The costs of diversity: higher prices for more diverse grassland seed mixtures

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Abstract

Globally, we face a dramatic biodiversity loss in agricultural systems as well as severe ecosystem degradation. In grasslands, higher biodiversity in terms of plant diversity was shown to increase the diversity of higher trophic levels and provide benefits for farmers such as higher and more stable yields. However, we lack a systematic overview of costs for more diverse seed mixtures, which are an essential tool in maintaining and increasing plant diversity in grasslands. We here investigated the prices and characteristics of 262 commercially available seed mixtures from six German or Swiss online shops and quantified the relationships between seed mixture prices and plant diversity. The most frequent seed mixtures contained 1–10 species and were designed for rather intensive grassland management. On the contrary, a smaller set of seed mixtures with particularly high plant diversity (>30 species), usually of native ecotypes, were offered for restoration purposes. More diverse seed mixtures were also more expensive. For example, a seed mixture with 10 or 30 species was on average +63% or +387% more expensive, respectively, than a product containing only one species. The relationship between plant diversity and seed mixture prices per ha was related to other seed mixture characteristics, of which plant provenance (i.e. native ecotypes vs. cultivars) was particularly important for the price. Seed mixtures containing only native ecotypes had considerably higher prices per ha (≥+75%) than those including cultivars. In conclusion, increasing biodiversity in grasslands can be costly. These costs need to be considered when making recommendations to farmers and other stakeholders. Measures to reduce such costs for maintaining and/or increasing plant diversity could promote establishment of grasslands with higher plant diversity, facilitate the restoration of semi-natural grasslands, and contribute to solving the biodiversity crisis in agroecosystems.

1. Introduction

Globally, we face major challenges of ecosystem degradation and decreasing biodiversity, especially in agricultural ecosystems, with negative feedbacks on many ecosystem services (Pe’er et al 2014, Newbold et al 2015, IPBES 2019, Seibold et al 2019, Resch et al 2021). Within grassland-based production systems, biodiversity-ecosystem functioning experiments have shown that increasing plant diversity can benefit farmers, especially by increasing productivity and decreasing production risks (e.g. Koellner and Schmitz 2006, Finn et al 2013, Binder et al 2018, Kleijn et al 2019, Manning et al 2019, Schaub et al 2020a, 2020b). Hence, plant diversity can contribute to the sustainable intensification of grassland-based milk and meat production and can be economically attractive for farmers. Moreover, plant diversity can also increase the diversity of further taxa and other non-production ecosystem services, such as pollination and cultural services (Scherber et al 2010, Isbell et al 2017, Le Clec’h et al 2019, Huber and Finger 2020). Some of those services, such as the cultural services of aesthetics, heritage, and recreation,
can create public benefits (Huber and Finger 2020). All these plant diversity benefits are important for both managed grasslands that are regularly renewed by re- or over-sowing and semi-natural grasslands (Resch et al 2021, Suter et al 2021). Including the costs of plant diversity and plant diversity-related public benefits into management considerations is hence crucial from a private and a societal perspective. Moreover, neglecting these aspects can potentially lead to a mismatch between levels of grassland plant diversity recommended to farmers by, for example, extension services, and the actual optimal levels for farmers and other land managers as well as for the public. Nonetheless, farmers’ and other land managers’ costs of maintaining and increasing plant diversity by using seed mixtures are not well studied, limiting their basis for decision-making about the economically optimal level of plant diversity. In this paper, we investigated the characteristics of German and Swiss seed mixtures, especially focusing on their plant diversity, and the relationship of plant diversity and market prices of various grassland seed mixtures.

The use of high-diversity seed mixtures for sowing or over-sowing grasslands is a relatively easy and quick method for increasing plant diversity in grasslands (Klaus et al 2017). Next to this, other methods, such as fresh hay transfer from species-rich sites located nearby, have been proven to be highly effective for increasing plant diversity, but are much more time consuming and resource-intensive than purchasing and planting commercially available seed mixtures (Walker et al 2004, Kiehl et al 2010). Moreover, plant diversity increases also over time when mowing and grazing intensities are reduced (Walker et al 2004). However, this increase can take a long time—even decades—after cessation of intensive management (Jacot and Lehmann 2001, Isbell et al 2013). All these practices for increasing and maintaining plant diversity usually come with considerable costs. These costs need to be better understood before farmers and other land managers, policymakers, as well as further stakeholders can take well-informed decisions on land management that affects plant diversity (Klaus et al 2020). The costs for increasing and maintaining plant diversity comprise, for example, direct input and labor costs but also opportunity costs. The latter can arise if profits decrease when adopting a lower management intensity (WalisDeVries et al 2002; see, e.g. Mewes et al 2015, for a systematic approach assessing costs).

