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Plant species richness of perennial flower strips on arable land is affected by seed diversity, provenance and seeding density

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A R T I C L E I N F O

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A B S T R A C T

Land-use intensification has caused drastic declines in the biodiversity of plants and insects in agricultural landscapes. To counteract these losses, the European Union introduced agri-environmental schemes that subsidise the establishment and maintenance of perennial flower strips on arable land. In practice, the large variety of flower strips makes it difficult to monitor their effectiveness, which calls for systematic experiments. This study reports on a field experiment to understand the effects of seed mixture and seeding density on the diversity of sown and unsown plant species. In spring 2020, we set up a field experiment with five seed mixtures differing in diversity, provenance and composition as well as three seed densities. Plant diversity was monitored after one and four years. There were clear effects of the seed mixtures on plant biomass and species richness, while the impact of seeding density was low. The moderately diverse regional mixture resulted in the highest richness; including insect-pollinated species, while the most diverse mixture and high-density seeding showed lowest colonisation by unsown species. Among the commercially available (and thus cheaper) mixtures, the one with lowest diversity performed worst in terms of sown species establishment, species richness and the proportion of unsown plants. Thus, we recommend usage of regional seeds with intermediate diversity at low to moderate seeding density when establishing perennial flower strips and aiming at high plant richness.

1. Introduction

Scientific and societal debates are currently focusing on the decline of biodiversity in many temperate regions. Not only insect abundance is decreasing (Hallmann et al., 2017), but several species groups get locally extinct, a trend seen in many land-use types (Seibold et al., 2019). Insects are of high significance, because they occur in almost all habitats, pollinate plants, disperse seeds, decompose biomass and serve as food source for amphibians, reptiles, birds and small mammals (Yang and Gratton, 2014). Insects are directly and indirectly affected by environmental change (Kotze et al., 2011), and their strongest declines are observed in agricultural landscapes (Seibold et al., 2019). Therefore, it is particularly important to develop and to implement improved arable land use and green infrastructure that support plant and insect diversity (Stadlmann and Adelmann, 2019).

There is general agreement that the intensification of arable systems has caused a deterioration of habitats and a decline of wildlife as well as ecosystem services (Stoate et al., 2001). This also concerns the diversity of arable plants that contribute to overall biodiversity via the food chain (Storkey et al., 2012). Agricultural intensification particularly affects endangered and low competitive plant species and associated insects (Twerski et al., 2022). To counteract these losses, the European Union introduced agri-environmental schemes (AES) which, among others, subsidise the establishment and maintenance of perennial flower strips on arable land to foster biodiversity. The flower strips are usually sown along field margins with seed mixtures containing a combination of seeds from wildflowers, ornamental plants and grasses (Haaland et al., 2011, Dietzel et al., 2019). The effects of these mixtures have been frequently discussed (Albrecht et al., 2021), but further critical studies on AES are needed, since they also have to cope with altered land use and climate change.

Haaland et al. (2011) and Dietzel et al. (2019) evaluated the success of flower strips by synthesising previous studies. They found generally positive effects on the abundance and diversity of insects (Haaland et al., 2011). Perennial strips also benefit farmland birds and small mammals (Arlettaz et al., 2010, Fischer and Wagner, 2016, Homberger et al., 2017). Flower strips do not only support specific animal groups, but also ecosystem functions through reducing natural pests (Tschumi et al.,

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2016) or supporting pollinators (Blaauw and Isaacs, 2014). Moreover, if these strips consist of native plant species they will attract a higher diversity of flower-visiting insects than mixtures including non-natives (Rollings and Goulson, 2019). However not only the species itself plays an important role in determining the strip's effect on pollinator abundance and diversity, but also plant provenance (Bucharova et al., 2021). Especially for pollinators, different flowering times caused by plants with different provenance can alter pollinator interactions, including their abundance (Durka et al., 2019). Genotypic differences of plants, in interaction with environmental factors for example, alter floral visitor communities (Burkle et al., 2013).

In fact, some studies only found moderate effects of flower strips on faunal biodiversity, and often no benefits for rare or endangered species (Kleijn Sutherland, 2003, Kleijn et al., 2006). Therefore, several authors suggested to better evaluate flower strips in order to improve their design (Ekroos et al., 2014, Nichols et al., 2022). So far, most studies have investigated the effects of flower strips 1–3 years after establishment (Uyttenbroeck et al., 2015, Ganser et al., 2019, Pfiffner et al., 2019, Uyttenbroeck et al., 2015), even though perennial strips can persist for about five years (Bayerisches Staatsministerium für Umwelt und Verbraucherschutz, 2024). Previous studies, that investigated flower strips older than three years, focused on associated pollinators and other insects (Buhk et al., 2018), while little is known about the development of the respective plant communities.

Flower strips vary in diversity, provenance and composition (e.g. legumes or grasses) of seed mixtures, as well as in seeding density (Dietzel et al., 2019). Consequently, a systematic comparison of flower strips is a complex task. The theory of plant community assembly suggests that species diversity and seeding density control the establishment of sown and unsown plants in flower strips, due to niche pre-emption, facilitation and competitive exclusion (Keddy and Laughlin, 2021). Recording sown species and their abundance (=biomass) provide evidence on plant establishment, while the unsown species inform about effects of seed bank and seed dispersal. These effects are of high relevance when designing and applying seed mixtures for flower strips on arable land, but their effects have yet been little investigated.

Thus, we set up a field experiment to evaluate the effects of seed mixture and seeding density on the plant species numbers ('richness'), biomass and community dynamics of flower strips. We included commercial mixtures that varied in plant diversity, provenance and species composition, with both native and non-native plants, rare arable species and grasses to evaluate the effect of mixtures that are practically sown by e.g. farmers. The experiment was designed to understand the driving factors of plant community assembly in flower strips and to develop practical advice on the most effective seed mixtures and seeding density, in terms of highest diversity. Specifically, we tested four hypotheses:

1. Due to niche pre-emption and stronger competition in high-diversity mixtures, we expect lower overall richness, while low-diversity mixtures consist of fewer species to begin with. This will therefore result in (a) the establishment of sown species to be highest in intermediate mixtures with moderate seeding density, and (b) this results also in the highest biomass of these treatments.
2. Due to niche pre-emption, high diversity mixtures and high seeding density of flower strips reduce colonisation by unsown species.
3. The effects of mixture diversity and seeding density become more pronounced over time, because of different competitions between the communities of each mixture due to the difference in sown species (numbers).
4. Thus, the sown plant communities diverge with time.

2. Material and methods

2.1. Experimental setup

The field experiment was established in Freising-Dürnast on an arable field near the TUM Greenhouse Laboratory Centre (N 48.405833, E 11.6975 WGS84; 465 m a.s.l.). Geologically the area belongs to the tertiary hills with loess deposits, resulting in very fertile soils. Soil samples for the whole site have been taken in the year of 2017 and 2023. The soil type was mineral soil and decalcified loess with a mean pH-value of 6.4–7.0, phosphate concentration of 11–12 mg/100 g soil and potassium 11–12 mg/100 g soil (Table A3). We performed a two-sided *t*-test to compare means of single parameters between the two years. Results are listed in the Appendix (Table A4). The climate is humid with 887 mm annual precipitations and 8.3 °C mean annual temperature (30-year mean values for Altomünster-Maisbrunn, DWD Climate Data Center, 2021). The site was located at the edge of an arable field that was previously used for conventional arable farming. The site is homogeneous, but slightly inclined (<5 % slope, NEE) and separated by two tall ash trees. Thus, the area around the trees was excluded from the experimental design.

The experiment was set up in May 2020 following a factorial design with five seed mixtures, three seed densities and four replicates (Fig. A1). This resulted in a total of 60 plots (5 m x 8 m), and each plot was sown with a random seed mixture. However, for practical reasons, mixtures were sown in a row of three plots separated by grass strips, with the three seed densities for each mixture sown in random order. After seeding and rolling, the plots were left unmanaged. The area between the plot rows was seeded with *Lolium perenne* and mown regularly. In October 2023, a cupping cut was done to reduce dominant plant species.

The five seed mixtures tested included three commercial products widely used in S Germany (composition of 2020) and two experimental mixtures to add regional seeds and a higher diversity of mixtures (Table A1, Fig. A2): (i) ***L.nr*** is a low diversity mixture (26 species) with (non)native species of non-regional provenance that is commercially available and called 'NaturPlus BW 900 Bienenweide' ('Bee Pasture'); (ii) ***M.nr*** is a moderate diversity mixture (42 species) with (non)native species of non-regional provenance that is commercially available and called '24 BY-KULAP Bayern, Lebendiger Acker – Trocken' ('Living Arable Land'); (iii) ***M.r*** is a moderate diversity mixture (41 species) with native species of regional provenance, including rare arable plants, that was specifically designed for the experiment; (iv) ***I.nr*** is an intermediate diversity mixture (47 species) with (non)native species of non-regional provenance that is commercially available and called 'NaturPlus BL 500 Blühende Landschaft' ('Flowering Landscape'); and (v) ***H.r*** is a high diversity mixture (61 species) with (non)native species of regional provenance, including grasses, that was suggested by the seed producer Johann Krimmer (Pulling).

The three commercial products are recommended mixtures in ecological funding programs on arable land in Bavaria, Germany (e.g. KULAP 'Kulturlandschaftsprogramm'). The seeding densities followed the recommendations of the producers (=100 %), i.e. 20 kg ha^{-1} for L.nr and M.nr, 10 kg ha^{-1} for I.nr, and 8 kg ha^{-1} for M.r and H.r.; this was compared to half (50 %) and double densities (200 %). In this study, we wanted to focus on commercial, practically used seed mixtures (nr) and compare them to 'newly' composed mixtures consisting of regional seeds (r). Since practically used mixtures do not exceed 50 species per mixture, we could not find an equivalent for H.r. The closest were mixtures as diverse as I.nr (around 47 species), which is why we included this mixture with no equivalent of a regional seed mixture.

2.2. Sampling protocol

Vegetation was sampled on all 60 plots in early (June–July) and late summer (August–September) 2021 by visually estimating the cover of each plant species as well as plant cover on the entire plot using the scale of Londo (1976). Additionally, a presurvey was done in May, and the mean cover of flowers was recorded in three randomly placed quadrats (1 m x 1 m) per plot. Biomass was harvested in May 2021 on one 25 cm× 50 cm quadrat per plot; it was dried for > 48 h at 65 °C before weighing. For later analysis, we converted measured biomass to biomass per m^2. In early and late summer 2024, we resampled plant cover on a smaller scale. A randomly placed quadrat with the size of 2 m × 2 m was used to estimate plant cover using the Londo scale.

