Deficits of biodiversity and productivity linger a century after agricultural abandonment

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At the global scale, human activities are threatening the extinction of many species. It remains debated, however, whether there has been corresponding loss of biodiversity at the smaller spatial scales at which species loss often erodes ecosystem functioning, stability and services. Here we consider changes in local biodiversity and productivity over 37 years in 21 grasslands and savannahs with known agricultural land-use histories. We show that, during the century following agricultural abandonment, local plant diversity recovers only incompletely and plant productivity does not significantly recover. By 91 years after agricultural abandonment, despite many local species gains, formerly ploughed fields still had only three quarters of the plant diversity and half of the plant productivity observed in a nearby remnant ecosystem that has never been ploughed. The large and growing extent of recovering ecosystems provides an unprecedented opportunity to reverse the impacts of habitat loss. Active restoration efforts are needed to enable and accelerate recovery.

Earth may be entering its sixth mass extinction event[1], this time caused by human activities[1–3], especially in the case of habitat loss[4]. There is concern that a loss in biodiversity will lead to the loss of ecosystem functioning, stability and services, such as the regulation of climate and the production of timber, livestock forage and fish[5]. There remains a mismatch, however, between the large scales of space and time at which species are going extinct and the smaller local scales at which species interact and at which the local loss of species is known to alter ecosystems[5–7]. Rapid species extinctions at the global scale do not necessarily translate into equally rapid rates of species loss at sub-global scales because extirpations (the loss of species at regional or local scales) can be offset by species gains due to the arrival of species from other places[8–10].

There is an ongoing debate regarding whether[11,12] or not[13,14] there has been any systematic loss of biodiversity at sub-global scales, within local communities of interacting species[5,15–18]. Studies of temporal trends in local biodiversity have found about as many places with species gains as losses during recent decades[13,14,19], leading to assertions that there has been no systematic loss of local biodiversity[13,14] and therefore no impact of global extinctions on ecosystem functioning[13] (grey lines in Fig. 1), because most of the evidence for the dependence of ecosystem functioning on biodiversity comes from experiments that manipulate local biodiversity[5–7]. By contrast, spatial comparisons of biodiversity and experiments have found systematic loss of biodiversity at locations that are influenced by agriculture and other human activities[11,12,20–22]. Temporal and spatial approaches each have unique strengths and limitations. Time series have the advantage of integrating all of the influences of anthropogenic drivers of biodiversity changes, including the well-studied drivers of species loss and the less-studied drivers of species gains. Space-for-time comparisons are uniquely able to consider biodiversity changes that may have occurred before the time series began, providing a way to account for shifted baselines. Here, by leveraging the strengths of both time series and space-for-time comparisons,
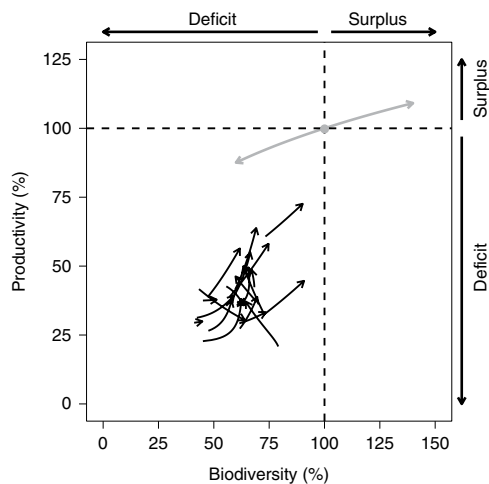
we show how the seemingly contrasting results of previous studies can be reconciled.

We consider changes in local plant diversity and productivity observed over 37 years in 21 grasslands with known land-use histories (Extended Data Fig. 1). Of these 21 fields, 4 were sampled during most years from 1982 to 2018 as control plots in a long-term fertilization experiment[23–25]. Three of these four fields were formerly cropped; the fourth field has never been ploughed and has had prescribed fire, and serves as our reference remnant ecosystem and primary vegetation. The remaining 17 fields were formerly cropped and sampled annually from 1988, or from the point in time at which they were abandoned from agriculture, to 2018 as part of a chronosequence study of old field succession[23,26,27]. Fields range in age from 1 to 91 years after agricultural abandonment. We use species-level plant community composition and aboveground plant biomass data that have consistently been sampled with exactly the same methods in all 21 fields (Methods).

Results

We find that local grassland plant diversity increased significantly over time (mixed effects model $F_{1,2,573} = 11.74$, $P = 0.0006$), but incompletely recovered during the century following agricultural abandonment (Fig. 2a, Extended Data Fig. 2). One year after agricultural abandonment, formerly ploughed old fields had, on average, slightly more than one third of the plant diversity (38%) and productivity (34%) observed in the nearby remnant ecosystem (Fig. 2a,b). By 91 years after agricultural abandonment, old fields had partially recovered, but still had only about three quarters (73%) of the plant diversity and only about half (53%) of the plant productivity observed in the remnant (Fig. 2a,b). This partial recovery of plant productivity was not statistically significant ($F_{1,2,573} = 1.95$, $P = 0.162$). If this slow and decelerating rate of increase in plant diversity continued, then it would take more than two or seven centuries to recover 80% or 90% of the plant diversity observed in the

Fig. 1 | Hypothesized and observed changes in local biodiversity and ecosystem functioning during recent decades. It has been suggested[10] that global biodiversity loss may have little impact on ecosystem functioning if local species gains in some locations (as indicated by the grey arrow pointing up and to the right) are leading to a surplus of biodiversity and ecosystem functioning that can compensate for the deficits in biodiversity and ecosystem functioning that may be occurring in other places[13] (as indicated by the grey arrow pointing down and to the left). Here we instead find that species gains during recent decades can be indicative of partial recovery and the reduction of deficits in biodiversity and productivity after agricultural abandonment (black lines). These deficits emerged before the beginning of the time series, shifting the baselines of black arrows to less than 100% of initial biodiversity and productivity. Grey arrows show hypothesized relationships between biodiversity and productivity based on results from 327 experiments that manipulated the diversity of primary producers[7]. Black arrows show observed trajectories for the 20 formerly ploughed fields included in our study, based on mixed-effects model predictions of temporal trends in biodiversity and productivity (Fig. 2a,b). Dotted horizontal and vertical lines are defined as the average levels of biodiversity and ecosystem functioning observed in never-ploughed primary vegetation over the same period of time, averaged across years and plots from 1982 to 2018.

remnant, respectively. Recovery of biodiversity was due to recovery of species richness ($F_{1,2,573} = 34.98$, $P < 0.0001$; Fig. 2c), whereas species evenness remained close to remnant levels and did not significantly change during old field succession (Fig. 2d; $F_{1,2,566} = 1.01$, $P = 0.316$). Further study will be needed to determine whether and how phylogenetic diversity, functional trait diversity and other dimensions of biodiversity recover following agricultural abandonment.