Although costs are important when making grassland management decisions and seed mixtures are commonly used for maintaining and increasing plant diversity in grasslands both in farming and restoration projects (Tórók et al 2011), we know still very little about the costs of seed mixtures. We specifically lack knowledge on the costs of seed mixtures in relation to their characteristics. Important characteristics include the number of plant species in a seed mixture and the provenance of seeds, i.e. if a seed mixture contains only native ecotypes of regional provenance, which are genetically adapted to the local environment (De Vitis et al 2017), or cultivars, which have been actively modified by plant breeding. Species-rich seed mixtures containing native ecotypes are mainly used by nature conservationists to restore semi-natural grasslands. Another important seed mixture characteristic is the intended use, such as for permanent grasslands, which are not included in crop rotations, vs. temporary grasslands, which are regularly resown and part of crop rotations for one to two years, or for conventional vs. organic forage production. Understanding the relationship of seed mixture costs and those characteristics is critical to improve farmers’ and other stakeholders’ basis for decision making. Furthermore, comprehensive economic assessments of the costs for grassland plant diversity are crucial for comparing positive economic benefits from plant diversity to plant diversity costs as well as designing effective agricultural policies and restoration schemes (e.g. Klimek et al 2008).

This study contributes to closing the above-mentioned knowledge gaps by providing an empirical assessment of 262 grassland seed mixtures and their prices obtained from six different online shops in Germany and Switzerland. To analyze seed mixture characteristics and quantify the relationship between prices and seed mixture composition, especially plant diversity, we specifically addressed the following two questions: (1) What are the characteristics of the most commonly offered seed mixtures, including their plant diversity, species combination, and provenance? (2) How does the price of seed mixtures relate to their plant diversity and other price determinants?

2. Materials and methods

2.1. Seed mixture data

We collected detailed information about seed mixtures and their prices from online price catalogs for shops in Germany and Switzerland during 2019 and 2020 (see Text S1 for further details). For the data collection, we systematically searched for price catalogs on Google using various combinations of German search terms (table S1 (available online at stacks.iop.org/ERL/16/094011/mmedia)). We only used data of seed mixtures if both price and species information were available and only if products were sold to farmers and other land managers for grassland production and/or restoration. Thus, we focused on online shops for a professional target audience, i.e. we excluded online shops that only offered...
very small quantities for private gardening. Based on these criteria, we used data from six online shops (see table S2), which sell within the respective country and do not restrict their sales to specific regions. Moreover, while we cannot assess the representativeness of the six online shops in our study compared to German and Swiss shops without online available price and species information due to unavailability of market information, we can assume that these six online shops offer a similarly large variety in seed mixtures as other shops and that their prices are comparable. This assumption is supported by the similarity of online and offline prices (Cavallo 2017).

We collected information on several characteristics of the seed mixture (table 1). First, we collected data about price per kg and recommended seed density (kg per ha). From these two variables, we calculated the seed mixture costs per ha. Second, we collected data on the proportions of individual species in seed mixtures. Based on this information, we computed two different plant diversity measures per seed mixture: (1) the number of species and (2) the Shannon index. The latter was calculated using information about the proportions of species in seed mixtures: 