2.3. Statistics

We used the statistical software R (version 4.3.2) for data analysis. Species richness (overall, unsown, grass and insect-pollinated plant species) and plant biomass were modelled with a generalised linear mixed model using the R package 'glmmTMB' (Brooks et al., 2017). As for the species richness of insect-pollinated plants we used the definition according to Landolt (2010). Assumptions like normal distribution were tested. We organized the plots into blocks that were sown together and sets of densities for seed mixture sown in one row to account for neighbouring effects. Each seed mixture was sown three times in a row with the three different seed densities in a random order. Hence, for the statistical model we added replication ID (of each combination of seed mixture and seed density), the ID of plot-blocks that were sown together and sets of densities for seed mixtures as random intercept factors. Furthermore, we added the interaction between the two explanatory variables: seed mixture and seed density. For the response variables of species richness (overall, unsown, grass and insect-pollinated plant species) we used the family of a Poisson distribution on a log-link scale.

In case of plant biomass, we transformed the response variable with log (biomass) + 1 to achieve a normal distribution and modelled it on an identity-link scale. Due to the high abundance of zeros, we transformed the counted number of grass species with + 1. To test for single variable differences, we performed for all response variables a Tukey-Kramer HSD post-hoc test. Additionally, we performed a Moran's *I* analysis as a function of contiguous neighbour with the Monte Carlo method ($n = 999$ simulations) to account for spatial patterns in biomass and species richness with the help of the package 'spdep' (Pebesma Bivand, 2023). In 2021 and 2024, neither biomass nor total species richness followed a non-random spatial pattern (biomass: statistic = 0.235, observed rank = 945, $p > 0.05$, species richness 2021: statistic = 0.003, observed rank = 537, $p > 0.4$, species richness 2024: statistic = 0.233, observed rank = 940, $p > 0.05$; see also Table A5).

We conducted non-metric multidimensional scaling (NMDS with two dimensions) within the R package 'vegan' (Oksanen et al., 2024) to check for differences within the species composition of plant communities resulting from the seed mixtures. The NMDS ordination was based on Bray-Curtis distances ranging from 0 (completely identical) to 1 (completely dissimilar). Plant species which were observed in less than four of the 60 plots, were considered as outliers (stray found) and therefore excluded from the NMDS-analysis. In 2021 one plot (Plot ID 39) of the intermediate diverse mixture (I.nr) showed a low coverage of plant species which is likely caused by a measurement error. Plant species cover data (Londo scale) were transformed to percentage values as described by Traxler (1997).

3. Results

3.1. Establishment of sown and unsown plant species

After one year, in total 70 plant species occurred in the experimental plots, with different vegetation structure depending on seed mixture (Fig. A2). Of these, 40 stemmed from the mixtures ('sown species'), and 52 had colonised the plots from the seedbank or adjacent vegetation ('unsown species'). Of the unsown plant species, 17 were not part of any of the five mixtures; the other 35 species were seeded in at least one of the other four mixtures of this experiment, but not in the one observed.

After this one year, mixture L.nr (low diversity, non-regional seeds) had the highest establishment rate, i.e., 69 % of the sown species. Mixture M.nr (moderate diversity, non-regional seeds) and H.r (high diversity, regional seeds) showed most species (both 39 in total), while mixture H.r had the fewest unsown plants in relation to the observed species within that mixture (28 %), i.e. plants, that were unsown (Fig. 1).

After four years, we recorded 74 plant species, i.e. 44 from the seed mixtures and 60 colonisers (Table A2). Of the 60 unsown species, 24 were not part of any of the mixtures. The other 36 species were sown in at least one of the other four mixtures of this study and probably had spread from nearby plots of the experiment. Mixture M.nr had the highest establishment rate, as 52 % of the sown species were recorded. Most plant species were recorded in mixtures M.nr and M.r with a total number of 50 species. Mixture H.r still had the fewest unsown species in relation to the observed species within that mixture (39 %; Fig. 1).

In the fourth year, the establishment rate was lower (31–52 %) compared to the first year (43–69 %), while the proportion of unsown species was higher for all mixtures. The largest difference occurred for L.nr in which the proportion of unsown species changed from 39 % to 77 %, while the smallest difference occurred in H.r (from 28 % to 39 %). The lower number of unsown plant species within H.r as compared to other mixtures became more pronounced after four years.

We observed significant effects of seeding density, but not of seed mixture on total species richness in the first year ($Chi^2_4 = 11.9$, $p = 0.003$; $Chi^2_2 = 8.8$, $p = 0.067$; Fig. 2a; see Table A6 for full statistical results). High seeding density resulted overall in significantly lower total species richness (not depicted in the graph, see Table A7 for full statistical results); however, this effect vanished when comparing single mixture densities (e.g. in H.r high seeding density vs. low seeding density: $z_{Inf} = 2.06$, $p > 0.05$; see Table A8 for full statistical results). We observed similar patterns for accounting established sown species richness alone. However, seed mixture, in contrast had a significant effect on established sown species richness ($Chi^2_4 = 29.1$, $p < 0.001$; Fig. 2c; see Table A9 for full statistical results). Sown species richness was lower for L.nr and I.nr compared to other mixtures. The number of unsown species was lowest in the two regional mixtures M.r and H.r compared to the least diverse one, i.e. L.nr ($z_{Inf} = 2.89$, $p = 0.032$; $z_{Inf} = 3.04$, $p = 0.02$; see Table A10 for full statistical results). Additionally, within mixture I.nr the number of unsown species was significantly lower for the highest density compared to the other densities ($z_{Inf} = 3.24$, $p = 0.018$; $z_{Inf} = 3.04$, $p = 0.035$; Fig. 2e; see Table A11 for full statistical results).

After four years, the low- (L.nr) and high-diversity (H.r) mixtures revealed a significantly lower total species number than intermediate (I.nr) or moderate diversity (M.nr and M.r; Fig. 2b; see Table A12 for full statistical results). If only taking established sown species in account, the low-diversity (L.nr) mixture, had lower establishment in both years, especially after four years (e.g. L.nr vs. M.r in 2021: $z_{Inf} = -2.92$, $p = 0.029$ or L.nr vs. M.r in 2024: $z_{Inf} = -4.63$, $p < 0.0001$; Fig. 2b–c; see Table A13 and Table A14 for full statistical results). A similar effect of total species number was observed after one year, but this effect was not significant (e.g. L.nr vs. M.nr: $z_{Inf} = -1.79$, $p > 0.05$; Fig. 2a; see Table A15 for full statistical results). Additionally, the number of unsown species remained low for H.r in both sampling years (Fig. 2e, f; see Table A10 & Table A16 for full statistical results). In contrast, the overall significant effect of seeding density on total species richness vanished after four years ($Chi^2_2 = 0.2$, $p > 0.05$; see Table A17 for full statistical results). There was also no longer an effect of seeding density on the number of unsown species ($Chi^2_2 = 1.1$, $p > 0.05$ see Table A18 for full statistical results). Thus, the seed mixture effect became more pronounced with time, while the effect of seed density disappeared. In general, total species number revealed similar patterns to established species numbers in both years (see Fig. 2a–d).

3.2. Plant biomass

The seed mixtures but not seed densities differed in their production of biomass in the first year of the experiment ($Chi^2_4 = 20.6$, $p < 0.001$; $Chi^2_2 = 0.2$, $p > 0.05$; see Table A19 for full statistical results). The moderately diverse regional mixture M.r yielded significantly more

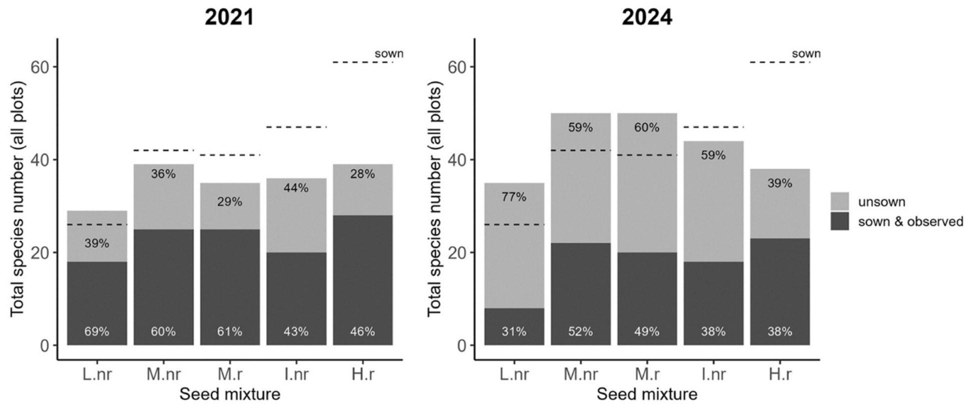

Fig. 1. Variation in plant species richness in perennial flower strips based on five seed mixtures in June–September of the first (2021) and fourth year (2024; L.nr, 26 non-regional spp.; M.nr, 42 non-regional spp.; M.r, 41 regional spp.; I.nr, 47 non-regional spp.; H.r, 61 regional spp.) across the three sowing densities. The dark grey bars show the number of observed species that were sown, while the light grey bars represent those unsown ones that spontaneously colonised the plots. The dashed lines indicate the species numbers of the mixtures. The white numbers represent the establishment rate, i.e. the percentage of observed sown species (dark grey bars). The black numbers display the proportion of unsown ones among all observed species of the respective seed mixture.