Simultaneously considering both temporal trends and spatial comparisons of local biodiversity (Fig. 2) shows that there was systematic loss of local biodiversity and productivity due to agricultural land-use before the start of the observations in each of these fields, and that there has been incomplete recovery of biodiversity during the century following agricultural abandonment. Increases in local biodiversity during recent decades are therefore indicative of a prolonged biodiversity deficit that has not yet undergone full recovery, rather than the accrual of a biodiversity surplus above the levels observed in nearby primary vegetation (Fig. 1). Although all fields experienced a similar climate during any particular calendar year, many fields experienced different climates during any particular year since agricultural abandonment, given that they were not all abandoned in the same year (Extended Data Fig. 1), thereby contributing to the variability that is observed across fields. Combining

temporal trends and space-for-time comparisons (Fig. 2) provides a more complete understanding of local changes in biodiversity and productivity than separately considering either temporal trends (Fig. 3a–d) or spatial comparisons (Fig. 3e–h).

Separately considering only temporal trends shows that there are local losses of biodiversity in some fields and local gains of biodiversity in other fields during recent decades (Fig. 3a–d), consistent with previous studies of biodiversity time series[13,14,19]. These temporal trends in biodiversity result from the integration of all factors that affected biodiversity during recent decades, including nearby habitat loss and fragmentation, nitrogen deposition, climate change and events, such as droughts, exotic species introductions and invasions, and other anthropogenic and natural disturbances. However, separately considering such temporal trends also ignores land-use history and all other factors that may have shifted the baseline of biodiversity before the start of the time series. Thus, it is impossible from the analysis of the time series alone to assess whether recent species gains are surpluses, as is often assumed, or the reduction in deficits of biodiversity and productivity, as we find here (Figs. 1, 2).

Separately considering only spatial comparisons shows that local biodiversity and productivity were systematically reduced in formerly ploughed fields compared to the never-ploughed primary vegetation (Fig. 3e–h), consistent with previous studies of spatial comparisons of biodiversity[13,14]. However, such spatial comparisons are unable to determine the temporal trajectories for recovery of biodiversity and productivity (Figs. 1, 2). For example, spatial comparisons show that plant species richness was reduced as much in intermediate secondary vegetation (30–91 years after agricultural abandonment) as in young secondary vegetation (<30 years after agricultural abandonment) (Fig. 3g), which masks the fact that plant species richness substantially recovered during the century following agricultural abandonment (Fig. 2c).

Local species gains could create a surplus of biodiversity, if new species arrived as a result of range shifts in response to climate change[10,28] or introductions from other locations[8,9]; however, we found little evidence for these explanations. Only 10 of the 176 plant species identified in our studies were near their northern range limit; the rest of the species are also present in Canada, more than 350 km north of the study site (Extended Data Fig. 3). Furthermore, all but one of these ten species were observed during the early years of the studies, and thus were not accrued as new arrivals during our study. Although 42 of the 176 plant species in our studies were introduced to the continental United States from elsewhere, all but 8 of these species were observed during the early years of the studies (Extended Data Fig. 4). Thus, we suspect less than 5% of the species identified in these studies may have arrived during recent decades. Instead, the recent species gains that we observed were more likely to be due to the return of formerly present species. Therefore, recent species gains are not necessarily evidence that there has been no systematic loss of local biodiversity, as previously suggested[13,14], because these gains can lead to the reduction of a deficit, rather than the accrual of a surplus, of biodiversity.

Discussion

Our results might underestimate or overestimate the effects of agricultural land-use history on biodiversity and productivity. Our reference levels of plant diversity and productivity came from 250 observations made between 1982 and 2018 in 10 plots in a single remnant that has never been ploughed. To improve our spatial comparisons of biodiversity, we also considered plant cover data collected in 44 nearby fields, 18 of which were never ploughed (Extended Data Fig. 5). Consistent with our results based on comparisons to the best-studied remnant, we found a higher plant diversity in these 18 remnants than in the 26 formerly ploughed fields (analysis of variance (ANOVA), $F_{1,42} = 15.21$, $P = 0.00034$; Extended Data Fig. 6). Given that many global change drivers such as nearby
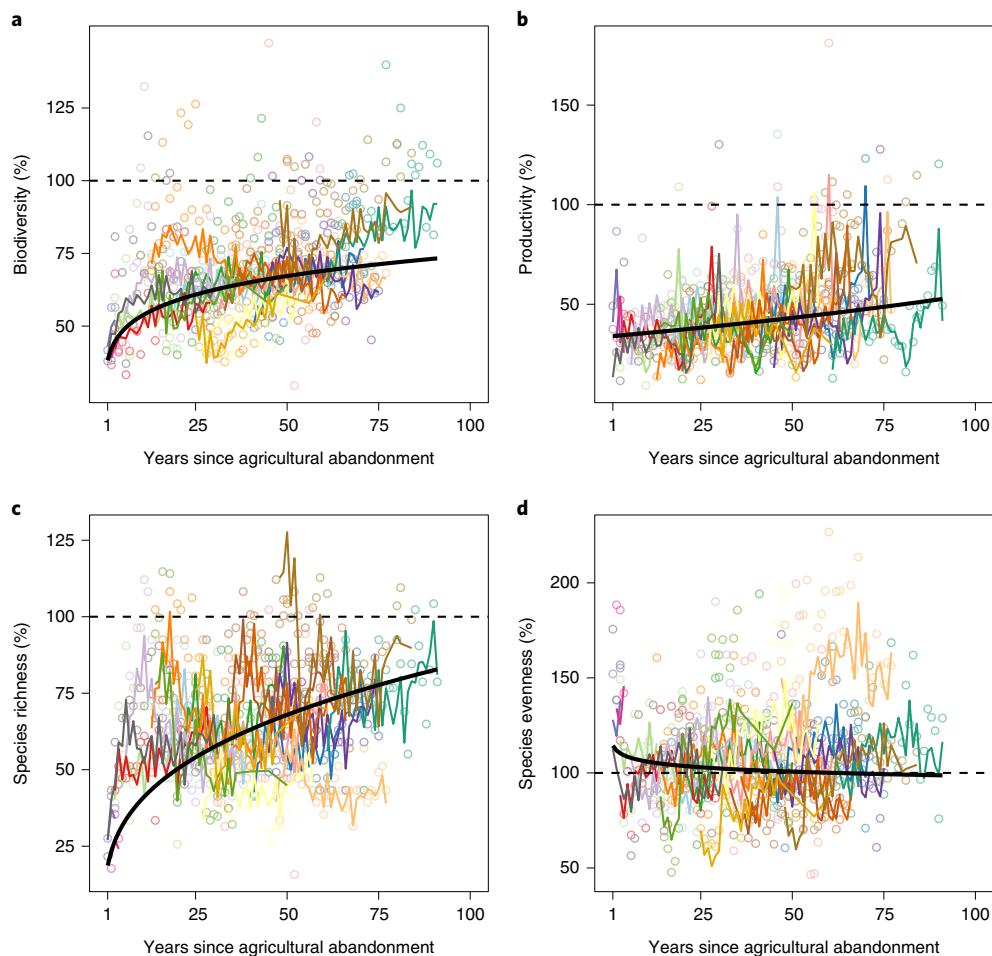
Fig. 2 | Trends in biodiversity, productivity, species richness and species evenness. a–d, Incomplete recovery of biodiversity (**a**) and species richness (**c**), lack of significant recovery of productivity (**b**) and no significant change in species evenness (**d**) during the century following agricultural abandonment. Combining space-for-time comparisons among fields with temporal trends observed within fields reveals that local biodiversity and productivity were systematically decreased and remain below the levels observed in the never-ploughed vegetation (horizontal dashed lines, which are based on 250 observations, averaged across plots and years), despite local increases in biodiversity during recent decades in many fields. Biodiversity was quantified by inverse Simpson's index, which gives species equivalents and accounts for both richness and evenness. The spatial scale for all panels is 0.3 m², which is relevant for local interactions among grassland plants. Predicted values are shown from the mixed-effects models averaged across all fields and plots (thick black line) and averaged across all plots within each field (thin, coloured lines). Points show observed values averaged across all replicate plots within each field and year. Total sample size = 2,710 observations. See Extended Data Fig. 1 for sample sizes and Extended Data Fig. 2 for parsimonious model structures.