$$\text{Shannon index} = -\sum_{n} S_n \ln (S_n)$$

where $S_n$ is the share of the species $n$ ($n = 1, \ldots, N$) in a seed mixture (Krebs 1999). For 5% of the seed mixtures, species identity but not their proportions were available. As a robustness check, we conducted an additional analysis for which we included these observations when using the Shannon index and assumed equal species distribution. As we focused our diversity assessment on the identity and the number of plant species, we did not distinguish between different genotypes or cultivars of the same species in a mixture. Third, we identified the provenance, i.e. native ecotype vs. cultivar, of the species in the seed mixture according to the production standards and origin of the seeds used for production. We categorized seed mixtures as ‘seed mixtures of native ecotypes’ when seed mixtures exclusively contained ecotypes of regional provenance, i.e. when seeds originated from and were propagated in a distinct region in Germany or in Switzerland as a whole (see Bucharova et al. 2017, Durka et al. 2017 for Germany, SKEW (Schweizerische Kommission für die Erhaltung von Wildpflanzen) 2009 for Switzerland). The alternative category ‘cultivar seed mixtures’ included all seed mixtures with native or non-native species that had been modified by plant breeding, i.e. cultivars, and which were frequently (though not in all cases) propagated outside of the specific regions or countries where they were used. Seed mixtures containing both cultivars and native ecotypes were also categorized as ‘cultivar seed mixtures’, as such seed mixtures are not suitable for ecological restoration in a strict sense. Fourth, we classified seed mixtures designed specifically for permanent grassland as ‘permanent grassland seed mixtures’ when the mixture was recommended to be used for more than three years (Suter et al. 2017). All other seed mixtures, e.g. grass-clover mixtures specifically for temporary grassland, were categorized as ‘other’ (temporary grass and other non-permanent forage mixtures). Seed mixtures with the declared purpose of introducing grass and/or clover species into existing swards through over-sowing were also categorized as ‘permanent grassland seed mixtures’. Finally, we classified if seed mixtures had an organic certification.

In total, our data consisted of 262 different seed mixtures (table S2) for which information was available about seed mixture name, number of species, individual species proportions, price per ha and kg, recommended seeding density, seed mixtures containing only native ecotypes, recommended use for permanent vs. other grasslands, organic certification, designation for over-sowing, presence of legumes, the share of legume plus herb species seeds, the share of grass species seeds, online shop, and country (see tables S2 and S3 and figures S1 to S2 for descriptive statistics).

### 2.2. Analysis of seed mixture characteristics

For simultaneously exploring a large number of different species combinations in seed mixtures, their frequency, species frequency, and price ranges, we used the UpSet approach (implemented in the R package ‘UpSetR’ (Gehlenborg 2019)). The UpSet

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4 We excluded two seed mixtures specifically designed for alpine grasslands and labeled by the producer as ‘rarity’. Furthermore, the Shop Rieger-Hoffmann sold the same type of seed mixture, e.g. for wet meadows (‘Feuchtwiesen’ in German), with different native ecotypes depending on the production region, but at the same price. To avoid multiple duplicates that do not contain additional price information, we selected the seed mixture from production region five, which includes the area of one of the longest-running biodiversity-ecosystem functioning experiments in Europe (the ‘Jena Experiment’).

5 We used an exchange rate of 1 EUR = 1.08 CHE. Furthermore, because price information for the online shop Saaten-Zeller was not available for commercial buyers (despite selling to them), we used prices for private buyers.

6 The regions are generally defined by climate, geology, and other biophysical parameters and can be quite large. Recent research discussed the suitability of such large regions for defining the production of native seed mixtures (see, e.g. Durka et al. 2017). Different regions also exist in Switzerland, but the online shops included in the study only provide information on whether seeds were produced in Switzerland or not. For an overview of seed provenance regions in several European countries see De Vitis et al. (2017).

7 While we observed more shops in Germany that had all required information available, the offer of seed mixtures in Swiss shops is considerably larger. This might be linked to the smaller and more concentrated market in Switzerland but could also be linked to other factors, such as culture or historical development of the markets. Moreover, we observed overall a higher number of different plant species for Germany than for Switzerland (table S2), which might be linked to the inclusion of specialized shops selling highly diverse mixture in Germany in our dataset.
We present in the supplementary information also the results for
In the quadratic plant diversity specification, the relationship
term. Second, we estimated a model that controls for
mies for the different online shops.

