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

Sergei Schaub[1,2,3], **Robert Finger**[1,*], **Nina Buchmann**[2], **Vera Steiner**[1] and **Valentin H Klaus**[2]

[1] Agricultural Economics and Policy Group, ETH Zürich, Zürich, Switzerland
[2] Grassland Sciences Group, ETH Zürich, Zürich, Switzerland
[3] Chair of Ecosystem Management, ETH Zürich, Zürich, Switzerland
[*] Author to whom any correspondence should be addressed.

E-mail: rofinger@ethz.ch

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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 ($\geqslant$+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 (WallisDeVries *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 (Török *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[4]. 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 i) offer a similarly large variety in seed mixtures as other shops and ii) that their prices are comparable. This assumption is supported by the large seed mixture variety in our dataset and 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)[5]. 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: $Shannnon\,index = -\sum_{n}^{N} S_n \ln(S_n)$, where S_n is the share of the species n $(n, \ldots, N)$ 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)[6]. 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)[7].

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

[4] We excluded two seed mixtures specifically designed for alpine grasslands and labeled by the producer as ‘rarity’. Furthermore, the Shop Rieger-Hofmann 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 CHF. 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.

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) per kg (b) per ha	(a) 13.25 (15.46) (b) 463.88 (533.80)	262
Seed density	Recommended seeding density (kg per ha)	34.65 (10.88)	262
Species composition	Name and proportions of species in seed mixtures	n.a.	n.a.
Plant diversity	Plant diversity was measured either (a) as the number of species (ranges from 1 to 62) or (b) as Shannon index (ranges from 0 to 3.70)	(a) 8.44 (10.37) (b) 1.51 (0.71)	(a) 262 (b) 255
Native ecotype	Seed mixtures exclusively containing ecotypes of regional provenance	0.07 (0.25)	Yes = 244 No = 18
Permanent grassland	Seed mixtures for permanent grassland use, i.e. for grasslands lasting longer than three years.	0.62 (0.49)	Yes = 100 No = 162
Organic	Seed mixture with an organic certification	0.27 (0.45)	Yes = 190 No = 72
Over-sowing	Seed mixture for over-sowing existing grasslands	0.13 (0.34)	Yes = 228 No = 34

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

approach is a matrix-based layout approach, which can be used to explore and visualize seed mixtures (Conway *et al* 2017). Hereby, we focused on (1) the 20 most frequent plant species and assigned all remaining species to the category 'Other Species', and (2) specific species combinations that occurred at least twice in the dataset.

2.3. Analysis of the relationship between seed mixture 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 models[8]. First, a simple model that focuses on the correlation between seed mixture price and plant diversity controlling only for systematic price differences among shops:

$$log\left(p_i\right) = \alpha_0 + \alpha_{Div} Div_{ij} + \alpha_{Shops} Shops_i + e_{1i} \quad (1)$$

where p_i is the price per ha of seed mixture i. Div_{ij} is the plant diversity of seed mixture i, expressed either as the number of species or the Shannon index depending on the index j. $Shops_i$ is a vector of dummies for the different online shops. e_{1i} is the error term. Second, we estimated a model that controls for online shops and other important price determinants that were likely linked to plant diversity:

$$log\left(p_i\right) = \beta_0 + \beta_{Div} Div_{ij} + \beta_{Eco} Eco_i + \beta_{PermG} PermG_i + \beta_{Org} Org_i + \beta_{Over} Over_i + \beta_{Shops} Shops_i + e_{2i} \quad (2)$$

where Eco_i 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_i 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). e_{2i} 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 bootstrapped 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 specification of plant diversity as it allows for diminishing and increasing marginal relationships between plant diversity and seed mixture price[9]. The marginal relationship between plant diversity and seed mixture price is $\Delta p_1 / \Delta Div_{ij}$.

