Tuexenia 41: 423–440. Göttingen 2021.
doi: 10.14471/2021.41.018, available online at www.tuexenia.de

Vegetation changes in urban grasslands over 25 years in the city of Zurich, Switzerland

Veränderung der Graslandvegetation in der Stadt Zürich (Schweiz) über 25 Jahre

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Abstract

Many studies have demonstrated significant alterations in the species composition of grasslands in Central Europe over the past decades due to multiple drivers of anthropogenic environmental change. Most such studies deal with dry, acidic, wet or alpine grassland types, while little is known about changes in mesic grasslands, particularly in urban areas. To investigate the effects of anthropogenic environmental change on such grasslands, we resurveyed a selection of plots in the city of Zurich (Switzerland) approximately 25 years after their original recording. First, we checked whether 241 extensively used mesic grasslands (belonging to the *Arrhenatheretalia elatioris*) in the city were still grasslands, and whether their management had changed. Then we resurveyed a representative subset of 30 quasi-permanent plots of 50 m². We tested whether biodiversity metrics, mean ecological indicator values, community weighted means (CWMs) of functional traits or the presence of individual vascular plant species had changed. We found that 15% of the original grasslands had been lost due to changes in land use during this period. Of the remaining grasslands, most of the former meadows were still mown, while many of the former pastures had been transformed into meadows. Measures of alpha diversity had not changed significantly for the 30 plots. However, species composition now indicated nutrient poorer, less base-rich and less ruderal site conditions, while CWMs of specific leaf area (SLA) had decreased and that of seed mass increased. In stands that were managed by mowing in both periods there was practically no change, while there was a pronounced change in those that had been transformed from grazing to mowing. In general, five species showed a significant increase and 16 species a significant decrease in frequency, with no obvious ecological difference between winners and losers. Alien species were rare in both periods and showed hardly any trend, except *Veronica persica*, which became rarer. In conclusion, more extensively used grasslands have survived to date than would be anticipated in such a rapidly growing city as Zurich. Their quality has hardly changed during the past

Manuscript received 09 May 2021, accepted 07 August 2021
Published online 31 October 2021
Co-ordinating Editor: Valentin Klaus

quarter century, and if changes occurred, they are rather attributable to the intentional change of management from grazing to mowing. The relatively good ecological state of these urban grasslands might be due to a lower agricultural land use pressure than outside urban areas, as well as a constant management of many of these grasslands with a conservation focus. By maintaining these grasslands in their current state, they may have the potential to contribute to the conservation of biodiversity in urban areas.

Keywords: *Arrhenatherion elatioris*, biodiversity, CSR-strategy, ecological indicator value, functional trait, green space, meadow, mesic grassland, *Molinio-Arrhenatheretea*, pasture, resurvey, Switzerland, urban ecology, vegetation change, Zurich

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Secondary grasslands are an important element of European landscapes. They exist due to centuries or millennia of human land use, mainly in the form of livestock grazing and mowing, in places that naturally would be forested (Dierschke & Briemle 2002, Poschlod 2015, Leuschner & Ellenberg 2017, Dengler et al. 2020). Despite being secondary (semi-natural), they are often very species rich in many taxonomic groups (Dengler et al. 2020), some of them even hosting world records for small-grain species richness of vascular plants among all vegetation types globally (Wilson et al. 2012). However, this huge biodiversity has strongly declined in recent decades due to multiple causes (Rounsevell et al. 2018, Dengler et al. 2020). In Central Europe, the intensification of the larger part of the secondary grasslands and underuse/abandonment of another part are considered the two main threatening factors (Dengler & Tischew 2018). Other potential reasons for the loss of biodiversity include eutrophication through deposition of atmospheric nitrogen, hydrological changes, homogenisation of the grassland patches, climate warming and invasion by non-native species (Dengler & Tischew 2018).

While still covering considerable areas, secondary grasslands have undergone drastic changes throughout Europe, particularly in Central Europe, where many of the drivers of change are most pronounced. Accordingly, few of the remaining secondary grasslands still qualify as semi-natural, and even semi-intensified grasslands have become rare, while the agronomically most productive, intensively used types now prevail (Stevens et al. 2004, Dengler et al. 2020). This development led to the inclusion of the majority of secondary grassland types into red lists of habitats, both at the European scale (Janssen et al. 2016) and in Switzerland (Delarze et al. 2016). While it has long been known that dry and wet grasslands are threatened habitats (e.g. Korneck et al. 1998), both in Switzerland and in all of Europe, the formerly widespread mesic meadows of the alliance *Arrhenatherion elatioris* (class *Molinio-Arrhenatheretea*) – at least the typically species-rich types – are now also considered vulnerable (Delarze et al. 2016, Janssen et al. 2016). These mesic meadows are mainly affected by the massive intensification of land use in grasslands throughout Europe during recent decades (Lachat et al. 2010, Bosshard et al. 2011). At the same time, even though agri-environmental schemes are implemented in grasslands, positive effects on the biodiversity of mesic grasslands remain limited (Riedel et al. 2019).

Details of the vegetation change in Central European grasslands have been studied via resurveys of historical vegetation plots (see meta-analysis by Diekmann et al. 2019), space-for-time substitutions (Gossner et al. 2016) and analyses of huge vegetation-plot databases (Jandt et al. 2011). In Switzerland, resurvey studies have been carried out in dry grasslands

(FISCHER & STÖCKLIN 1997, BOCH et al. 2019), wet grasslands (RION et al. 2018, BERGAMINI et al. 2019), montane-subalpine managed grasslands (PETER et al. 2008, 2009, HOMBURGER & HOFER 2012) and alpine grasslands (MATTEODO et al. 2016). However, there seem to be no prior resurvey studies in mesic grasslands of the lowlands and especially not in urban areas.

Urban grasslands can cover quite large areas in cities. In Berlin, for example, grasslands cover 5% of the city, not counting those in small parks and private gardens (FISCHER et al. 2013a). Urban grasslands have a clear potential for biodiversity conservation (FISCHER et al. 2013a, KLAUS 2013,) and there has been quite some research on different aspects. Several studies show that low-maintenance urban grasslands can harbour quite a high species richness (e.g. RUDOLPH et al. 2017, CHOLLET et al. 2018, NORTON et al. 2019, SEHRT et al. 2020). However, their species richness was still lower than in comparable semi-natural agricultural grasslands (RUDOLPH et al. 2017). Other studies on mesic grasslands in an urban context deal with aspects of ecosystem functioning (e.g. ONANDIA et al. 2019), the establishment of novel grasslands (e.g. FISCHER et al. 2013b) and with their species and trait composition along the urbanisation gradient (e.g. ALBRECHT & HAIDER 2013). However, we are not aware of any prior study that analysed vegetation change in low-maintenance urban grasslands over time.

For this study, we made use of the PhD thesis of WILHELM (1997), who comprehensively sampled the urban grasslands (meadows and pastures, meadows all with less than four cuts per year) within the city of Zurich (Switzerland) during the years 1990–1993. Zurich is a well-researched city from a floristic point of view. The complete flora of Zurich has been described in detail by LANDOLT (2001) and, apart from the study of WILHELM (1997), there have been other studies on different aspects like the flora of pavement gaps (KRÜSI & TRACHSEL 2012) or the vegetation of compacted grounds (WISKEMANN 1989). All these studies present a valuable knowledge base for further research. In our study, we first asked which of the 241 historical vegetation plots sampled by WILHELM (1997) were still grasslands, and, if so, whether their management had changed. Then we took a representative subset of 30 historical plots in the urban District 7 and resurveyed these plots in 2018. We assessed whether and how species diversity and species composition had changed, and which conclusions regarding the underlying drivers and grassland conservation values could be drawn.