depending on the index
either as the number of species or the Shannon index
is the plant diversity of seed mixture
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price and plant diversity controlling only for system-
that focuses on the correlation between seed mixture
mixture price and plant diversity
2.3. Analysis of the relationship between seed
price and plant diversity
For identifying the relationship between the price per
ha and the plant diversity of seed mixtures, i.e. either
number of species or Shannon index, we employed
two different linear models8. First, a simple model that
focuses on the correlation between seed mixture
price and plant diversity controlling only for system-
atic price differences among shops:
\[
\log(p_i) = \alpha_0 + \alpha_{Div}Div_{ij} + \alpha_{Shops}Shops_i + \epsilon_{ij} \quad (1)
\]
where \(\alpha_0\) is a dummy variable indicating if seed
mixture \(i\) consists of native ecotypes (= 1) or not (= 0),
\(PermG_i\) is a dummy variable indicating if seed
mixture \(i\) is designed for permanent grasslands (yes = 1,
no = 0), \(Org\) is a dummy variable indicating if seed
mixture \(i\) is organic (yes = 1, no = 0), and \(Over_i\)
is a dummy variable indicating if seed mixture \(i\)
is designed to be used for over-sowing (yes = 1,
no = 0). \(\epsilon_{ij}\) is the error term. We reported standard
errors that are corrected (i) for the clustered nature
of the collected data, i.e. online shops, and (ii) for
heteroscedasticity, e.g. due to changing variance with
increasing plant diversity. To this end, we used wild
cluster bootstrap standard errors (Cameron et al
2008), implemented in the R package ‘multiwayvcov’
(Graham et al 2016).

In the main analysis, we used a linear specification
of plant diversity to understand the relationship
between seed mixture prices and plant diversity. In
a sensitivity analysis, we also used a quadratic spe-
cification of plant diversity as it allows for dimin-
ishing and increasing marginal relationships between
plant diversity and seed mixture price9. The marginal
relationship between plant diversity and seed mixture
price is \(\Delta p_i / \Delta Div_{ij}\).

### 3. Results

#### 3.1. Seed mixture characteristics

The number of different seed mixtures was 262 in
Germany and Switzerland (55 in Germany and 207

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**Table 1. Overview of the main characteristics of the seed mixtures.**

| Variable               | Description                                                                 | Mean (Standard Deviation) | Number of observations |
|------------------------|-----------------------------------------------------------------------------|---------------------------|------------------------|
| Price                  | Price of the seed mixture                                                   | (a) 13.25 (15.46)         | 262                    |
|                        | (a) per kg                                                                  |                           | 262                    |
|                        | (b) per ha                                                                  | 463.88 (533.80)           |                        |
| Seed density           | Recommended seeding density                                                 | 34.65 (10.88)             | 262                    |
|                        | (kg per ha)                                                                 |                           |                        |
| Species composition    | Name and proportions of species in seed mixtures                            | n.a.                      | n.a.                   |
| Plant diversity        | Plant diversity was measured either                                          | (a) 8.44 (10.37)          | 262                    |
|                        | (a) as the number of species (ranges from 1 to 62)                           |                           |                        |
|                        | (b) as Shannon index (ranges from 0 to 3.70)                                 | (b) 1.51 (0.71)           | 255                    |
| Native ecotype         | Seed mixtures exclusively containing ecotypes of regional provenance        | 0.07 (0.25)               | Yes = 244              |
| Permanent grassland    | Seed mixtures for permanent grassland use, i.e.                             | 0.62 (0.49)               | No = 18                |
|                        | for grasslands lasting longer than three years.                              |                           |                        |
| Organic                | Seed mixture with an organic certification                                  | 0.27 (0.45)               | Yes = 190              |
| Over-sowing            | Seed mixture for over-sowing existing grasslands                            | 0.13 (0.34)               | Yes = 228              |

Remark: The data includes 262 seed mixtures from six online shops. n.a. = not applicable.

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8 We present in the supplementary information also the results for seed mixture price per kg (text S2).

9 In the quadratic plant diversity specification, the relationship between plant diversity and seed mixture prices at a given level of plant diversity (\(Div_i\)) is \(\beta_{Div}Div_i^2 + \beta_{Div}Div_{ij}^2\).
in Switzerland) and comprised in total 181 different species (159 in Germany and 81 in Switzerland, respectively; table S2). The three most commonly used species within all seed mixtures were *Lolium perenne* (180 times; 69%), *Poa pratensis* (142 times; 54%), and *Trifolium repens* (141 times; 54%; figure 1).

