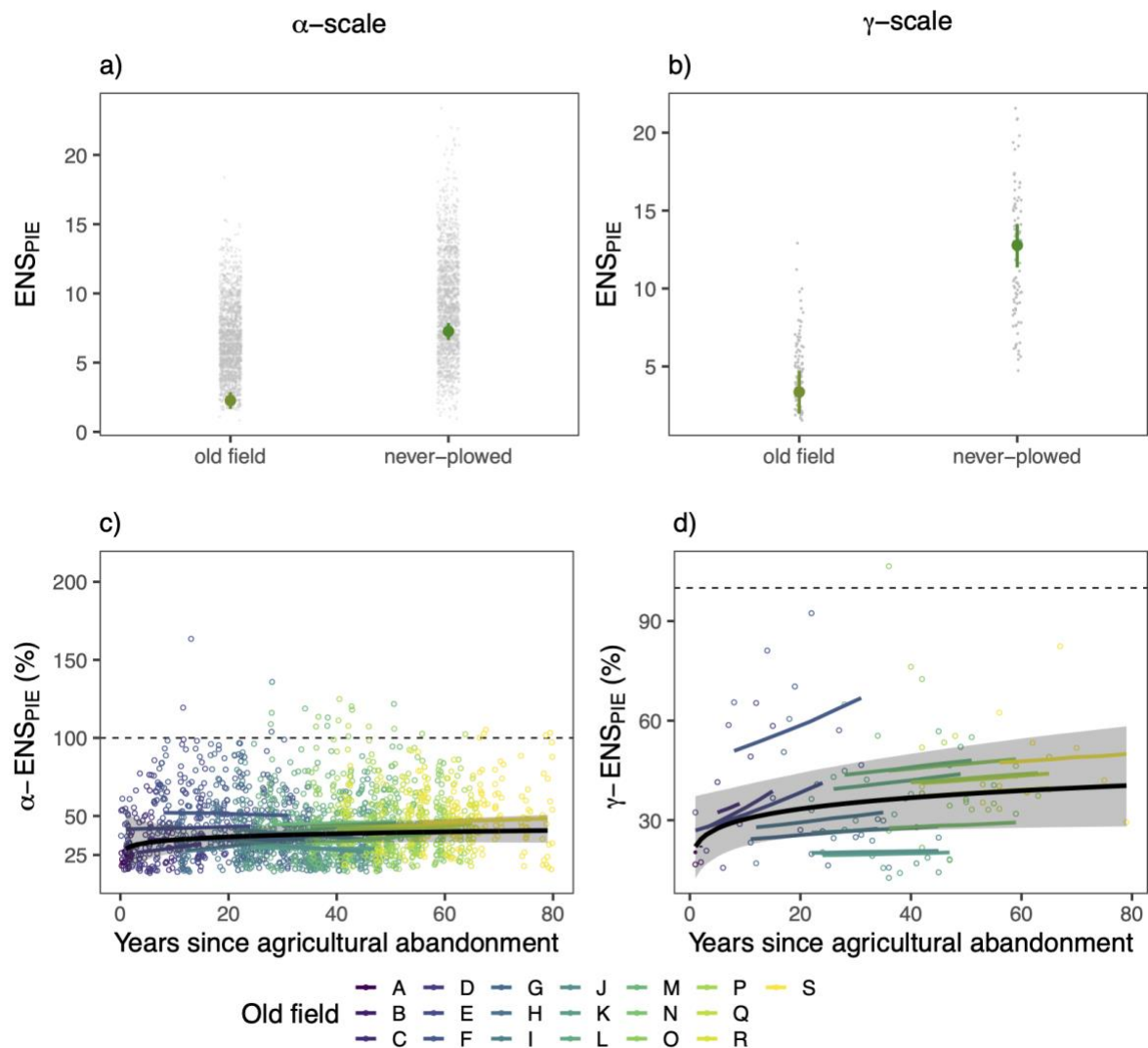
Figure 2: α-scale and γ-scale ENS_PIE a) α-scale and b) γ-scale ENS_PIE as a function of site status. Small points show data models were fit to; large points are the conditional effects of site status and the lines show the 95% credible intervals of conditional effects. c) α-scale and d) γ-scale species evenness as a function of 'years since agricultural abandonment'. Black dashed line represents the mean diversity metric of all never-ploughed sites (18 sites). The thick black line represents the mean fitted line of years since agricultural abandonment on species richness across all old-fields. The grey shading around the black line represents the 95% credible interval of that mean effect estimate. Each colored line represents the average predicted values for each site. Each open point represents an old-field plot (α-scale) or a site (γ-scale) calculated as the percentage of evenness, compared to never-ploughed sites. Y-axes vary for clarity.