habitat loss and nitrogen deposition can erode plant diversity over time within remnants, and that we observed declines in plant diversity over time in our best-studied remnant (top line at the start of the time series in Fig. 3a,c), perhaps partly due to long-term nitrogen deposition and/or nitrogen spillover effects from fertilization in nearby experimental plots (Methods), we suspect that our results probably underestimate the extent to which agricultural land-use history decreased biodiversity. It is less clear whether our comparisons with the best-studied remnant underestimate or overestimate the extent to which agricultural land-use history decreased productivity. If farmers tended to choose highly productive sites for croplands, then remnants might have escaped cultivation partly because they were less productive than the other fields before agricultural land use. This could make our comparisons underestimates of the extent to which agricultural land-use history decreased productivity. Alternatively, spillover from fertilization in nearby experimental plots might instead have artificially increased the productivity that we observed in the control plots of the remnant relative to levels of productivity in the other fields, which could make our comparisons

overestimates of these effects. Fully resolving the extent to which agricultural land-use history has shifted baselines of biodiversity and productivity will require high-frequency multidecadal observations across many remnant ecosystems and chronosequences of land-use history.

The slow and incomplete recovery of biodiversity following agricultural abandonment that we observed is probably occurring in many ecosystems across the planet. Recovering secondary vegetation, which includes old fields and recovering forests, currently covers approximately 2.9 billion ha, nearly twice the area of current croplands, and is projected to cover approximately 4.1 to 5.2 billion ha by the end of this century[29]. Furthermore, in addition to shifting locations, the global footprint of agriculture has also started decreasing in size during the past two decades, with more land now being abandoned from agriculture than converted to it, especially in western Europe and North America (Extended Data Fig. 7). Thus, given that many ecosystems worldwide are recovering after relaxation of anthropogenic disturbances, we suspect many of the gains in local plant species that have been observed during recent decades
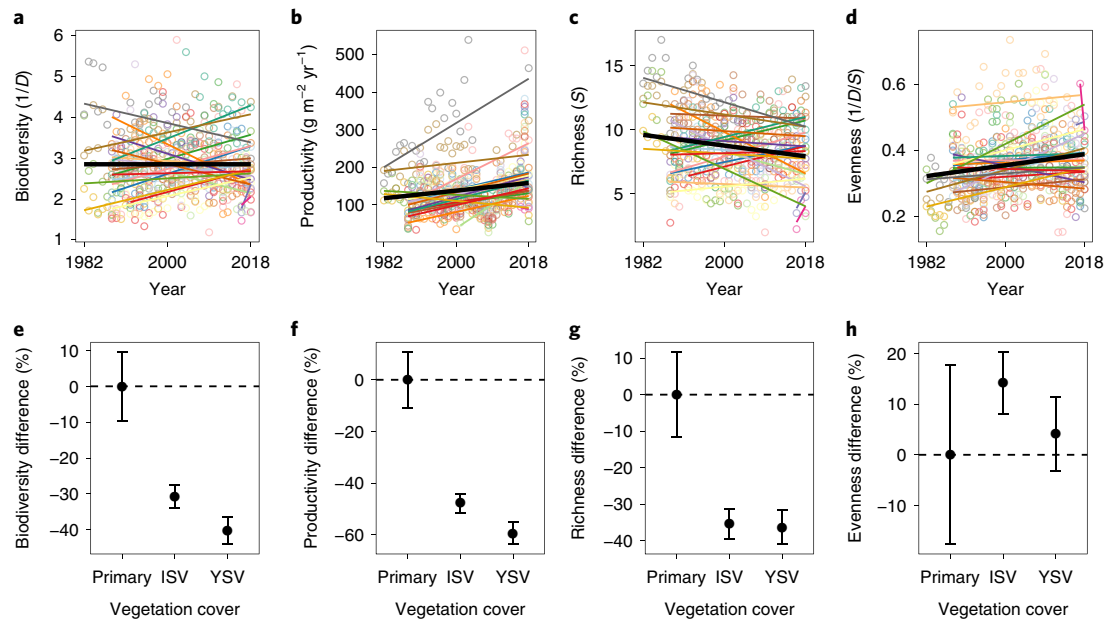
Fig. 3 | Analyses of temporal and spatial trends in biodiversity. a–h, Two contrasting views of the same data: separately considering temporal trends in biodiversity (**a–d**) or spatial comparisons of biodiversity (**e–h**). Temporal trends in biodiversity (**a**), productivity (**b**), richness (**c**) and evenness (**d**) show increases in some fields and decreases in others during recent decades. Lines show the linear fit for each field, as in previous studies of biodiversity time series[14]. Thick black lines show the mean trend. In the early years, the never-ploughed remnant (top grey line) had the highest biodiversity (**a**), productivity (**b**) and richness (**c**), but lost plant diversity and increased productivity over time. Points are observed means of all replicate plots within each field and year. Sample sizes are given in Extended Data Fig. 1. By contrast, spatial comparisons between vegetation land cover classes show systematic loss of local biodiversity (**e**), productivity (**f**) and richness (**g**) in secondary (previously ploughed) vegetation. ISV, intermediate secondary vegetation (30–91 yr after agricultural abandonment); YSV, young secondary vegetation (<30 yr after agricultural abandonment). For these spatial comparisons, biodiversity was averaged across all years within plots and fields. Thus, the variation shown is shown across all plots and fields within each vegetation cover class. Data are mean and 95% confidence intervals analysed using ANOVA and the Tukey method for comparing a family of three estimates. Sample sizes are 10, 85 and 63 for primary vegetation, intermediate secondary vegetation and young secondary vegetation, respectively.

represent the gradual reduction of a biodiversity deficit[21], as we observed (Fig. 1), rather than the accrual of a biodiversity surplus.