2. Methods

2.1 Study area

Zurich (Switzerland, 47º22’ N, 8º33’ E with a population of approx. 434,600 people and an area of 91.9 km^2 (STADT ZÜRICH 2021) is a green city, with 24% of its area covered by forest, 9% by agricultural area, 6% by water bodies and 4% by parks and cemeteries. 40% of the vascular plant flora of the whole country is present within the city (GRÜN STADT ZÜRICH 2019). From 1990 to 1993, WILHELM (1997) carried out a vegetation survey of mown and grazed grasslands in the city of Zurich. His study covered the whole area of the city, with 241 grasslands being surveyed (WILHELM 1997). Based on coordinates and site descriptions, we first checked satellite images of SWISSTOPO (2018) taken between 2015 and 2017 to verify whether the grasslands still existed. Based on the results of this check and due to time constraints, we restricted our resurvey to the urban District 7 (*Stadtkreis* 7) within the city of Zurich (Fig. 1). This district is divided into four different quarters and has an area of 15 km^2 (STADT ZÜRICH 2018a). WILHELM (1997) surveyed 76 grasslands in this district between 1990 and 1993. For

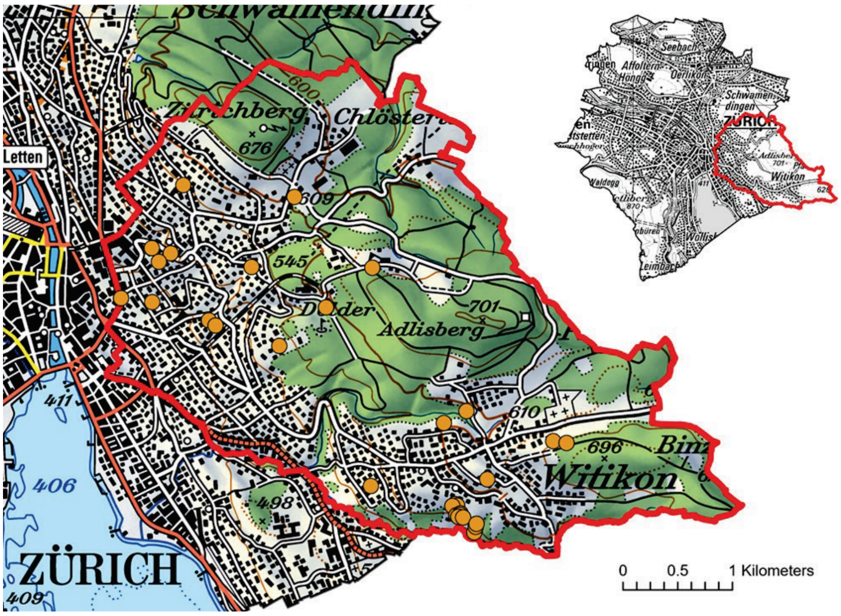

Fig. 1. Map showing the distribution of plots surveyed (orange dots) in the District 7 (red outline) in the southeast of the city of Zurich. Background map: © swisstopo.

Abb. 1. Karte der Positionen der Aufnahmeflächen (orange Punkte) im Kreis 7 (rot markiert), sowie der Lage des Kreis 7 (rot markiert) innerhalb der Stadt Zürich (kleine Karte oben rechts). Hintergrundkarte: © swisstopo.

our resurvey, we first assessed the current land-use of the still existing sites by interviewing landowners, then chose 30 grasslands in this district (for examples see Fig. 2) based on this information (see Supplement E1 for detailed information). The grasslands were selected so that they represented the four district quarters evenly (Fig. 1).

2.2 Data collection and measurements

The plots for the resurvey were placed in the 30 selected grasslands as accurately as possible using the coordinates and descriptions given in WILHELM (1997). The resurvey was carried out between May and June 2018 using 50-m^2 plots (like WILHELM 1997). The new plots were square-shaped with a side length of 7.07 m, as there was no information on the shape of the old plots available. The diagonal of the new plots was oriented North-South, with these two corners permanently marked by buried magnets for later resurvey, except for two plots (sites 660 and 839) where we did not get permission from the landowners. Additionally, the coordinates of the northern and southern corners were recorded with the application GNSS Status (version 3.0.1.359, Trimble) to a precision of 10 m.

In the new plots, all vascular plants were recorded and their percentage cover estimated visually on a continuous scale, while WILHELM (1997) had used the 7-step cover-abundance scale of BRAUN-BLANQUET (1964). The plant nomenclature of the old and new plots was harmonized according to JUILLERAT et al. (2017). We defined alien species according to LANDOLT et al. (2010) and threated species according to the red list of the Swiss vascular plants (BORNAND et al. 2016). Cover of the different vegetation layers (total vegetation, herbs, shrubs, trees, mosses and litter) was also estimated in percent. The mean height of the herb layer in the new plots was measured with the drop disc method (DENGLER et al. 2016). The vegetation plots are provided in Supplement E1 and will be contributed to the emerging Swiss National Vegetation Database (J. Dengler et al. in prep.) and the ReSurveyEurope database (F. Essl et al. in prep., see http://euroveg.org/eva-database-re-survey-europe).

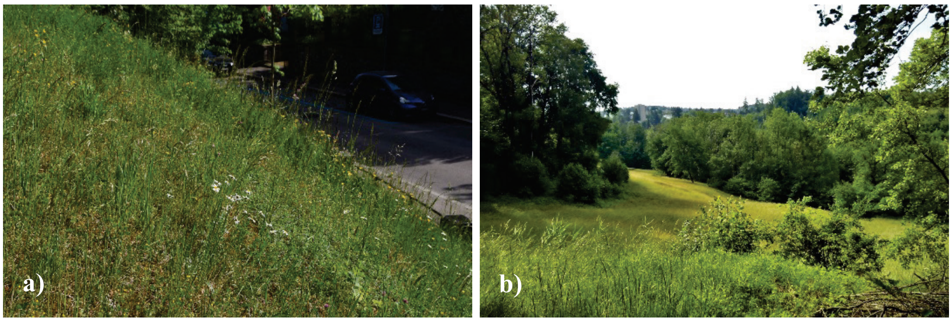

Fig. 2. Two examples of surveyed grasslands in District 7 of the city of Zurich; **a)** shows the grassland surrounding the Kreuzkirche (Dolderstrasse) inside the built-up area (Photo: J. Dengler, 07.05.2018), **b)** shows the surveyed grasslands in Segeten (Witikon) at the edge of the city (Photo: J. Kummli, 05.06.2018).

Abb. 2. Zwei Beispiele von untersuchen Wiesen im Kreis 7 in der Stadt Zürich; **a)** zeigt die Wiese bei der Kreuzkirche (Dolderstrasse) in der überbauten Zone (Foto J. Dengler, 07.05.2018), **b)** zeigt eine Wiese im Gebiet Segeten (Witikon) am Rande der Stadt (Foto J. Kummli, 05.06.2018).

2.3 Statistical analyses

The Braun-Blanquet-scale used by WILHELM (1997) was transformed into percentages using the arithmetic mean of the borders of the Braun-Blanquet classes. The Software VEGEDAZ (KÜCHLER 2019) was used to calculate Shannon diversity, Shannon evenness, mean cover-weighted indicator values (LANDOLT et al. 2010) and cover-weighted mean plant strategies (LANDOLT et al. 2010) for each plot. For the latter, the original nominal measure based on the C-S-R triangle by GRIME (1977) was decomposed into the three dimensions: "competition," "stress" and "ruderality," each with values ranging from 0–3. Following the leaf-height-seed (LHS) plant strategy scheme (WESTOBY 1998), the community weighted means (CWM) of the functional traits specific leaf area (SLA), plant height and seed mass obtained from the LEDA Database (KLEYER et al. 2008) were calculated using the function "functcomp" of the R package "FD" (LALIBERTÉ et al. 2014) after standardising the trait measurements with $\log_{10}$. Beta diversity was defined as Jaccard similarity coefficient (1 – Dissimilarity index), calculated separately for the plots sampled 1991–1993 and the plots sampled in 2018 using the function "vegdist" of the R package "vegan" (OKSANEN et al. 2018).

A paired *t*-test was used to test for differences in species diversity, indicator values and plant strategies between the two sampling periods. To analyse which species decreased and which increased in their frequency, we ran a sign test with the base R function "binom.test" to compare the number of plots where the species had newly appeared vs. the number of plots where the species had disappeared. The species pairs *Crepis capillaris*/*biennis* and *Prunella vulgaris/grandiflora* were not taken into account, as systematic identification errors had apparently occurred and could not be resolved *post hoc*.

All statistical analyses were run in R 4.0.4 (R CORE TEAM 2021).

3. Results

3.1 Land use change

Of the 241 grasslands sampled in 1990–1993, 205 (85%) were still present in satellite imagery recorded between 2015 and 2017, 33 (14%) former grassland patches had meanwhile mainly been built over and three grasslands (1%) could not be retrieved using the available information.

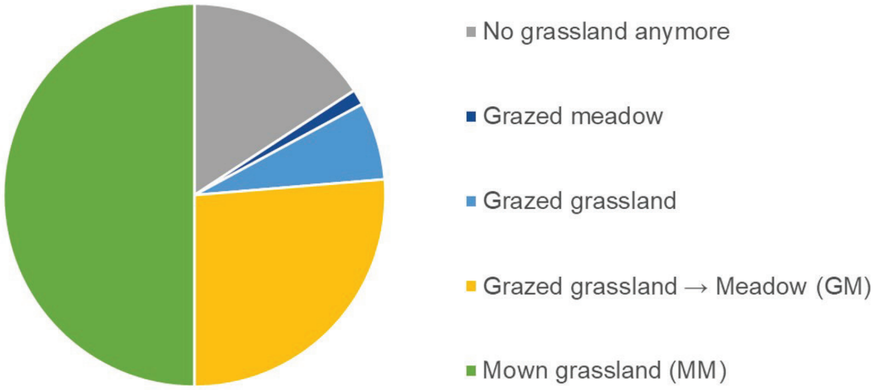

Fig. 3. Fate of the 76 grasslands sampled 1990–1993 in District 7 of the city of Zurich. Some disappeared, one remained as a grazed meadow and some remained as pastures. In this publication, we focus on those grasslands that were mown in both periods (MM) and those that were grazed in 1990–1993 and are now mown (GM).

