The long-term effects of monoculture maize cultivation on plant diversity

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Abstract

Biodiversity loss is one of the most serious global environmental problems caused by human activities. The intensification of agriculture and the increasing presence of monocultures is one of the main reasons for this. To study the long-term effects of maize monocultures compared to crop rotation systems on vegetation and biodiversity, two nearby sites in the small village of Metschach in Central Carinthia, Austria, were monitored for 30 years. These two test sites with intensively used arable land, divided into maize and crop rotation (14.5 ha in total) were taken out of production in 1989 as part of a nature conservation project. Changes in the composition and abundance of vascular plant species were recorded in 29 permanent plots. The monitoring showed that the previous use has long-lasting effects on species richness and ecological indicator values of the fallow land: The species numbers of the former maize field remained on average 10 species below those of the former crop rotation field over the entire study period. After 30 years, the plant communities in the former crop rotation revealed tendencies towards species-rich grassland communities, whereas in the former maize monoculture *Elymus repens* or tall herbaceous fringe communities remained dominant. Ecological indicator values showed predominantly higher moisture and nutrients values in the former maize cultivation over the entire study period. Overall, this study underlines the importance of monitoring to unravel long-term effects of different crop types on biodiversity. In particular, it highlights the need for additional monitoring programmes in comparable ecosystems, including in-situ measurement of temperature, moisture and nitrogen.

Keywords: maize cultivation, biodiversity, long-term vegetation monitoring, vegetation dynamics, nature conservation, land use change

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Introduction

The loss of biological diversity is one of the most severe global environmental problems caused by human activity. The average abundance of native species in most major terrestrial biomes worldwide has fallen by at least 20 per cent, potentially affecting ecosystem processes and hence nature's contributions to people, i. e. ecosystem services: provisioning, climate regulation, wastewater treatment, erosion control, pollination, biological pest control etc. The decline in native species has mostly taken place since 1900 and may be accelerating (IPBES 2019). While the reasons for this development are manifold, some of the important causes are the transformation of natural ecosystems, climate change and the intensification of agriculture with increasing use of pesticides and fertilizers (Koch et al. 2019, Magurran & Dornelas 2010).

Ecosystems such as wetlands, including bogs and mires, have experienced considerable degradation and losses. Across Europe, around 60% of the original bogs and mires have been destroyed (Joosten 1997). In the decades after World War II, 265,000 hectares of wetlands were drained in Austria alone (Jungmeier & Werner 1999) and continued to be used for agricultural crop production. Today, only 0.3% (approx. 26,500 ha) of the Austrian territory (84,000 km²) is covered by bogs and mires (Keusch & Steiner 2005). As a global phenomenon, systematic drainage was accompanied by an intensification of agriculture on the now arable land.

The EU's agricultural production is among the most intensive in the world and is responsible for various negative environmental impacts (*EuroStat* 2017). Meanwhile, the demand for food and energy production is constantly increasing (Diaz et al. 2019). Modern agriculture now

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faces the challenge of reconciling agricultural intensification, i.e. the continuous cultivation of the same land area with increased use of the same resources, with the reduction of negative environmental impacts (see ecological intensification; Tittonell 2014).

The world's most important staple crop and a major source of food and nutritional security for millions of people is maize (*Zea mays L.*), with a global production of over one billion tonnes (1,147,621,938 t) (*FAOStat* 2017). The combination of the required pesticides and fertilization for maize cultivation leads to an excess of nutrients in the soil and groundwater, which is further increased by the traditional form of maize cultivation without crop rotation (Dowswell et al. 1996).

There are studies on maize production and its immediate negative impacts on the abundance and diversity of wildlife (Gevers et al. 2011), birds (Brandt & Glemnitz 2014, Heldbjerg et al. 2018, Sauerbrei et al. 2014), wild bees (Le Féon et al. 2010), and nutrients (Nkonya et al. 2005). Negative effects are often results of the structural conversion of rotational set-aside fields that function as wildlife habitats to energy crop production fields. There are significantly fewer studies on the effects of monoculture maize production on accompanying arable plants: (Fanfarillo et al. 2019) surveyed arable plant communities in maize cultivation in Italy over 50 years and found a relevant decrease in the number of species, accompanied by a major species turnover. An increase in neophyte, geophyte, C4 photosynthetic pathway, and monocotyledons was observed, while the incidence of insect-pollinated taxa decreased. A study on restored grassland in Hungary identified invasion of invasive alien species and noxious weeds as major threats to both biodiversity and agriculture (Valkó et al. 2016).

Less or no attention, however, is paid to the question of the long-term effects of maize monoculture compared to crop rotation systems on vegetation and biodiversity once cultivation is abandoned. Therefore, a monitoring project was started in 1990 to document the development of abandoned arable land on former wetland sites (Jungmeier 1997, Jungmeier & Werner 1999, Jungmeier & Wieser 1993, Keusch et al. 2009).

