The recovery of biodiversity and species composition after agricultural abandonment across spatial scales

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

Word count (main text and references): 7099

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 or active ecological restoration. The recovery of biodiversity following the removal of disturbance (passive) is often incomplete. The magnitude of recovery can very much depend on the landscape matrix in which a local (within plots) community or patch (site) is embedded. Our detection of recovery depends on the temporal and spatial scales at which biodiversity is measured.

2. We measured the recovery of biodiversity and species composition over 27 years in 17 temperate grasslands with known agricultural land-use histories, comparing them to never-disturbed sites as benchmarks. We specifically measured aspects of diversity at the local plot-scale (α-scale, 0.5m^2), site-scale (γ-scale, 10m^2), as well as the within-site heterogeneity (β-diversity) and among-site variation in species composition (turnover and nestedness).
3. At the α-scale (within-plot), sites recovering after agricultural abandonment only had 70% of the plant species richness (and ~30% of the evenness), even up to 80 years post-recovery, compared to never-ploughed sites. Within-site β-diversity (heterogeneity) recovered following agricultural abandonment to around 90% after 80 years. This effect, however, was not enough to lead to recovery at the γ-scale (site-scale) richness in recovering sites was ~65% of that in remnant never-ploughed sites. The presence of species characteristic of the never disturbed sites increased in the recovering sites through time, suggesting the lack of full recovery was at least partially due to dispersal limitation.
4. ***Synthesis.*** We found that, during the 80 years after agricultural abandonment, old-fields did not recover to the level of biodiversity in remnant never-ploughed sites at any scale. β-diversity recovered more than α-scale or γ-scales, and plant species composition recovered, but not completely, over time. Time to full recovery is predicted to take an extremely long time, and to take different time spans at different spatial scales without intervention. Patterns of ecological recovery in degraded ecosystems across space and long time-scales can inform effective, targeted active restoration interventions and perhaps, help to lead to better outcomes.

Introduction

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

restoration of those ecosystems (Jones et al., 2018). Indeed, the United Nations has recently announced 2021-2030 as the Decade on Ecosystem Restoration, with the goal of restoring 350 million hectares of degraded land to achieve higher biodiversity and ecosystem functions (UNEA, 2019).

Restored ecosystems, including those that are passively (e.g., removal of disturbance) and actively (e.g., enhancement of environmental conditions or increasing species colonisation) restored, typically have increased biodiversity and ecosystem functions when compared to degraded systems (Rey Benayas et al., 2009). However, this recovery is typically incomplete (Jones et al., 2018; Moreno-Mateos et al., 2017; Rey Benayas et al., 2009). In addition, communities in restored/recovered ecosystems are often composed of more generalist and alien species when compared to reference sites that usually have more narrow-ranged and endemic species (Kaul & Wilsey, 2021).

Despite frequent studies on how biodiversity responds to anthropogenic impact and recovery (Murphy & Romanuk, 2014; Newbold et al., 2015), less attention has been paid to how inference of restoration on biodiversity depends on the ecological scale in which diversity is observed (Catano et al., 2021; Martin et al., 2005). Nevertheless, most measures of biodiversity inherently depend on the spatial scale on which samples are taken (i.e., a $1m^2$ quadrat compared to an entire site), and on the temporal scales which are measured (i.e., a year or a decade) (Matthews et al., 2021; Rosenzweig, 1995). As a result, scale can critically influence the magnitude in which biodiversity changes are quantified, even when sample effort is standardised (Chase et al., 2018; Chase & Knight, 2013; Field et al., 2009; Hill & Hamer, 2004; Sax & Gaines, 2003).

While the scale-dependence of biodiversity responses to anthropogenic activities are well known, the direction of scale dependence is less clear. Scale-dependent biodiversity responses to anthropogenic activities are most often studied in the context of changes to β-diversity, or the site differences in species composition (Chase et al., 2019; Socolar et al., 2016). Often, anthropogenic activities are thought to create a homogenization effect, reducing β-diversity (Gossner et al., 2016; Hautier et al., 2018; Martin et al., 2005). When β diversity is reduced by an anthropogenic driver, this can lead to cases where small to moderate effects of a driver at smaller scales (i.e., α-diversity) can become exacerbated at larger spatial scales. For example, (Smith et al., 2009) found that neotropical anuran communities that were impacted by an invasive fungal disease had fewer species in each locality (α-diversity). However, because more narrowly distributed species were more strongly influenced by the disease than more widespread species, β-diversity decreased, and the effect at the larger (γ-diversity) spatial scale was greater.

On the other hand, anthropogenic activities can lead to communities becoming more different between sites (higher β-diversity), which can lead to cases where relatively larger effects of a driver occur at smaller spatial scales (i.e., α-diversity). These negative effects weaken as scale increases (i.e., γ-diversity). For example, (Powell et al., 2013) found that the invasion of forested sites by dominant alien plant species lead to a strong reduction in small-scale species richness, but this negative effect dissipated as scale increased.

There are many underlying factors that can influence the direction and magnitude of scale-dependence resulting from anthropogenic drivers, with numerous examples supporting each (Chase et al. 2018, 2019). In the literature of tropical forest disturbances (i.e., logging), opposite scale-dependent patterns among birds

and butterflies have been found (Hill & Hamer, 2004). In this case, disturbance generally decreased bird diversity at small scales, but increased it at larger scales by increasing β-diversity. On the other hand, disturbance generally increased small scale diversity of butterflies, but decreased large scale diversity by decreasing β-diversity.