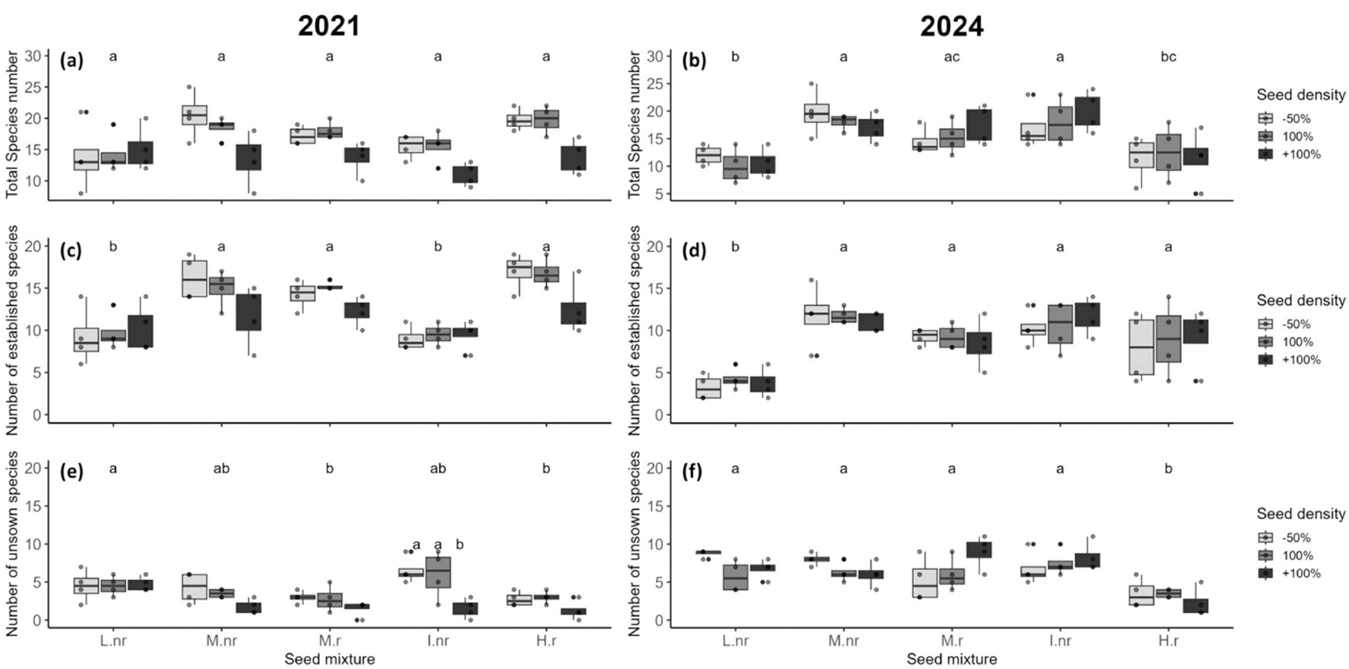

Fig. 2. Variation in plant species richness of all (a and b), of established sown (c and d) and of unsown species (e and f) in perennial flower strips, based on five seed mixtures with three seeding densities (L.nr, 26 non-regional spp.; M.nr, 42 non-regional spp.; M.r, 41 regional spp.; I.nr, 47 non-regional spp.; H.r, 61 regional spp.) in the first (2021) and the fourth year (2024). Plant species richness was plotted in box plots distinguishing seed mixture and seeding density (light grey = low; grey = moderate; dark grey = high density), while dark grey dots depict respective raw data points (four plots per mixture and density combination). Two-way ANOVA followed by Tukey-HSD-tests; letters indicate significant differences ($p < 0.05$). For the differences between seeding densities within single seed mixtures, we only added letters if a significant difference ($p < 0.05$) between the three densities of the mixture was given.

biomass compared to M.nr, I.nr and H.r ($t_{41} = -3.5$, $p = 0.009$; $t_{41} = 4.06$, $p = 0.002$; $t_{41} = 2.94$, $p = 0.04$; Fig. 3; see Table A20 for full statistical results). The least diverse mixture (L.nr) did not differ from the others and produced an intermediate amount of biomass.

3.3. *Insect-pollinated plants and grasses*

The richness of insect-pollinated species was significantly affected by mixture ($Chi^2_4 = 11.6$, $p = 0.021$; see Table A21 for full statistical results) but not by seeding density in the first sampling year ($Chi^2_2 = 1.5$, $p > 0.05$; Fig. 4a). It was lower in plots with low-diversity (L.nr) compared to the moderate-diversity mixture with non-regional seeds (M.nr; $z_{Inf} = -2.8$, $p = 0.038$; see Table A22 for full statistical results). Similar effects occurred in the fourth year, but the total species richness of insect-pollinated plants was lower in plots with L.nr and H.r compared to M.r and M.nr and I.nr (Fig. 4b; see Table A23 for full statistical results). When only analysing the sown species, the proportion of established to sown insect-pollinated species differed among seed mixtures in the fourth year (L.nr 26.1 %, M.nr 57.6 %, M.r 61.3 %, I.nr 58.1 % and H.r 51.5 %). Again, we did not observe a significant effect of seed density in the fourth year ($Chi^2_2 = 0.15$, $p > 0.05$; see Table A24 for full statistical results).

As for the species richness of grasses, mixture but not seeding density showed significant effects in the first ($Chi^2_4 = 16.8$, $p = 0.002$; $Chi^2_2 = 0.12$, $p > 0.05$; Fig. 4c; see Table A25 for full statistical results) and fourth year ($Chi^2_4 = 12.9$, $p = 0.011$; $Chi^2_2 = 0.89$, $p > 0.05$; Fig. 4d; see

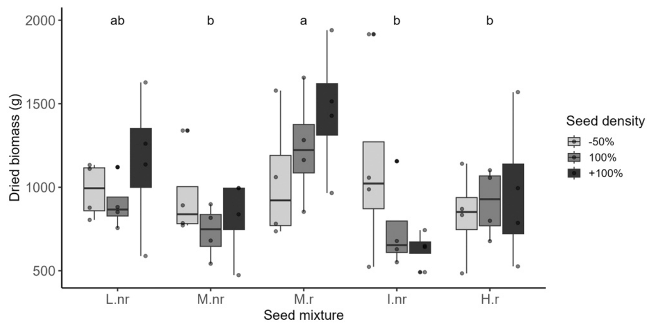

Fig. 3. Variation in plant biomass in perennial flower strips based on five seed mixtures with three seeding densities in the first year (L.nr, 26 non-regional spp.; M.nr, 42 non-regional spp.; M.r, 41 regional spp.; I.nr, 47 non-regional spp.; H.r, 61 regional spp.). Dark grey dots depict raw data points (four plots per mixture and density combination). Biomass was log-transformed prior to analysis with two-way ANOVA followed by Tukey-HSD-tests; letters indicate significant differences ($p < 0.05$). The dried biomass (g) is depicted as g biomass per m^2 (y-axis).

Table A26 for full statistical results). While in the first year the mixture with high diversity (H.r) had higher grass richness compared to the moderate-diversity mixtures (M.r and M.nr; $z_{Inf} = -3.01$, $p = 0.022$ and $z_{Inf} = -2.86$, $p = 0.035$; see Table A27 for full statistical results), this effect disappeared in the fourth year (see Table A28 for full statistical results).

3.4. Plant community characteristics

The NMDS ordination accounted for 81.1 % of total variance in seed mixture and sampling year (Fig. 5). Comparing both sampling years and all five mixtures, a divergence of the plant communities in the fourth year occurred. In the first year, species composition was similar across seed mixtures. Only the moderate-diversity mixture consisting of regional seeds (M.r) and containing arable (e.g. *Legousia speculum-veneris* and *Papaver rhoeas*) and grassland species (e.g. *Campanula rapunculoides* and *Knautia arvensis*; Fig. A2), showed a greater distance to the other mixtures. Similar effects were seen in the fourth year.

In the NMDS, leguminous species (e.g. *Melilotus officinalis*) occurred close to the plots of the first year, while most grass species (e.g. *Dactylis glomerata*) were situated close to the plots of the fourth year. The plots of the most diverse mixture (H.r) consisted of regional seeds including grasses like *Arrhenatherum elatius*, and were closer to the grass species than plots of moderate diversity (M.r and M.nr). Species like *Phleum pratensis* or *Geranium pratense* in the NMDS were located closest to the plots of M.r and M.nr from the year 2024 while furthest from plots of 2021, especially L.nr. This effect was the opposite for species like *M. officinalis* and *Lolium perenne*, which were located closer to plots sown with L.nr in the year 2021. Additionally, in the NMDS, species like *Centaurea scabiosa* or *Vicia sativa* were closer located to the 2021 plots than to those of 2024, while especially closely located to plots consisting of M.r and M.nr. *Dactylis glomerata* and *Epilobium parviflorum*, however, were closer located to plots from 2024, especially L.nr and H.r.

4. Discussion

The purpose of this study was to evaluate the contribution of different seed mixtures for flowering strips to plant biodiversity on arable land. The experiments showed how seeding density, seed provenance and mixture diversity influence the plant communities within flowering strips in arable land. Although, we could not contrast each regional seed mixture with one non-regional, commercial mixture due to logistic reasons, the following conclusions can be drawn.

4.1. Drivers of species' establishment

About two-third of sown species established in the first year of almost all of the sown seed mixtures, which is in accordance to other studies about establishment of seed mixtures in grass land (Kaulfuß et al. 2022, Kiehl et al., 2010). Over the four years, the presence of sown species decreased, while the proportion of unsown ones increased across seed mixtures, in contrast to the findings of Lepš et al. (2007), where the proportion of unsown species decreased. Additionally, our results partly confirmed hypothesis 1a, stating that seed mixtures with moderate diversity (M.r, M.nr) had the highest establishment of species in relation to sown species. In the fourth year, total species richness and that of sown species were lower for low- (L.nr) and high-diversity mixtures (H.r) compared to the moderate (M.r and M.nr) and intermediate diverse (I.nr) mixtures, suggesting that moderate and intermediate mixtures fill

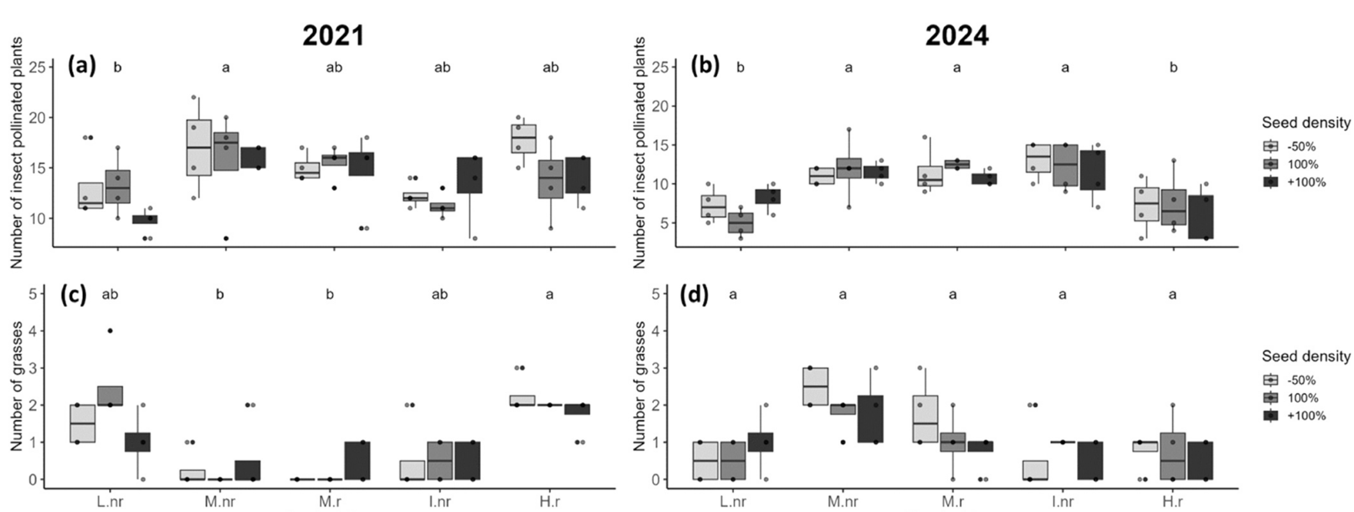

Fig. 4. Variation in the species richness of insect-pollinated plants (a and b) and grasses (c and d) in perennial flower strips based on five seed mixtures with three seeding densities (L.nr, 26 non-regional spp.; M.nr, 42 non-regional spp.; M.r, 41 regional spp.; I.nr, 47 non-regional spp.; H.r, 61 regional spp.) in the first (2021) and fourth year (2024). Plant species richness was plotted in box plots determined by seed mixture and seeding density (light grey = low; grey = moderate; dark grey = high density) combinations, while dark grey dots depict respective raw data points (four plots per mixture and density combination). Definition of insect-pollinated plants according to Landolt (2010). Two-way ANOVA followed by Tukey-HSD-tests; letters indicate significant differences ($p < 0.05$). For the differences between seeding densities within single seed mixtures, we only added letters if a significant difference ($p < 0.05$) between the three densities of the mixture was given.