Abb. 3. Verbleib der 76 Flächen, die 1990–1993 im Kreis 7 in der Stadt Zürich untersucht wurden. Einige sind verschwunden, eine Fläche wird immer noch als Mähweide bewirtschaftet und wenige werden immer noch als Weide genutzt. In dieser Publikation fokussieren wir auf die Flächen, die in beiden Untersuchungsperioden gemäht wurden (MM) oder deren Bewirtschaftung von Beweidung in 1990–1993 auf Mahd in 2018 umgestellt wurde (GM).

Of the 76 grasslands originally surveyed in the District 7, 64 (84%) still existed in 2018 while 12 grasslands (16%) had vanished. For 44 grasslands (58%), the management had remained unchanged since 1990–1993 (38 mown grasslands (MM-grasslands), five pastures, one grassland with combined mowing/grazing; Fig. 3). For 20 grasslands (26%), the management had changed from grazing to mowing (GM-grasslands; Fig. 3). The grasslands surveyed in this study belonged either to the MM-grasslands (15 sites) or to the GM-grasslands (15 sites, i.e. all surveyed grasslands were managed as meadows.

3.2 Changes in biodiversity

We could determine a total of 192 different vascular plant species on the 30 surveyed grasslands in 2018. In comparison, 157 plant species were found in 1990–1993. Across all 30 grasslands, there were no significant changes in the diversity metrics (i.e. mean species richness, Shannon diversity and evenness) over the intervening 25 years (Supplement E2). Also in the two subgroups (MM- and GM-grasslands), all three diversity metrics remained unchanged between the two surveys (Supplement E2). At the individual species level, we found a significant increase in frequency for five species between 1990–1993 and 2018, while 16 species significantly decreased in frequency (Table 1).

There was no significant difference in beta diversity between the two surveys (mean Jaccard index 1990–1993: 0.285; 2018: 0.274; p = 0.077) for the combined dataset. However, the results differed considerably between the two subgroups. While the MM-grasslands became more dissimilar to each other over the years (mean Jaccard index 1990–1993: 0.284; 2018: 0.254; p = 0.009), the similarity of the GM-grasslands did not change significantly (mean Jaccard index 1990–1993: 0.332; 2018: 0.329; p = 0.790).

Table 1. List of all species that showed significant or marginally significant positive or negative changes in frequency between 1990–1993 and 2018. The *p*-values are from sign tests.

Tabelle 1. Liste der Arten, die eine signifikante Zunahme oder Abnahme oder zumindest einen Trend in der Frequenz zwischen zwei Aufnahme-Zeitpunkten zeigten. Die *p*-Werte beziehen sich auf Vorzeichentests.

Species name	Frequency 1990–1993	Frequency 2018	Difference	*p*-value
Winners				
Bromus erectus	8	16	+8	0.057
Carex caryophyllea	1	7	+6	0.070
Galium mollugo aggr.	18	25	+7	0.065
Holcus lanatus	9	21	+12	0.008
Quercus sp.	0	5	+5	0.063
Rhinanthus alectorolophus	2	16	+14	0.001
Sanguisorba minor	5	13	+8	0.021
Stachys officinalis	0	7	+7	0.016
Vicia sepium	13	21	+8	0.021
Losers				
Agrostis stolonifera	15	1	-14	< 0.001
Bellis perennis	16	7	-9	0.035
Capsella bursa-pastoris	8	0	-8	0.008
Cardamine hirsuta	13	0	-13	< 0.001
Cardamine pratensis aggr.	11	4	-7	0.039
Carex hirta	6	1	-5	0.063
Cerastium fontanum	28	21	-7	0.016
Clinopodium vulgare	9	0	-9	0.004
Festuca arundinacea	11	3	-8	0.039
Festuca pratensis	9	1	-8	0.021
Lolium perenne	22	13	-9	0.049
Polygonum aviculare aggr.	5	0	-5	0.063
Primula elatior	5	0	-5	0.063
Ranunculus bulbosus	8	3	-5	0.063
Ranunculus ficaria	11	1	-10	0.002
Rumex obtusifolius	12	2	-10	0.013
Sonchus asper	7	0	-7	0.016
Taraxacum officinale aggr.	27	17	-10	0.013
Verbena officinalis	11	0	-11	0.001
Veronica arvensis	5	0	-5	0.063
Veronica persica	10	2	-8	0.039

3.3 Changes in species composition

The analyses of the complete dataset revealed significant decreases in the indicator values for reaction and nutrient supply (Supplement E2). The two subgroups showed different patterns. While there were no significant differences for the MM grasslands, we found significant decreases in the indicator values for moisture and light and a significant increase for the temperature indicator value in the GM grasslands (Fig. 4; Supplement E2).

Looking at the plant strategies, the value for ruderality decreased significantly in the complete dataset (Supplement E2). This result was mainly due to the significant decrease of this value in the GM grasslands, while the MM grasslands showed no significant differences (Supplement E2). A similar pattern emerged in the analysis of functional traits: seed mass and plant height differed significantly between the two surveys in the complete dataset and in the GM grasslands, but not in the MM grasslands (Fig. 5; Supplement E2).

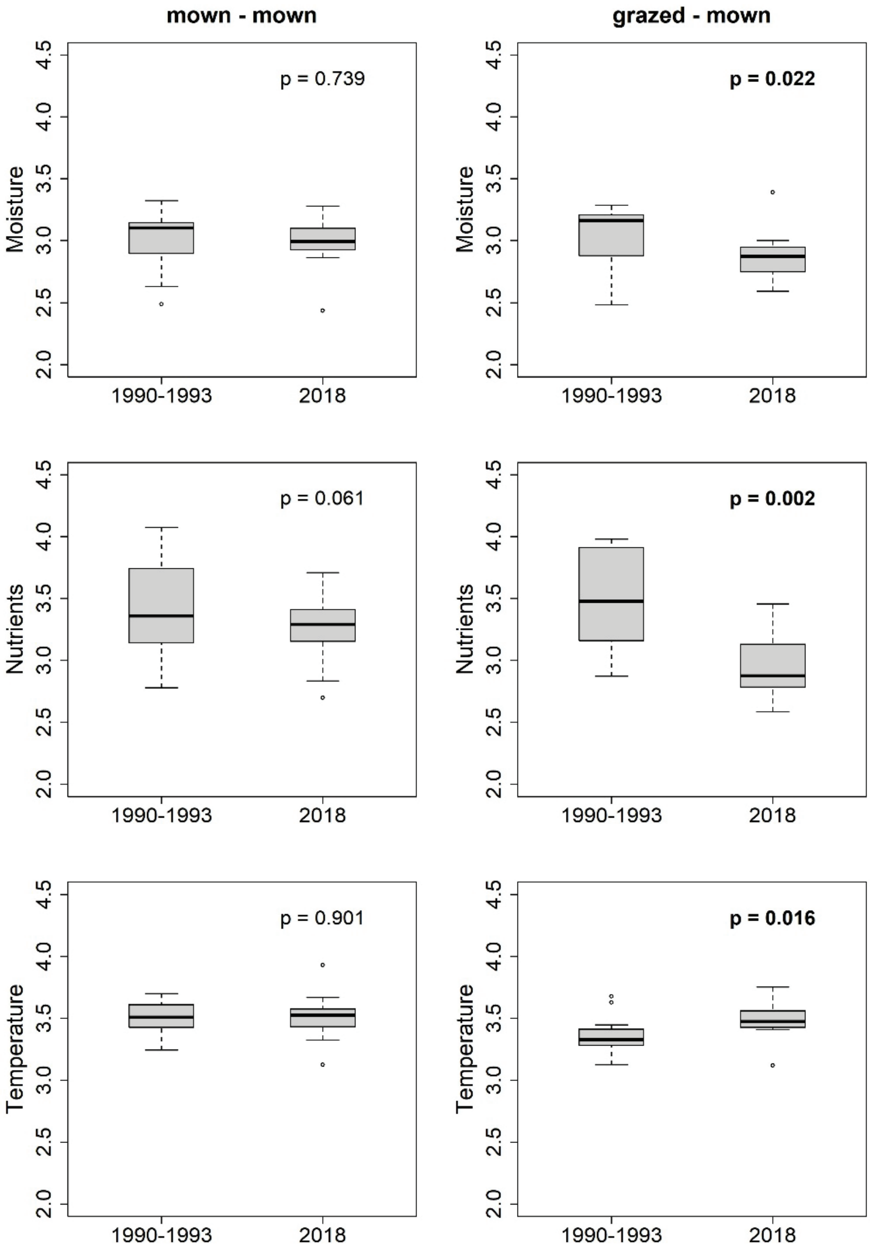

Fig. 4. Temporal changes in mean ecological indicator values according to LANDOLT et al. (2010). Values of the original survey (1990–1993) and the resurvey (2018) are shown. Results are given for the two types of grasslands, in which management (mowing) remained unchanged over the years and in which management changed from grazing to mowing. The given *p*-values originate from paired *t*-tests.