When considering how biodiversity recovers following cessation of disturbance, scale-dependence of biodiversity responses can emerge. For example, following removal of an anthropogenic effect, even with active restoration actions, small-scale (α) diversity usually does not fully recover to pre-disturbance levels (Isbell et al., 2019; Moreno-Mateos et al., 2017; Rey Benayas et al., 2009). What is less clear, however, is how β and γ-diversity respond during recovery. If β-diversity is not influenced by the removal of disturbance and does not increase through time, the incomplete recovery of diversity following restoration would be equivalent at both α (within-plot) and γ (site) scales. If β-diversity is reduced by removal of disturbance (i.e., via homogenization) and does not recover during restoration, the incomplete recovery of α diversity would be exacerbated at larger (γ) scales. Finally, if β-diversity increases following removal of the disturbance, incomplete recovery of α diversity could be accompanied by a more complete recovery of diversity at larger spatial scales. To date, few studies have examined the influence of recovery and restoration on the scale-dependence of biodiversity and β-diversity in particular, and those that have measured β-diversity in a number of different, often incomparable ways. There is some evidence that β-diversity and γ- diversity recover even less than α-diversity (Martin et al., 2005; Passy & Blanchet, 2007; Polley et al., 2005; Wilsey et al., 2005). In a meta-analysis of grassland studies, however, (Catano et al., 2017) showed that the effects of disturbance can lead to homogenization (lower β-diversity) or

differentiation (higher β-diversity) depending on the effects of disturbance on stochastic factors and dispersal rates. Furthermore, β-diversity can be enhanced in restoration, for example, when restoration actively targets β-diversity via larger species pools (Grman & Brudvig, 2014).

While there is evidence of deficits of α, β and γ-diversity in recovering and restored ecosystems, and in grassland systems in particular (Martin et al., 2005; Polley et al., 2005), it remains unclear how long these potential deficits are manifest on the landscape. Grasslands are one of the most endangered and least protected biomes globally (Hoekstra et al., 2004), and are experiencing extreme levels of land use change both within sites due to changing agricultural practises within the surrounding regional landscape matrices (Carbutt et al., 2017; Roch & Jaeger, 2014). Here, we take advantage of long-term surveys of prairie vegetation in remnant savannah prairies and recovering grasslands at the Cedar Creek Ecosystem Science Reserve in Minnesota (USA). Isbell et al. (2019) used data from remnant prairies and a 37-year survey of old-fields with different levels of time since agricultural abandonment (ranging from 1 to 91 years) to examine how α-scale (within-plot) species richness, species diversity, evenness and productivity recovered (measured in 0.3 m^2 plots). They found that even after more than 91 years since abandonment of agriculture, the numbers of species only recovered to 75% of their values in the reference site that was never-ploughed and that α-scale species evenness was not substantially altered by land use changes. However, because species richness is a scale-dependent metric, it is unclear how larger scale diversity recovered. Using the same system, but different sampling sites as Isbell et al. (2019), and taking spatial scale explicitly into account, we asked the following: (1) how do larger scale measures of diversity (i.e., β and γ-diversity) vary through time across the chronosequence following agricultural

abandonment and how do they compare to the smaller scale (α) measures? (2) How do measures of diversity other than species richness, such as those that incorporate evenness, respond at the α, β and γ - scales? (3) How has species composition, as a different component of recovery compared to measures of richness and diversity, responded through time? (4) How long can we expect recovery to take without intervention across each scale?

Methods

Study system

Cedar Creek Ecosystem Science Reserve is a 2,200-hectare long-term ecological science reserve (LTER) run by the University of Minnesota (USA) in cooperation with the Minnesota Academy of Science 50 km north of Minneapolis. Cedar Creek is a mosaic of prairie and forest including oak savanna, prairie, abandoned agricultural sites (old-fields) and preserved pre-agricultural ecosystems (never-ploughed remnants). The natural history of Cedar Creek is described in detail in (Clark et al., 2019; Inouye et al., 1987). Relevant summarised points include that agricultural land use began after 1900, but aerial photography suggests some areas of forest and savanna were never cleared (MHAPO, 2015; Pierce, 1954).

Study design and sampling

We analysed vegetation from several sites that were part of long-term research at the Cedar Creek Ecosystem Science Reserve. Specifically, we used data from otherwise comparable sites that could be categorised into two treatments (see Table S1 for details): (1) Never-ploughed sites, which included 18 upland oak

savannas (plots of “Experiment 133”); (2) recovery plots that included 17 old-fields which were ploughed and used for agriculture, but were abandoned so that natural succession and recovery of the vegetation could be followed (“Experiment 014”). Old-fields were abandoned between 1927 and 2015 (Clark et al., 2019). Each field was measured approximately 6 times, with ~5-6 year measurement intervals from 1983- 2010 (27 years). At the start of the surveys, old-fields ranged from 1 year since agricultural abandonment to 48 years (Figure S1). For surveys in both experiments, plants were estimated using species-level percent cover (“Experiment 14”) and percent cover classes (“Experiment 133”) in 0.5 m^2 plots.

Data preparation

We did not include sites from the never-ploughed sites that had also never been burned. This is because fire is a natural disturbance that maintains these systems, and woody encroachment ensues when there is human-induced fire suppression (Clark et al., 2019). Within the old-fields, we kept all plots surveyed in years before the first year of burning, or those that have not been burned to represent site recovery after abandonment before fire. We also did not include sites that contained many trees (Clark et al., 2019). For the purposes of our comparisons, and because sample effort was not equal between all of the sites, we used 20 randomly selected survey plots from each site (site E014 was sub-sampled to match the number of samples in site E133). We took the midpoint of each cover class to quantify percent cover of species, so that the summed cover of all species could exceed 100%. Species cover relative to each plot's summed cover was quantified as a proportion.