447
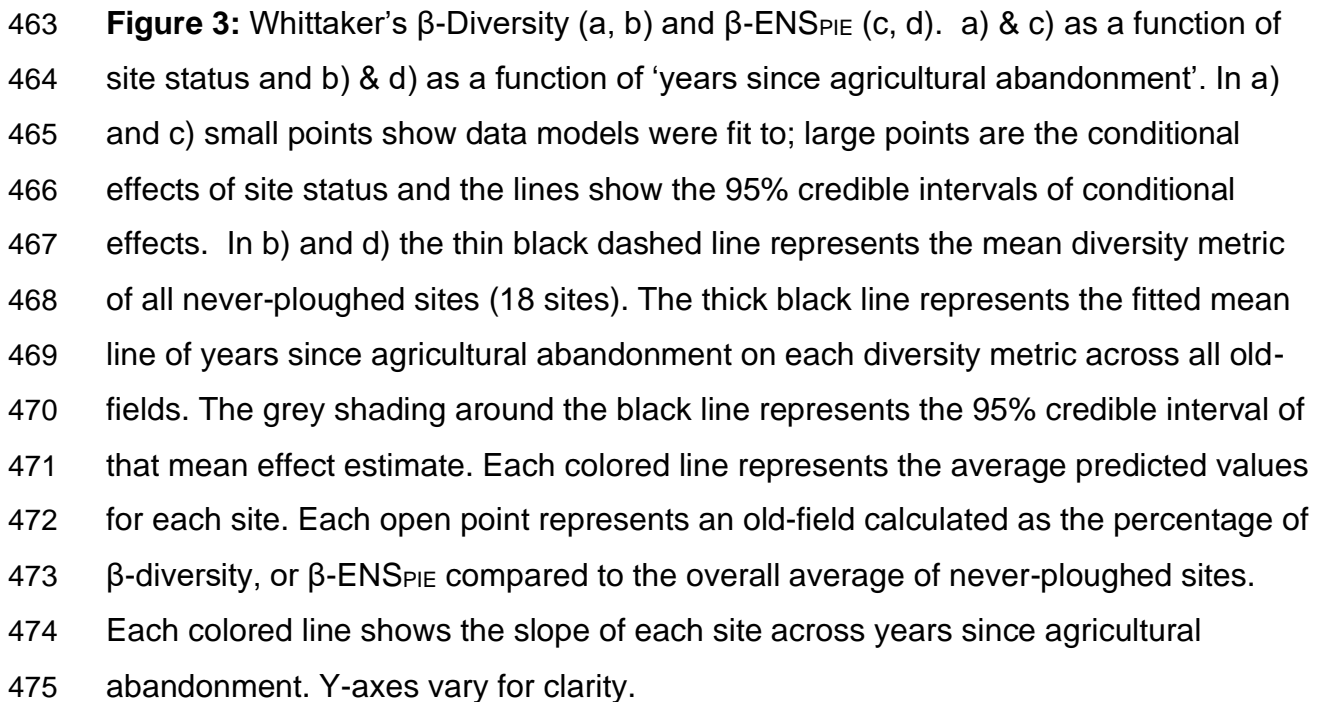
448

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, ß-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, $\beta\text{-ENS}_{PIE}$ 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, $\beta\text{-ENS}_{PIE}$ 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