Abb. 4. Veränderung der ökologischen Zeigerwerte nach LANDOLT et al. (2010) zwischen 1990–1993 und 2018. Dargestellt sind die Werte der ursprünglichen Untersuchung und die Werte der neuen Untersuchung. Die Ergebnisse sind für die zwei untersuchen Wiesentypen (in beiden Perioden gemähte versus ursprünglich beweidete und jetzt gemähte) separat dargestellt. Die *p*-Werte stammen aus gepaarten *t*-Tests.

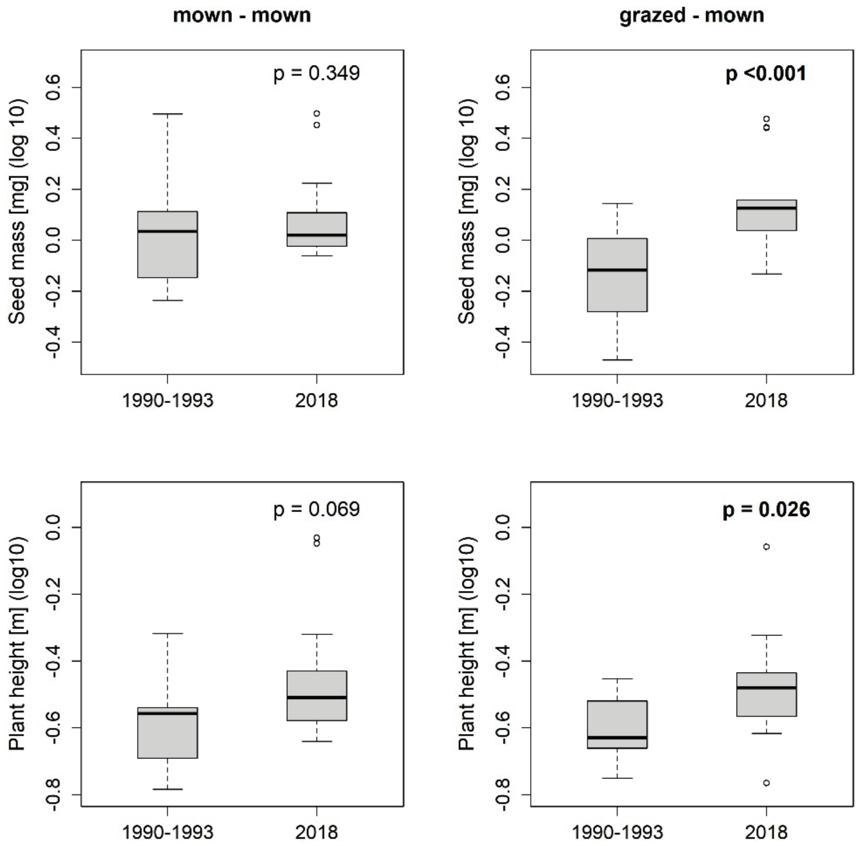

Fig. 5 Temporal changes in CWMs of two functional traits. Values of the original survey (1990–1993) and the resurvey (2018) are shown. Results are given for the two types of grasslands, in which management (mowing) remained unchanged over the years and in which management changed from grazing to mowing. The given *p*-values originate from paired *t*-tests.

Abb. 5. Veränderung der CWMs zweier funktioneller Eigenschaften zwischen 1990–1993 und 2018. Dargestellt sind die Werte der ursprünglichen Untersuchung und die Werte der neuen Untersuchung. Die Ergebnisse sind für die zwei untersuchen Wiesentypen (in beiden Perioden gemähte versus ursprünglich beweidete und jetzt gemähte) separat dargestellt. Die *p*-Werte stammen aus gepaarten *t*-Tests.

We recorded 15 alien species in 2018, while in 1990–1993 there were eleven such species (Supplement E3). Of the 15 species, seven species were new compared to the old survey (Supplement E3). On the other hand, four alien species were no longer present in the new plots, and two had become rarer (Supplement E3). Of the new species, five were woody species and had been planted on purpose. When comparing the proportion of alien species in the complete dataset as well as in the two subgroups between the two surveys, there were no significant differences (Supplement E4).

In 1990–1993, the near-threatened species *Narcissus pseudonarcissus* was recorded on four grasslands. In 2018, it could be found in only one grassland. On the other hand, we recorded two new near-threatened species (*Carex distans* in two grasslands and *Medicago falcata* in one grassland) in 2018, which were not present in the plots in 1990–1993.

4. Discussion

4.1 Land use change

Since 1976, the city of Zurich grew mainly in height, i.e. the average building nowadays is twice as high as a hundred years ago but little open area was lost to new building ground (STADT ZÜRICH 2018b). This is reflected in the fact that between the two surveys only around 15% of the grasslands had been built over and the majority still existed as meadows and pastures. This was true for the whole city of Zurich as well as for the selected District 7. During the same time-period, the population of Zürich grew by approximately 13.5% from around 383,000 to 434,600 inhabitants (STADT ZÜRICH 2021).

For approximately two thirds of the remaining grasslands in District 7, the management remained unchanged between the two surveys. Approximately one third of the grasslands were converted from grazing to mowing. Of all existing grasslands, only approximately nine percent were still used for grazing. This conversion is very likely due to a general decrease in livestock farming in the city of Zurich (STADT ZURICH 1993) and to changes in conservation practice partly based on the studies of WILHELM (1996, 1997). WILHELM (1996) suggested that the conversion of these grasslands from grazing to low-intensity mowing would remove nutrients from the topsoil and lead to changes in plant species composition promoting species adapted to mowing.

4.2 Changes in biodiversity

We did not find any significant changes in diversity metrics between the two surveys, which is in contrast other studies. Some resurvey studies showed an increase in species richness for grasslands (339 meadows and pastures across all Switzerland) in Switzerland (BÜHLER & ROTH 2011), while others showed a decline in species richness for semi-natural grasslands in general (see meta-analysis by DIEKMANN et al. 2019). The observed changes in these studies were mainly attributed to an increase in common and low altitude species (BÜHLER & ROTH 2011), to changes in management and to an increase in nutrient availability, especially of nitrogen (DIEKMANN et al. 2019). Also, unlike other studies (BÜHLER & ROTH 2011, ZEEMANN et al. 2017), we did not find signs of floristic homogenization at the plot level. In a resurvey study of urban grasslands in Melbourne (Australia) by ZEEMANN et al. (2017), the observed homogenization was driven mainly by the invasion of non-native species as well as a decline in traditional disturbance regimes such as prescribed burning. On the contrary, in BÜHLER & ROTH (2011) the observed increase in common species led to homogenization. In our case, these processes do not seem to play a role, probably due to lower agricultural pressure in the urban context–there is hardly any intensive farming within the city of Zurich–and due to the continuous management of these grasslands, many of which are maintained by farmers. Unlike the situation described in ZEEMANN et al. (2017), European grasslands do not seem to be generally affected as much by invasions of non-native species as man-made habitats or grasslands on other continents (AXMANOVÁ et al. 2021). This is reflected in our results, as there were no significant changes in the proportion of alien species between the two surveys, even though many of them lie within close proximity to private gardens and allotments, which could be potential sources for alien species. However, this finding is probably also associated with the management of many of these grasslands for conservation purposes. Therefore, it is very likely, that at least on some of these grasslands, alien species are actively removed.

Interestingly, beta diversity between plots decreased over time in the grasslands whose management remained unchanged (MM), but not in the formerly grazed grasslands that are now mown (GM). One reason for this result could be connected to the fact that ten out of 15 grasslands, which have been transformed from grazing to mowing, lie in close proximity to each other and are managed for conservation purposes by the same farmer. The mown grasslands, in contrast, are more evenly distributed over District 7 and more heterogeneous concerning their surrounding land use and probably also concerning their management. This could have led to different pathways of development of these mown grasslands. However, further research would be needed looking at this question in more detail to strengthen this argument.