3. Results

3.1. Seed mixture characteristics

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

[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 $(\widehat{Div}_{ij})$ is $\beta_{Div}\widehat{Div}_{ij} + \beta_{Div^2}\widehat{Div}_{ij}^2$

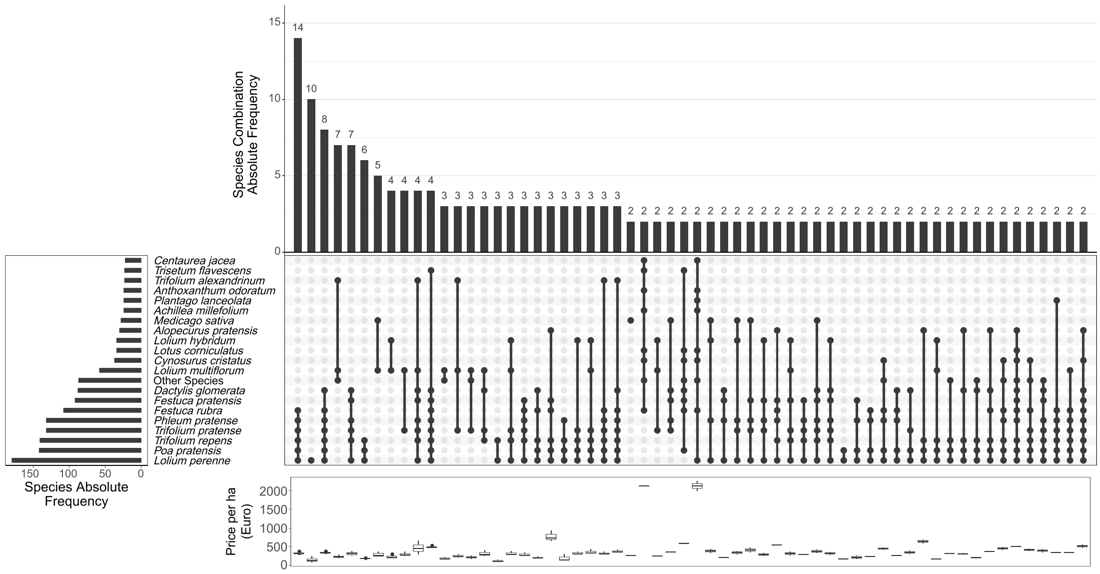

Figure 1. Differences in seed mixture composition and their prices: absolute frequency of species combinations and species, and seed mixture prices per ha. Only the 20 most frequent species are presented; all other species are assigned to the category 'Other Species'. Only species combinations of seed mixtures that occurred at least twice are depicted. See figures S3 and S4 for information on German and Swiss online shops separately.

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, Phleum 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, Phleum pratense, Festuca rubra,* and *Dactylis glomerata* (8 times; 3%; figure 1)[10]. 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. We generally found higher per ha prices for seed mixtures that included less commonly used species (summarized in the category 'Other Species') than for seed mixtures that included one or more of the 20 most commonly used species. Moreover, out of the 20 most commonly used species *Achillea millefolium, Anthoxanthum odoratum, Centaurea jacea, Cynosurus cristatus, Festuca rubra*, and *Lotus corniculatus* were characteristics of the four most expensive seed mixtures (figure 1).

Seed mixtures with native ecotypes had considerably higher plant diversity (figure 2). Moreover, seed mixtures with native ecotypes were always designed for permanent grassland and not organic (figure S1). In contrast, seed mixtures with cultivars (i.e. not only native ecotypes) were designed for both permanent grasslands and other use (i.e. temporary grass and other non-permanent forage mixtures) as well as were for both organic and conventional production systems.

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

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

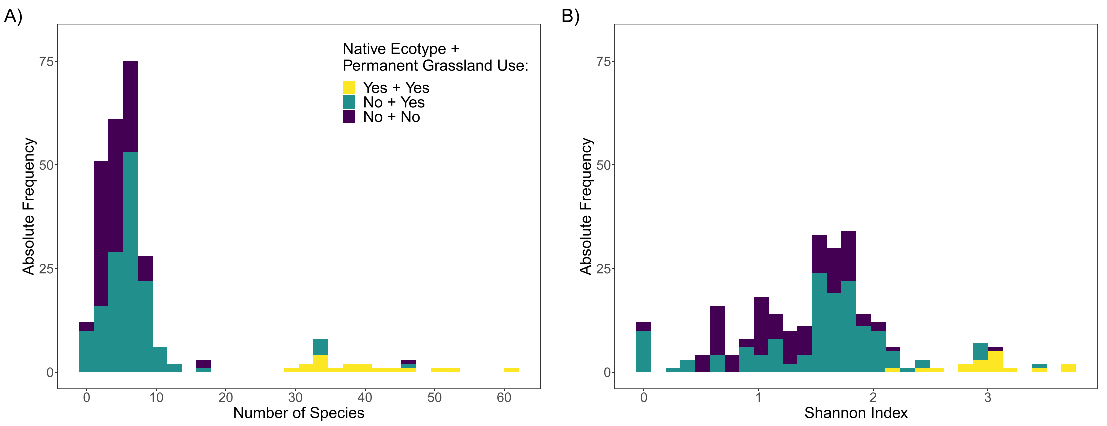

Figure 2. Absolute frequencies of seed mixtures with a specific plant diversity level described as (A) the number of species and (B) the Shannon index with an indication of whether mixtures contain only native ecotypes and are designed for permanent grassland use or not (see tables S5 and S6)[11].