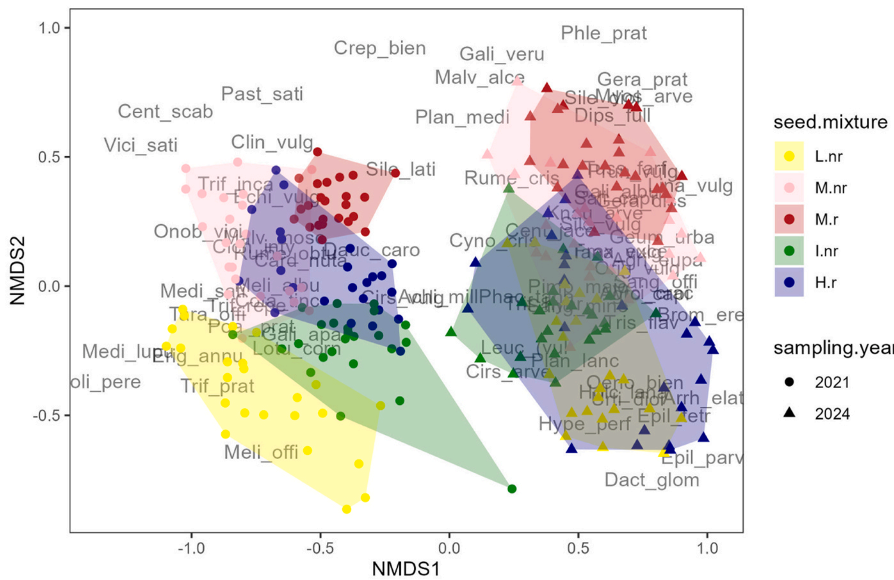

Fig. 5. Trends in the plant communities in perennial flower strips based on five seed mixtures (L.nr, 26 non-regional spp.; M.nr, 42 non-regional spp.; M.r, 41 regional spp.; I.nr, 47 non-regional spp.; H.r, 61 regional spp.) sampled in the first (2021) and fourth year (2024). The NMDS ordination (two-dimensional, final stress = 0.206) shows each plot as one point. Different colours depict different mixtures and different symbols indicate sampling year. Black text depicts abbreviations of plant species' scientific names (species listed in Table A1); NMDS Axis 1 and 2 are shown. Species considered as outliers (present in less than four out of 60 plots) are excluded from the ordination.

the niches for plant establishment better than low-diversity mixtures. In these mixtures, there was most likely less competition between plant species compared to high-diversity ones, as also reported by Barr et al. (2017) and Schmidt et al. (2020). This effect fully occurred in the fourth year, while only a tendency was seen in the first year. It thus became more pronounced over time, thus, confirming hypothesis 3. Lepš et al. (2007) also found the number of sown species to decrease from the second season onwards. A decrease of sown and an increase of unsown species within less diverse seed mixture has also been observed by Roscher et al. (2011).

Interestingly, effects of seeding density on species richness were negligible, contrary to hypothesis 1a. Overall, a tendency for higher seeding density resulting in lower species richness was shown in the first but not in the fourth year, suggesting that in perennial flowering strips seeding densities are of little relevance compared to the impact of seed mixture, which confirms findings of Carter and Blair (2012), Nemec et al. (2013) and Barr et al. (2017).

While seeding density did not have a significant effect on total species richness, within the intermediate-diversity mixture (I.nr), the number of unsown species was reduced in the highest seeding density. However, this effect disappeared in the fourth year. There is a high possibility that this effect is a false significant effect, as this was observed neither in other mixtures of similar diversity (M.r and M.nr), nor in the other year. Since we could not include an I.r mixture (intermediate-diversity consisting of regional seeds) and no samples of the years between 2021 and 2024 due to logistic reasons, this effect needs further investigations to draw clear conclusions. Additionally, the mixture with the highest seed diversity (H.r) had the lowest number of unsown species, even in the fourth year, most likely due to niche pre-emption. This result confirmed hypothesis 2, which matches the observations by Carter and Blair (2012). Thus, in the high-diversity mixture (H.r), low establishment rates, especially after four years, and low numbers of unsown species led to a lower total number of species. We therefore recommend mixtures with moderate diversity, especially when financial resources are limited. In turn, a high-diversity mixture is more efficient in reducing the number of unwanted plants (Barr et al., 2017), likely because a high diversity of native plants increases invasion resistance, probably due to stronger interspecific competition and niche pre-emption (Lepš et al. 2007, Nemec et al., 2013, Schmidt et al., 2020).

4.2. Diversity effects on plant biomass

The lower biomass for the high-diversity mixture (H.r) but not for the low diversity one (L.nr) partly confirmed hypothesis 1b. This is in contrast to other studies (Lepš et al. 2007, Han et al., 2021, Rychtecká et al. 2014) which compared mixtures of different diversities and found that high-diversity mixtures produced more biomass. However, these studies compared mixtures with far lower species numbers, i.e. their highest diversity mixture corresponded to our lowest seed mixture, which renders a valid comparison difficult. In fact, biomass always highly depends on the identity of the sown species, which can lead to contradicting results when comparing seed mixtures. For example, the tall *Dipsacus fullonum* produces a high amount of biomass, while smaller but more abundant species like *Plantago lanceolata* produce less. Especially *D. fullonum* was more abundant in the moderate-diversity mixture with regional seeds (M.r) compared to the high-diversity mixture (H.r), which most likely caused the higher biomass found within this mixture.

4.3. Understanding plant community dynamics

Taking a closer look at species composition, plant communities of the different mixtures diverged over time, which is in line with hypothesis 4. This is in contrast to the observation made by Lepš et al. (2007), and given that plots were located rather close to each other, i.e. that seeds from adjacent treatments likely spread, as suggested by the higher numbers of unsown species in adjacent plots in the fourth year. Notably, grass species (Poaceae) occurred less in the mixture with moderate diversity consisting of regional plants (M.r), indicating that strips sown with this mixture were more resistant against grass invasion. This finding is similar to Walker et al. (2015) and Schmidt et al. (2020), who found that mixtures with regional provenances were more resistant against invasion by unsown species. Our second mixture with regional provenance and high diversity (H.r) did not support this result, which might be because grass species were already present in that mixture. Moreover, the number of insect-pollinated plants was similarly low in the high-diversity mixture (H.r), especially in the fourth year, which might also arise from the competition by grasses probably causing the cover of insect-pollinated plants to reduce over the years.

Leguminous species (e.g. *M. officinalis*) were more present in the first than in the fourth year, indicated by the NMDS (these species were closer located to plots from 2021 than from 2024). This group consists of annual and short-lived perennial plants (Beuselinck et al., 1994). Consequently, in later years, these species tend to disappear, especially due to their low ability to re-establish into existing fields (Woodcock et al., 2014). Species, which were sown in neither mixture and were mostly present in the fourth year, as *E. parviflorum*, *D. glomerata* or *P. pratense*, caused higher numbers of unsown species in the fourth year. *P. pratense* was mostly present in plots of M.r in the fourth year, contrary to *E. parviflorum* and agricultural species (*D. glomerata* mostly present in L.nr). Since all three species are common (Metzing et al., 2018, Müller et al., 2021), an occurrence in flowering strips within arable land, is unsurprising despite not being contained it the seed mixtures. Even though we did not consider surrounding fields, it is very likely that seeds from these species dispersed from close by fields, margins or even the seedbed causing them to appear more frequently, the longer the fields exist.

Centaurea scabiosa on the other hand, tended to occur mostly in plots in the first year, especially sown with M.nr, which is most likely due to the fact, that this species was solely sown in M.nr. This plant species is dependent on dispersal via ants (Müller et al., 2021). In freshly established fields, ant presence and therefore their activity is rather low, compared to older fields (Dauber and Wolters, 2005). Consequently, with low chance of dispersal due to missing ant activity, other plant species outperformed *C. scabiosa* over the years, leading this species neither to disperse to other plots nor to re-establish at later years.

The presence of *Lolium perenne* in the first, but not in the fourth year, can be explained by the method of establishing the experiment. Despite not being part of any seed mixture sown, this species was sown as walking paths between the plots, causing some of the seeds to disperse onto the plots. Consequently, this species occurred in all plots, despite not being present in the mixtures. While we could not record this species in the fourth year, it is very likely that *L. perenne* was outperformed by other species in light competition. This is also in accordance to Roscher et al. (2011), where the population size of *L. perenne* decreased with increasing species richness of experimental grasslands.

5. Conclusions

In sown flower strips there are clear effects of seed mixture, but not of seeding density, on plant establishment, biomass and community dynamics. Since intermediate-diversity mixtures with high seeding density reduced the number of unsown plants in the first year, we do not recommend this option for perennial flowering strips. Instead, moderate or low seeding densities should be applied. Moreover, mixtures with 40–50 species result in the highest plant richness, while increasing the number of sown species to 60 is not effective in supporting plant richness on arable land. To benefit biodiversity, we therefore recommend the use of a moderate to intermediate mixtures (40–50 species) which resulted in highest richness and did not reduce the number of unsown species. For further studies in this area, we recommend to compare regional and non-regional mixtures of similar diversities for all variations to receive clearer results.