4.3 Changes in species composition

Total species composition indicated significantly nutrient-poorer and less base-rich soil conditions in 2018. This is in contrast to studies on agriculturally managed grassland, which found increases in nutrients, especially nitrogen, to be an important driver of changes in grassland composition (DIEKMANN et al. 2019, BÜCHLER et al. 2020, CHARMILLOT et al. 2021). In our study, no significant change was found in the ecological indicator values of the MM-grasslands, while the GM-grasslands showed highly significant reductions in these indicator values. Therefore, we attribute these changes mainly to the conversion of these grasslands from grazing to mowing, as well as to the continuous management of the meadows, some of which lie in nature protection areas. In grazed grasslands, the vast majority of the nutrients harvested remain in the system through re-distribution by defaecation (WHITEHEAD 2000). After the change of management from grazing to mowing, these nutrients are being removed from the system through mowing. This pattern fits changes predicted by WILHELM (1996) for conversion from sheep grazing to mowing. Also, MANNINEN et al. (2010) could show in their study on urban grasslands in Finland, that a regular mowing and hay-making regime was associated with lower nutrient concentrations in the soil. In our study, the significant overall decrease in ruderality of the species composition can very likely also be attributed to these changes in management.

Likewise, the CWM of functional traits mainly reacted to the changes in management. The significant overall increase in seed weight and plant height was mostly due to the highly significant increase of these CWMs in GM grasslands. An increase in seed weight due to changes in management was also found by MOOG et al. (2005) and KAHMEN & POSCHLOD (2008) in grassland management experiments. Lower seed weight can be advantageous for regeneration in the open gaps created by grazing (MOOG et al. 2005), while higher individual seed mass is associated with a higher persistence of seedlings in undisturbed grasslands (BU et al. 2016). The increase in plant height after the change from grazing to mowing also fits into this picture. Grazing may promote smaller plants as well also more stoloniferous or rosette-forming plants (DÍAZ et al. 2007, KAHMEN & POSCHLOD 2008, LANTA et al. 2009) than under a mowing regime.

Species, which significantly increased or decreased in occurrence, did not show an obvious ecological pattern apart from their association with either grazing or mowing. These changes in species occurrence fit more or less exactly the predictions made by WILHELM (1996) for sheep pastures transformed to hay meadows (published in WILHELM 1997): an increase in *Vicia sepium* (and a marginally significant increase in *Bromus erectus* and *Gallium mollugo* aggr.) as well as a decrease in *Taraxacum officinale* aggr., *Bellis perennis* and

Lolium perenne. So overall, the changes found in species composition between the two surveys clearly show the changes in management but else do not indicate other typical changes in environmental conditions such as an eutrophication or climate warming.

5. Conclusions

Our resurvey of mesic urban grasslands revealed that a large majority of the grasslands originally surveyed in 1990–1993 have remained intact to date. This is a positive result considering the high building pressure that currently exists in cities. For two thirds of the grasslands surveyed in Zurich's District 7 the management remained the same, for one third it changed from grazing to mowing. Our survey showed that the quality of these grasslands in terms of species richness and composition was comparable to the original survey. Any observed changes were largely connected to the conversion of management. The widely discussed drivers of change in rural grasslands such as nutrient enrichment and invasion of non-native species did not seem to affect these urban grasslands between the two surveys. While plant species may react with a certain time lag to changed conditions, a time span of 25 years between the two surveys, as shown in other studies on grassland changes (e.g. VAN DEN BERG et al. 2011, KOCH et al. 2017, PEPPLER-LISBACH & KÖNITZ 2017), seems long enough to detect such changes and show pathways of development. In conclusion, our results show that continuously managed urban grasslands can maintain their quality over many years, even under the pressures of global changes such as land-use change or climate change. Especially under low-intensity management, as shown by others (e.g. CHOLLET et al. 2018, SEHRT et al. 2020), urban grasslands can provide habitat for many species and may have the potential to help conserving biodiversity in cities.

Erweiterte deutsche Zusammenfassung

Einleitung – Viele Studien konnten signifikante Veränderungen in der Artenzusammensetzung von Grasland in den letzten Jahrzehnten in Zentraleuropa nachweisen. Mögliche Gründe für diese Veränderungen sind die Intensivierung der Nutzung oder die Nutzungsaufgabe, aber auch eine Eutrophierung durch Stickstoffeintrag, eine Homogenisierung der Flächen, der Klimawandel sowie das Einwandern von nicht-einheimischen Arten (DENGLER & TISCHEW 2018). Viele dieser Studien stammen von trockenen, feuchten oder alpinen Grasland-Typen, während das mesische Grasland, vor allem auch im urbanen Kontext, noch wenig untersucht wurde. Urbanes Grasland kann relative grosse Flächen umfassen und stellt somit in grosses Potential für die Förderung der Biodiversität dar (FISCHER et al. 2013a, KLAUS 2013). Diverse Studien konnten zeigen, dass extensiv bewirtschaftetes urbanes Grasland eine relativ grosse Artenvielfalt hervorbringen kann (z. B. RUDOLPH et al. 2017, CHOLLET et al. 2018, NORTON et al. 2019, SEHRT et al. 2020).

Inwiefern diese urbanen Grasland-Flächen von den oben erwähnten Faktoren beeinflusst werden, ist Gegenstand dieser Studie. Wir wiederholten 25 Jahre alte Vegetationsaufnahmen aus der Stadt Zürich (WILHELM 1997) und verglichen diese mit den ursprünglichen Aufnahmen, um mögliche Veränderungen zu erfassen und mögliche Gründe dafür aufzuzeigen.

Methoden – Diese Untersuchung basiert auf der Studie von WILHELM (1997), beschränkt sich jedoch bezüglich der Vegetationskartierung auf den Kreis 7 der Stadt Zürich. In einem ersten Schritt wurde die Existenz der Flächen auf Satellitenbildern überprüft. Danach eruierten wir die aktuelle Landnutzung der noch existierenden Flächen und wählten 30 Flächen für die Untersuchung aus.

Auf diesen Flächen führten wir eine Wiedererhebung der damals durchgeführten Vegetationsaufnahmen durch. Wir relokalisierten die Plots so genau wie möglich und erhoben alle Gefässpflanzenarten und schätzen deren Deckungsgrad in Prozent. Wir berechneten u. a. verschiedene Diversitätsindizes, gewichtete mittlere ökologische Zeigerwerte, gewichtete mittlere Pflanzenstrategien sowie funktionelle Eigenschaften für alle Aufnahmen. Mit gepaarten *t*-Tests verglichen wir die Werten zwischen den Aufnahmen von 1990–1993 und 2018. Mit einem Vorzeichentest analysierten wir, welche Arten zwischen den Aufnahmen signifikant zu oder abgenommen haben in ihrer Frequenz.

Ergebnisse – Von den 1990–1993 im Kreis 7 untersuchten Flächen waren 2018 16 % durch Landnutzungsänderungen verschwunden. Von den übrigen Flächen wurde der grösste Teil (58 %) der ehemals gemähten Flächen immer noch gemäht (MM-Grasland), während viele der ehemals beweideten Flächen (26 %) nun auch gemäht wurden (GM-Grasland). Die restlichen Flächen wurden immer noch beweidet oder als Mähweide genutzt. In dieser Untersuchung wurden nur MM- und GM-Wiesen angeschaut.

Bei den Vegetationsaufnahmen im Jahr 2018 wurden insgesamt 192 Gefäßpflanzenarten bestimmt, während es 1990–1993 157 Arten waren. Die Diversitätsindizes zeigten keine signifikanten Unterschiede zwischen den Untersuchungen, weder für alle Aufnahmen gemeinsam noch für die zwei untersuchten Gruppen (MM- und GM-Grasland). Auf Artniveau fanden wir eine signifikante Zunahme in der Frequenz bei fünf Arten und eine signifikante Abnahme bei 16 Arten.

Bei den ökologischen Zeigerwerten zeigte sich eine signifikante Abnahme der Reaktionszahl und der Nährstoffzahl für alle Aufnahmen zusammen. Die zwei Gruppen zeigten wiederum unterschiedliche Muster. Das MM-Grasland zeigte keine signifikanten Unterschiede, während beim GM-Grasland die Feuchtigkeitszahl und Lichtzahl signifikant abnahm und die Temperaturzahl signifikant zunahm.

Ein ähnliches Muster zeigte sich bei den Strategietypen und den funktionellen Eigenschaften. Signifikante Veränderungen bei der Analyse aller Aufnahmen zusammen waren gekoppelt mit signifikanten Änderungen beim GM-Grasland aber keinen Änderungen beim MM-Grasland. Der Anteil nicht-einheimischer Arten veränderte sich nicht signifikant zwischen den zwei Aufnahmezeitpunkten, weder für alle Aufnahmen zusammen noch in den zwei Gruppen.