Through continuous vegetation monitoring over 30 years, the vegetation dynamics in the study area and its value for biodiversity and nature conservation were to be studied and documented. The entire region was initially characterised by wet meadows, bogs and fens until well into the 19th century and was known as 'the largest fen area in Carinthia' (Rieder 1904). These wetlands have largely disappeared due to systematic drainage and agricultural intensification pressure. After a change in the management regime from intensive agriculture to extensive grassland practices in 1989, the aim of the monitoring was to document the following vegetation transformation. Since two different intensive management regimes were carried out on separate sections, the long-term

effects of monoculture maize and crop rotation on vegetation patterns could be compared.

Specifically, we ask whether the long-term effects of maize cultivation are reflected in (1) divergent patterns of plant communities, (2) different tendencies in species richness, and (3) deviating mean ecological indicator values (EIV). Therefore, a site with former monoculture maize cultivation is compared with a site with former crop rotation. The findings are expected to improve our understanding of the reversibility of intensively used cropland under different agricultural practices in formerly moisture-dominated ecosystems. Furthermore, the feasibility and validity of three common measures in vegetation ecology, namely phytosociological relevés, species richness and EIVs, will be assessed.

Material and methods

Study area

The study area is located in Metschach (Carinthia, Austria, 47°42' 24.65"N and 14°14' 25.69"E) in a valley bottom at an altitude of 520 m above sea level (Fig. 1). During the period 1981–2019 the annual soil temperature ranged between 6–9°C (mean = 8°C) and the annual mean
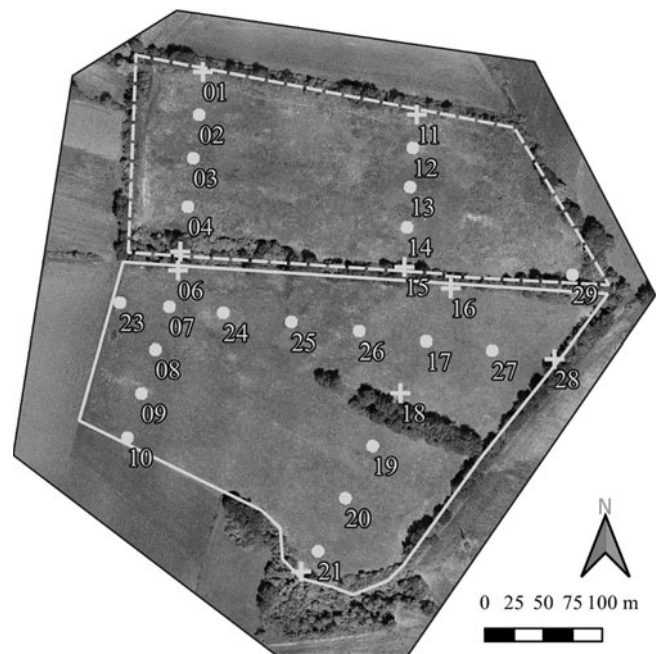

Fig. 1. Location of 29 permanent plots during a spring-aspect in Metschach, Austria. Northern site with dashed line: the former maize field including 11 permanent plots; southern field with solid line: the former crop rotation; mowing work on right field visible including 18 permanent plots. Circles denote grassland locations, while crosses denote fringe locations. Source: E.C.O. Institute of Ecology.

precipitation varied between 787–1333 mm (mean = 1063 mm) based on ERA5 reanalysis data (C3S Copernicus Climate Change Service, 2020; Fig. S1). Within the study area, two sites were distinguished with different previous land use covering a total of 14.5 hectares (Fig. 1). The northern site (6.1 ha) was used exclusively for maize before it was taken out of production and the southern site (8.4 ha) was under crop rotation (cereals, vegetables and grassland). Both sites, which are separated only by a ditch, have a similar elevation and inclination. It can be assumed that the ecological site conditions (climate, soil type, water level) are the same. Both sites were mowed once or twice a year to hinder development of a forest (Tab. S1). The study area was drained at considerable expense in the 1930s. Besides several ditches, clay pipes were laid in a dense herringbone pattern. With the incipient decay of the clay pipes during agricultural use, the effectiveness of this drainage system was reduced and temporary rewetting of the study area could be observed.

Study design

The nature conservation department of the Carinthian provincial government developed a nature conservation project for the rehabilitation of a wet meadow habitat in the study area. Human interventions were to be kept to a minimum and only be carried out through targeted maintenance measures (mowing). Comprehensive maintenance measures started from the fourth fallow year and included annual mowing but selected areas were mowed twice (Tab. S1). Mowing was done mainly to push back the couch grass (*Elymus repens*).

With a total number of 29 permanent plots (11 on the northern former maize field, 18 on the southern former crop rotation field) and 20 repetitions in the period 1990–2020, this resulted in 580 phytosociological relevés. The size of the plots was set at 5 × 5 m according to the minimum area (MA) assessment (the smallest area which adequately represents community composition). For the relocation of the permanent plots, a combination of buried metal pipes and movably attached wood was used for marking.