Calculating Within-Site Metrics of Diversity

We examined how biodiversity recovered across scales by calculating and comparing multiple metrics of diversity at multiple scales between the never-ploughed and recovery treatments. We followed the recommendations of (Chase et al., 2018), and estimated diversity at two spatial scales: (i) the α-scale, which was the diversity in a given 0.5m^2 plot in a given treatment and year, and (ii) the γ-scale, which here we define as the total diversity in 20 0.5m^2 plots within a site in a given treatment and year. Note, here we simply use α and γ- diversity to denote smaller and larger scales, and make no assumptions whether these scales correlate with any local or regional coexistence mechanisms. Finally, from these α and γ estimates, we calculate (iii) Whittaker's multiplicative β-diversity ($\beta = \gamma/\alpha$, (Whittaker, 1972) to quantify plot-to-plot variation, or the heterogeneity of plots within sites at each time point. While the sampling approach was not designed to sample the range of variation in the whole site, the amount and the equal number of samples across sites allows an estimation of this variation. Additionally, we extrapolated expected species accumulation across 50 samples for species richness to estimate a γ-scale for a larger spatial area (Chao et al., 2014).

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

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

Across treatment differences in species composition

The measures of biodiversity (species richness and ENS_{PIE}) explored here across scales (α, β, γ) allow us to compare numbers and types of species from plots within a given site status (i.e., never-ploughed versus ploughed sites). They do not, however, allow us to quantify the difference in species composition between the sites. For example, many highly specialised prairie and savanna plants rarely establish in the early phase of old-field recovery, which instead is dominated by weedy species that are less frequently found in pristine sites (Inouye et al., 1987). To quantify the difference in species composition between never-ploughed sites and recovering sites, we calculated Jaccard's dissimilarity index indicating the dissimilarity in species composition between treatments (ranging from 0 to 1). We then partitioned the difference between the turnover and nestedness components of Jaccard's index using the R package beta.part (Baselga, 2009; Baselga & Orme, 2012).

The presence of species across all never-ploughed sites was quantified at each time point measured (1984, 1990, 1995, 2000, 2005, 2010) to determine the 'regional-γ' species pool for the never-ploughed sites. The species within each old-field at each time point (1983, 1989, 1994, 1997, 2002, 2006) (γ-diversity) was then compared to the regional-γ-scale species pool for never-ploughed sites at the closest calendar year measured (eg. 1983 compared to 1984) as a single pairwise comparison (Marion et al., 2017). We also compared each old-field to every individual never-ploughed site within a given time bracket, which yielded qualitatively similar results. Here, we present a comparison between each old-field at every time-point to the entire regional-γ never-ploughed species pool at the nearest comparable time point. This quantifies the compositional change of each old-field since agricultural abandonment compared to the total diversity of all never-ploughed sites across space and time. If species from the regional-γ species pool of never-ploughed sites were recolonizing old-fields over time, we expect nestedness to increase in each old-field as years since agricultural abandonment progress. If species colonising old-field sites since abandonment are different from that of never-ploughed sites, then we would expect the turnover component to increase across time.

Statistical analysis

All data preparation, manipulation, calculation of diversity metrics, analysis and graphic visualisation of results were conducted in the R Environment for Statistics and Computing (R Core Development Team, 2019). We used the iNEXT package (Chao et al., 2014; Hsieh, T.C. et al., 2020) to interpolate and extrapolate (up to 50 samples) species accumulation across scales based on average observed samples across each site status and year since agricultural abandonment (Figure

S2, S3). To quantify diversity metrics we used tidyverse and vegan packages and for dissimilarity we used the beta.part package (Baselga & Orme, 2012; Oksanen et al., 2019).

Field status (old-field vs never-ploughed) effects on biodiversity were quantified using hierarchical linear models (Discrete analysis). All models included site status as old-field or never-ploughed as a categorical fixed effect. Site and calendar year were modelled as random intercepts and random effects (Supplementary Information Table S2, Figure S4-S8 for all model details).

The effect of years of agricultural abandonment on the recovery of old-fields compared to the never-ploughed sites at each scale of diversity were quantified using hierarchical linear models (continuous analysis). Year since agricultural abandonment (YSA) was modelled as a continuous fixed effect and was log-transformed. We found logarithmic trends to be the most parsimonious for all statistical models similar to previous work (Isbell et al., 2019). Each diversity component in old-fields at each scale was quantified as the percentage compared to the mean of the never-ploughed sites at that same metric and scale and was log-transformed. Random intercepts and slopes were allowed to vary for years since agricultural abandonment, and intercepts for categorical calendar year, assuming variation between each site, the year it was abandoned and each calendar year sampling started (Supplementary Information for all model details). For the α-scale, plot nested within transect, nested within site were modelled as random effects and for β and γ-scales, site was modelled as a random effect. We then predicted overall estimates for species richness across each scale (α-scale, γ-scale, β-scale) as function of year since agricultural abandonment to quantify the predicted time to ~95%-100 recovery for each scale of measurement. We predicted values in intervals

of 25 years for each metric up to a maximum of 1000 years. β-diversity was predicted from the β-diversity model, but also by using predicted α and γ values to calculate and estimate predicted β-diversity, and estimates were extremely similar. These predictions harbour an enormous amount of uncertainty, and represent predictions of recovery only for these sites, under only this type (agricultural) of disturbance, incorporating no other factors that might affect recovery other than the trajectory of recovery at each scale according to the data we currently have.

Year of abandonment effects on the turnover and nestedness components of Jaccard's dissimilarity were quantified using two univariate hierarchical linear models (dissimilarity analysis). Year since abandonment (YSA) was modelled as a continuous fixed effect. Site was modelled as a random effect. Random intercepts and slopes were allowed to vary for years since agricultural abandonment, for calendar year, assuming there was variation in each site and each year.

For Bayesian inference and estimates of uncertainty, models were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter et al., 2017), and coded using the brms package (Bürkner, 2018). All models were fit with four chains and differing iterations (See Supplementary Information for all model details). We used weakly regularizing priors and visual inspection of the HMC chains showed excellent convergence.

Results

α-scale and γ-scale species richness

For the discrete analysis (top row Figure 1), at the α-scale (0.5 m^2), old-field plots overall had on average 59% of species richness (5.65, 95% credible interval:

4.66 to 6.56) found in never-ploughed sites (9.59, CI: 8.70 to 10.51, Figure 1a). At the γ-scale (the combination of 20 plots and thus $10m^2$) old-field sites had approximately 55% fewer species (23.6, 21.2 to 26.1) than never-ploughed sites (42.6, 38.6 to 47.1, Figure 1b). We found a similar difference between old-fields and never-ploughed sites when we extrapolated species richness estimates based on incidence-based species accumulation out to 50 samples (Figure S2, S3).

In the continuous analysis (bottom row Figure 1), at the α-scale, richness weakly increased across years since agricultural abandonment, but with high uncertainty (Slope: 0.13, 95% credible interval: -0.17 to 0.53, Figure 1c). After ~80 years since abandonment, α-scale species richness in old-fields was about 70% of that found in never-ploughed sites. At the γ-scale, grassland species richness increased across years since agricultural abandonment (Fig. 1d), but again with high uncertainty (Slope: 0.13, CI: -0.11 to 0.40). γ-scale richness in old-fields was about 65% of that found in never-ploughed sites after 80 years. That is, at both the α-scale and γ-scale recovery after agricultural abandonment at this temporal resolution (sites measured ~ every six years) there is a weak positive trend of species richness recovery.

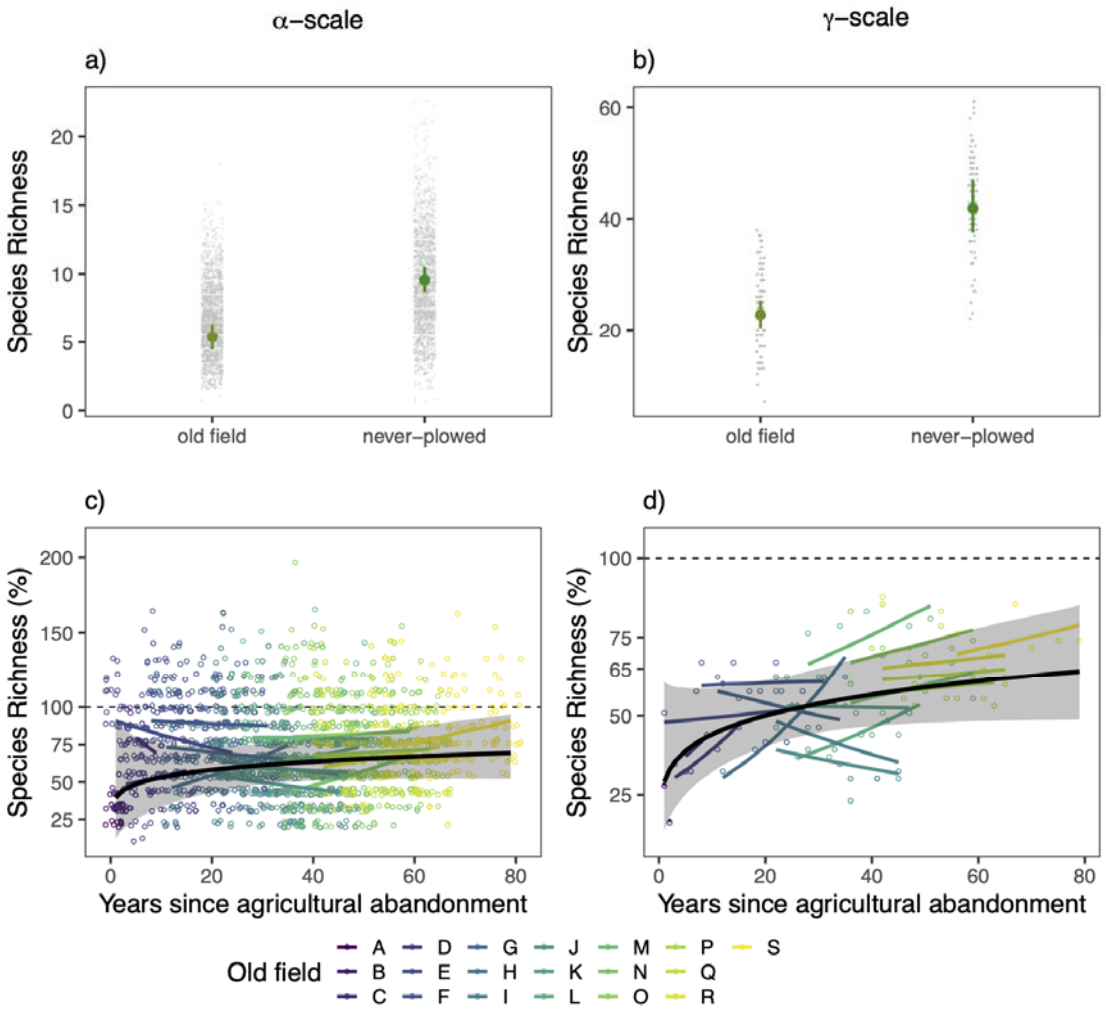

Figure 1: α-scale and γ-scale species richness. a) α-scale and b) γ-scale species richness as a function of site status. Small points show data models were fit to; large points are the conditional effects of site status and the lines show the 95% credible intervals of conditional effects. c) α-scale and d) γ-scale species richness 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 average effect 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 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 richness, compared to never-ploughed sites. Y-axes vary for clarity.

α-scale and γ-scale ENS_{PIE}

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

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

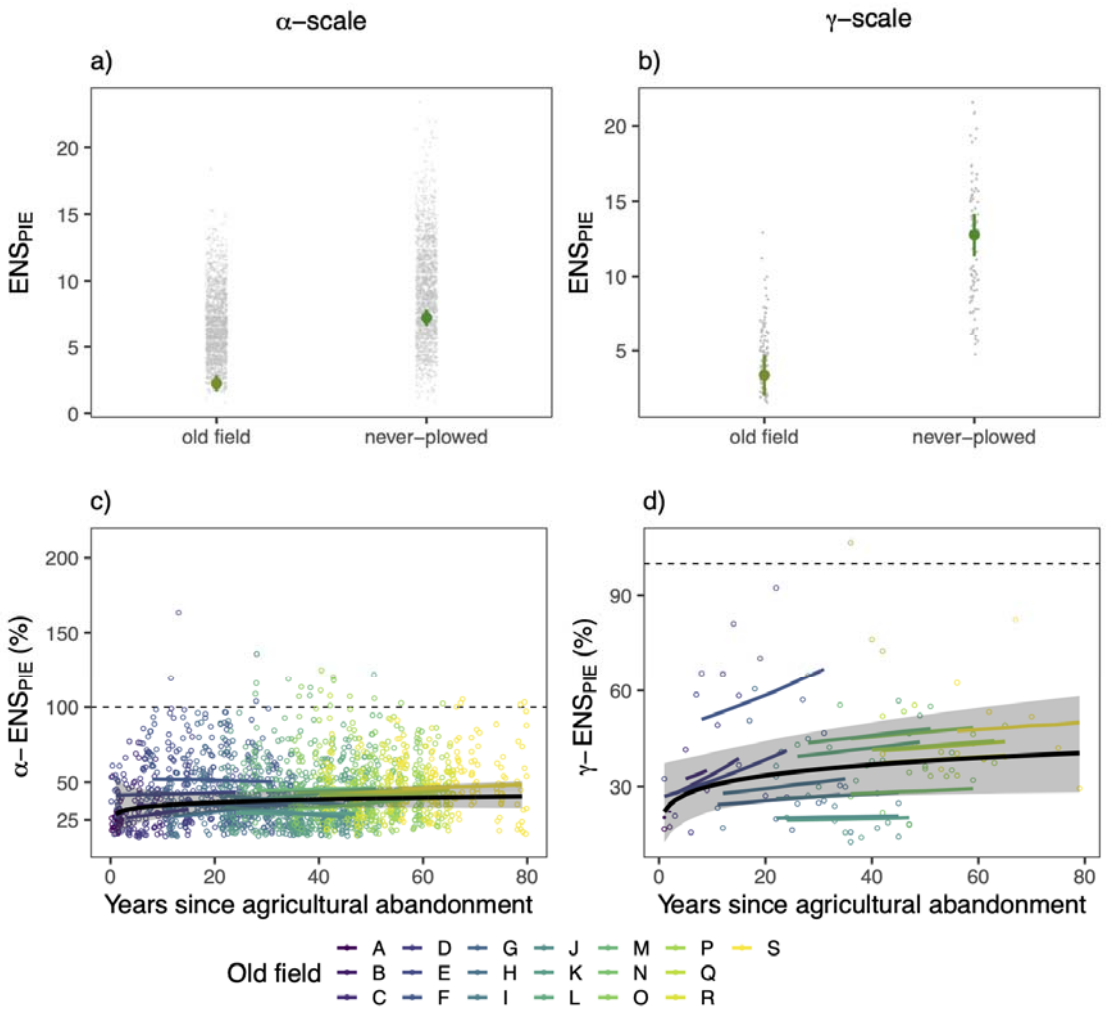

Figure 2: α-scale and γ-scale ENS_{PIE} a) α-scale and b) γ-scale ENS_{PIE} as a function of site status. Small points show data models were fit to; large points are the conditional effects of site status and the lines show the 95% credible intervals of conditional effects.

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.

β-diversity

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

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

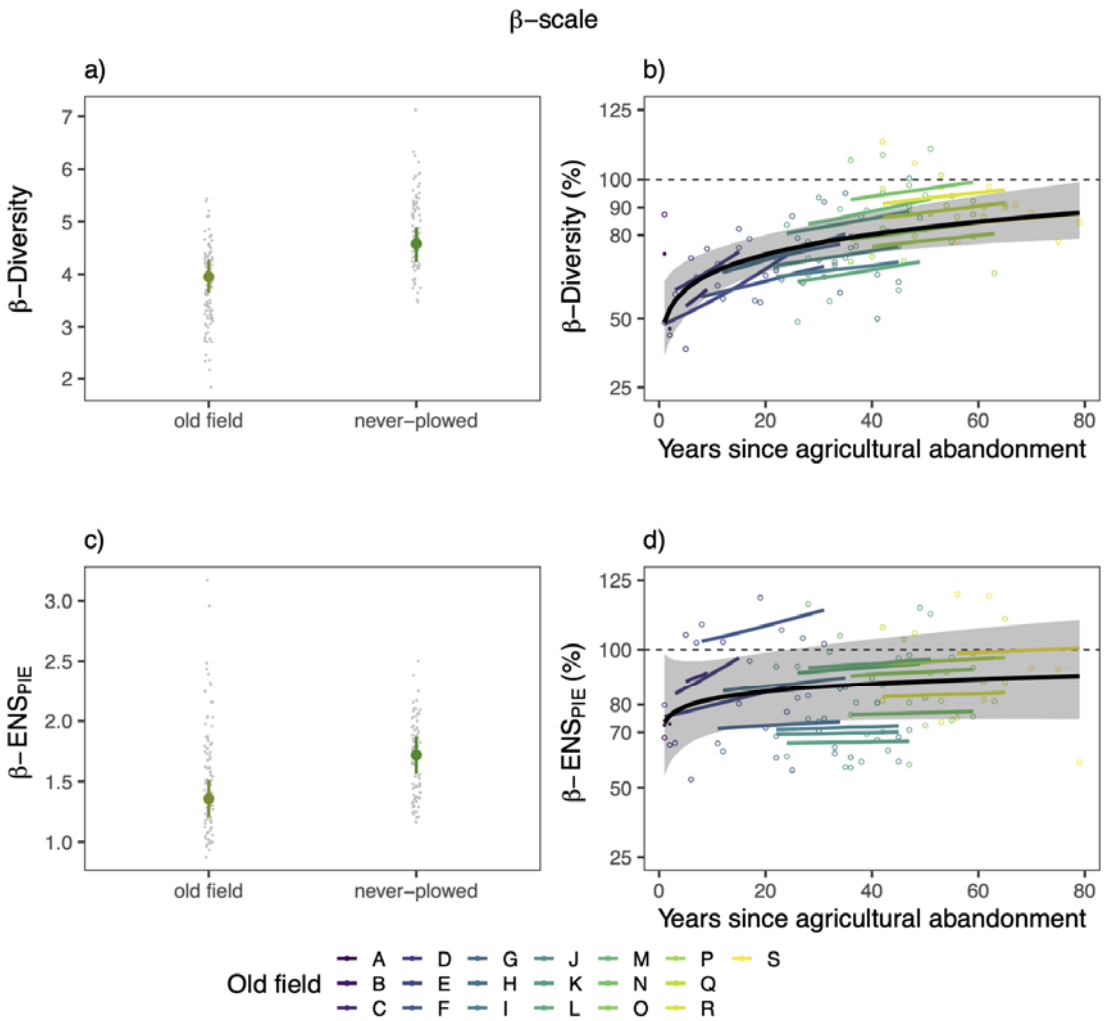

Figure 3: Whittaker's β-Diversity (a, b) and β-ENS_{PIE} (c, d). a) & c) as a function of site status and b) & d) as a function of 'years since agricultural abandonment'. In a) and c) small points show data models were fit to; large points are the conditional effects of site status and the lines show 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.

Community Composition

In total, we found 63 species that occurred in never-ploughed sites, but never in any old-fields. There is evidence that old-fields are colonised by exotic weeds at the start of abandonment and are slowly replaced by native species characteristic of never-ploughed sites over time. Dissimilarity due to turnover in old-fields compared to never-ploughed sites decreased across years since abandonment (Slope: -0.02, 95% Credible Interval: -0.03 to -0.01). That is, old-fields were colonised with species that were unique to old-field sites, when first abandoned, and this decreased over time. Dissimilarity due to nestedness in old-fields compared to never-ploughed sites increased across years since abandonment (Slope: 0.01, CI: 0.001 to 0.02). That is, old-fields were increasingly colonised by species characteristic of the never-ploughed sites over time since abandonment, but never fully converged.

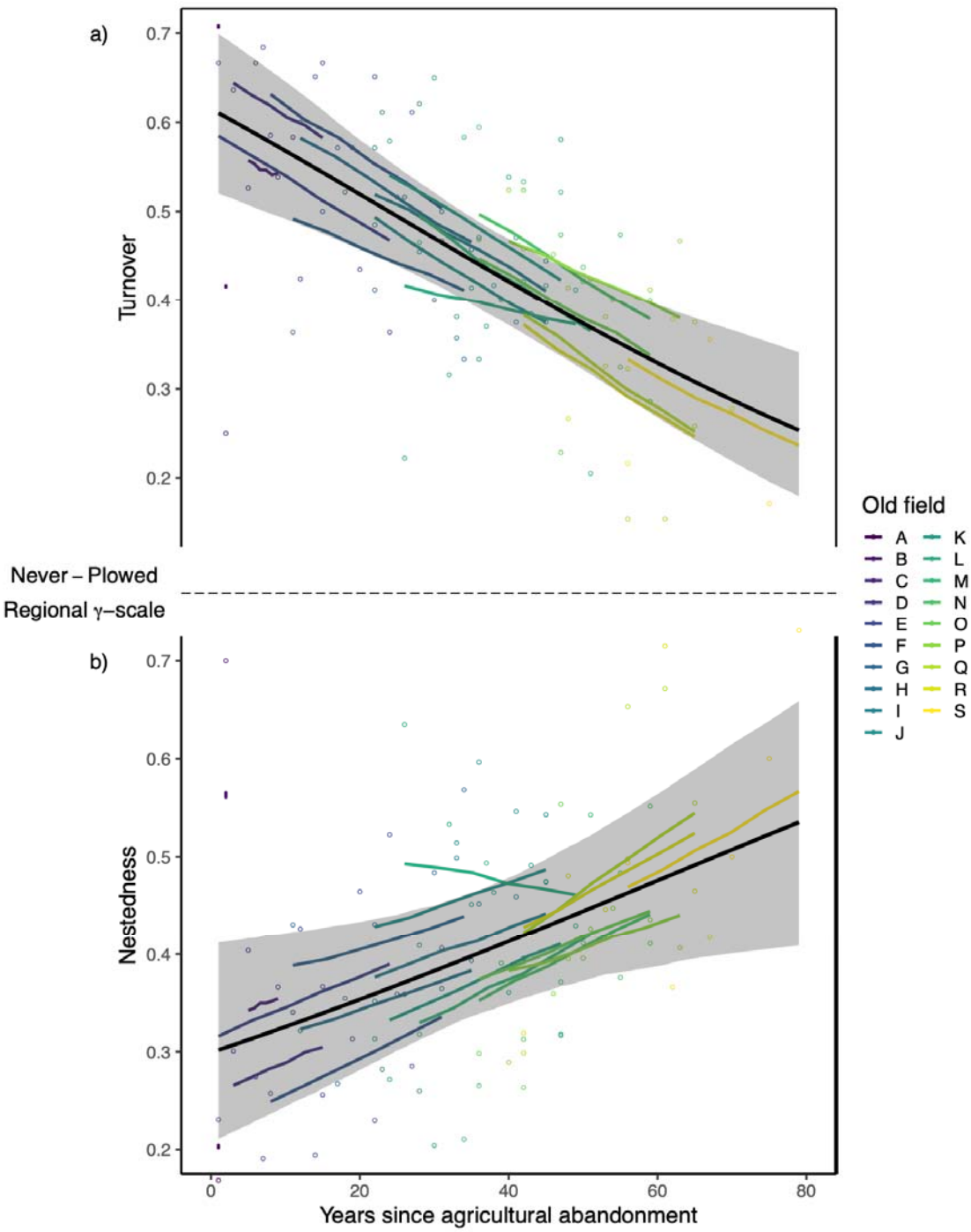

Figure 4: a) Spatial turnover and b) spatial nestedness components of Jaccard's dissimilarity index as a function of 'years since agricultural abandonment'. Each old-field at each time point was compared to the regional-γ species pool of all never-ploughed sites. The black dashed line represents a value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

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

Predicted Recovery

By predicting percent recovery across each scale as a function of years since agricultural abandonment, we quantify how long old-fields might take to recover across time without intervention (active restoration). We project that at the α-scale species richness is expected to recover to approximately 95% after 1000 years of abandonment, that γ-scale species richness is expected to recover to approximately 95% after 750 years of abandonment, and that β-Diversity is expected to recover to 95% of that seen in never-ploughed sites after approximately 150 years. We predict that heterogeneity and γ-scale species richness recover faster than species richness at α-scales.

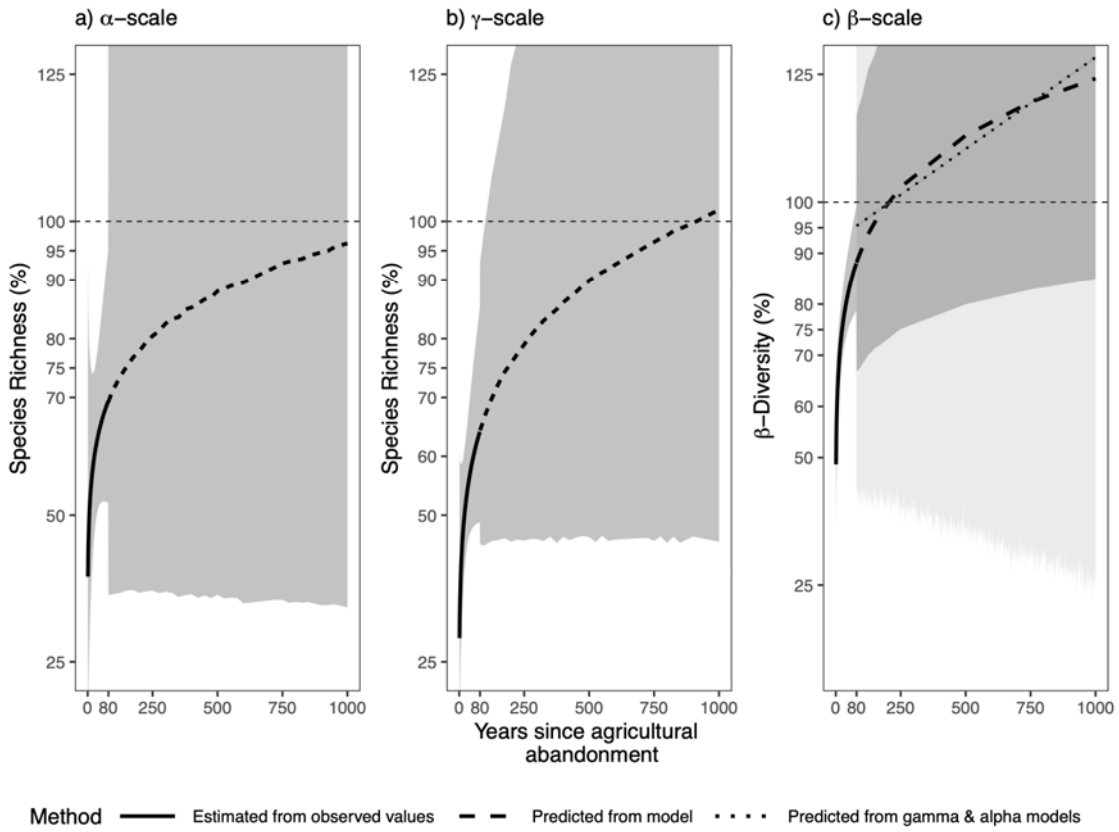

Figure 5: a) α-scale species richness b) γ-scale species richness c) and β-Diversity, % recovery as a function of 'years since agricultural abandonment'. Thin horizontal black dashed lines represent the mean diversity metric of all never-ploughed sites (18 sites). The thick black solid curved lines represent the average estimated effect of years since agricultural abandonment from observed values for each metric, and thick black dashed portions of the curve represent predicted estimates across years since abandonment. Dotted line in c) represents β-Diversity estimated from predicted α and γ values.

Discussion

A major tenet in disturbance ecology has traditionally been that, given enough time, removal of anthropogenic disturbances such as agriculture will allow biodiversity to recover (Moreno-Mateos et al., 2017). At the same time, accruing evidence suggests that, in the absence of active restoration interventions (and even

in their presence), this recovery can take an exceedingly long time and is often incomplete (Buisson et al., 2018; Isbell et al., 2013; Nerlekar & Veldman, 2020). For example, using many of the same sites as in the present study (see Supplementary Table 1 for details), Isbell et al. (2019) showed that species richness in α-scale ($0.3m^2$) plots had recovered to only ~75% of that of the never-ploughed sites even after 91 years of recovery. Unsurprisingly, we found similar results at the α-scale (0.5 m^2), where within-plot species richness increased slightly through time, but remained ~70% lower than never-ploughed plots, even after 80 years of recovery (Figure 1c).

Importantly, coexistence and diversity are highly scale-dependent patterns and it is less clear how larger-scale patterns of diversity recover. Anthropogenic disturbances are known to often influence β-diversity in grassland ecosystems, both positively and negatively (Catano et al., 2017; Eskelinen & Harrison, 2015; Martin et al., 2005; Polley et al., 2005). As a result, we might expect exacerbated effects of that driver and recovery at larger spatial scales (if β-diversity is lower) or enhanced effects of that driver and recovery at larger spatial scales (if β-diversity is higher). We found that β-diversity was indeed lower than in never-ploughed sites following agricultural abandonment, and while this diversity showed signs of recovery over time, it remained lower overall than in the never-ploughed sites. Complementary results have been found in successional sites that showed heterogeneity among plots increasing and across sites decreasing as succession progressed (Li et al., 2016).

Given the lower β-diversity in recovering compared to never-ploughed sites (Fig 3a), we might expect that the magnitude of the deficit of species richness in recovered relative to never-ploughed sites might increase with spatial scale. This was true for the absolute number of species; the deficit in recovering relative to

never-ploughed sites was ~4 species at the α-scale (Figure 1a), but ~19 species at the γ-scale (Figure 1b). But it was not true for the ratio of the deficit; the deficit of species richness was 59% at the α scale (Figure 1a), with a similar recovery deficit of 55% at the γ-scale (Figure 1b). In addition, there was little evidence that the deficit in species richness declined through time over the course of the observations. Although we cannot explicitly discern the mechanism underlying the continued deficit of species richness at α and γ-scales in these recovering old-fields, we suspect dispersal limitation might play a key role. Several previous studies at the study site have shown that seed additions can lead to significantly increased levels of species richness (Fargione et al., 2011; Ladouceur et al., 2020; Symstad, 2000; Tilman, 1997). Even seeds added to a never-ploughed prairie-savanna led to a doubling of α plant diversity that persisted for 13 years or longer (Catford et al., 2019; Tilman, 1997). This is also consistent with our results comparing the nestedness and turnover components of compositional dissimilarity, which indicated that species composition in the old-fields was becoming more similar to the never-ploughed sites over time (Figure 4), likely through species gains (Foster & Tilman, 2000). However, it is also quite possible that the soils in recovering sites have been significantly altered so that environmental filters also play a role in limiting recovery (Seabloom et al., 2020). Another explanation is extinctions might be occurring across the system following long time periods since fragmentation and habitat destruction, leading toan extinction debt (Tilman et al., 1994).

By comparing the results of how species richness recovered following agricultural abandonment to those of ENS_{PIE}, a diversity metric that accounts for the most common species, we can see how patterns of recovery are influenced by more common versus rare species. In this case, ENS_{PIE} following agricultural

abandonment recovered to only ~31% of that observed in the never-ploughed sites at the α-scale (Figure 2a). Compared to the ~59% recovery of species richness at the α-scale (Figure 1a), this suggests that much of the recovery of species richness was among species that are relatively rare in the community and that there is less recovery of evenness in the community. At the site scale, ENS_{PIE} in old-fields recovered to 28% of that in never disturbed sites (Figure 2b), compared to the 55% recovery of species richness at the site scale (Figure 1b). The higher recovery of species richness than ENS_{PIE} is also consistent with previous studies (Martin et al., 2005; Sluis, 2002; Wilsey et al., 2005), suggesting that rarer species drive a lot of the passive recovery in abandoned old-fields.

Finally, despite the fact that measurements of species diversity (richness and evenness) only partially recovered across scales even after nearly a century of agricultural abandonment, species composition has consistently recovered through time (Figure 4). Early in the time series, recovering old-fields were colonised by species not typically found in never-ploughed sites. These species, such as *Agrostis scabra, Agropyron repens, Vicia villosa and Berteroa incana,* are often rapid colonising and weedy species indicative of early successional sites (Inouye et al., 1987). However, through time, these early colonising species went extinct and were replaced by species more characteristic of native prairies and savannahs of the region, such as *Andropogon gerardii, Schizachyrium scoparium, Solidago rigida, and Liatris aspera*.

Finally, we predict that without intervention, recovery to 95% of reference sites may take hundreds of years more, but this time to recovery is different for each scale (Figure 5). Of course, this prediction has many limitations. First, it does noorporate might interact with disturbance cessation. Second, this represents

recovery from one type of disturbance, at this one location, and this model can only represent the range of data we have. Consistent with observed values, we expect β-Diversity to recover the fastest, followed by g-Diversity and a-Diversity taking up to 1000 years, but with considerable uncertainty around these estimates. To accelerate or assist this recovery, intervention via restoration may be considered a favourable option. Predicting recovery across scales, across space, and time, can help to improve the use of ecological references and possibly help to target restoration efforts at different spatial and temporal scales (Shackelford et al., 2021).

Overall, our results show that analyses of multiple metrics across scales more fully reveals how ecological communities recover following disturbance in space and time. We specifically examined a system without active restoration, and found that recovery is incomplete across scales for a very long time. To initiate or accelerate recovery at α and γ-scales, active restoration treatments may prove necessary to achieve more complete recovery.

Acknowledgements

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

Author Contributions

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

Data Availability

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

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