Diskussion und Schlussfolgerungen – Entgegen den Erwartungen hat ein Grossteil der 1990–1993 untersuchten Flächen bis 2018 unverbaut, und die Flächen werden immer noch als Wiesen und Weiden genutzt. Für ca. 2/3 der Flächen hat sich an der Bewirtschaftung nichts geändert seit 1990–1993, für etwa 1/3 wurde allerdings die Bewirtschaftung von Beweidung auf Mahd umgestellt. Diese Umstellung ging einher mit einer generellen Abnahme von Weidehaltung in der Stadt Zürich (STADT ZÜRICH 1993) und wahrscheinlich einer Anpassung der Bewirtschaftung auch teilweise basierend auf den Empfehlungen von WILHELM (1996).

Wir konnten keine signifikanten Veränderungen in der Diversität zwischen im Untersuchungszeitraum feststellen. Dies steht im Kontrast zu anderen Studien, die entweder eine Zunahme an Arten im Grasland in der Schweiz (BÜHLER & ROTH 2011) oder eine generelle Abnahme an Arten feststellten (z. B. DIEKMANN et al. 2019). Auch fanden wir keine Anzeichen für eine Homogenisierung der Vegetation auf Plot-Niveau. In anderen Studien wurde eine Homogenisierung aufgrund von Einwanderungen nicht einheimischer Arten, dem Wegfallen der traditionellen Bewirtschaftung (ZEEMANN et al. 2017) oder aufgrund einer Zunahme von häufigen Arten (BÜHLER & ROTH 2011) beobachtet. Dass dies auf den untersuchten Flächen nicht passierte, liegt möglicherweise an einem geringeren landwirtschaftlichen Intensivierungsdruck im urbanen Kontext, sowie an der konstanten Bewirtschaftung der Flächen.

Die beobachtete Abnahme insbesondere der Nährstoffzahl auf unseren Flächen steht im Kontrast zu vielen andern Untersuchungen auf landwirtschaftlich genutzten Flächen. Diese zeigten, dass insbesondere die Zunahme von Nährstoffen (v. a. Nitrat) zu Veränderungen in der Zusammensetzung von Grasland führte (DIEKMANN et al. 2019, BÜCHLER et al. 2020). In unserer Untersuchung nahm jedoch insbesondere auf den Flächen, die von Beweidung auf Mahd umgestellt wurden, die Nährstoffzahl ab, so dass diese Umstellung der Bewirtschaftung der Hauptgrund für diese Veränderung sein dürfte. Auch andere Untersuchungen in einem urbanen Kontext konnten zeigen, dass mit einem regelmässigen Mahd-Regime die Nährstoffverfügbarkeit reduziert werden konnte (MANNINEN et al. 2010). Ebenso können die beobachteten Veränderungen bei den Strategien und funktionellen Merkmalen der Vegetation unserer Flächen, sowie den Veränderungen auf Artniveau, mehrheitlich auf die Anpassungen bei der Bewirtschaftung zurückgeführt werden.

Zusammenfassend lässt sich sagen, dass die in der Literatur vielfach diskutierten Treiber von Veränderung, wie z. B. die Anreicherung von Nährstoffen oder die Einwanderung von nicht-einheimischen Arten oder der Klimawandel, die hier untersuchten Flächen in den letzten 25 Jahren nicht beeinträchtigt haben. Solch extensiv bewirtschaftete Wiesen können, wie auch andere Studien gezeigt haben (z. B. CHOLLET et al. 2018, SEHRT et al. 2020), Lebensraum für viele Arten bieten und damit zum Schutz der Biodiversität im urbanen Kontext beitragen.

Acknowledgements

We thank Hallie Seiler for linguistic editing and Kevin Antonio Vega, Valentin H. Klaus and one anonymous reviewer for their helpful comments on the initial version of the manuscript.

Author contributions

M.W. carried out the original field sampling and J.K. the resurvey as a Bachelor thesis supervised by R.B. and J.D. S.W. performed the statistical analyses, while R.B. and J.D. led the writing and all authors contributed to the revised manuscript.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Complete vegetation table of the old and new survey.

Anhang E1. Vollständige Vegetationstabelle der alten und neuen Aufnahmen.

Supplement E2. Mean value as well as standard deviation (SD), minimum and maximum for the diversity indices, indicator values, plant strategies and functional traits over all plots as well as for the two subgroups separately.

Anhang E2. Mittelwerte, Standardabweichung, Minimum und Maximum für die Diversitätsindizes, ökologischen Zeigerwerte, Pflanzenstrategien und funktionellen Eigenschaften aller Aufnahmeflächen zusammen sowie getrennt in die zwei Gruppen (MM- und GM-Grasland).

Supplement E3. Changes in frequency of alien species found in the two surveys.

Anhang E3. Veränderungen in der Frequenz nicht-einheimischer Arten zwischen den zwei Untersuchungen.

Supplement E4. Changes in the proportion of alien species (%) between the two surveys. Results are shown for all plots combined as well as for the two subgroups based on land use history.

Anhang E4. Veränderungen im Anteil nicht-einheimischer Arten (%) zwischen den zwei Untersuchungen für alle Aufnahmeflächen zusammen, sowie getrennt in die zwei Gruppen nach Nutzungshistorie.

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Supplement S1. Complete vegetation table of the old and new survey. All plots are 50 m² in size, species cover is given in %.

Beilage S1. Vollständige Vegetationstabelle der alten und neuen Aufnahmen. Alle Aufnahmeflächen waren 50 m² groß und die Artdeckungen sind in % angegeben.

Plot ID	%	%	**200**	**605**	**615**	**635**	**660**	**665**	**666**	**669**	**677**	**679**	**680**	**684**	**685**	**690**	**736**	**737**	**747**	**812**	**839**	**852**	**853**	**855**	**856**	**857**	**859**	**860**	**861**	**862**	**863**	**913**	**200**	**605**	**615**	**635**	**660**	**665**	**666**	**669**	**677**	**679**	**680**	**684**	**685**	**690**	**736**	**737**	**747**	**812**	**839**	**852**	**853**	**855**	**856**	**857**	**859**	**860**	**861**	**862**	**863**	**913**
Recording date	**1990-1993**	**2018**	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	90-93	02.06.2018	09.05.2018	05.06.2018	02.06.2018	01.06.2018	17.05.2018	09.05.2018	31.05.2018	07.05.2018	07.05.2018	25.05.2018	01.06.2018	08.05.2018	02.06.2018	31.05.2018	31.05.2018	02.06.2018	02.06.2018	31.05.2018	29.05.2018	02.06.2018	04.06.2018	05.06.2018	05.06.2018	04.06.2018	08.06.2018	05.06.2018	24.05.2018	24.05.2018	04.06.2018
recorded by			M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	M.W.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.	J.K.
Managment			grazed	mown	mown	mown	mown	mown	mown	grazed	mown	mown	mown	mown	mown	mown	mown	mown	mown	grazed	grazed	grazed	grazed	grazed	grazed	grazed	grazed	grazed	grazed	grazed	grazed	grazed	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown	mown
Aspect (°)			225	225	180	270	225	225	315	20	225	135	250	N.A.	225	180	250	N.A.	45	250	155	180	180	205	205	205	180	180	155	205	155	N.A.	225	280	170	5	235	225	285	5	250	120	255	255	230	220	190	350	320	260	205	230	200	200	170	180	200	180	200	200	170	250
Slope (°)			21.8	21.8	30.9	9.6	26.5	8.5	19.2	5.7	14	33	28.8	0	19.2	2.8	4	0	11.3	43.5	8.5	11.3	2.8	5.7	19.2	13.4	6.8	6.8	13.4	33	35	0	11.5	23.5	4.2	9.6	23.8	2.4	20.2	1.2	29.4	27	41.4	4.2	8.1	8.2	4.9	2.1	9.1	6.8	10.4	26.1	15.3	14.4	6.2	5.4	11.8	8.2	13.4	12.3	11.8	0.5
Cover of tree layer (%)			N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	0	2	2	0	0	15	1	20	1	8	0	0	10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cover of shrub layer (%)			N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	0	1	0	0	8	10	0	3	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cover of herb layer (%)			N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	90	85	85	90	50	50	50	80	60	60	60	100	80	70	70	100	90	100	70	99	80	90	100	100	80	95	85	95	100	95
Cover of litter (%)			N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	30	8	70	30	20	4	5	35	3	5	20	50	10	30	10	10	40	30	8	80	60	60	80	85	60	80	70	70	80	60
Cover of mosses (%)			N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	40	60	5	20	50	90	0	60	60	80	40	40	5	30	60	60	80	45	60	50	20	20	70	70	20	65	45	45	70	25
Vascular plant species richness	36.4	35.8	49	34	42	25	22	29	38	38	48	44	43	18	55	27	32	23	30	36	29	58	31	38	32	24	33	54	41	41	46	33	29	29	24	30	32	28	33	32	50	51	32	28	57	38	29	27	33	37	35	37	28	33	36	31	35	53	36	31	26	32