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

476

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.
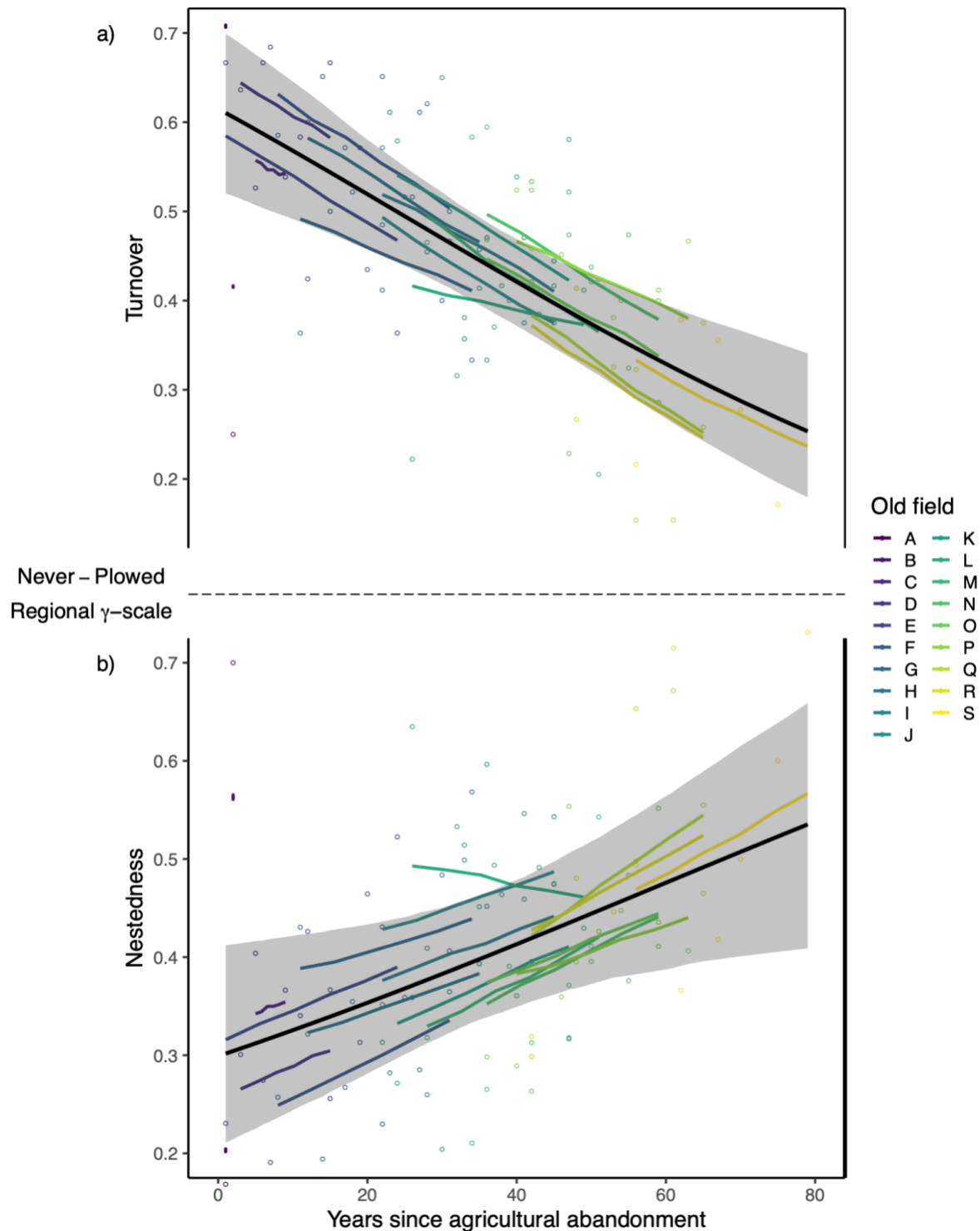
Figure 4: a) Spatial turnover and b) spatial nestedness components of Jaccard's dissimilarity index as a function of 'years since agricultural abandonment'. Each old-field at each time point was compared to the regional-γ species pool of all never-ploughed sites. The black dashed line represents a value of zero (0). The thick 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   fobs decreased (-0.57, CI: -0.98 to -0.20) and introduced legumes decreased (-0.10,