In Germany, the three most commonly used species were *Lolium perenne* (30 times; 55%), *Poa pratensis* (29 times; 53%), and *Phleum pratense* (26 times; 47%), while in Switzerland, they were *Lolium perenne* (150 times; 72%), *Trifolium repens* (123 times; 59%), and *Trifolium pratense* (120 times; 58%; figures S3 and S4).

Some rather species-poor mixtures were identified as the most commonly offered products with a distinct species combination. The three most common seed mixtures consisted of: (1) *Lolium perenne, Poa pratensis, Trifolium repens, Trifolium pratense,* and *Festuca rubra* (14 times; 5%), (2) *Lolium perenne* (10 times; 4%; note that these seed mixtures usually contained several different genotypes/cultivars of one species), and (3) *Lolium perenne, Poa pratensis, Trifolium repens, Trifolium pratense,* and *Dactylis glomerata* (8 times; 3%; figure 1). Of all 262 seed mixtures, 32 (12%) seed mixtures did not include any legumes (table S4). These mixtures were often offered for over-sowing of existing swards and establishing new swards such as clover-free pastures. In Germany, 25% of the seed mixtures did not include legumes, compared to only 9% in Switzerland.

The same online shop sometimes offered different seed mixture products with the same species combination (e.g. once as organic and once as conventional).

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3.2. Relationship between seed mixture price and plant diversity

Seed mixture price per ha significantly increased with the number of species in the mixture (figure 3(A)). The relationship of plant diversity with the absolute price per ha showed on average a +6% (95%-confidence interval (95%-CI): +4% to +7%) increase in price per plant species in the simple model that only controlled for online shops (equation (1), table 2). Thus, the price per ha for seed mixtures with, for example, 10 species were predicted to be on average +142 (95%-CI: +134 to +150) Euro per ha higher than the price for seed products containing one species only, which had a predicted absolute
Figure 2. Absolute frequencies of seed mixtures with a specific plant diversity level described as (A) the number of species and (B) the Shannon index with an indication of whether mixtures contain only native ecotypes and are designed for permanent grassland use or not (see tables S5 and S6).

Figure 3. Seed mixture price per ha and plant diversity expressed as (A) the number of species, and (B) the Shannon index with an indication of native ecotypes. The lines indicate the linear relationship between plant diversity and log-transformed prices. Y-axes are logarithmic.

price of +223 (95%-CI: +206 to +242) Euro per ha. This represents a price increase of +63%. Along these lines, prices for seed mixtures with 30 and 60 species were predicted to be on average +864 (95%-CI: +683 to +1087) and +5366 (95%-CI: +3404 to +8409) Euro per ha, respectively, higher than seed products containing only one species. These increases represent average price markups of +387% and +2402% for a 30- and 60-species mixture, respectively.

In the model that controlled for shops and other important price determinants likely linked to plant diversity (i.e. native ecotypes, permanent grassland use, organic, and designed for over-sowing; equation (2)), we found again a positive, though weaker correlation between plant diversity and seed mixture price (+3% (95%-CI: +2% to +5%); table 2). Seed mixtures containing only native ecotypes had a substantially higher price per ha, namely +75% (95%-CI: +53% to +99%), than those containing cultivars. Seed mixtures designed for permanent grassland use and organic seed mixtures exhibited +30% (95%-CI: +9% to +54%) and +20% (95%-CI: +4% to +38%), respectively, higher prices per ha compared to their counterparts. Seed mixtures designed for over-sowing of permanent grasslands had −29% (95%-CI: −44% to −25%) lower prices per ha, linked to their lower recommended seeding density.