Species	% 1990-1993	% 2018
Acer campestre	7	3
Acer platanoides	0	13
Acer pseudoplatanus	13	7
Achillea millefolium aggr.	27	20
Aegopodium podagraria	0	10
Aesculus hippocastanum	0	7
Agrimonia eupatoria	3	0
Agrostis capillaris	3	0
Agrostis cf. stolonifera	0	3
Agrostis stolonifera	50	3
Ajuga reptans	73	73
Alchemilla splendens aggr.	0	3
Alchemilla vulgaris aggr.	0	7
Alliaria petiolata	0	3
Allium ursinum	3	3
Allium vineale	0	7
Alopecurus pratensis	10	13
Anagallis arvensis	0	0
Anemone nemorosa	13	13
Angelica sylvestris	7	0
Anthoxanthum odoratum	47	63
Anthriscus sylvestris	17	7
Aquilegia cf. atrata	0	3
Aquilegia vulgaris	3	0
Arrhenatherum elatius	77	80
Arum maculatum	0	3
Barbarea vulgaris	7	0
Bellis perennis	53	23
Brachypodium pinnatum	17	3
Brachypodium sylvaticum	10	23
Briza media	7	13
Bromus cf. hordeaceus	0	3
Bromus erectus	27	53
Bromus hordeaceus	20	7
Bromus sterilis	7	3
Calystegia sepium	7	20
Campanula glomerata	0	3
Capsella bursa-pastoris	27	0
Cardamine hirsuta	43	0
Cardamine pratensis agg.	37	13
Carex caryophyllea	3	23
Carex cf. caryophyllea	0	3
Carex distans	0	3
Carex divulsa	0	3
Carex flacca	17	23
Carex hirta	20	3
Carex leersii	0	3
Carex montana	0	3
Carex pairae	0	10
Carex pallescens	0	3
Carex spicata	17	7
Carex sylvatica	33	50
Carpinus betulus	7	17
Cedrus sp.	0	3
Centaurea jacea	20	40
Centaurea scabiosa	0	3
Cerastium fontanum	93	70
Cerastium glomeratum	3	13
Chionodoxa luciliae	3	0
Circaea lutetiana	0	13
Cirsium arvense	13	7
Cirsium oleraceum	10	3
Cirsium vulgare	7	0
Clinopodium vulgare	30	0
Colchicum autumnale	7	7
Convolvulus arvensis	30	27
Conyza canadensis	3	0
Cornus mas	0	7
Cornus sanguinea	3	0
Corydalis cava	3	0
Corylus avellana	0	7
Crataegus laevigata	0	3
Crataegus monogyna aggr.	3	0
Crataegus persimilis	0	3
Crataegus sp.	0	3
Crepis biennis	3	57
Crepis capillaris	57	0
Crepis vesicaria	3	0
Crocus chrysanthus	7	0
Cynosurus cristatus	7	10
Dactylis glomerata	100	90
Daucus carota	27	27
Deschampsia cespitosa	3	0
Echinochloa crus-galli	13	0
Elymus repens	10	27
Equisetum arvense	3	20
Equisetum telmateia	0	3
Erigeron annuus	10	13
Fagus sylvatica	0	13
Festuca arundinacea	37	10
Festuca ovina aggr. s.l.	0	7
Festuca pratensis	30	3
Festuca rubra aggr.	67	77
Filipendula ulmaria	3	3
Forsythia sp.	0	3
Fragaria vesca	20	30
Fraxinus excelsior	20	13
Galanthus nivalis	7	0
Galium aparine	0	3
Galium mollugo aggr.	60	83
Galium odoratum	0	3
Galium pumilum	0	3
Galium verum	3	13
Geranium molle	3	3
Geranium pusillum	7	0
Geranium pyrenaicum	7	0
Geranium robertianum	10	0
Geranium rotundifolium	0	3
Geranium sp.	0	3
Geranium sylvaticum	0	7
Geum urbanum	27	33
Glechoma hederacea subsp. hederacea	77	70
Hedera helix	10	10
Helictotrichon pubescens	13	20
Heracleum sphondylium	17	20
Hieracium murorum aggr.	0	3
Hieracium pilosella	0	13
Holcus lanatus	30	70
Hypericum perforatum	13	0
Hypochaeris radicata	23	17
Ilex aquifolium	0	3
Iris sp.	0	3
Juglans regia	0	3
Juncus articulatus	3	0
Juncus inflexus	0	3
Knautia arvensis	20	27
Koeleria pyramidata	0	3
Lamium galeobdolon	0	10
Lapsana communis	3	0
Lathyrus pratensis	23	23
Leontodon hispidus	23	27
Leontodon saxatilis	3	0
Leucanthemum vulgare aggr.	20	20
Ligustrum vulgare	0	3
Linum catharticum	7	10
Listera ovata	0	3
Lolium multiflorum	27	17
Lolium perenne	73	43
Lotus corniculatus	33	53
Luzula campestris	13	13
Lysimachia nemorum	7	3
Lysimachia nummularia	43	20
Lysimachia punctata	0	7
Mahonia aquifolium	0	7
Malva neglecta	0	3
Medicago falcata	0	3
Medicago lupulina	60	63
Mentha arvensis	0	3
Muscari racemosum	10	7
Myosotis arvensis	10	7
Myosotis scorpioides aggr.	7	3
Narcissus pseudonarcissus	13	3
Onobrychis viciifolia	0	3
Origanum vulgare	0	10
Ornithogalum umbellatum	3	0
Papaver dubium	0	7
Phleum pratense aggr.	20	17
Phyteuma orbiculare	0	3
Phyteuma spicatum	10	0
Picea abies	0	3
Picris hieracioides	7	0
Plantago lanceolata	83	97
Plantago major	30	10
Plantago media	20	10
Poa annua	27	7
Poa pratensis aggr.	70	53
Poa trivialis	30	33
Polygonatum multiflorum	0	3
Polygonum aviculare aggr.	17	0
Potentilla anserina	3	0
Potentilla erecta	3	10
Potentilla reptans	30	43
Potentilla sterilis	40	40
Primula acaulis	23	23
Primula elatior	17	0
Prunella cf. grandiflora	0	37
Prunella vulgaris	40	7
Prunus laurocerasus	0	3
Prunus sp.	0	7
Pyrus sp.	0	3
Quercus sp.	0	17
Ranunculus acris	90	77
Ranunculus bulbosus	27	10
Ranunculus ficaria	37	3
Ranunculus repens	43	30
Rhinanthus alectorolophus	7	53
Rosa sp.	20	10
Rubus caesius	3	0
Rubus fruticosus aggr. s.l.	0	13
Rubus idaeus	0	7
Rumex acetosa	53	33
Rumex crispus	10	0
Rumex obtusifolius	40	7
Salvia pratensis	13	3
Sambucus racemosa	0	3
Sanguisorba minor	17	43
Scabiosa columbaria	3	0
Scilla bifolia	3	0
Sedum album	0	3
Sedum rupestre	0	3
Sedum sexangulare	13	0
Silene dioica	3	0
Silene vulgaris subsp. vulgaris	7	3
Sisymbrium officinale	3	0
Solidago canadensis	3	0
Sonchus arvensis	0	3
Sonchus asper	23	0
Stachys officinalis	0	23
Stellaria media	7	3
Syringa vulgaris	0	3
Taraxacum officinale aggr.	90	57
Taxus baccata	0	3
Thuja occidentalis	0	3
Thymus pulegioides	7	0
Tilia sp.	0	3
Tragopogon pratensis	0	10
Trifolium dubium	10	7
Trifolium pratense	83	87
Trifolium repens	80	77
Trisetum flavescens	50	57
Urtica dioica	13	7
Verbena officinalis	37	0
Veronica arvensis	17	0
Veronica chamaedrys	80	83
Veronica filiformis	37	37
Veronica hederifolia	7	0
Veronica persica	33	7
Veronica serpyllifolia	33	17
Vicia cracca	10	3
Vicia sativa	0	7
Vicia sepium	43	70
Vincetoxicum hirundinaria	0	3
Viola hirta	20	10
Viola odorata	13	0
Viola reichenbachiana	13	20
Viola riviniana	0	3

Supplement E2. Mean value as well as standard deviation (SD), minimum and maximum for the diversity indices, indicator values, plant strategies and functional traits over all plots as well as for the two subgroups separately. All *p*-values are from paired *t*-tests.

Anhang E2. Mittelwerte, Standardabweichung, Minimum und Maximum für die Diversitätsindizes, ökologischen Zeigerwerte, Pflanzenstrategien und funktionellen Eigenschaften aller Aufnahmeflächen zusammen sowie getrennt in die zwei Gruppen (MM- und GM-Grasland). Die *p*-Werte stammen aus gepaarten *t*-Tests.