CRediT authorship contribution statement

Franziska Katharina Mück: Writing – review & editing, Writing – original draft, Visualization, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Katharina Strobl:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Data curation. **Sara Diana Leonhardt:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Johannes Kollmann:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing 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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Appendix

Table A1
Species list of sown seed mixtures of arable flower strips. Numbers indicate the proportion of species within the mixture. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Species	Abbrevation	Seed mixture proportion (%)				
		L.nr	M.nr	M.r	I.nr	H.r
Acer campestre	Acer_camp					
Acer pseudoplatanus	Acer_pseu					
Achillea millefolium	Achi_mill	0.4	1.2	3.00	1	0.75
Agrimonia eupatoria	Agri_eupa		0.5			3
Agrostis capillaris	Agro_capi					
Ajuga reptans	Ajug_rept					
Allium fistulosum	Alli_fist				2	
Anethum graveolens	Anet_grav	1				
Anthoxanthum odoratum	Anth_odor					3
Anthriscus sylvestris	Anth_sylv			2		
Anthyllis vulneraria	Anth_vuln					1.13
Arenaria serpyllifolia	Aren_serp					

(*continued on next page*)

Table A1 (*continued*)

Species	Abbrevation	Seed mixture proportion (%)				
		L.nr	M.nr	M.r	I.nr	H.r
Arrhenatherum elatius	Arrh_elat					1.5
Barbarea vulgaris	Barb_vulg		0.2			1.5
Betonica officinalis	Beto_offi					1.5
Borago officinalis	Bora_offi	3				
Brassica napus	Bras_napu					
Bromus erectus	Brom_erec					3
Calendula officinalis	Cale_offi				6	3
Camelina sativa	Came_sati	5			2.9	2
Campanula patula	Camp_patu			1		0.15
Campanula persicifolia	Camp_pers				0.1	
Campanula rapunculoides	Camp_rapu			0.5		
Capsella bursa-pastoris	Caps_burs					
Carduus nutans	Card_nuta					0.75
Carum carvi	Caru_carv	4	5	3		2.63
Centaurea cyanus	Cent_cyan	1.1	2	2	4.2	4.5
Centaurea jacea	Cent_jace	0.5		3	1	2.25
Centaurea scabiosa	Cent_scab		0.2			
Cerastium arvense	Cera_arve					
Cichorium intybus	Cich_inty	1	3.2	3	2	1.35
Cirsium arvense	Cirs_arve					
Cirsium vulgare	Cirs_vulg					
Clinopodium vulgare	Clin_vulg		0.1			
Coriandrum sativum	Cori_sati		2.5		2.9	1.5
Cota tinctoria	Cota_tinc		0.5		1	1.5
Crepis biennis	Crep_bien			2		
Cynosurus cristatus	Cyno_cris		2.1			4.5
Dactylis glomerata	Dact_glom					
Daucus carota	Dauc_caro	0.5	2	3	2	1.5
Dianthus carthusianorum	Dian_cart					1.13
Dipsacus fullonum	Dips_full		0.2	3		
Echium vulgare	Echi_vulg	1	1	5	1.5	1.5
Elymus repens	Elym_repe					
Epilobium palustre	Epil_palu					
Epilobium parviflorum	Epil_parv					
Epilobium tetragonum	Epil_tetr					
Equisetum arvense	Equi_arve					
Erigeron annuus	Erig_annu					
Fagopyrum esculentum	Fago_escu		10		8	4
Festuca ovina	Fest_ovin					
Foeniculum vulgare	Foen_vulg	1.1	2			
Fraxinus excelsior	Frax_exce					
Galium album	Gali_albu		1.5	3		
Galium aparine	Gali_apar					
Galium verum	Gali_veru		0.5	3		
Geranium dissectum	Gera_diss					
Geranium pratense	Gera_prat			3		
Geranium robertianum	Gera_rober					
Geum urbanum	Geum_urba					
Glebionis segetum	Gleb_sege					1.5
Helianthus annuus	Heli_annu		10		9	
Holcus lanatus	Holc_lana					1.5
Hypericum perforatum	Hype_perf		0.3		0.5	0.38
Hypochaeris radicata	Hypo_radi					0.38
Isatis tinctoria	Isat_tinc		0.3		3.5	
Knautia arvensis	Knau_arve			3	0.4	1.13
Legousia speculum-veneris	Lego_spec			1		
Leucanthemum sp.	Leuc_(vul	1	0.5	3	2.5	2.25
Linaria vulgaris	Lina_vulg		0.1			
Linum perenne	Linu_pere				2.5	
Linum rubrum	Linu_rubr					2
Linum usitatissimum	Linu_usit		15		1.5	3.5
Lolium perenne	Loli_pere					
Lotus corniculatus	Lotu_corn	7		3	1.5	0.75
Malva alcea	Malv_alce			5		
Malva moschata	Malv_mosc		0.6		0.4	0.75
Malva sylvestris	Malv_sylv	5			2	
Medicago lupulina	Medi_lupu	10				
Medicago minima	Medi_mini					
Medicago sativa	Medi_sati	4	4		2	1.25
Melilotus albus	Meli_albu	3		2	0.9	0.38
Melilotus officinalis	Meli_offi	3	2		0.5	0.38
Myosotis arvensis	Myos_arve			0.5		
Nigella sativa	Nige_sati	0.9				
Oenothera biennis	Oeno_bien					1.13

(*continued on next page*)

Table A1 (*continued*)

Species	Abbrevation	Seed mixture proportion (%)				
		L.nr	M.nr	M.r	I.nr	H.r
Onobrychis viciifolia	Onob_vici	10	6.5		2.9	3
Origanum vulgare	Orig_vulg		0.2		0.2	0.38
Papaver rhoeas	Papa_rhoe		2	1	1.7	1.87
Pastinaca sativa	Past_sati		1	3	1	1.5
Phacelia tanacetifolia	Phac_tana	5.5	5.5		5	2.5
Phleum pratense	Phle_prat					
Pimpinella major	Pimp_majo			3		
Plantago lanceolata	Plan_lanc	1	3.5		2	1.5
Plantago major	Plan_majo					
Plantago media	Plan_medi		0.2			
Poa annua	Poa _annu					
Poa pratensis	Poa _prat					
Poa trivialis	Poa _triv					
Prunella vulgaris	Prun_vulg		0.2	2		1.13
Ranunculus acris	Ranu_acri					
Ranunculus repens	Ranu_repe					
Reseda luteola	Rese_lute		0.5		0.3	0.38
Rumex crispus	Rume_cris					
Rumex obtusifolius	Rume_obtu					
Salix caprea	Sali_capr					
Salvia pratensis	Salv_prat		2.5	3	1.2	3.75
Sanguisorba minor	Sang_mino	1	2	3	2	1.12
Sanguisorba officinalis	Sang_offi			2.5		
Saponaria officinalis	Sapo_offi				0.5	0.75
Scorzoneroides autumnalis	Scor_autu					0.38
Sherardia arvensis	Sher_arve			3		
Silene dioica	Sile_dioi			2	0.8	2.25
Silene flos-cuculi	Sile_flos			2		1.13
Silene latifolia	Sile_lati		0.4	2	0.8	1.13
Silene vulgaris	Sile_vulg		1.8	3	1.3	1.5
Sinapis alba	Sina_alba				2	1.5
Sinapis arvensis	Sina_arve				1	
Solidago virgaurea	Soli_virg				0.2	
Sonchus asper	Sonc_aspe					
Stellaria media	Stel_medi					
Tanacetum vulgare	Tana_vulg			0.5	0.1	
Taraxacum officinale	Tara_offi					
Tragopogon pratensis	Trag_prat			2		1.5
Trifolium hybridum	Trif_hybr	10				
Trifolium incarnatum	Trif_inca				4	1.25
Trifolium pratense	Trif_prat	10		3		1.13
Trifolium repens	Trif_repe	10		3		
Trisetum flavescens	Tris_flav					1.5
Tussilago farfara	Tuss_farf					
Urtica dioica	Urti_dioi					
Valeriana dentata	Vale_dent			1.5		
Valeriana rimosa	Vale_rimo			1.5		
Verbascum densiflorum	Verb_dens				0.6	
Verbascum lychnitis	Verb_lych		0.2			
Verbascum nigrum	Verb_nigr				0.5	0.75
Verbascum thapsus	Verb_thap			2		
Veronica arvensis	Vero_arve					
Veronica chamaedrys	Vero_cham					
Veronica hederifolia	Vero_hede					
Veronica persica	Vero_pers					
Vicia cracca	Vici_crac					0.75
Vicia sativa	Vici_sati		6.3		5	2.5
Viola arvensis	Viol_arve					
Viola tricolour	Viol_tric					

Table A2
Established plant species in the field experiment on 60 plots in 2021 and 2024, separated by five seed mixtures ('x' means species was observed on plots sown with the respective seed mixture); for 2021, data sampled in May is included. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Species	Abbreviation	Seed mixture - Species observed in 2021					Seed mixture - Species observed in 2024				
		L.nr	M.nr	M.r	I.nr	H.r	L.nr	M.nr	M.r	I.nr	H.r
Acer campestre	Acer_camp										x
Acer pseudoplatanus	Acer_pseu									x	
Achillea millefolium	Achi_mill	x	x	x	x	x	x	x	x	x	x

(*continued on next page*)

Table A2 (*continued*)