Considering the Shannon index, which is based on the number of species and their species proportions in the seed mixture, as a measure for plant diversity, we also found a positive relationship between plant diversity and seed mixture price per ha when considering price differences among online shops (figure 3(B), table 2). On average, an increase of the Shannon index by 1 was associated with a rise of +59% (95%-CI: +40% to +81%) in the per ha price (the range of the Shannon index in our sample was 0–3.70). Again, we found a weaker, but still significant positive relationship between the Shannon index and the seed mixture price when also controlling for

8 out of 12 seed products with 1 species were designed for over-sowing.
Table 2. Coefficient estimates of the relationship of seed mixture price per ha with plant diversity, either as number of species or Shannon index, and other price determinants.

| Model | Coefficient (Euro; log) | ∆%  | Coefficient (Euro; log) | ∆%  | Coefficient (Euro; log) | ∆%  | Coefficient (Euro; log) | ∆%  |
|-------|--------------------------|-----|--------------------------|-----|--------------------------|-----|--------------------------|-----|
| Number of species | 0.05** *(0.04–0.06)* | 6%  | 0.03*** *(0.02–0.04)* | 3%  | 0.46*** *(0.33–0.6)* | 59% | 0.27*** *(0.21–0.32)* | 31% |
| Shannon Index |                            |     |                          |     |                          |     |                          |     |
| Native ecotype* (Yes = 1, No = 0) | 0.56*** *(0.42–0.69)* | 75% |                            |     |                          |     | 0.96** *(0.28–1.64)* | 161% |
| Permanent grassland (Yes = 1, No = 0) | 0.26** *(0.09–0.43)* | 30% |                            |     |                          |     | 0.21* *(0.03–0.38)* | 23% |
| Organic (Yes = 1, No = 0) | 0.18** *(0.05–0.31)* | 20% |                            |     |                          |     | 0.16* *(0.03–0.29)* | 18% |
| Over-sowing (Yes = 1, No = 0) | −0.43*** *(−0.58 to −0.29)* | −35% |                            |     |                          |     | −0.34*** *(−0.5 to −0.18)* | −29% |
| Online shop dummies | Yes |     | Yes |     | Yes |     |                          |     |

Remark: In Models 1 and 2, the number of species, and in Models 3 and 4, the Shannon index was used to measure plant diversity. Models 1 and 3 included only dummies for online shops as control variables (equation (1), and Models 2 and 4 also other control variables (equation (2)). The ‘Coefficient (Euro; log)’ shows point estimates and in parentheses their 95% confidence interval. ∆% is the percentage change associated with the point estimate. Standard errors and confidence intervals are corrected for clusters and heteroscedasticity using wild cluster bootstrapped standard errors. ***, ** and * indicate significance at the 0.1%, 1% and 5% level. The full model results and predictions (for price per ha and kg) can be found in table S7, figures S5 and S6. Our sensitivity analysis results, i.e. when using a quadratic specification of plant diversity, supported our main analysis results, i.e. when using a linear specification of plant diversity (table S8). Note that all seed mixtures with native ecotypes are exclusively designed for permanent grasslands.
other price determinants than only online shops (i.e. +30% (95%-CI: +23% to +37%)).

4. Discussion

We investigated the characteristics of commercially available grassland seed mixtures with regard to plant diversity, mixture composition, and provenance, i.e. native ecotype vs. cultivar. Additionally, we assessed the relationships of plant diversity and the other characteristics with the price of the seed mixtures.

4.1. Seed mixture characteristics

Sowing and over-sowing grasslands with seed mixtures are important tools for sward renewal as well as increasing and maintaining grassland plant diversity (Walker et al. 2004, Kiehl et al. 2010, Merritt and Dixon 2011, Ladouceur et al. 2020). The three most frequent species in seed mixtures in our study were Lolium perenne, Poa pratensis, and Trifolium repens which are rather low-growing, valuable forage species, indicative of intensive management, and commonly found in temperate European grasslands (Suter et al. 2017, Arbeitsverband der norddeutschen Landwirtschaftskammern 2020). All three species are typical dominant species of grazed swards, the backbone of European grassland-based dairy and beef production, and of high nutritive value for ruminants (Mielke and Wohlert 2019, Van Den Pol-Van Dasselaar et al. 2019). The most abundant plant species typical of mown grasslands was Trifolium pratense. Most seed mixtures included legumes, in particular clover species. Legumes can have several positive benefits, such as substituting mineral fertilization due to symbiotic N₂ fixation, reducing greenhouse gas emissions by reducing fertilization in general, mitigating drought-induced yield losses, as well as increasing forage nutritive quality and quantity (Temperton et al. 2007, Nyfeler et al. 2011, Lüscher et al. 2014, Fuchs et al. 2018). Other frequently found species were mainly grass seeds in mixtures for high to mid productive (mown) swards, such as Phleum pratense, Festuca rubra, and Daucus glomerata. All these frequent species were competitive and relatively fast-growing, following acquisitive strategies such as a high specific leaf area that makes them winners of land-use intensification in grasslands (Busch et al. 2019). Thus, the most frequent seed mixtures were designed for intensive grassland management and production of forage with high nutritive value for ruminants.