Field recording

The collection of species data involved the recording and visual estimation of the cover of all vascular plants present on each plot and in each survey year. The estimation of the visual cover followed the ordinal scale according to Braun-Blanquet (Braun-Blanquet 1964) (Tab. S2). In view of the strong seasonally changing field vegetation, the plots were documented twice in the first two years of the study. The first investigation took place in 1990 between early and mid-June (stem fruit set), while the second investigation date in 1991 was scheduled for early to mid-August (root crop set). Starting in the third year of the survey, one documentation date (middle of June) was sufficient to document the declining seasonal formation.

Abiotic site conditions

Differences in abiotic factors between the two study sites could have strong shaping impacts on species richness, but also on vegetation succession within the permanent plots. However, *in situ* measurements in the field, especially over longer periods of time, are difficult and Ellenberg Indicator Values (EIV) for light, moisture and nutrients have proven to be reliable alternatives (Descombes et al. 2020, Lamprecht et al. 2018). The EIVs are derived from a numerical scheme to categorise plants in Central Europe according to their habitat requirements. In the present monitoring, the mean value of a given EIV of all species occurring in a given plot and year was used as a proxy for the respective site condition. In order to be able to make statements about site conditions and changes, mean EIVs were calculated for each site according to (Ellenberg 1996), but modified and adapted to Austrian conditions (Englisch et al. 1991, Karrer & Kilian 1990).

To illustrate the climatic characteristics within the study region, two climate indices (soil temperature level 1, total precipitation) were extracted from the monthly ERA5-Land dataset (C3S 2019). Soil temperature level 1 refers to the soil temperature at 0–7 cm depth and total precipitation includes all liquid and frozen water at the surface.

Species turnover

The species turnover was computed from one monitoring period to the next as the proportion of species gained or lost in relation to the total number of species observed in both periods since 1992, in order to avoid methodical changes.

Data analysis

For all statistical analyses and graphical data representations, except for the classification of plant communities, the statistical software R Version 4.0.2 (2020-06-22, (R Core Team 2019) was used. In addition to the cross-checks mentioned above, the package *taxonstand* (Cayuela et al. 2012) was used to detect nomenclatural inconsistencies between relevés of different field workers and years. To identify shifts in the presence and absence of species over the entire period, the species turnover was calculated using the R package *codyn* – Community Dynamics Metrics' (Hallett et al. 2016).

The statistical analysis of differences in species richness and EIVs between plots with former maize cultivation and crop rotation was performed using linear mixed effects models (Bates et al. 2014). Either species richness

or a single EIV was used as the response, the former cultivation type as a fixed effect and the plot and survey year as random effects. This allowed control of a non-random sample design and imbalances in the number of plots between both cultivation types. A likelihood-ratio test from the *multcomp* package (function *glht*, (Hothorn et al. 2008) was used to test for differences in the cultivation type.

Classification of plant communities

A modified Two-Way-INdicator-SPecies-ANalysis, known as twinspan analysis, (Hill 1979, Roleček et al. 2009) was used for the classification of permanent plots within the phytosociological software Juice (Tichý 2002). The parameters were set to a minimum dissimilarity of 0.5 for the division of groups and pseudospecies cut levels of 10. The latter resulted in a division of relevés with low dissimilarity in ecological space but relatively high differences in species presence. This was needed as the study site was seemingly characterised by low differences in ecological gradients and partly by a high number of widespread species within the plots. This is a side-effect of the use of permanent plots in an ongoing succession, which leads to heterogenous plant communities within each plot.

The modified twinspan algorithm allows an analysis of heterogeneity before each division, which was performed with the average Sørensen dissimilarity. A nomenclature of vegetation types follows Mucina et al. (1993) with translations modified from EUNIS (https://eunis.eea.europa.eu/habitats-code-browser.jsp).

Results

Plant communities

The twinspan analysis resulted in 60 vegetation clusters, which showed a high correspondence with eight different plant communities (Fig. 2, Tab. S4). These are described in detail thereafter:

Annual community of periodically flooded edges of water bodies (*Bidentetea tripartiti*)
Regardless of the former crop type, the first two survey years were characterised by a community associated with arable land combined with high levels of groundwater and nutrients. Among the predominant species are *Rorippa palustris* and *Persicaria lapathifolia,* but also relations to the segetal vegetation (*Stellarietea mediae*), wet meadows (*Molinietalia*) and the *Elymus repens* community could still be observed.
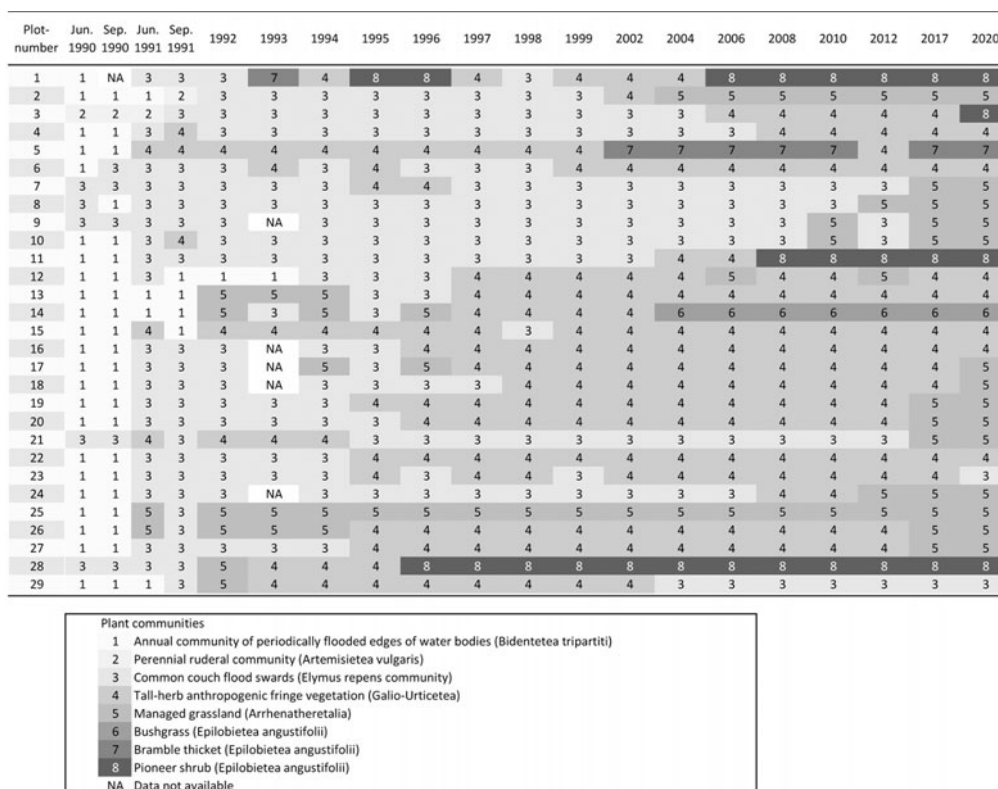

Fig. 2. Plant communities in 29 permanent plots, located in Metschach, Austria during the study period 1990–2020. A modified twinspan analysis (Hill 1979, Roleček et al. 2009) was used to classify 580 vegetation relevés. For details see Tab. S4.

Perennial ruderal community (*Artemisietea vulgaris*)

While many plots included ruderal fragments throughout the entire study period, only one single plot, which was located in the former maize cultivation, showed typical species of this community in the first two survey years at a higher abundance. These included competitive and ruderal specialists such as *Erigeron annuus*, *Ranunculus repens* and *Elymus repens*.

Common couch flood swards (*Elymus repens* community)

From the second year onwards, a tendency towards monodominant patterns can be observed in *Elymus repens*, which later on is accompanied by tall-herb anthropogenic fringe vegetation (*Galio-Urticetea*), wet meadows (*Molinietalia*), managed grassland (*Arrhenatheretalia*), but also ruderal elements (*Artemisietea vulgaris*). After a maximum in the second year, including 70% of the plots, this type remains predominantly in the western part of both sites, but is replaced in the following years by managed grassland (*Arrenatheretalia*) in plots with former crop rotation.

Tall-herb anthropogenic fringe vegetation (*Galio-Urticetea*)

After about five years, the eastern plots showed a transitional change with decreasing abundance of graminoids and an increase of tall herbaceous and nitrophilous plants, such as *Galium aparine*, *Urtica dioica* and *Rubus fruticosus* agg. Besides a high number of transitional types, this type has diminished within the last decade in most plots of the former crop rotation, where it is mainly replaced by managed grassland (*Arrhenatheretalia*).

Managed grassland (*Arrhenatheretalia*)

During the last decade, a species-rich community characterised by *Arrhenatherum elatius*, *Dactylis glomerata* and *Campanula patula* developed predominantly in the southern site. Initially rich in segetal and ruderal species such as *Urtica dioica* and *Erigeron annuus*, the community also hosted the endangered *Potentilla norvegica* in higher abundances than other plots. Later, an association with dominant *A. elatius*, constant *Holcus lanatus* and *Anthriscus sylvestris* was shown (*Pastinaco-Arrhenatheretum*). A variant associated with higher soil moisture is evident by constant occurrence of *Juncus effuses*, *Deschampisa cespitosa*, *Carex leporina* and *C. hirta* (*Molinietalia*).

Bushgrass (*Epilobietea angustifolii*)

Forest clearings promote light-demanding nitrophilous species such as *Calamagrostis epigejos* with fast vegetative growth. The latter showed monodominant behaviour where the tree species remained small and shadowing effects diminished. Small patches of this vegetation type were found mixed in areas at the margins of both study sites, nearby forests, and taller-growing shrub vegetation. Within the study area, this type emerged only on a single plot in 2004 and remained for the duration of the study.

Bramble thicket (*Epilobietea angustifolii*)

A mixture of woody species such as *Fraxinus excelsior* and *Sambucus nigra*, together with nitrophilous and herbaceous species characteristic of pioneer forests and clearings, such as *Fragaria vesca*, *Epilobium angustifolium* and *Rubus fruticosus* agg. distinguished this vegetation type from the tall herbaceous fringe vegetation (*Galio-Urticetea*). Bramble thickets occurred only on two plots in the western part of the former maize cultivation.