In many recovering ecosystems, active restoration efforts are needed to restore biodiversity and ecosystem functioning[20]. For example, in the abandoned agricultural fields that we studied, fully restoring biodiversity may require several forms of active management, such as using prescribed fire to restore natural disturbance regimes[27], using seed additions to alleviate dispersal limitations that have been created by habitat loss and fragmentation[30], using haying to remove excess nutrients added through nitrogen deposition, and reintroducing extirpated herbivores, predators and other key components of the food web. In many ecosystems worldwide, active restoration efforts have substantially increased levels of biodiversity, ecosystem functioning and many ecosystem services, speeding up what would otherwise be slower or insignificant recovery[20,21]. The enormous and growing extent of recovering ecosystems worldwide provides an unprecedented opportunity for ecological restoration efforts to help to mitigate a sixth mass extinction and its consequences for human wellbeing.

Methods

Study designs. We analysed plant diversity and productivity data from 21 fields that were part of 2 long-term studies at Cedar Creek Ecosystem Science Reserve in Minnesota, USA. All fields were within 7 km of one another and thus experienced the same climatic conditions. Four fields (Cedar Creek experiment number E001, fields A, B, C and D) were studied as part of a long-term fertilization study[23–25]. Here we use the control plots from this study, which received no nitrogen fertilizer. The other 17 fields (Cedar Creek experiment number E054, fields 4, 5, 10, 24, 26, 28, 35, 39, 41, 45, 53, 70, 72, 77, LS, 600 and 601) were studied as part of an old field chronosequence[23,26,27]. Extended Data Figure 1 provides the range of years sampled, range of years since agricultural abandonment, number of years in which

sampling occurred and number of observations for fields sampled in the old field chronosequence study and in the control plots of the long-term fertilization study. Field D is the primary vegetation remnant that has never been ploughed.

Some other areas of the remnant have been influenced by experimental manipulations of fertilizer or seed additions. These two experimental treatments might indirectly decrease or increase, respectively, the level of plant diversity that we observed in the control plots. If anything, we suspect that plant diversity might be slightly reduced in the control plots because fertilization substantially decreased plant diversity[23–25] and occurred much closer (1 m) than seed additions (>100 m) to control plots. If nearby fertilization has reduced plant diversity in these control plots, then this could lead to the underestimation of plant diversity in the remnant, thereby underestimating the extent to which agricultural land-use history decreased biodiversity and overestimating the extent to which recovery is occurring in the old fields.

To help to avoid this treatment spillover issue, as well as other issues that could arise from using a single remnant as the primary vegetation reference, we also compared plant cover data collected in many nearby (within 7 km) remnants and formerly ploughed fields. Specifically, we analysed plant cover data from 44 fields that were part of 2 other long-term studies that are also located at Cedar Creek Ecosystem Science Reserve (Extended Data Fig. 5). The 18 remnants were sampled as part of a long-term prescribed fire study[31–33] (Cedar Creek experiment number E133). Given that fire is a natural disturbance in these ecosystems and that prescribed fires are now needed to maintain these ecosystems and compensate for anthropogenic fire suppression across the wider landscape, we excluded all experimental plots that received no burns. We also excluded three plots for which the former land-use history was unclear (that is, for which historical aerial images suggested cropping, but some large trees were not removed), leaving us with 18 remnant plots that have never been ploughed (Extended Data Fig. 5). The local plant species richness of these remnants were compared to that of 26 formerly ploughed fields (Extended Data Fig. 5), in which plant cover data were collected across an old field chronosequence[23,26,27] (Cedar Creek experiment number E014) that includes 16 of the 17 old fields included in the aforementioned chronosequence study (E054, Extended Data Fig. 1), plus 10 additional old fields.

Plant sampling. Peak aboveground plant biomass was sampled in exactly the same manner in all fields listed in Extended Data Fig. 1 and for all years. For each

plot in each field in each study, aboveground biomass was clipped in a 10 cm by 300 cm strip, sorted to species, dried to constant mass and weighed. At our site, all herbaceous aboveground plant tissues die each winter, and therefore aboveground peak biomass of herbaceous plant species is a reasonable proxy for aboveground annual net primary productivity. The aboveground biomass of woody species was excluded, given that it accumulates over time and is therefore not a proxy for aboveground annual net primary production. Furthermore, four plots that became invaded by trees, and thus had exceptionally low biomass of herbaceous species (<0.25 g m^{-2}), were excluded from the analysis.

Plant cover was sampled in replicated quadrats of the same size area (0.5 m^2) in all fields listed in Extended Data Fig. 5. For each plot in each field in each study, the percentage cover of aboveground plant biomass was estimated for each species present in a 50 cm by 100 cm quadrat. In the fields of E133, cover was sampled at 10-m intervals along four parallel 50-m transects, which were located 25 m apart, for a total of 24 quadrats for each year of sampling in each field[31–33]. In E014, cover was sampled at 1.5-m intervals along four parallel 40-m transects, which were located 25 m apart, for a total of 100 quadrats for each year of sampling in each field[23,26,27]. Cover was estimated approximately every 5 or 6 years from 1984 to 2015 for E133 and from 1983 to 2016 for E014. Herbaceous plant species richness was averaged across all observations (that is, quadrats and years) within each field.

Biodiversity and productivity measures. Biodiversity was quantified by the inverse Simpson's index, $1/D$, where $D = p_i^2$ and p_i is the relative biomass of species i. Productivity was quantified as the sum of peak aboveground biomass for all herbaceous species. Species richness (S) is the number of species. Evenness was quantified by the inverse Simpson's evenness index ($1/D/S$). We use the inverse Simpson's diversity index because it gives the effective number of species, which is directly comparable to other diversity indices[34], and because its associated evenness index is directly comparable between communities with different numbers of species[35]. In total, 7 of the 2,710 observations included only one species. These observations were included for analyses of diversity and richness, with a value of one, but were excluded for the analysis of evenness because there is no evenness when only one species is present.