Non-legume herbs were absent in the most frequently found seed mixtures, which indicates that even the most frequent herb species were not elements of seed mixture that were designed for intensively managed grasslands. The most frequent herbs observed in seed mixtures, such as Achillea millefolium, Plantago lanceolata, and Centaurea jacea indicate mid-intensive grassland use. While Achillea millefolium and Plantago lanceolata can benefit from intensive grazing of permanent grasslands, Centaurea jacea is often found in extensively managed lowland hay meadows and negatively affected by land-use intensification, primarily by mowing and fertilization (Busch et al. 2019).

The number of species of the most frequently offered seed mixtures ranged from one to nine species, which makes them suitable for agricultural production purposes, but not for restoration efforts as semi-natural grasslands are considerably more diverse (Buchmann et al. 2018). Monocultures have generally been strongly discouraged for both intensive and extensively managed grasslands because of their poor performance and low sustainability (Nyfeler et al. 2011, Isbell et al. 2017). However, most of these one-species seed products were designed for the over-sowing of established grasslands. On the other end of the diversity gradient, high-diversity seed mixtures consisting of native ecotypes are used mostly for nature conservation purposes to restore semi-natural grasslands, often on arable land or after topsoil removal (Baasch et al. 2016, Resch et al. 2021). However, the availability of these seed mixtures can be limited by regional and production constraints (Nevill et al. 2016, Bucharova et al. 2019). The limited availability of native seed mixtures led in the past to large-scale restoration projects using species-poor mixtures of cultivars even for nature conservation purposes (Török et al. 2010). Furthermore, farmers can use native seed mixtures to establish key plant species needed for result-oriented agri-environmental schemes, e.g. in extensively managed permanent grasslands (e.g. Mack et al. 2020). In Switzerland, specific low-intensity grasslands, so-called biodiversity priority areas, are eligible for additional subsidies when specific key species are present. If these key species are lacking, they can be introduced by re- and over-sowing of existing species-poor grasslands with appropriate seed mixture (FOAG (Federal Office for Agriculture) 2021). Assessing the characteristics of the most frequently available seed mixtures for grasslands revealed two distinct types of seed mixtures: first, most mixtures contained 1–10 species, designed for mostly intensive grassland swards;
second, very diverse mixtures with 30 to more than 60 species, and a Shannon index >2 for grassland restoration.

4.2. Relationship between seed mixture price and plant diversity
We found strong positive relationships between plant diversity and the price of seed mixtures. For example, seed mixtures with 10 species were on average +63% (95%-CI: +62% to +65%) and with 30 species +387% (95%-CI: +331% to +449%) more expensive than seed products with one species. Besides seed costs, also other costs, such as opportunity and direct costs, can increase with plant diversity, with considerable differences between sites (Török et al. 2011). For example, maintaining certain species, especially valuable forage species, over time in more intensively used grasslands can require regular over-sowing (Van Den Pol-Van Dasselaar et al. 2019), causing costs, such as labor and fuel costs, to farmers. While plant diversity increases some costs, it can also reduce others, including mineral fertilizer costs due to N₂ fixation by legumes (Nyfeler et al. 2011). Therefore, seed costs and other costs are important when evaluating farmers’ potential economic benefits of plant diversity (e.g. Koellner and Schmitz 2006, Binder et al. 2018, Schaub et al. 2020a, 2020b).