Pioneer shrubland (*Epilobietea angustifolii*)

Taller growing woody species occurred in the last decade at the margins of the study area, next to ditches. With one exception, all plots were classified as fringe with regard to their location type. Typical species were small trees such as *Salix caprea* and *Populus tremula*, but also herbaceous plants such as *Angelica sylvestris*, *Tanacetum vulgare*, *Urtica dioica* and the small woody species *Rubus idaeus*. Additionally, this type shared a high species number with the tall herbaceous fringe vegetation (*Galio-Urticetea*).

The development of species numbers and species turnover

Considering the entire study period 1990–2020, the mean species richness was highest in plots of the former crop rotation, independent of the location type (Tab. 1, Tab. S1).

Similar tendencies could be observed for each survey year for the two crop types but were less evident between plots on the fringe or in grassland (Fig. 3). The 30-year trend of mean species richness in grassland decreased from 45/28 species in the baseline year to about 23/17 species in the period of 1991–1995 in former crop-rotation and maize-plots respectively. This was caused mainly by disappearance of a community typical for arable land with high groundwater-levels. After the five years, competitive species such as *Galium aparine*, *Urtica dioica* and *Rubus fruticosus* agg. became more abundant.

In 1996, however, the species richness increased continuously. This change appeared clearer in plots with former crop rotation. The species turnover reveals considerable changes in species composition even in years with small changes in richness (Fig. 3). Overall, its pattern drops during the first decade, but less obvious compared to the richness and shows distinctive declines during the last decade. Additionally, the differences between both cultivation types are less obvious and seem to be more pronounced between grassland and fringe vegetation.
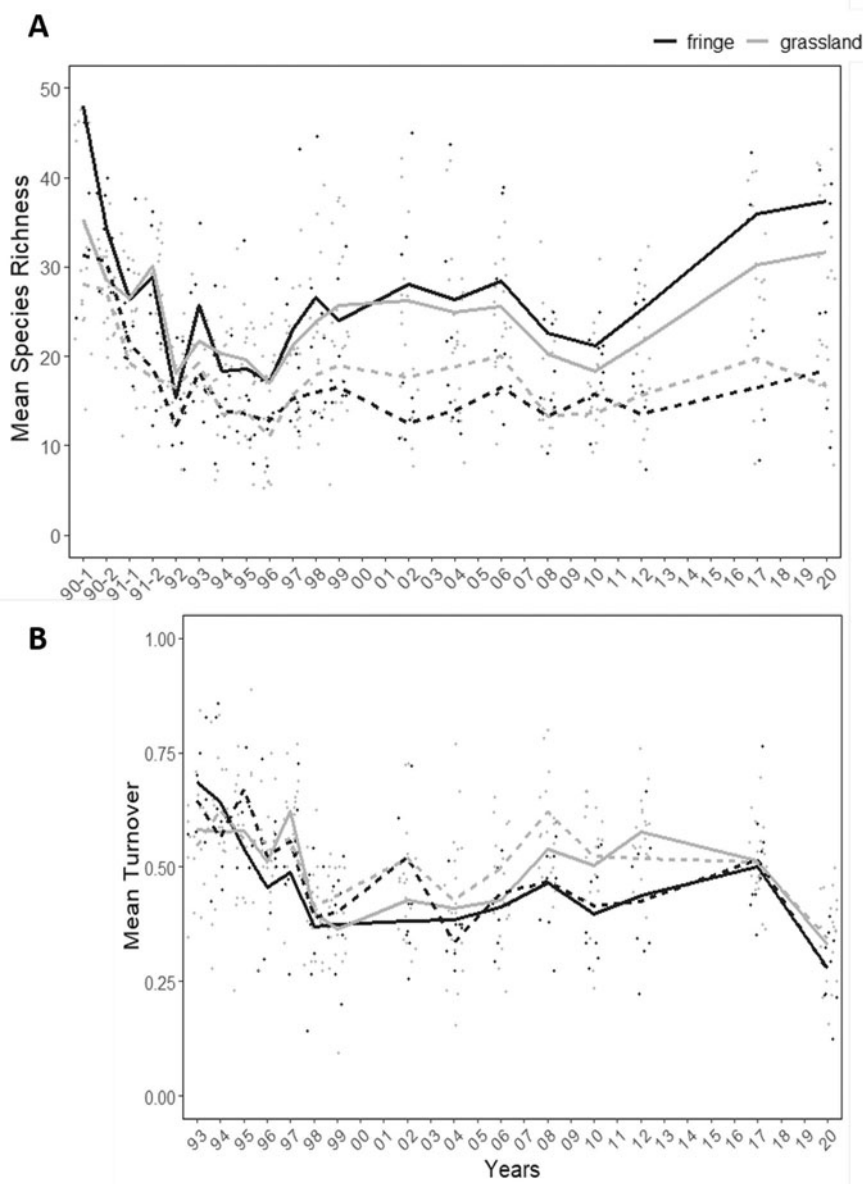
Fig. 3. Mean species richness (A) and mean turnover (B) in 29 permanent plots, located in Metschach, Austria during the period 1990–2020. Shown is raw data per plot (points) and mean values (lines). Solid line indicates mean values of former crop-rotation and dashed line of former maize plots. For further details on mean species richness, see Tab. 1.