All plots (*n* = 30)	**1990–1993**				**2018**				
	Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	***p***
Diversity metrics									
Species richness	36.4	10.2	18	58	34.4	8.1	24	57	0.226
Shannon diversity	2.7	0.3	2.2	3.3	2.7	0.3	1.7	3.1	0.762
Shannon evenness	0.8	0.1	0.6	0.9	0.8	0.1	0.5	0.9	0.422
Ecological indicator values									
Moisture (F)	3.0	0.2	2.5	3.3	2.9	0.2	2.4	3.4	0.056
Reaction (R)	3.2	0.2	2.8	3.7	3.1	0.2	2.8	3.8	**0.037**
Nutrients (N)	3.5	0.4	2.8	4.1	3.1	0.3	2.6	3.7	**<0.001**
Light (L)	3.6	0.2	3.0	3.9	3.6	0.3	2.9	3.9	0.722
Temperature (T)	3.4	0.2	3.1	3.7	3.5	0.2	3.1	3.9	0.068
Continentality (K)	3.0	0.2	2.6	3.6	3.0	0.2	2.6	3.4	0.545
Mowing tolerance (MV)	3.3	0.6	1.9	4.1	3.2	0.6	1.8	3.9	0.260
Anthropogenic influence (EM)	3.0	0.3	2.2	3.7	3.0	0.3	2.0	3.5	0.821
Plant strategies C-S-R									
Competition value	1.3	0.2	0.8	1.8	1.4	0.2	1.1	2.1	0.125
Ruderality value	0.9	0.3	0.4	1.7	0.8	0.1	0.5	1.1	**0.012**
Stress value	0.8	0.2	0.3	1.2	0.8	0.2	0.4	1.2	0.233
Functional traits									
Specific leaf area [mm^2/mg] (log$_{10}$)	1.39	0.05	1.26	1.52	1.37	0.05	1.24	1.46	0.059
Seed dry mass [mg] (log$_{10}$)	-0.06	0.20	-0.47	0.50	0.12	0.18	-0.13	0.50	**0.001**
Plant height [m] (log$_{10}$)	-0.59	0.11	-0.78	-0.32	-0.47	0.17	-0.77	-0.03	**0.004**

Subset MM grasslands (n = 15)	**1990–1993**				**2018**				
	Mean	SD	Min	Max	Mean	SD	Min	Max	p
Diversity metrics									
Species richness	34	10.7	18	55	34.7	9.9	24	57	0.732
Shannon diversity	2.6	0.3	2.2	3.1	2.8	0.2	2.5	3.1	0.058
Shannon evenness	0.7	0.1	0.6	0.8	0.8	0.1	0.7	0.9	0.090
Ecological indicator values									
Moisture (F)	3.0	0.2	2.5	3.3	3.0	0.2	2.4	3.3	0.739
Reaction (R)	3.2	0.2	3.0	3.5	3.1	0.2	2.8	3.5	0.069
Nutrients (N)	3.5	0.4	2.8	4.1	3.2	0.3	2.7	3.7	0.061
Light (L)	3.5	0.3	3.0	3.9	3.5	0.3	2.9	3.8	0.487
Temperature (T)	3.5	0.1	3.2	3.7	3.5	0.2	3.1	3.9	0.901
Continentality (K)	2.9	0.2	2.6	3.6	3.0	0.2	2.6	3.3	0.714
Mowing tolerance (MV)	3.3	0.7	1.9	4.0	3.1	0.7	1.8	3.9	0.409
Anthropogenic influence (EM)	3.1	0.2	2.4	3.3	3.1	0.2	2.9	3.5	0.606
Plant strategies C-S-R									
Competition value	1.4	0.2	0.8	1.8	1.4	0.2	1.1	2.1	0.729
Ruderality value	0.8	0.2	0.5	1.1	0.8	0.2	0.5	1.1	0.904
Stress value	0.8	0.2	0.5	1.1	0.8	0.2	0.4	1.1	0.733
Functional traits									
Specific leaf area [mm2/mg] (log10)	1.41	0.05	1.34	1.52	1.38	0.06	1.24	1.46	0.219
Seed dry mass [mg] (log10)	0.02	0.20	-0.24	0.50	0.09	0.17	-0.06	0.50	0.349
Plant height [m] (log10)	-0.58	0.13	-0.78	-0.32	-0.45	0.19	-0.64	-0.03	0.069

Subset GM grasslands (*n* = 15)	**1990–1993**				**2018**				
	Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	***p***
Diversity metrics									
Species richness	38.9	9.5	24	58	34.1	6.2	26	53	0.064
Shannon diversity	2.8	0.4	2.2	3.3	2.6	0.4	1.7	3.1	0.466
Shannon evenness	0.8	0.1	0.6	0.9	0.8	0.1	0.5	0.9	0.871
Ecological indicator values									
Moisture (F)	3.0	0.3	2.5	3.3	2.9	0.2	2.6	3.4	**0.022**
Reaction (R)	3.2	0.2	2.8	3.7	3.1	0.2	2.9	3.8	0.195
Nutrients (N)	3.5	0.4	2.9	4.0	3.0	0.3	2.6	3.5	**0.002**
Light (L)	3.6	0.2	3.3	3.9	3.7	0.2	3.1	3.9	0.173
Temperature (T)	3.3	0.2	3.1	3.7	3.5	0.1	3.1	3.8	**0.016**
Continentality (K)	3.1	0.2	2.9	3.4	3.1	0.2	2.7	3.4	0.628
Mowing tolerance (MV)	3.4	0.5	2.5	4.1	3.3	0.4	2.3	3.8	0.459
Anthropogenic influence (EM)	3.0	0.3	2.2	3.7	3.0	0.3	2.0	3.3	0.590
Plant strategies C-S-R									
Competition value	1.2	0.2	0.9	1.5	1.3	0.2	1.1	1.9	0.071
Ruderality value	1.1	0.3	0.4	1.7	0.8	0.1	0.5	1.0	**0.003**
Stress value	0.7	0.3	0.3	1.2	0.9	0.2	0.5	1.2	0.086
Functional traits									
Specific leaf area [mm^2/mg] (log$_{10}$)	1.4	0.0	1.3	1.4	1.4	0.0	1.3	1.4	0.117
Seed dry mass [mg] (log$_{10}$)	-0.1	0.2	-0.5	0.1	0.1	0.2	-0.1	0.5	**0.000**
Plant height [m] (log$_{10}$)	-0.6	0.1	-0.8	-0.5	-0.5	0.2	-0.8	-0.1	**0.026**

Supplement E3. Changes in frequency of alien species found in the two surveys, sorted from winners to losers.

Anhang E3. Veränderungen in der Frequenz nicht-einheimischer Arten zwischen den zwei Untersuchungen, sortiert von zunehmenden zu abnehmenden Arten.

Species name	Frequency 1990–93	Frequency 2018	Difference
Aesculus hippocastanum	0	2	+2
Lysimachia punctata	0	2	+2
Mahonia aquifolium	0	2	+2
Erigeron annuus	3	4	+1
Onobrychis viciifolia	0	1	+1
Prunus laurocerasus	0	1	+1
Syringa vulgaris	0	1	+1
Thuja occidentalis	0	1	+1
Veronica filiformis	11	11	0
Conyza canadensis	1	0	-1
Scilla luciliae	1	0	-1
Solidago canadensis	1	0	-1
Crocus chrysanthus	2	0	-2
Lolium multiflorum	8	5	-3
Veronica persica	10	2	-8

Supplement E4. Changes in the proportion of alien species (%) between the two surveys. Results are shown for all plots combined as well as for the two subgroups based on land use history. The *p*-values are from paired *t*-tests.

Anhang E4. Veränderungen im Anteil nicht-einheimischer Arten (%) zwischen den zwei Untersuchungen für alle Aufnahmeflächen zusammen, sowie getrennt in die zwei Gruppen nach Nutzungshistorie. Die *p*-Werte stammen aus gepaarten *t*-Tests.

	1990–1993				2018				
	Mean	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**	***p***
Cover-based									
All Plots	2.5	4.6	0.0	22.7	2.9	5.2	0.0	22.0	0.741
Mown – mown (MM grasslands)	3.3	5.9	0.0	22.7	4.5	6.5	0.0	22.0	0.582
Grazed – mown (GM grasslands)	1.7	2.8	0.0	10.1	1.3	3.0	0.0	9.8	0.715
Richness-based									
All Plots	3.7	3.1	0.0	11.1	3.2	3.3	0.0	14.3	0.389
Mown – mown (MM grasslands)	4.7	3.7	0.0	11.1	4.0	3.6	0.0	14.3	0.461
Grazed – mown (GM grasslands)	2.7	1.9	0.0	6.3	2.4	2.8	0.0	9.4	0.681