Statistical analyses. We used linear mixed-effects models to test whether biodiversity and productivity depended on years since agricultural abandonment (Fig. 2). Fixed effects were included for 'year' as a factor, with calendar years ranging from 1982 to 2018, and 'years since agricultural abandonment', quantified as an integer ranging from 1 to 91. Including year as a factor controlled for the inter-annual variability that was observed across all fields and plots. For example, in the late 1980s, a severe drought reduced both biodiversity and productivity in all fields at our field site[36,37]. By including year as a factor, we controlled for such inter-annual variability when testing for recovery trends. We considered linear and decelerating (logarithmic) recovery trends, finding linear recovery trends to be most parsimonious for productivity and species evenness and decelerating recovery trends to be most parsimonious for inverse Simpson's diversity and species richness, according to the Akaike information criterion (AIC) (Extended Data Fig. 2). Random intercepts and slopes were included for 'plots' nested within 'fields'. Models that excluded random slopes or intercepts were less parsimonious, according to AIC (Extended Data Fig. 2). The error structure accounted for repeated measurements within plots nested within fields across years. For all response variables, a first-order autoregressive covariance structure provided a better fit than a compound symmetry (split-plot-in-time) covariance structure, according to AIC (Extended Data Fig. 2). For all models, the response variable was log-transformed to meet model assumptions. Models were fitted with the lme function in the nlme package[38] in R[39].

In ecosystems in which plants evolved with fire as a natural disturbance[40], prescribed burning can speed up the recovery of plant diversity during old field succession[27]. Although the grasslands and savannahs at our study site evolved with fires[33], in recent decades, there have been varying amounts of fire suppression in the fields that we studied. The never-ploughed remnant has had the least fire suppression, with burning occurring approximately two out of every three years since 1964, when a fire management study began[31–33]. Prescribed burning probably contributes to the high levels of plant diversity in this remnant[31–33]. The formerly ploughed old fields have experienced fire suppression for most of the study period and for decades before observations began, although some of the old field plots were burned in recent years. Specifically, since 2006, experimental burning treatments have been applied to half of the replicate plots in most of the old fields[27]. Furthermore, since 2005, prescribed burning affected all observations in fields A, B and C. To assess whether the recovery of plant diversity that we observed after agricultural abandonment was explained by recent burning, we repeated our analyses after excluding the 281 observations that were affected by prescribed burning, which is about 10% of the 2,710 total observations. We found similar results after excluding all observations of burned plots. Specifically, there remained a significant increase in plant diversity ($F_{1,2,094} = 12.492$, $P = 0.0004$) and species richness ($F_{1,2,094} = 42.428$, $P < 0.0001$) with years since agricultural abandonment when only the unburned observations were considered. Thus, although burning probably contributes to high levels of plant diversity in the remnant ecosystem and to recovery of plant diversity in the old fields, it does not, by itself, fully explain the partial recovery of plant diversity that we observed.

To visualize temporal trends in biodiversity, its richness and evenness components and productivity, we used the lm function in R to fit linear relationships over time (Fig. 3a–d), as has been done in previous studies of biodiversity temporal trends[13,14]. These changes in biodiversity over time appear similar to results reported in previous global meta-analyses of biodiversity temporal trends[13,14,19], which have found species gains in some places and species losses in others.

To assess changes across space in biodiversity, its richness and evenness components and productivity (Fig. 3e–h), we classified vegetation cover (that is, type of land cover) as in previous studies[12], and used the aov function in R to conduct an ANOVA for a vegetation cover factor that had three levels: primary vegetation (never-ploughed), intermediate secondary vegetation (last ploughed 30 or more years ago) or young secondary vegetation (last ploughed less than 30 years ago). These biodiversity changes across space appear similar to results reported in previous global meta-analyses of biodiversity spatial comparisons[12], which have found that biodiversity is often lower in young and intermediate secondary vegetation than in primary vegetation.

Drivers of local species gains. To investigate the drivers of local species gains, we used the US Department of Agriculture Plants Database[41] to identify the plant species observed in our study that were near their northern range limit and that were introduced to the continental United States. First, we used the plant distribution data from the database to generate a list of plant species that were considered to be at their northern range limit, defining this as plant species that are known to be present in Minnesota, but not in Manitoba or Ontario, which are the two neighbouring Canadian provinces to the north of Minnesota, more than 350 km north of the study site (Extended Data Fig. 3). This is an inclusive definition of species that may be near their northern range limit because some of these species are known to be present more than 300 km north of the study site, within the state of Minnesota. Second, we used the native status data from the database to generate a list of plant species that are known to be introduced to the continental United States (Extended Data Fig. 4). Third, we determined the years in which the species on these two lists were first observed in any of four studies of plant communities that were conducted in the same fields during the early 1980s. These included the two studies described above (E001 and E054), as well as a survey plants in the old fields (E014, which is adjacent to E054) and a second fertilization study (E002, which is adjacent to E001). Details of all these studies can be found in previous publications[23–27].

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
The plant biomass and cover data that support the findings of this study are available from the Cedar Creek Long-Term Ecological Research project website (www.cedarcreek.umn.edu/research/data).

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Acknowledgements

Author contributions

D.T. designed and conducted three of the long-term studies (E001, E014 and E154); P.B.R. conducted one of the long-term studies (E133); A.T.C. contributed to data collection; and F.I. conceived this project, contributed to data collection, analysed the data and wrote the paper, with input from all coauthors.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-1012-1.

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Study	Field	Last Year Cultivated	Range of Years	Range of YSA	# Years	# Observations
E054	600	2015	2016-2018	1-3	3	12
E054	601	2014	2016-2018	2-4	3	12
E054	10	1998	2001-2018	3-20	18	72
E054	28	1989	1992-2018	3-29	27	108
E054	LS	1987	1988-2018	1-31	31	124
E054	41	1982	1988-2018	6-36	31	124
E054	39	1975	1988-2018	13-43	31	124
E054	4	1971	1988-2018	17-47	31	124
E054	24	1968	1988-2018	20-50	31	92
E054	53	1961	1988-2018	27-57	31	124
E054	26	1957	1988-2018	31-61	31	31
E054	70	1955	1988-2018	33-63	31	124
E054	77	1952	1988-2018	36-66	31	123
E054	5	1947	1988-2018	41-71	31	124
E054	45	1943	1988-2018	45-75	31	124
E054	35	1941	1988-2018	47-77	31	124
E054	72	1927	1988-2018	61-91	31	124
E001	A	1968	1982-2018	14-50	26	312
E001	B	1957	1982-2018	25-61	26	312
E001	C	1934	1982-2018	48-84	33	396
E001	D	Never-plowed	1982-2018	Never-plowed	25	250

Extended Data Fig. 1 | Field details for plant biomass data. Range of years sampled, range of years since agricultural abandonment (YSA), number of years in which sampling occurred, and number of observations for fields sampled in the old field chronosequence study (Cedar Creek study E054) and in the control plots of the long-term fertilization study (Cedar Creek study E001). Field D is the never-plowed primary vegetation reference.