Species	Abbreviation	Seed mixture - Species observed in 2021					Seed mixture - Species observed in 2024				
		L.nr	M.nr	M.r	I.nr	H.r	L.nr	M.nr	M.r	I.nr	H.r
Agrimonia eupatoria	Agri_eupa		x			x	x	x			x
Agrostis capillaris	Agro_capi						x	x	x	x	x
Ajuga reptans	Ajug_rept		x			x					
Allium fistulosum	Alli_fist				x						
Anethum graveolens	Anet_grav										
Anthoxanthum odoratum	Anth_odor		x		x	x					
Anthriscus sylvestris	Anth_sylv										
Anthyllis vulneraria	Anth_vuln										
Arenaria serpyllifolia	Aren_serp				x						
Arrhenatherum elatius	Arrh_elat			x	x	x	x	x		x	x
Barbarea vulgaris	Barb_vulg					x					
Betonica officinalis	Beto_offi										
Borago officinalis	Bora_offi	x	x								
Brassica napus	Bras_napu	x									
Bromus erectus	Brom_erec					x		x	x		x
Calendula officinalis	Cale_offi				x	x					
Camelina sativa	Came_sati	x			x	x					
Campanula patula	Camp_patu			x							
Campanula persicifolia	Camp_pers										
Campanula rapunculoides	Camp_rapu			x					x		
Capsella bursa-pastoris	Caps_burs				x						
Carduus nutans	Card_nuta					x					
Carum carvi	Caru_carv	x	x	x		x					
Centaurea cyanus	Cent_cyan	x		x	x	x					
Centaurea jacea	Cent_jace	x		x	x	x	x	x	x	x	x
Centaurea scabiosa	Cent_scab		x			x					
Cerastium arvense	Cera_arve				x						
Cichorium intybus	Cich_inty	x	x	x	x	x					
Cirsium arvense	Cirs_arve	x		x	x		x	x	x	x	x
Cirsium vulgare	Cirs_vulg		x	x	x	x		x	x	x	x
Clinopodium vulgare	Clin_vulg		x					x			
Coriandrum sativum	Cori_sati										
Cota tinctoria	Cota_tinc	x	x	x	x	x		x	x	x	
Crepis biennis	Crep_bien			x					x		
Cynosurus cristatus	Cyno_cris		x		x	x	x	x	x	x	x
Dactylis glomerata	Dact_glom	x			x		x		x	x	
Daucus carota	Dauc_caro	x	x	x	x	x	x	x	x	x	x
Dianthus carthusianorum	Dian_cart										
Dipsacus fullonum	Dips_full		x	x		x	x	x	x	x	x
Echium vulgare	Echi_vulg	x	x	x		x			x		
Elymus repens	Elym_repe	x							x		
Epilobium palustre	Epil_palu								x		
Epilobium parviflorum	Epil_parv	x					x		x	x	x
Epilobium tetragonum	Epil_tetr	x					x	x	x	x	x
Equisetum arvense	Equi_arve										
Erigeron annuus	Erig_annu	x	x		x						
Fagopyrum esculentum	Fago_escu	x			x						
Festuca ovina	Fest_ovin	x									
Foeniculum vulgare	Foen_vulg		x								
Fraxinus excelsior	Frax_exce		x				x	x	x	x	x
Galium album	Gali_albu	x	x	x	x	x	x	x	x	x	x
Galium aparine	Gali_apar	x	x	x	x		x				
Galium verum	Gali_veru		x	x				x	x		
Geranium dissectum	Gera_diss						x		x	x	x
Geranium pratense	Gera_prat			x			x	x	x	x	x
Geranium robertianum	Gera_rober								x		
Geum urbanum	Geum_urba						x	x	x		
Glebionis segetum	Gleb_sege					x					
Helianthus annuus	Heli_annu		x								
Holcus lanatus	Holc_lana	x	x	x	x	x	x	x	x	x	x
Hypericum perforatum	Hype_perf		x		x			x		x	
Hypochaeris radicata	Hypo_radi			x	x	x					
Isatis tinctoria	Isat_tinc		x		x						
Knautia arvensis	Knau_arve	x		x	x	x	x	x	x	x	x
Legousia speculum-veneris	Lego_spec			x							
Leucanthemum sp.	Leuc_(vul	x	x	x	x	x	x	x		x	x
Linaria vulgaris	Lina_vulg		x					x	x		x
Linum perenne	Linu_pere				x			x			
Linum rubrum	Linu_rubr										
Linum usitatissimum	Linu_usit		x								
Lolium perenne	Loli_pere	x	x	x	x	x					
Lotus corniculatus	Lotu_corn	x		x	x	x					x
Malva alcea	Malv_alce			x				x			x
Malva moschata	Malv_mosc		x		x	x	x	x	x		

(*continued on next page*)

Table A2 (*continued*)

Species	Abbreviation	Seed mixture - Species observed in 2021					Seed mixture - Species observed in 2024				
		L.nr	M.nr	M.r	I.nr	H.r	L.nr	M.nr	M.r	I.nr	H.r
Malva sylvestris	Malv_sylv										
Medicago lupulina	Medi_lupu	x	x	x		x					
Medicago minima	Medi_mini										
Medicago sativa	Medi_sati	x	x		x	x					
Melilotus albus	Meli_albu	x	x	x	x	x		x		x	x
Melilotus officinalis	Meli_offi	x	x	x	x	x				x	x
Myosotis arvensis	Myos_arve		x	x			x	x	x	x	
Nigella sativa	Nige_sati										
Oenothera biennis	Oeno_bien					x		x			x
Onobrychis viciifolia	Onob_vici	x	x	x	x	x				x	
Origanum vulgare	Orig_vulg		x		x		x	x	x	x	x
Papaver rhoeas	Papa_rhoe			x							
Pastinaca sativa	Past_sati		x	x	x	x			x		
Phacelia tanacetifolia	Phac_tana	x	x		x	x		x	x	x	
Phleum pratense	Phle_prat						x		x	x	
Pimpinella major	Pimp_majo							x		x	
Plantago lanceolata	Plan_lanc	x	x	x	x	x	x	x	x	x	x
Plantago major	Plan_majo		x			x					
Plantago media	Plan_medi	x	x			x		x	x		
Poa annua	Poa _annu		x	x	x	x					
Poa pratensis	Poa _prat	x							x		
Poa trivialis	Poa _triv	x	x	x	x	x					
Prunella vulgaris	Prun_vulg		x			x		x	x	x	x
Ranunculus acris	Ranu_acri		x			x					
Ranunculus repens	Ranu_repe				x						
Reseda luteola	Rese_lute		x	x	x			x			
Rumex crispus	Rume_cris	x	x	x	x		x	x	x	x	
Rumex obtusifolius	Rume_obtu	x	x	x	x	x		x	x	x	
Salix caprea	Sali_capr							x	x	x	
Salvia pratensis	Salv_prat		x	x	x	x		x			
Sanguisorba minor	Sang_mino	x	x	x	x	x	x	x	x	x	x
Sanguisorba officinalis	Sang_offi						x	x	x	x	x
Saponaria officinalis	Sapo_offi					x				x	
Scorzoneroides autumnalis	Scor_autu					x					
Sherardia arvensis	Sher_arve										
Silene dioica	Sile_dioi	x	x	x	x	x	x	x	x	x	x
Silene flos-cuculi	Sile_flos	x		x	x	x					
Silene latifolia	Sile_lati	x	x	x	x	x	x		x	x	x
Silene vulgaris	Sile_vulg	x	x	x	x			x	x	x	x
Sinapis alba	Sina_alba										
Sinapis arvensis	Sina_arve			x	x						
Solidago virgaurea	Soli_virg				x						
Sonchus asper	Sonc_aspe						x				
Stellaria media	Stel_medi	x		x							
Tanacetum vulgare	Tana_vulg			x	x				x	x	
Taraxacum officinale	Tara_offi	x	x	x	x	x					
Tragopogon pratensis	Trag_prat			x							
Trifolium hybridum	Trif_hybr	x	x			x	x	x		x	
Trifolium incarnatum	Trif_inca					x					
Trifolium pratense	Trif_prat	x	x	x	x	x					
Trifolium repens	Trif_repe	x	x	x	x	x					
Trisetum flavescens	Tris_flav						x	x	x	x	x
Tussilago farfara	Tuss_farf		x	x	x			x	x		
Urtica dioica	Urti_dioi		x				x	x	x	x	x
Valeriana dentata	Vale_dent										
Valeriana rimosa	Vale_rimo										
Verbascum densiflorum	Verb_dens				x						
Verbascum lychnitis	Verb_lych		x								
Verbascum nigrum	Verb_nigr							x			
Verbascum thapsus	Verb_thap			x							
Veronica arvensis	Vero_arve			x	x						
Veronica chamaedrys	Vero_cham				x			x			
Veronica hederifolia	Vero_hede	x		x							
Veronica persica	Vero_pers			x	x						
Vicia cracca	Vici_crac					x					x
Vicia sativa	Vici_sati		x		x						
Viola arvensis	Viol_arve		x								
Viola tricolor	Viol_tric				x						

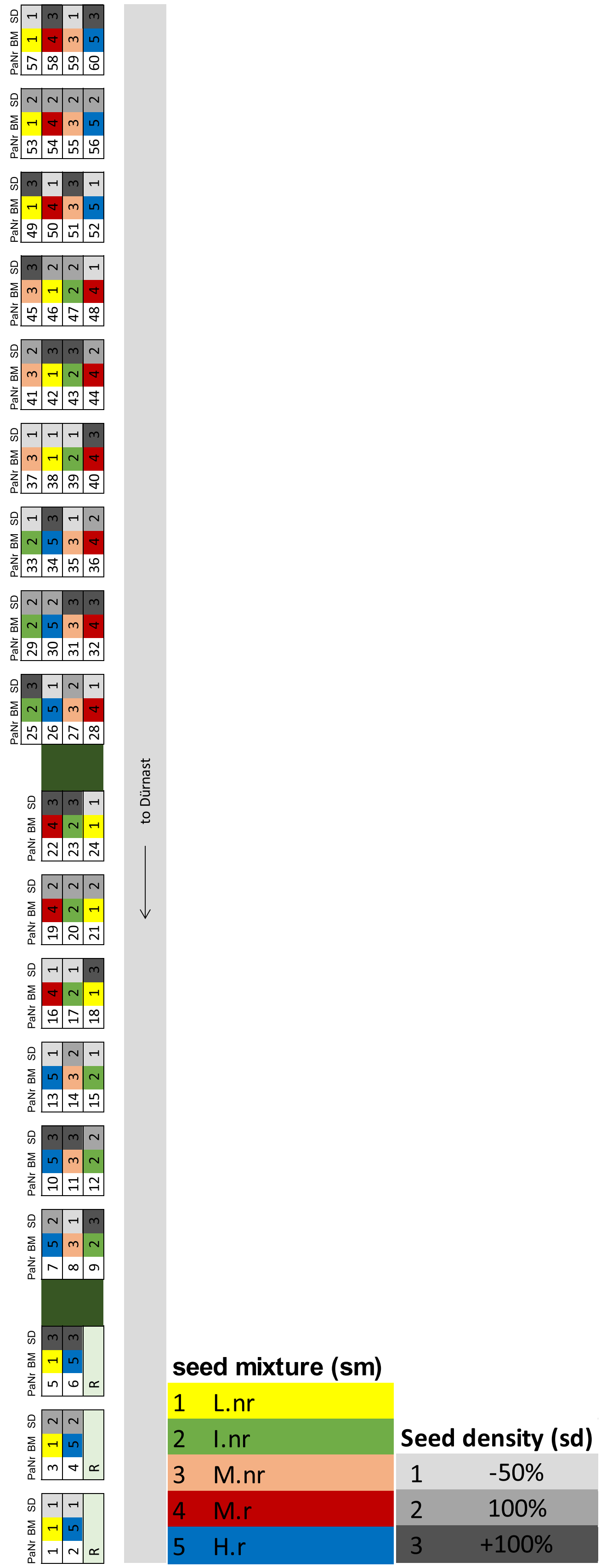

Fig. A1. Setup of the experiment with the five different seed mixtures and three different seed densities (numbers with white background depict plot IDs). Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