The development of the site factors (EIVs)

Soil moisture values are slightly higher on the former maize cultivated site during the entire study period (Fig. S3), with the highest mean value of 5.91 and 5.73 for maize and crop-rotation respectively in the plots of the fringe (Tab. 1, Tab. S3). Almost the same values of 5.73 and 5.71 were obtained between the fringe with former crop rotation and grassland with former maize cultivation respectively. Grassland from both crop types revealed significantly higher values of 5.71 in plots with former maize, compared to 5.48 to former crop rotation.

The indicator value for light availability (illuminance) showed the highest values of 7.03 in grassland with former maize cultivation followed by 6.98 in grassland with former crop rotation. Plots with fringe vegetation had the lowest values.

As far as nutrients are concerned, former maize cultivation plots had significantly higher values of 6.91 and 6.37 for fringe and grassland respectively (Tab. 1, Tab. S3).

The temperature values of 5.72 and 5.69 were highest in the grassland of former maize and crop rotation respectively (Tab. 1, Tab. S3), while the lowest values of 5.56 were found for the fringe vegetation irrespective of

Table 1. Mean and standard error (SE) of species richness and four different ecological indicator values (EIV) in 29 permanent plots located in Metschach, Austria during the study period 1990–2020. Prior to the study, two different cultivation types were applied, and the dataset was split into two subsets, including either plots located in the central grassland area or the marginal fringe zone of both crop-types. P-values were derived from linear mixed effects models (lme4, Bates et al. 2015), with either richness or a EIV as response, crop type as fixed effect and plot as well as survey year as random effects. Significant p-values in bold. For number of plots in each crop- and vegetation-type see Fig. 1 and for model details Tab. S3 in the supplement.

Species Richness	Crop-type	Location	Mean	SE	P-value
Richness	crop rotation	grassland	26.41	0.86	
	maize		18.93	0.83	**0.000**
	crop rotation	fringe	28.16	1.5	
	maize		17.31	1.22	**0.000**
Ellenberg Indicator Values	**Crop-type**	**Location**	**Mean**	**SE**	**P-value**
Moisture	crop rotation	grassland	5.48	0.02	
	maize		5.71	0.04	**0.022**
	crop rotation	fringe	5.73	0.03	
	maize		5.91	0.04	0.107
Light	crop rotation	grassland	6.98	0.01	
	maize		7.03	0.02	0.267
	crop rotation	fringe	6.77	0.03	
	maize		6.66	0.05	0.473
Nutrients	crop rotation	grassland	5.89	0.04	
	maize		6.37	0.06	**0.018**
	crop rotation	fringe	6.15	0.07	
	maize		6.91	0.04	**0.012**
Temperature	crop rotation	grassland	5.69	0.01	
	maize		5.72	0.02	0.248
	crop rotation	fringe	5.56	0.02	
	maize		5.56	0.03	0.920

former crop type. The latter reflects slightly colder conditions due to shadowing-effects next to adjacent trees and taller growing fringe vegetation.

Discussion

The main goal at the start of the nature conservation project in 1990 was to re-establish wet meadows and peatland after the abandonment of intensive agricultural cultivation. This was followed by extensive management with one or two mowing operations per year. The ongoing monitoring in the former intensive cropland Metschach, Austria, reveals partly unexpected results regarding vegetation dynamic, species richness and community structure according to EIVs. Moisture-dominated wet meadows and peatlands are of high importance both for the preservation of biodiversity and for meas-

ures to mitigate climate change by carbon sequestration in the soil (Grzybowski & Glińska-Lewczuk 2020, Parish et al. 2008). In contrast to the initial management aims, the reestablishment of wet meadows and peatland could not yet be realised, but diverging ecological patterns depending on former agricultural management regime became apparent.

Plant communities

After the abandonment of intensive agricultural crop cultivation in 1989, three main successional pathways emerged during the period 1990–2020 (Fig. 2, Tab. S4). Starting from the initially annual segetal and ruderal types, these can be further summarised in order of their appearances as transformations towards: (1) graminoid dominated communities (*E. repens*-community, bush-

grass, managed grassland), (2) nitrophilous, herbaceous communities (tall herbaceous fringe vegetation) and (3) communities with taller growing shrubs and trees (bramble thicket, pioneer shrubland). In line with other long-term studies on abandoned croplands with different intensities of mowing, these reflect typical patterns of early secondary succession (Prach et al. 2007, Ruprecht 2005).

With respect to the first research question, whether maize cultivation has different long-term effects on plant communities, our results indicate that the longevity of certain successional stages depends on the former cultivation type. Although only minor differences were observed in the first twenty years, considerable differences were observed over the last decade (Fig. 2, Tab. S4).

In the latter period, the plots with former crop rotation shifted mainly to species-rich communities of managed grassland, while the former maize cultivation remained in its previous species configuration with predominantly *E. repens*-community and tall herbaceous fringe vegetation. Given a vast vegetative growth, our findings likely reflect the competitive abilities of *E. repens* (Boström et al. 2013), which allows the formation of stable communities on some plots in the second year of the survey for almost two decades.