Response	YSA fixed effect		Random effects		Autocorrelation	df	AIC
	Linear	Decelerating	Intercept	Slope			
Diversity	X		X	X	corAR1	46	1788
Diversity		**X**	**X**	**X**	**corAR1**	**46**	**1783**
Diversity		X	X		corAR1	42	1821
Diversity		X		X	corAR1	42	1838
Diversity		X	X	X	corCompSymm	46	1964
Productivity	**X**		**X**	**X**	**corAR1**	**46**	**3093**
Productivity		X	X	X	corAR1	46	3095
Productivity	X		X		corAR1	42	3205
Productivity	X			X	corAR1	42	3231
Productivity	X		X	X	corCompSymm	46	3124
Richness	X		X	X	corAR1	46	1646
Richness		**X**	**X**	**X**	**corAR1**	**46**	**1617**
Richness		X	X		corAR1	42	1677
Richness		X		X	corAR1	42	1689
Richness		X	X	X	corCompSymm	46	1830
Evenness	X		X	X	corAR1	46	2072
Evenness		**X**	**X**	**X**	**corAR1**	**46**	**2071**
Evenness		X	X		corAR1	42	2084
Evenness		X		X	corAR1	42	2094
Evenness		X	X	X	corCompSymm	46	2145

Extended Data Fig. 2 | Model selection results. The most parsimonious model, based on the Akaike Information Criterion (AIC), is bolded for each response variable. In each case, models with linear or decelerating (logarithmic) fixed effects for YSA (years since agricultural abandonment) were first compared. The most parsimonious of these fixed effect structures was retained for subsequent comparisons of alternative random effects and autocorrelation structures. df = degrees of freedom; YSA = years since agricultural abandonment.

| Plant species	USDA PLANTS Symbol	Cedar Creek species ID	First observation(s)	
			Year	Study
Chenopodium leptophyllum	CLE4	Chenlept	1982	E001
Coreopsis palmata	COPA10	Corepalm	1982	E001
Dichanthelium villosissimum	DIVIP	Paniprae	1982	E001
Lepidium densiflorum	LEDE	Lepidens	1982	E001
Mirabilis hirsuta	MIHI	Oxybhirs	1982	E001
Penstemon grandiflorus	PEGR7	Pensgran	1982	E001
Silene latifolia	SILAA3	Lychalba	1982	E001
Bouteloua hirsuta	BOHI2	Bouthirs	1983	E014
Tradescantia bracteata	TRBR	Tradbrac	1984	E002
Aristida tuberculosa	ARTU	Aristube	1994	E001

Extended Data Fig. 3 | Plant species that are near their northern range limit at our study site. That is, these ten species are found in Minnesota, including at our study site, but not in Manitoba or Ontario, the Canadian Provinces that are more than 350 km north of study site. Gains of these species during our study could possibly be attributable to range shifts in response to climate change. However, 9 of these 10 species were already present at the beginning of these studies, observed in 1982, the first year of observations, or in 1983, the first year of observations in another survey of plants in these fields (E014), or in 1984 in another experiment (E002) that is also located in these same fields. Furthermore, an additional 166 plant species observed in our study are found in Minnesota and in Manitoba or Ontario and thus are not near their northern range limit. Thus, only 1 of the 176 plant species identified in our studies, *Aristida tuberculosa*, possibly arrived at the study site during recent decades due to a range shift in response to climate change. Even this species may have been present, but failed to be detected, during early years, due to dormancy or observation error.

| Plant species	USDA PLANTS Symbol	Cedar Creek species ID	First observation(s)	
			Year	Study
Ambrosia artemisiifolia	AMARE	Ambrarte	1982	E001
Artemisia ludoviciana	ARLU	Arteludo	1982	E001
Berteroa incana	BEIN2	Bertinca	1982	E001
Chenopodium album	CHAL7	Chenalbu	1982	E001
Crepis tectorum	CRTE3	Creptect	1982	E001
Digitaria ischaemum	DIIS	Digiisch	1982	E001
Digitaria sanguinalis	DISA	Digisang	1982	E002
Elymus repens	ELRE4	Agrorepe	1982	E001
Lactuca serriola	LASE	Lactserr	1982	E002
Lepidium densiflorum	LEDE	Lepidens	1982	E001
Melilotus officinalis	MEOF	Melialba	1982	E001
Poa pratensis	POPRP2	Poaprate	1982	E001
Polygonum convolvulus	POCOC2	Polyconv	1982	E001
Potentilla recta	PORE5	Poterect	1982	E001
Rumex acetosella	RUAC3	Rumeacet	1982	E001
Salsola tragus	SATR12	Salskali	1982	E002
Setaria pumila	SEPUP2	Setalute	1982	E001
Setaria viridis	SEVIV	Setaviri	1982	E001
Silene latifolia	SILAA3	Lychalba	1982	E001
Taraxacum officinale	TAOFO	Taraoffi	1982	E002
Tragopogon dubius.	TRDU	Tragdubi	1982	E001
Trifolium repens	TRRE3	Trifrepe	1982	E001
Verbascum thapsus	VETH	Verbthap	1982	E001
Agrostis stolonifera	AGST2	Agroalba	1983	E014
Cirsium arvense	CIAR4	Cirsarve	1983	E002
Hieracium aurantiacum	HIAU	Hieraura	1983	E014
Panicum miliaceum	PAMI2	Panimili	1983	E014
Poa compressa	POCO	Poacompr	1983	E014
Potentilla argentea	POAR8	Potearge	1983	E001
Vicia villosa	VIVI	Vicivill	1983	E002
Asparagus officinalis	ASOF	Aspaoffi	1984	E001
Bromus inermis	BRIN2	Brominer	1985	E002
Trifolium hybridum	TRHY	Trifhybr	1986	E001
Medicago sativa	MESA	Medisati	1988	E001
Linaria vulgaris	LIVU2	Linavulg	1989	E054
Setaria italica	SEIT	Setaital	1990	E001
Stellaria media	STMEM	Stelmedi	1991	E054
Sisymbrium altissimum	SIAL2	Sisyalti	1992	E054
Trifolium arvense	TRAR4	Trifarve	1996	E054
Polygonum persicaria	POPE3	Polypers	1997	E001
Solanum dulcamara	SODUD	Soladulc	2003	E001
Convolvulus arvensis	COAR4	Convarve	2004	E001

Extended Data Fig. 4 | Introduced species. The 42 plant species listed here were introduced to Minnesota. About half of these species were already observed in 1982, during the first year of observations. About three quarters of the species were observed by 1988, the first year of the annual sampling of the old field chronosequence (E054). This leaves only 8 of the 176 plant species identified in our studies that possibly arrived at the study site during recent decades due to biotic homogenization resulting from species introductions. Even these eight species may have been present from the start, but failed to be detected, during early years, due to dormancy or observation error.