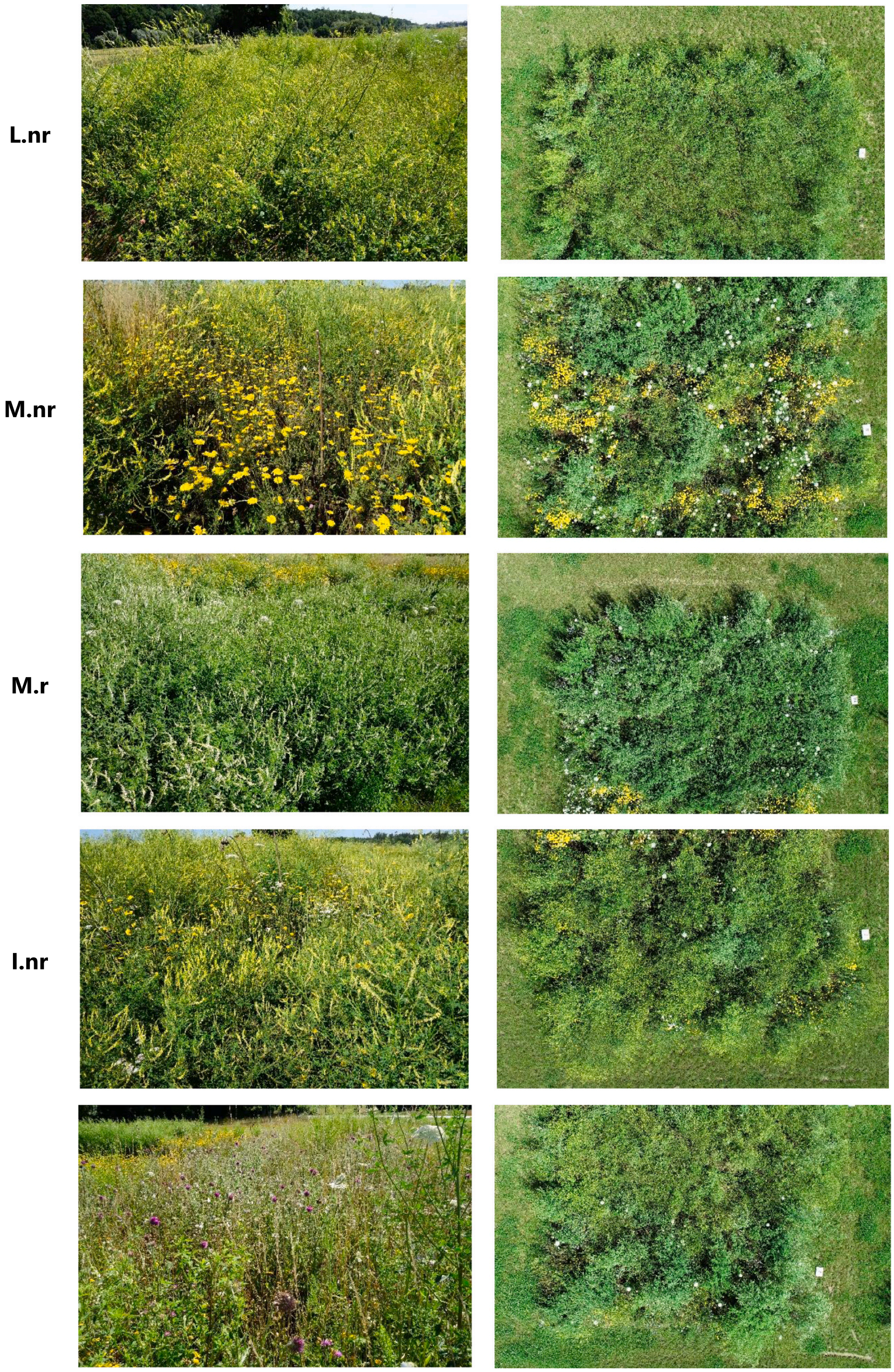

Fig. A2. The five seed mixtures of the field experiment seen in profile (Katharina Strobl, 12 July 2021) and from above (Jürgen Plass, 12 July 2021). Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Table A3
Results of the soil sample analyses of the study site from two years (2017 and 2023)

	2017				2023				Soil type	Land use
	pH-value	phosphor (mg/100 g)	potassium (mg/100 g)	magnesium (mg/100 g)	pH-value	phosphor (mg/100 g)	potassium (mg/100 g)	magnesium (mg/100 g)		
Mean	6.4	11	12	NA	7.0	12	11	8.5	uL	arable farming
SE	0.2	2.2	2.8	NA	0.1	1.7	1.2	1.4		

Table A4
Output-table of the *t*-test between the years (2017 and 2023) for soil parameters

	pH	Phosphor	potassium
p-value	9.22E−07	0.342	0.564
t	−7.7	−0.98	0.59
df	16	16	16

Table A5
Results of one run from the Moran's *I* Monte Carlo approach with contiguous neighbour definition

	Number of simulations	Statistic	Observed rank	p
Biomass	999	0.235	937	0.063
Total species richness 2021	999	0.003	547	0.453
Total species richness 2024	999	0.233	943	0.058

Table A6
ANOVA result table of total species richness in 2021

	Chisq	Df	Pr(>Chisq)
seed.density	11.9449	2	0.0025
seed.mixture	8.7784	4	0.0669
seed.density x seed.mixture	5.8255	8	0.6668

Table A7
Post-hoc Tukey HSD-test result table of total species richness in 2021. Comparison of different seeding density levels (low: 50 %, moderate: 100 %, high: 200 %)

Seeding density pair	estimate	SE	df	z.ratio	p
50 % / 100 %	0.0049	0.0768	Inf	0.063	0.9978
50 % / 200 %	0.2525	0.082	Inf	3.081	0.0059
100 % / 200 %	0.2476	0.082	Inf	3.021	0.0071

Table A8
Post-hoc Tukey HSD-test result table of total species richness in 2021. Comparison of different seeding density levels (low: 50 %, moderate: 100 %, high: 200 %) within single mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture	Seeding density pair	ratio	SE	df as	ymp.LCL as	ymp.UCL	null	z.ratio	p
L.nr	**50 % / 100 %**	0.965	0.182	Inf	0.555	1.68	1	−0.189	1
L.nr	**50 % / 200 %**	0.917	0.171	Inf	0.531	1.58	1	−0.466	1
L.nr	**100 % / 200 %**	0.95	0.176	Inf	0.553	1.63	1	−0.277	1
M.nr	**50 % / 100 %**	1.108	0.178	Inf	0.693	1.77	1	0.64	1
M.nr	**50 % / 200 %**	1.519	0.266	Inf	0.909	2.54	1	2.384	0.2285
M.nr	**100 % / 200 %**	1.37	0.245	Inf	0.811	2.31	1	1.76	0.7058
M.r	**50 % / 100 %**	0.958	0.161	Inf	0.585	1.57	1	−0.253	1
M.r	**50 % / 200 %**	1.255	0.227	Inf	0.739	2.13	1	1.255	0.9707
M.r	**100 % / 200 %**	1.309	0.234	Inf	0.775	2.21	1	1.504	0.8816
I.nr	**50 % / 100 %**	1	0.18	Inf	0.591	1.69	1	0	1
I.nr	**50 % / 200 %**	1.409	0.278	Inf	0.791	2.51	1	1.74	0.7224
I.nr	**100 % / 200 %**	1.409	0.278	Inf	0.791	2.51	1	1.74	0.7224
H.r	**50 % / 100 %**	1	0.159	Inf	0.628	1.59	1	0	1
H.r	**50 % / 200 %**	1.436	0.252	Inf	0.859	2.4	1	2.062	0.4512
H.r	**100 % / 200 %**	1.436	0.252	Inf	0.859	2.4	1	2.062	0.4512

Table A9
ANOVA result table of established sown species richness in 2021

	Chisq	Df	Pr(>Chisq)
seed.density	3.824	2	0.1478
seed.mixture	29.0574	4	0.00000761
seed.density x seed.mixture	4.0739	8	0.8504

Table A10
Post-hoc Tukey HSD-test result table of unsown species richness in 2021. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	0.4357	0.22	Inf	1.977	0.277
L.nr - M.r	0.6835	0.237	Inf	2.887	0.0318
L.nr - I.nr	0.1658	0.214	Inf	0.776	0.9376
L.nr - H.r	0.7443	0.244	Inf	3.044	0.0198
M.nr - M.r	0.2479	0.261	Inf	0.949	0.8776
M.nr - I.nr	−0.2699	0.24	Inf	−1.123	0.7945
M.nr - H.r	0.3086	0.268	Inf	1.151	0.7793
M.r - I.nr	−0.5178	0.256	Inf	−2.026	0.2533
M.r - H.r	0.0608	0.282	Inf	0.216	0.9995
I.nr - H.r	0.5786	0.263	Inf	2.202	0.1787

Table A11
Post-hoc Tukey HSD-test result table of unsown species richness in 2021. Comparison of different seeding density levels (low: 50 %, moderate: 100 %, high: 200 %) within single mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture	Seeding density pair	ratio	SE	df as	ymp.LCL	asymp.UCL	null	z.ratio	p
L.nr	**50 % / 100 %**	1	0.333	Inf	0.377	2.65	1	0	1
L.nr	**50 % / 200 %**	0.947	0.312	Inf	0.362	2.48	1	−0.164	1
L.nr	**100 % / 200 %**	0.947	0.312	Inf	0.362	2.48	1	−0.164	1
M.nr	**50 % / 100 %**	1.214	0.438	Inf	0.422	3.49	1	0.538	1
M.nr	**50 % / 200 %**	2.429	1.091	Inf	0.652	9.04	1	1.976	0.5232
M.nr	**100 % / 200 %**	2	0.926	Inf	0.516	7.76	1	1.497	0.885
M.r	**50 % / 100 %**	1.091	0.455	Inf	0.321	3.7	1	0.208	1
M.r	**50 % / 200 %**	2	1	Inf	0.463	8.65	1	1.386	0.9339
M.r	**100 % / 200 %**	1.833	0.93	Inf	0.415	8.1	1	1.194	0.9811
I.nr	**50 % / 100 %**	1.083	0.307	Inf	0.473	2.48	1	0.283	1
I.nr	**50 % / 200 %**	4.333	1.963	Inf	1.151	16.32	1	3.238	0.0179
I.nr	**100 % / 200 %**	4	1.826	Inf	1.051	15.22	1	3.037	0.0352
H.r	**50 % / 100 %**	0.917	0.383	Inf	0.27	3.11	1	−0.208	1
H.r	**50 % / 200 %**	2.2	1.187	Inf	0.454	10.67	1	1.462	0.9026
H.r	**100 % / 200 %**	2.4	1.277	Inf	0.505	11.4	1	1.645	0.7942

Table A12
Post-hoc Tukey HSD-test result table of total species richness in 2024. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	−1	0.111	Inf	−4.708	< .0001
L.nr - M.r	0	0	Inf	−3.273	0.0094
L.nr - I.nr	−1	0	Inf	−4.749	< .0001
L.nr - H.r	0	0	Inf	−0.744	0.946
M.nr - M.r	0	0	Inf	1.493	0.5671
M.nr - I.nr	−0.00419	0.0957	Inf	−0.044	1
M.nr - H.r	0.43211	0.1079	Inf	4.006	0.0006
M.r - I.nr	−0.1528	0.0995	Inf	−1.536	0.5387
M.r - H.r	0.2835	0.1113	Inf	2.548	0.0803
I.nr - H.r	0.4363	0.1078	Inf	4.048	0.0005