Similar results were also reported from abandoned fields in Transylvanian croplands, where annual species dominated in the first year and were replaced by *E. repens* in the second year (Ruprecht 2005). Vegetative spread is also an important strategy for characteristic species of tall herbaceous fringe vegetation (*Galio-Urticetea*), which became more abundant after about five years. However, an obvious diversification between maize and crop rotation plots was still missing (Fig. 2, Tab. S4). As shown in other studies, management has a strong shaping impact on richness and abundance of vascular plants in anthropogenic grasslands (Klimek et al. 2007, Stadler et al. 2017). This was also evident at the margins of both the maize and the crop rotation site (Fig. 1), where successional stages dominated by graminoids or herbaceous vegetation showed tendencies towards early successional forest communities (bramble thicket, pioneer shrubland), once mowing was stopped (Tab. S1). Consequently, even the application of mowing once or twice a year may not be sufficient to replace herbaceous dominated communities.

Other studies have reported long-term effects of agriculture on soil conditions, such as C- and N levels (Knops & Tilman 2000, Nkonya et al. 2005, Richter et al. 2000) that can last for decades or even centuries (Foster et al. 2003). Our results suggest that such effects might even differ depending on crop type. One explanation arehigh amounts of artificial fertilizers and herbicides used more intensively in monoculture maize cultivation compared with other crops (Fanfarillo et al. 2019). However, at this stage, our results must be considered with caution and additional *in-situ* measurements of soil characteristics such as soil moisture or nitrogen would be necessary to clarify this point.

The development of species numbers and species turnover

Numerous studies analysing secondary succession found continuously increasing numbers of species in abandoned old fields (Chytrý et al. 2001, Keever 1950, Lepš 1987). Our contrasting finding of decreasing species richness in the first years can be explained by the recent abandonment of an intensive agriculture regime, which led to germination of a high number of species present in the soil-seed bank into an uncompetitive environment. This initially high species richness declines with the abandonment of intensive agricultural practice and the increasing abundance of more competitive species such as *E. repens* or *Urtica dioica*. Similar results have been reported from abandoned old-fields in North America, were a decline in species richness occurred due to the disappearance of the annual community (Collins et al. 2001) but also from different managements regimes applied to grassland communities in Germany (Stadler et al. 2017). Abandoned crop fields are also prone to invasive plant species, as reported from the Czech Republic (Prach et al. 2007). Within the study area, the two introduced species *Erigeron annuus* and *Solidago canadensis* have been found in higher abundances since 1996 (Tab. S3) and could potentially lead to lower species numbers in the first surveys (Hejda et al. 2009).

Divergent patterns in species richness with higher values on the former crop rotation site and lower values at former maize cultivation have been present since the beginning of the study and remain so over the entire 30-year study period (Fig. 3A, Tab. 1, Tab. S3). With strong ecological gradients, species richness can also vary considerably between nearby sites (Diamond et al. 2020, Moeslund et al. 2013). Differences between the northern and southern sites might therefore be an artifact of heterogenous topography. However, the study design was applied to a homogenous valley bottom with minimal slope and homogenous soil structure, which should minimize the differences in microtopography and microclimate. Additionally, the data set was divided into two location types, fringe and grassland, to account for small differences between plots. The only major difference between the two sites is the respective land-use history, which was pointed out by Benjamin et al. 2005 as one of the major explaining factors for current state of vegetation in abandoned farmlands. We therefore conclude that the former maize cultivation is the main reason for the lower numbers in species richness at the northern site. A less clear pattern was observed in the mean species turnover, which did not show a clear diversification between the two cultivation types (Fig. 3B).

Remarkably, the mean species richness tended to increase on almost all plots during the last decade, while the mean turnover decreased consistently. In the past, such declines were related to steady states during vegetation succession (Lewis et al. 2017, Shugart & Hett 1973) and might therefore indicate an approach towards a more stable species equilibrium.

Most strikingly, this would further imply that substantially lower species numbers associated with maize cultivation would remain within the current vegetation for at least 30 years, but probably several decades longer once equilibrium is reached. Given the challenges involved in maintaining a long-term permanent plot study and the setup itself, which was originally designed to monitor the re-establishment of wet meadows, this observation must be made with caution.. Nevertheless, given the scarcity of comparable datasets, especially for the prevailing extent of time, the patterns observed should be emphasized. Furthermore, we suggest continuing the vegetation surveys in Metschach to broaden the understanding of the long-term effects of maize cultivation on biodiversity in the temperate climate zone.

The development of the site factors (EIVs)

Abiotic factors, such as temperature, moisture or nutrients are known to have strong shaping impacts on biodiversity and plant communities (Lewis et al. 2017) but are closely linked to biotic interactions (Loreau et al. 2001). The analysis of the EIVs revealed minor differences in grassland moisture and nutrients between the former crop-rotation and maize cultivation for both sites (Fig. S3, Tab. 1, Tab. S1). The common couch flood swards community and tall anthropogenic fringe vegetation, both adapted to higher levels of moisture and nutrients were preserved in most of the survey years on former maize cultivation plots and differed significantly from crop-rotation plots. In the latter, managed grassland became dominant during the last decade revealing significantly higher number of species. While higher values of moisture might also explain the lower richness in former maize plots (Moeslund et al. 2013), this only holds true considering grassland plots.