511   CI: -0.86 to 0.56).

512
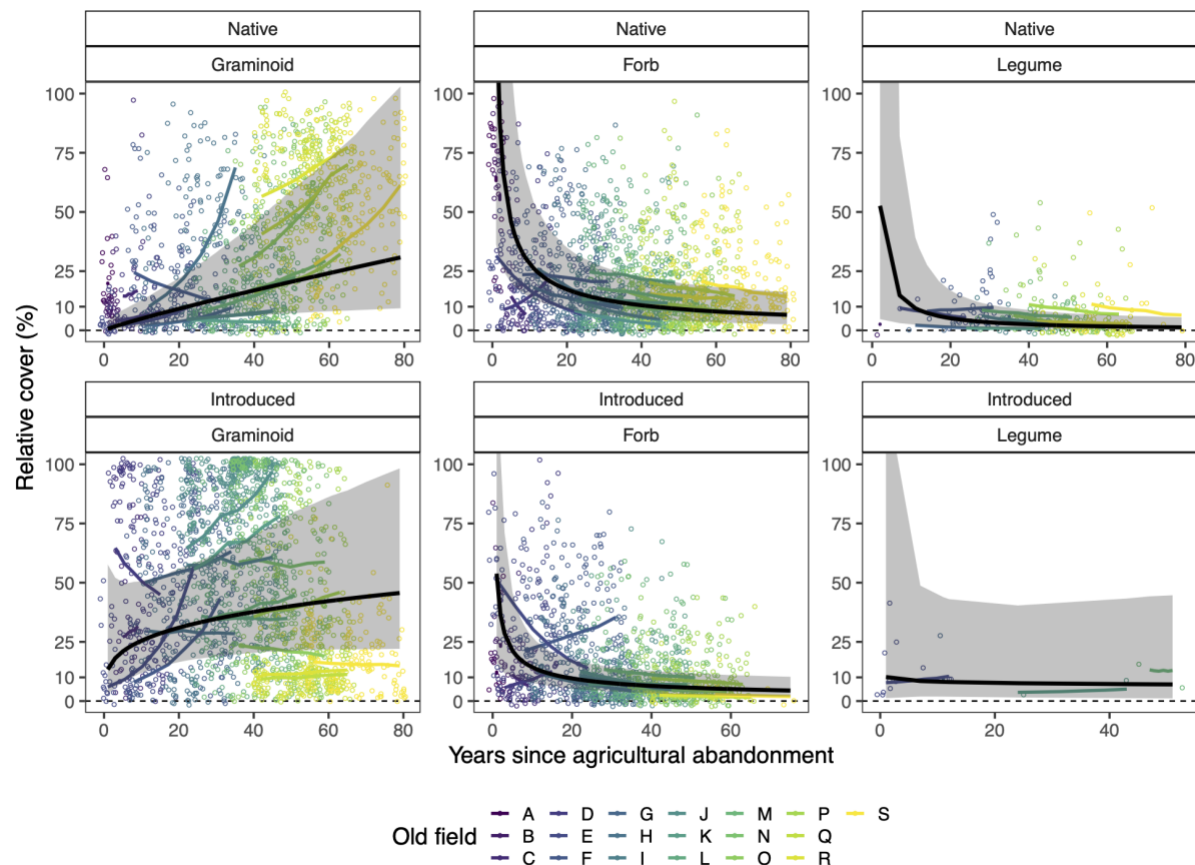
Figure 5: Relative cover of native a) graminoids b) forbs and c) legumes, and introduced d) graminoids e) forbs and f) legumes, characteristic of never-ploughed sites as a function of 'years since agricultural abandonment'. The thick black line represents the average effect of years since agricultural abandonment on species growth form and origin groups across all old-fields. The grey shading around the black line represents the 95% credible interval of that effect estimate. Each open point represents the relative cover of each respective growth form and origin in an old-field plot at a time since agricultural abandonment. Each colored line shows the predicted slope of each old-field across years since agricultural abandonment for each growth form and origin.

523

Discussion

524

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 (0.3m^2) 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 m^2)

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

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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