Table A13
Post-hoc Tukey HSD-test result table of established sown species richness in 2021. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	−0.3769	0.12	Inf	−3.132	0.015
L.nr - M.r	−0.3526	0.121	Inf	−2.918	0.029
L.nr - I.nr	0.0431	0.132	Inf	0.326	0.9976
L.nr - H.r	−0.4494	0.119	Inf	−3.788	0.0014
M.nr - M.r	0.0244	0.109	Inf	0.223	0.9995
M.nr - I.nr	0.4201	0.122	Inf	3.446	0.0052
M.nr - H.r	−0.0724	0.107	Inf	−0.677	0.9614
M.r - I.nr	0.3957	0.122	Inf	3.234	0.0107
M.r - H.r	−0.0968	0.107	Inf	−0.901	0.8967
I.nr - H.r	−0.4925	0.12	Inf	−4.097	0.0004

Table A14
Post-hoc Tukey HSD-test result table of established sown species richness in 2024. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	−1	0.185	Inf	−6.089	< .0001
L.nr - M.r	−0.8818	0.19	Inf	−4.629	< .0001
L.nr - I.nr	−1.0654	0.186	Inf	−5.718	< .0001
L.nr - H.r	−0.8492	0.191	Inf	−4.439	0.0001
M.nr - M.r	0	0.145	Inf	1.691	0.4395
M.nr - I.nr	0.0616	0.14	Inf	0.441	0.9922
M.nr - H.r	0.2778	0.146	Inf	1.9	0.3175
M.r - I.nr	−0.1837	0.147	Inf	−1.252	0.7204
M.r - H.r	0.0326	0.153	Inf	0.213	0.9995
I.nr - H.r	0.2162	0.148	Inf	1.463	0.5865

Table A15
Post-hoc Tukey HSD-test result table of total species richness in 2021. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	−0.185	0.1036	Inf	−1.786	0.3819
L.nr - M.r	−0.1245	0.1049	Inf	−1.187	0.759
L.nr - I.nr	0.0354	0.1092	Inf	0.324	0.9976
L.nr - H.r	−0.2005	0.1032	Inf	−1.942	0.2948
M.nr - M.r	0.0606	0.1004	Inf	0.603	0.9747
M.nr - I.nr	0.2204	0.105	Inf	2.1	0.2202
M.nr - H.r	−0.0155	0.0987	Inf	−0.157	0.9999
M.r - I.nr	0.1599	0.1062	Inf	1.505	0.5591
M.r - H.r	−0.076	0.1	Inf	−0.76	0.9419
I.nr - H.r	−0.2359	0.1046	Inf	−2.255	0.1597

Table A16
Post-hoc Tukey HSD-test result table of unsown species richness in 2024. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	0	0.157	Inf	0.263	0.9989
L.nr - M.r	0.0602	0.159	Inf	0.38	0.9956
L.nr - I.nr	−0.069	0.153	Inf	−0.452	0.9914
L.nr - H.r	0.8371	0.201	Inf	4.168	0.0003
M.nr - M.r	0	0.16	Inf	0.118	1
M.nr - I.nr	−0.1103	0.154	Inf	−0.716	0.9529
M.nr - H.r	0.7958	0.202	Inf	3.941	0.0008
M.r - I.nr	−0.1291	0.156	Inf	−0.83	0.9213
M.r - H.r	0.7769	0.203	Inf	3.826	0.0012
I.nr - H.r	0.9061	0.199	Inf	4.564	< .0001

Table A17
Post-hoc Tukey HSD-test result table of total species richness in 2024. Comparison of different seeding density levels (low: 50 %, moderate: 100 %, high: 200 %)

	Chisq	Df	Pr(>Chisq)
seed.density	0.2262	2	0.8931
seed.mixture	38.9785	4	7.038E−08
seed.density x seed.mixture	3.897	8	0.8663

Table A18
Post-hoc Tukey HSD-test result table of unsown species richness in 2024. Comparison of different seeding density levels (low: 50 %, moderate: 100 %, high: 200 %)

	Chisq	Df	Pr(>Chisq)
seed.density	1.103	2	0.5760797
seed.mixture	22.2416	4	0.0001794
seed.density x seed.mixture	9.4061	8	0.3092077

Table A19
ANOVA result table of plant biomass per m^2 in 2021

	Chisq	Df	Pr(>Chisq)
seed.density	0.21	2	0.9003143
seed.mixture	20.616	4	0.0003773
seed.density x seed.mixture	11.831	8	0.1589076

Table A20
Post-hoc Tukey HSD-test result table of plant biomass per m^2 in 2021. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	t.ratio	p
L.nr - M.nr	0.1818	0.111	41	1.639	0.4822
L.nr - M.r	−0.2	0.109	41	−1.84	0.3656
L.nr - I.nr	0.2418	0.11	41	2.203	0.1991
L.nr - H.r	0.1237	0.11	41	1.124	0.7928
M.nr - M.r	−0.3818	0.109	41	−3.501	0.0094
M.nr - I.nr	0.06	0.11	41	0.544	0.982
M.nr - H.r	−0.0581	0.109	41	−0.533	0.9834
M.r - I.nr	0.4418	0.109	41	4.059	0.0019
M.r - H.r	0.3237	0.11	41	2.943	0.0402
I.nr - H.r	−0.118	0.11	41	−1.07	0.8208

Table A21
ANOVA result table of insect pollinated plant species richness in 2021

	Chisq	Df	Pr(>Chisq)
seed.density	1.4734	2	0.47869
seed.mixture	11.5723	4	0.02083
seed.density x seed.mixture	4.7998	8	0.77875

Table A22
Post-hoc Tukey HSD-test result table of insect pollinated plant species richness in 2021. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	−0.31214	0.111	Inf	−2.824	0.0382
L.nr - M.r	−0.23797	0.112	Inf	−2.119	0.2117
L.nr - I.nr	−0.03412	0.118	Inf	−0.29	0.9985
L.nr - H.r	−0.23676	0.112	Inf	−2.105	0.2178
M.nr - M.r	0.07417	0.103	Inf	0.718	0.9524

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Table A22 (*continued*)

Seed mixture pairs	estimate	SE	df	z.ratio	p
M.nr - I.nr	0.27802	0.109	Inf	2.546	0.0808
M.nr - H.r	0.07539	0.103	Inf	0.729	0.9499
M.r - I.nr	0.20385	0.111	Inf	1.836	0.3524
M.r - H.r	0.00122	0.105	Inf	0.012	1
I.nr - H.r	−0.20263	0.111	Inf	−1.822	0.3605

Table A23
Post-hoc Tukey HSD-test result table of insect pollinated plant species richness in 2024. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	−0.5415	0.141	Inf	−3.828	0.0012
L.nr - M.r	−0.54744	0.141	Inf	−3.873	0.001
L.nr - I.nr	−0.60406	0.14	Inf	−4.318	0.0002
L.nr - H.r	−0.029	0.158	Inf	−0.184	0.9997
M.nr - M.r	−0.00594	0.12	Inf	−0.049	1
M.nr - I.nr	−0.06256	0.119	Inf	−0.527	0.9846
M.nr - H.r	0.5125	0.139	Inf	3.678	0.0022
M.r - I.nr	−0.05661	0.118	Inf	−0.478	0.9894
M.r - H.r	0.51844	0.139	Inf	3.723	0.0018
I.nr - H.r	0.57505	0.138	Inf	4.174	0.0003

Table A24
ANOVA result table of insect pollinated plant species richness in 2024

	Chisq	Df	Pr(>Chisq)
seed.density	0.1482	2	0.9286
seed.mixture	33.2497	4	1.06E−06
seed.density x seed.mixture	4.8583	8	0.7726

Table A25
ANOVA result table of grass (Poaceae) species richness in 2021

	Chisq	Df	Pr(>Chisq)
seed.density	0.124	2	0.939895
seed.mixture	16.7817	4	0.002131
seed.density x seed.mixture	2.7179	8	0.950797

Table A26
ANOVA result table of grass (Poaceae) species richness in 2024

	Chisq	Df	Pr(>Chisq)
seed.density	0.893	2	0.63986
seed.mixture	12.87	4	0.01193
seed.density x seed.mixture	3.7917	8	0.87541

Table A27
Post-hoc Tukey HSD-test result table of grass (Poaceae) species richness in 2021. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	0.7445	0.319	Inf	2.337	0.1331
L.nr - M.r	0.8189	0.327	Inf	2.503	0.0898
L.nr - I.nr	0.5486	0.297	Inf	1.844	0.3481
L.nr - H.r	−0.1422	0.247	Inf	−0.577	0.9785
M.nr - M.r	0.0744	0.378	Inf	0.197	0.9997
M.nr - I.nr	−0.1959	0.352	Inf	−0.556	0.9812
M.nr - H.r	−0.8868	0.311	Inf	−2.856	0.0349

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Table A27 (*continued*)

Seed mixture pairs	estimate	SE	df	z.ratio	p
M.r - I.nr	−0.2703	0.36	Inf	−0.751	0.9444
M.r - H.r	−0.9611	0.319	Inf	−3.01	0.022
I.nr - H.r	−0.6908	0.289	Inf	−2.391	0.1176

Table A28
Post-hoc Tukey HSD-test result table of grass (Poaceae) species richness in 2024. Comparison of different seed mixture levels. Abbreviations of seed mixtures: L: low, M: moderate, I: intermediate, H: high diversity; nr: non-regional, r: regional provenance

Seed mixture pairs	estimate	SE	df	z.ratio	p
L.nr - M.nr	−1.14E+ 00	0.426	Inf	−2.675	0.0576
L.nr - M.r	−5.53E−01	0.469	Inf	−1.18	0.7631
L.nr - I.nr	−9.00E−07	0.527	Inf	0	1
L.nr - H.r	−3.93E−02	0.518	Inf	−0.076	1
M.nr - M.r	5.88E−01	0.351	Inf	1.672	0.4511
M.nr - I.nr	1.14E+ 00	0.426	Inf	2.675	0.0576
M.nr - H.r	1.10E+ 00	0.415	Inf	2.652	0.0614
M.r - I.nr	5.53E−01	0.469	Inf	1.18	0.7631
M.r - H.r	5.13E−01	0.459	Inf	1.12	0.7962
I.nr - H.r	−3.93E−02	0.518	Inf	−0.076	1

Data availability

I have shared the link to my data and code at the Attach File step Duernast_FloweringFields (FranziskaMueck/Duernast_Flowering-Fields: 0.0.3)

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