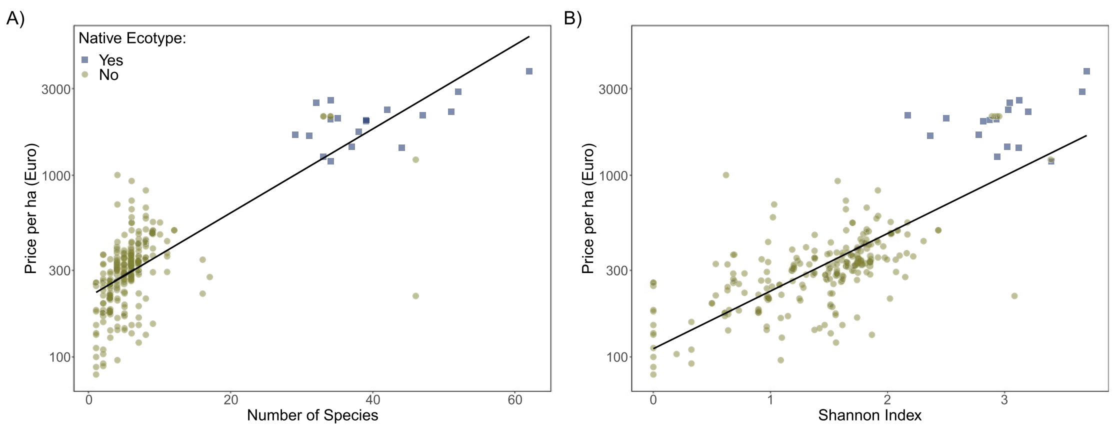

Figure 3. Seed mixture price per ha and plant diversity expressed as (A) the number of species, and (B) the Shannon index with an indication of native ecotypes. The lines indicate the linear relationship between plant diversity and log-transformed prices. Y-axes are logarithmic.

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

[11] 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 1		Model 2		Model 3		Model 4	
	Coefficient (Euro; log)	Δ%	Coefficient (Euro; log)	Δ%	Coefficient (Euro; log)	Δ%	Coefficient (Euro; log)	Δ%
Number of species	0.05^{***} (0.04–0.06)	6%	0.03^{***} (0.02–0.04)	3%				
Shannon Index					0.46^{***} (0.33–0.6)	59%	0.27^{***} (0.21–0.32)	31%
Native ecotype[1] (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		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. Δ% 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).[1] 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[12].

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 Landwirtschafskammern 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 N_2 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 species in mixtures for high to mid productive (mown) swards, such as *Phleum pratense, Festuca rubra,* and *Dactylis 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;

[12] Costs of grassland management and restoration despite seed costs are highly variable and depend on many different factors (e.g. country, soil, management factors, production aim, and restoration technique; Török *et al* 2011). For example, the variable costs producing fresh feed from grasslands with five cuts and average yield were estimated to be 529 Euro per ha in Germany (excluding seed costs; KTBL (Kuratorium für Technik und Bauwesen in der Landwirtschaft e.V.) 2021). These costs can vary, for example, due to the distance of grassland plots to the farm or the number of cuts. Restoration costs of grasslands in 200 European projects (including different restoration techniques) were estimated to be on average 1227 Euro per ha (Dietzel and Maes 2015). However, the cost range was substantial (100–3043 Euro per ha), and the authors indicated caution when interpreting the costs, which also varied substantially with environmental and socio-economic factors.

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 N_2 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 grasslands[13] 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, FiBl 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, FiBl 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.

References

Arbeitsverband der norddeutschen Landwirtschafskammern 2020 Qualitätsstandard mischungen für grünland—sortenempfehlung 2020–2022 (available at: www.landwirtschaftskammer.de/landwirtschaft/ackerbau/gruenland/index.htm) (accessed 1 March 2021)

Baasch A, Engst K, Schmiede R, May K and Tischew S 2016 Enhancing success in grassland restoration by adding regionally propagated target species *Ecol. Eng.* **94** 583–91

Binder S, Isbell F, Polasky S, Catford J A and Tilman D 2018 Grassland biodiversity can pay *Proc. Natl Acad. Sci.* **115** 3876–81

Bio Suisse 2020 Richtlinien für die erzeugung, verarbeitung und den handel von knospe-produkten (Basel: Bio Suisse)

Bucharova A, Bossdorf O, Hölzel N, Kollmann J, Prasse R and Durka W 2019 Mix and match: regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration *Conserv. Genet.* **20** 7–17

Bucharova A, Michalski S, Hermann J M, Heveling K, Durka W, Hölzel N, Kollmann J and Bossdorf O 2017 Genetic differentiation and regional adaptation among seed origins used for grassland restoration: lessons from a multispecies transplant experiment *J. Appl. Ecol.* **54** 127–36

Buchmann T *et al* 2018 Connecting experimental biodiversity research to real-world grasslands *Perspect. Plant Ecol. Evol. Syst.* **33** 78–88

Busch V *et al* 2019 Will I stay or will I go? Plant species specific response and tolerance to high land-use intensity in temperate grassland ecosystems *J. Veg. Sci.* **30** 674–86

Cameron A C, Gelbach J B and Miller D L 2008 Bootstrap-based improvements for inference with clustered errors *Rev. Econ. Stat.* **90** 414–27

Cavallo A 2017 Are online and offline prices similar? Evidence from large multi-channel retailers *Am. Econ. Rev.* **107** 283–303

Conway J R, Lex A and Gehlenborg N 2017 UpSetR: an R package for the visualization of intersecting sets and their properties *Bioinformatics* **33** 2938–40

De Vitis M, Abbandonato H, Dixon K W, Laverack G, Bonomi C and Pedrini S 2017 The European native seed industry: characterization and perspectives in grassland restoration *Sustainability* **9** 1682

Dietzel A and Maes J 2015 Costs of restoration measures in the EU based on an assessment of LIFE projects *Report EUR 27494 EN* (Luxembourg: European Commission) (https://doi.org/10.2788/235713)

Durka W, Michalski S G, Berendzen K W, Bossdorf O, Bucharova A, Hermann J M, Hölzel N and Kollmann J 2017 Genetic differentiation within multiple common grassland plants supports seed transfer zones for ecological restoration *J. Appl. Ecol.* **54** 116–26

FiBl 2021 Database of organic seed availability (available at: www.organicxseeds.com) (accessed 1 March 2021)

Finn J A *et al* 2013 Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: a 3-year continental-scale field experiment *J. Appl. Ecol.* **50** 365–75

FMFA (Federal Ministry of Food and Agriculture) 2021 Die EU-Rechtsvorschriften für den ökologischen Landbau (available at: www.bmel.de/DE/themen/landwirtschaft/oekologischer-landbau/eg-oeko-verordnung-folgerecht.html) (accessed 1 March 2021)

FOAG (Federal Office for Agriculture) 2020 Überblick: direktzahlungen an schweizer ganzjahresbetriebe (Bern: FOAG)

FOAG (Federal Office for Agriculture) 2021 Weisungen und Erläuterungen 2021 November 2020 (Änderung gegenüber 2020) Verordnung über die Direktzahlungen an die Landwirtschaft (Direktzahlungsverordnung, DZV; SR 910.13) vom 23 Oktober 2013 (Bern: FOAG)

Fuchs K, Hörtnagl L, Buchmann N, Eugster W, Snow V and Merbold L 2018 Management matters: testing a mitigation strategy for nitrous oxide emissions using legumes on intensively managed grassland *Biogeosciences* **15** 5519–43

Gehlenborg N 2019 UpSetR: a more scalable alternative to venn and euler diagrams for visualizing intersecting sets *R package version 1.4.0* (available at: https://CRAN.R-project.org/package=UpSetR) (accessed 1 March 2021)

Graham N, Arai M and Hagströmer B 2016 multiwayvcov: multi-way standard error clustering *R package version 1.2.3* (available at: https://CRAN.R-project.org/package=multiwayvcov) (accessed 1 March 2021)

Huber R and Finger R 2020 A meta-analysis of the willingness to pay for cultural services from grasslands in Europe *J. Agric. Econ.* **71** 357–83

IPBES 2019 Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services (Bonn: IPBES Secretariat) (https://doi.org/10.5281/zenodo.3831673)

Isbell F *et al* 2017 Benefits of increasing plant diversity in sustainable agroecosystems *J. Ecol.* **105** 871–9

Isbell F, Tilman D, Polasky S, Binder S and Hawthorne P 2013 Low biodiversity state persists two decades after cessation of nutrient enrichment *Ecol. Lett.* **16** 454–60

Jacot K and Lehmann J 2001 Wie können artenreiche Wiesen neu angelegt werden? In: schriftenreihe FAL 39, 69–75 *Eidgenössische Forschungsanstalt für Agrarökologie und Landbau* (Switzerland: Zürich-Reckenholz)

Kiehl K, Kirmer A, Donath T W, Rasran L and Hölzel N 2010 Species introduction in restoration projects–Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe *Basic Appl. Ecol.* **11** 285–99

Klaus V H, Schäfer D, Kleinebecker T, Fischer M, Prati D and Hölzel N 2017 Enriching plant diversity in grasslands by large-scale experimental sward disturbance and seed addition along gradients of land-use intensity *J. Plant Ecol.* **10** 581–91

Klaus V H, Whittingham M J, Báldi A, Eggers S, Francksen R M, Hiron M, Lellei-Kovács E, Rhymer C M and Buchmann N 2020 Do biodiversity-ecosystem functioning experiments inform stakeholders how to simultaneously conserve biodiversity and increase ecosystem service provisioning in grasslands? *Biol. Conserv.* **245** 108552

Kleijn D, Bommarco R, Fijen T P, Garibaldi L A, Potts S G and Van Der Putten W H 2019 Ecological intensification: bridging the gap between science and practice *Trends Ecol. Evol.* **34** 154–66

Klimek S, Steinmann H H, Freese J and Isselstein J 2008 Rewarding farmers for delivering vascular plant diversity in managed grasslands: a transdisciplinary case-study approach *Biol. Conserv.* **141** 2888–97

Koellner T and Schmitz O J 2006 Biodiversity, ecosystem function, and investment risk *BioScience* **56** 977–85

Krebs C J 1999 *Ecological Methodology* 2nd edn (Menlo Park, CA: Addison Wesley)

KTBL (Kuratorium für Technik und Bauwesen in der Landwirtschaft eV) 2021 Leistungs-Kostenrechnung Pflanzenbau *KTBL* (available at: https://daten.ktbl.de/dslkrpflanze/postHv.html) (accessed 5 January 2021)

Ladouceur E, Stanley Harpole W, Blowes S A, Roscher C, Auge H, Seabloom E W and Chase J M 2020 Reducing dispersal limitation via seed addition increases species richness but not above-ground biomass *Ecol. Lett.* **23** 1442–50

Le Clec'h S, Finger R, Buchmann N, Gosal A, Hörtnagl L, Huguenin-Elie O, Jeanneret P, Lüscher A, Schneider M K and Huber R 2019 Assessment of spatial variability of multiple ecosystem services in grasslands of different intensities *J. Environ. Manage.* **251** 109372

Lüscher A, Mueller-Harvey I, Soussana J F, Rees R M and Peyraud J L 2014 Potential of legume-based grassland–livestock systems in Europe: a review *Grass Forage Sci.* **69** 206–28

Mack G, Ritzel C and Jan P 2020 Determinants for the implementation of action-, result-and multi-actor-oriented agri-environment schemes in Switzerland *Ecol. Econ.* **176** 106715

Manning P *et al* 2019 Transferring biodiversity-ecosystem function research to the management of 'real-world' ecosystems *Adv. Ecol. Res.* **61** 323–56

Merritt D J and Dixon K W 2011 Restoration seed banks—a matter of scale *Science* **332** 424–5

Mewes M, Drechsler M, Johst K, Sturm A and Wätzold F 2015 A systematic approach for assessing spatially and temporally differentiated opportunity costs of biodiversity conservation measures in grasslands *Agric. Syst.* **137** 76–88

Mielke H and Wohlert W 2019 *Praxishandbuch Grünland: Nutzung Und Pflege* 2nd edn (Clenze: Agrimedia)

Nevill P G, Tomlinson S, Elliott C P, Espeland E K, Dixon K W and Merritt D J 2016 Seed production areas for the global restoration challenge *Ecol. Evol.* **6** 7490–7

Newbold T *et al* 2015 Global effects of land use on local terrestrial biodiversity *Nature* **520** 45–50

Nyfeler D, Huguenin-Elie O, Suter M, Frossard E and Lüscher A 2011 Grass-legume mixtures can yield more nitrogen than legume pure stands due to mutual stimulation of nitrogen uptake from symbiotic and non-symbiotic sources *Agric. Ecosyst. Environ.* **140** 155–63

Pe'er G *et al* 2014 EU agricultural reform fails on biodiversity *Science* **344** 1090–2

Pedrini S, Gibson-Roy P, Trivedi C, Gálvez-Ramírez C, Hardwick K, Shaw N, Frischie S, Laverack G and Dixon K 2020 Collection and production of native seeds for ecological restoration *Restor. Ecol.* **28** 228–38

Resch M C, Schütz M, Buchmann N, Frey B, Graf U, Van Der Putten W H, Zimmermann S and Risch A C 2021 Evaluating long-term success in grassland restoration: an ecosystem multifunctionality approach *Ecol. Appl.* **31** e2271

Rieger E, Feucht B and Wieden M 2014 Agricultural propagation of native seeds and development of a certification procedure in Germany *Guidelines for Native Seed Production and Grassland Restoration* ed K Kiehl, A Kirmer, N Shaw and S Tischew (Newcastle upon Tyne: Cambridge Scholars Publishing) pp 101–17

Schaub S, Buchmann N, Lüscher A and Finger R 2020b Economic benefits from plant species diversity in intensively managed grasslands *Ecol. Econ.* **168** 106488

Schaub S, Finger R, Buchmann N, Steiner V and Klaus V H, 2021 Data: German and Swiss seed mixture prices and characteristics (Zürich: ETH Zürich Research Collection) (available at: https://doi.org/10.3929/ethz-b-000485215) (accessed 15 July 2021)

Schaub S, Finger R, Leiber F, Probst S, Kreuzer M, Weigelt A, Buchmann N and Scherer-Lorenzen M 2020a Plant diversity effects on forage quality, yield and revenues of semi-natural grasslands *Nat. Commun.* **11** 768

Scherber C *et al* 2010 Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment *Nature* **468** 553–6

Seibold S *et al* 2019 Arthropod decline in grasslands and forests is associated with landscape-level drivers *Nature* **574** 671–4

SKEW (Schweizerische Kommission für die Erhaltung von Wildpflanzen) 2009 Empfehlungen für den anbau und die verwendung von pflanz- und saatgut einheimischer wildpflanzen (Nyon: Sekretariat SKEW)

Suter D, Rosenberg E, Mosimann E and Frick R 2017 Standardmischungen für den Futterbau. Revision 2017–2020 *Agrarforsch. Schweiz* **8** 1–16

Suter M, Huguenin-Elie O and Lüscher A 2021 Multispecies for multifunctions: combining four complementary species enhances multifunctionality of sown grassland *Sci. Rep.* **11** 1–16

Temperton V M, Buchmann N, Buisson E, Durigan G, Kazmierczak Ł, Perring M P, De Sá Dechoum M, Veldman J W and Overbeck G E 2019 Step back from the forest and step up to the Bonn Challenge: how a broad ecological perspective can promote successful landscape restoration *Restor. Ecol.* **27** 705–19

Temperton V M, Mwangi P N, Scherer-Lorenzen M, Schmid B and Buchmann N 2007 Positive interactions between nitrogen-fixing legumes and four different neighbouring species in a biodiversity experiment *Oecologia* **151** 190–205

Török P, Deák B, Vida E, Valkó O, Lengyel S and Tóthmérész B 2010 Restoring grassland biodiversity: sowing low diversity seed mixtures can lead to rapid favourable changes *Biol. Conserv.* **148** 806–12

Török P, Vida E, Deák B, Lengyel S and Tóthmérész B 2011 Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs *Biodivers. Conserv.* **20** 2311–32

Van Den Pol-Van Dasselaar A, Bastiaansen-Aantjes L, Bogue F, O'Donovan M and Huyghe C 2019 *Grassland Use in Europe—A Syllabus for Young Farmers* (Versailles: Quae Editions)

Walker K J, Stevens P A, Stevens D P, Mountford J O, Manchester S J and Pywell R F 2004 The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK *Biol. Conserv.* **119** 1–18

WallisDeVries M F, Poschlod P and Willems J H 2002 Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna *Biol. Conserv.* **104** 265–73