Furthermore, the relationship of plant diversity and seed mixture prices per ha as well as the price per ha overall were related to other seed mixture characteristics such as provenance and organic certification. Our results showed that especially seed mixtures of native ecotypes were substantially more expensive (≥+75% (95%-CI: +53% to +99%)) than those not classified as such. This price increase is mainly relevant for the restoration of semi-natural grasslands, for which these seed mixtures are primarily used, and not for intensively used grasslands that are regularly renewed by re- or over-sowing. Many grassland restoration projects are financed or at least supported by public entities, such as the European Commission (Török et al. 2011). Therefore, public entities are often indirectly paying for seed mixtures containing native ecotypes. Moreover, subsidies that farmers receive for low-intensity and species-rich permanent grasslands¹³ can be a motivation to use species-rich seed mixtures of native ecotypes to introduce missing key species, as discussed above.

The higher costs for seed mixtures of native ecotypes can be linked to production processes, including time-consuming seed collection from local populations, limited number of propagations, hand harvest, complicated cleaning of harvested seeds, and quality control standards (Rieger et al. 2014, Bucharova et al. 2017, De Vitis et al. 2017), and can thus limit the use of native ecotypes on larger spatial scales. Previous studies highlighted the critical issue of the shortage of native seed supply (Nevill et al. 2016), which can lead to higher prices of native seed mixtures under an increasing restoration demand in the future. Moreover, although the restoration of species-rich grasslands is crucial and the main focus of our study, we note that conserving the few existing semi-natural grasslands should still be a major priority for policymakers (Temperton et al. 2019).

Furthermore, price markups for organic certification, regularly required in Germany and Switzerland for organic farming (Bio Suisse 2020, FiBi 2021, FMFA (Federal Ministry of Food and Agriculture) 2021)¹⁴, mainly affect seed mixtures for organic forage production, while mixtures consisting of native ecotypes never had an organic certification in our study. Under current policy trajectories, which often promote organic farming, e.g. the EU ‘Farm to Fork Strategy’, the demand for organic seed mixtures might increase in the future.

Aside from the seed mixture price and the other characteristics considered in our analysis, also other characteristics, such as the species’ palatability and drought resistance, can influence farmers’ and other land managers’ selection of seed mixtures. Those characteristics can also be connected to the recommended use of seed mixtures by seed producers to farmers, such as for permanent or temporary grassland use. The analysis of these other characteristics of available seed mixtures should be addressed by researchers as it remains an important area for future research. Moreover, while it is plausible to assume that online shops represent the available seed mixtures and prices, extending our research by including data from offline shops and sales data might offer interesting future research avenues.

In conclusion, it is important to consider plant diversity costs together with private and public benefits of grassland plant diversity when farmers and other land managers, policymakers, and other stakeholders decide about land management and grassland plant diversity. Neglecting these aspects can lead to a divergence between plant diversity levels recommended to farmers by, for example, extension services, and the actual optimal levels for farmers as well as the public. We showed that plant diversity, and related seed mixture characteristics, especially provenance, are considerable drivers of seed mixture costs, which carries implications beyond the focus of our analysis: reducing farmers’ costs of plant diversity could be an effective option for policymakers to support

¹³ For example, subsidies in Switzerland for low-intensity and species-rich grasslands that require certain plant species to be present can be up to 1920 CHF per year and per ha (~1778 Euro per year and per ha), depending on the type and location of the grassland (FOAG (Federal Office for Agriculture) 2020, 2021, Mack et al. 2020).

¹⁴ Note that whether single seeds need to be organic or not depends on the species and its availability (Bio Suisse 2020, FiBi 2021, FMFA (Federal Ministry of Food and Agriculture) 2021).
the increase in grassland plant diversity. Furthermore, high costs for plant diversity could also have significant financial implications for restoration activities and might therefore inhibit the realization of farming practices connected to specific agri-environmental schemes. However, reducing seed costs will require considerable efforts, such as competition among seed providers as well as research to develop more cost-effective production and operations (Merritt and Dixon 2011, Pedrini et al. 2020).

Data availability

The data that support the findings of this study are openly available at the following URL/DOI: 10.3929/ethz-b-000485215.

Code availability

The R-code for reproduction of this study is available online on Github (https://github.com/AECP-ETHZ/seed_price).

Authors’ contributions

SS, RF, and VHK conceived the ideas. SS, VHK, and VS collected the data. SS analyzed the data. SS and VHK led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

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

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