Study	Field	Last Year Cultivated	Range of Years	# Years	# Observations
E014	600	2015	2016-2016	1	100
E014	601	2014	2016-2016	1	100
E014	10	1998	2002-2016	4	400
E014	28	1989	1994-2016	6	600
E014	41	1982	1983-2016	8	800
E014	39	1975	1983-2016	8	800
E014	40	1972	1983-2016	8	800
E014	4	1971	1983-2016	8	800
E014	24	1968	1983-2016	8	747
E014	29	1968	1983-1989	2	300
E014	44	1961	1983-2016	8	799
E014	53	1961	1983-2016	8	800
E014	47	1959	1983-2016	8	800
E014	21	1957	1983-2016	8	800
E014	22	1957	1983-1989	2	188
E014	26	1957	1983-2016	8	730
E014	70	1955	1983-2016	8	800
E014	76	1952	1983-2016	8	800
E014	77	1952	1983-2016	8	795
E014	5	1947	1983-2016	8	800
E014	27	1947	1983-2016	8	800
E014	45	1943	1983-2016	8	800
E014	32	1941	1983-2016	8	800
E014	35	1941	1983-2016	8	794
E014	69	1934	1983-1989	2	176
E014	72	1927	1983-2016	8	800
E133	1	Never-plowed	1984-2015	7	168
E133	3	Never-plowed	1984-2015	8	176
E133	4	Never-plowed	1984-2015	8	176
E133	5	Never-plowed	1984-2015	8	175
E133	6	Never-plowed	1990-2015	7	152
E133	7	Never-plowed	1984-2015	8	176
E133	8	Never-plowed	1984-2015	7	152
E133	11	Never-plowed	1984-2015	7	151
E133	13	Never-plowed	1984-2015	7	152
E133	16	Never-plowed	1984-2015	6	144
E133	17	Never-plowed	1995-2015	5	120
E133	19	Never-plowed	1990-2015	6	144
E133	24	Never-plowed	1995-2015	6	127
E133	901	Never-plowed	1995-2015	5	120
E133	902	Never-plowed	1995-2015	5	120
E133	903	Never-plowed	1990-2015	6	144
E133	904	Never-plowed	1995-2015	5	120
E133	905	Never-plowed	1990-2015	6	144

Extended Data Fig. 5 | Field details for plant cover data. Range of years sampled, number of years in which sampling occurred, and number of observations for fields sampled in the old field chronosequence study that collected plant cover data (Cedar Creek study E014) and in the long-term prescribed fire study that collected plant cover data (Cedar Creek study E133). The Field numbers given for E014 correspond to the Field numbers given for E054 in Extended Data Fig. 1. The Field numbers given for E133 are its plot numbers and do not correspond to the field numbers of E014 or E054.
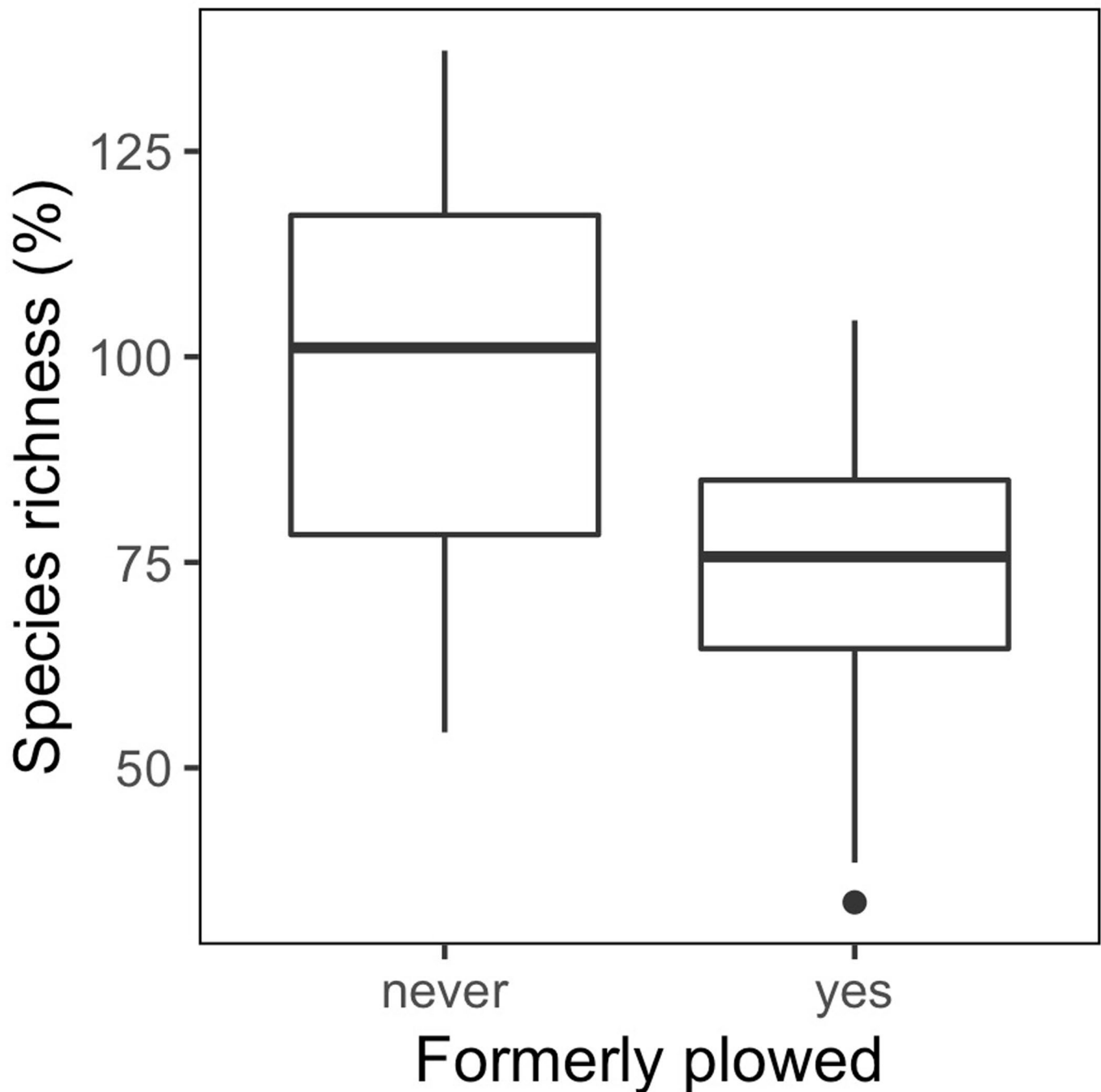
Extended Data Fig. 6 | Spatial comparison of local (0.5 m²) plant species richness between 18 fields that were never-plowed and 26 fields that were formerly-plowed. Data shown are based on plant cover measurements and were averaged over all observations (quadrats and years) within fields, such that the variation shown is only across fields. Here, rather than having a single never-plowed field as a reference remnant (as in Fig. 2), values are shown as a percentage of the average plant species richness observed in 18 fields that were never-plowed. Note that these percentages are not directly comparable to those shown in Fig. 2 because they were collected by a different method (cover estimates, rather than clipped biomass) and at a different spatial scale (0.5 m², rather than 0.3 m²). Nevertheless, the results are similar in that, in both cases, formerly-plowed fields tend to have lower local plant species richness than never-plowed fields. Details for each field are provided in Extended Data Fig. 5. Box plots summarize observed data: black band, median; bottom and top of boxes respectively correspond to lower and upper quartiles; error bars show 1.5 times the interquartile range.
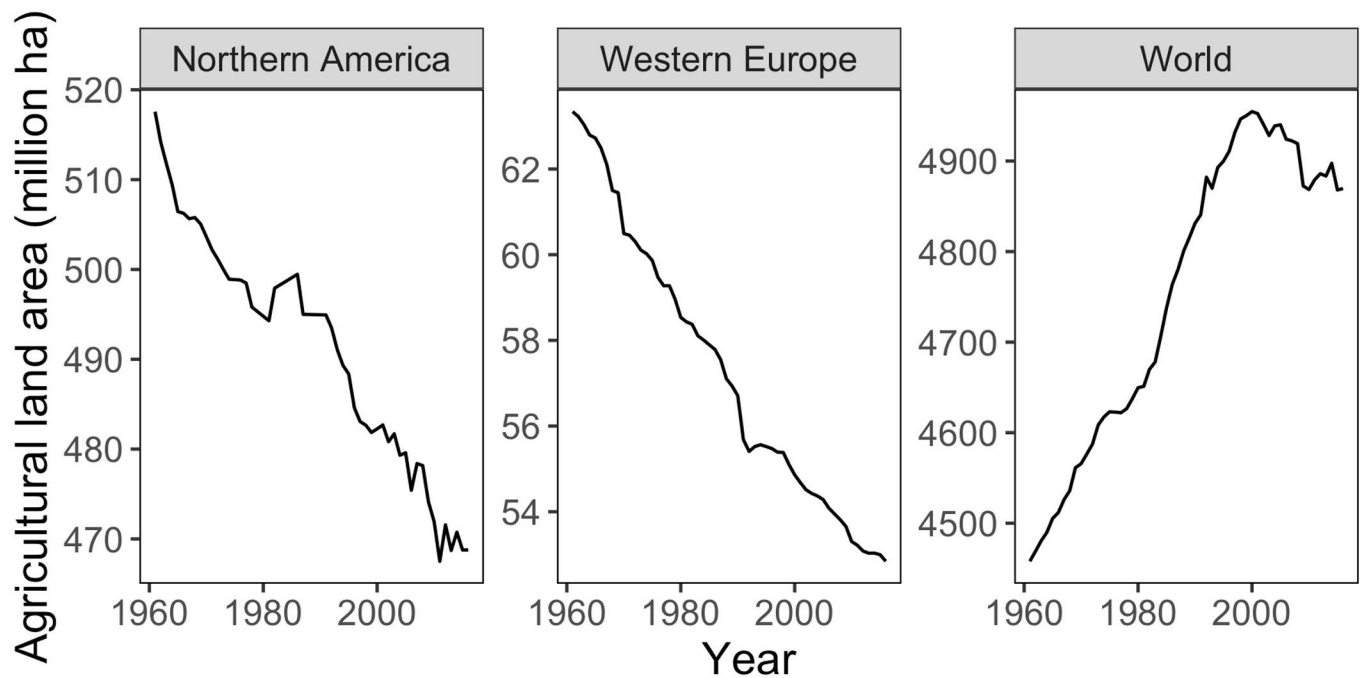
Extended Data Fig. 7 | Many lands worldwide are now recovering after agricultural abandonment, especially in the regions where most biodiversity monitoring has occurred in recent decades (that is, Northern America and Western Europe). Decreases in agricultural land area over time indicate that more land is being abandoned from agriculture than is being converted to it. Given that abandoned agricultural lands are now widespread, and that it can take more than a century for recovery of biodiversity following agricultural abandonment (Fig. 2), many species gains observed during recent decades may be the reduction of a biodiversity deficit, rather than a local biodiversity surplus (Fig. 1). Data shown are from the Food and Agriculture Organization (FAO) of the United Nations (www.fao.org/faostat). Agricultural area includes arable land (temporary crops, temporary pastures and hay meadows, gardens), permanent crops (crops that do not need to be replanted after each harvest), and permanent pastures (herbaceous forage crops, either sown or natural vegetation).