In contrast, plots covered by fringe vegetation, did not show comparable moisture values, but the richness was nevertheless significantly lower. A higher moisture indicator value in former maize plots might be a result of the species composition itself. For example, a recent study found evidence that plant communities themselves can alter soil properties in a way that leads to drier soils (Fischer et al. 2019). The authors reported that higher species richness was associated with advanced topsoil organic carbon in later successional grasslands, likely because of advanced soil aggregation resulting in a better drainage. Therefore, even higher moisture values might be associated with maize cultivation as it could reflect delayed successional development.

The observed higher EIVs for nutrients in former maize cultivation are well in line with the resource-ratio hypothesis (Tilman 1985). The latter describes the dominance of certain species during succession in relation with long-term supply of limiting resources. This is probably due to intensive fertilization during former maize cultivation (Nkonya et al. 2005) resulting in high amounts of nutrients, especially nitrogen. Nitrogen is well-known to promote competitive species, with negative effects on species richness (Midolo et al. 2019).

Lessons learned and outlook

The continuous collection of biodiversity data over a period of 30 years is a methodological and logistical challenge. It is important to keep the collection independent of changes in the field staff (Futschik et al. 2020) and of taxonomic changes and to ensure a consistent and systematic data storage.

Over the past 30-years, improvements in various measurement and data processing technologies have been enormous. These should be implemented in ongoing biodiversity monitoring programmes to improve the cost-efficiency of field work, combined with more detailed information on abiotic site conditions and data consistency.

This in turn would support the interpretation of biodiversity trends, all the more so in case of unexpected results. In view of the numerous international and national conventions for the protection of biodiversity (e.g. Convention on Biological Diversity – Aichi Biodiversity Targets, Berne Convention, Bonn Convention, International Convention for the Protection of Birds), there is also an urgent need for increased use of modern technologies to meet the increased demands on monitoring systems.

The balance between costs-and-benefits of long-term monitoring remains on the cost side, at least in the initial years, but in view of the scarcity of longer time series in biodiversity research, there is an enormous benefit with every survey year. Therefore a continuation of the present monitoring is highly recommended and will further improve our understanding of biodiversity patterns in abandoned croplands.

For a better understanding of the present results obtained in Metschach, further studies at additional sites with similar land-use history are necessary to verify our findings. This in turn would also put the results in a wider spatial context. Further research should include samples from the seed bank, chemical analyses of soil properties (nitrogen, heavy metals, etc.), in-situ measurements of temperature and moisture, but also short-term manipulation experiments. Given the longevity of the current monitoring programme, continuation is highly recommended to ensure comparability with other monitoring

sites and to further document ongoing changes in vegetation. Currently, this study focuses solely on plants, but since various species groups often show diverging tendencies (Winkler et al. 2018), a comparative study including e.g. soil arthropods would support a comprehensive understanding of the relevant ecological processes.

Finally, results of the current study, as well as expected outcomes from related studies will be part of further teachings and lectures in the framework of nature conservation and restoration ecology.

Conclusion

This study highlights the importance but also reflects the difficulties associated with long-term biodiversity monitoring programmes. These include, on the one hand, consistent commissioning and implementation, which is strongly related to funding opportunities and inevitably affects the number of study units and the measurement of site conditions, and, on the other hand, long-term monitoring often inevitably involves changes in researchers, methods, or technologies, but these should be avoided or limited where possible. Furthermore, a clean documentation of the management history is necessary to be able to interpret changes in plant composition.

Overall, we found that abandoned maize cultivation at least delays succession towards managed grassland communities, negatively affects species richness and promotes a community adapted to higher nutrient levels. Should these unexpected results be further confirmed, the impact of crop cultivation on biodiversity would urgently need to be reassessed, including other crop types. As the initial goal of the monitoring, the reestablishment of a wet meadow could not be reached, an evaluation of the intended actions and assessment of their impact is necessary. These will focus on improved water logging and adaptation of management plans. Additionally, the challenging effects of rising temperatures (Fig. S1) for the restoration of moisture dominated habitats must be considered (Joyce et al. 2016). However, the current study strengthens the importance of monitoring to reveal the impacts of biodiversity management.

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work in this paper.

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Tab. S1: Different management activities of 29 permanent plots in Metschach, Austria
Tab. S2: Ordinal abundance scale (Braun-Blanquet 1964), used for cover estimation
Tab. S3: Results of models analysing effects of different crop cultivation across different location types
Tab. S4: Vegetation relevés of 29 permanent plots in Metschach, Austria between 1990-2020
Fig. S1: Mean annual soil temperature and mean annual precipitation in Metschach, Austria between 1981-2019
Fig. S2: Weighted ecological indicator values (EIV) according to Ellenberg

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