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No code was used to collect the data in this study.
Data analysis	All analyses were conducted in R version 3.6.0

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Here we consider changes in local plant diversity and productivity observed over 37 years in 21 grasslands with known land use histories (Extended Data Table 1). Four of these 21 fields were sampled during most years from 1982-2018 as control plots in a long-term fertilization experiment. Three of these four fields were formerly cropped; the fourth field has never been plowed and has had less fire suppression, and serves as our reference remnant ecosystem and primary vegetation. The remaining 17 fields were formerly cropped and sampled annually from 1988, or whenever they were abandoned from agriculture, to 2018 as part of a chronosequence study of old field succession. Fields range in age from 1 to 91 years after agricultural abandonment.
Research sample	The research sample consists of 2,960 observations, which includes 2,710 observations from recovering secondary vegetation and 250 observations from unplowed primary vegetation. These observations come from 114 plots located in 21 fields that were consistently sampled from 1982 to 2018.
Sampling strategy	Plant aboveground biomass data were collected by clipping all plants in a 10 by 300 cm strip in each plot, sorting to species, drying to constant mass, and weighing. Sample sizes were not based on a formal power analysis, but were based on results of prior studies.
Data collection	Plant aboveground biomass data were collected under the supervision of Dave Tilman.
Timing and spatial scale	Plant aboveground biomass data were collected annually from 1982 until 2018 at a spatial scale of 10 by 300 cm.
Data exclusions	Four plots that became invaded by trees, and thus had exceptionally low biomass of herbaceous species (< 0.25 g m-2), were excluded from the analysis.
Reproducibility	Every effort was made to ensure that data were collected in a consistent manner across fields and years.
Randomization	For the long-term fertilization study, fertilization treatments were randomized at the plot level. No treatments were applied to the old-field chronosequence, and thus there was no randomization in the study.
Blinding	Plant samples were collected by research technicians, and thus the PIs were blinded from the data until collection was completed.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The study was conducted on infertile, sandy soils at a site with mean annual precipitation of 682 mm and mean annual temperature of 7.5 degrees C.
Location	This research was conducted at Cedar Creek Ecosystem Science Reserve, near East Bethel, Minnesota, USA, in recovering grasslands and savannas within 7 km of 43.39715 N, -93.18032 W.
Access and import/export	All data collection was done in compliance with all local, national, and international laws.
Disturbance	The only disturbance caused by this study was clipping aboveground plant biomass, which regrows.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging