Plant provenance affects pollinator network: Implications for ecological restoration

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Abstract

1. The selection of plant provenance for ecological restoration is an intensively debated topic. Throughout this debate, arguments mostly focus on plant performance, but little attention is paid to the effects of provenance on other members of the restored ecosystem. On the other hand, in restoration projects that focus specifically on supporting interacting biota, for example, wildflower strips among fields to support pollinators, the provenance choice is often not considered, partly because the effect of provenance on pollinators is unknown. In this pioneering case study, we tested whether pollinators differentiate between experimental plant communities of different provenances.

2. We established experimental plant communities with the same species composition but with plants originating from three different provenances. We then recorded plant phenology and observed pollinators and flower visitors interacting with these experimental communities and related the pollinator visitation to the provenance identity.

3. The provenances of the experimental plant communities had a strong and significant effect on the diversity and abundance of flower–pollinator interactions, with one provenance interacting two times as often as the other two provenances. The effect was driven by the differences in flowering phenology among provenances.

4. Synthesis and applications. Plant provenances substantially differ in their interactions with local pollinators. Therefore, the selection of plant provenance should be considered when planning restoration projects for the support of pollinators.

KEYWORDS
ecological restoration, ecosystem restoration, flowering phenology, plant–pollinator interaction, pollinator, provenance, seed sourcing, wildflower strip

1 | INTRODUCTION

As the UN declared the decade 2021-2030 The Decade on Ecosystem Restoration, ecological restoration is now a political priority (www.decadeonrestoration.org). In terrestrial ecosystems, successful restoration often requires the re-establishment of plant communities. These communities may establish via natural succession, but in modern, fragmented landscapes, natural succession often
leads to incomplete recovery of vegetation, partly because of missing seeds in the soil or absence of natural habitats that could serve as diaspore source to recolonize the new habitat (Isbell et al., 2019). Plant introduction thus became a major tool in ecological restoration (Hölzel et al., 2012). When selecting species for introduction, there is a general agreement that restoration should prioritize native species (McDonald et al., 2016). However, there is a substantial debate on which provenance will ensure the best restoration outcome (Breed et al., 2013, 2018; Broadhurst et al., 2008; Bucharova, 2017; Kettenring et al., 2014; Prober et al., 2015).

Traditionally, the local provenance was considered to be the best choice (Hamilton, 2001). This is based on the observation that populations of the majority of plant species are genetically differentiated and this differentiation partly reflects adaptation to the local environment. As a result, plants of local provenance perform on average better than plants from foreign provenances, a pattern termed local adaptation (Bucharova, Durka, et al., 2017; Leimu & Fischer, 2008; Oduor et al., 2016). However, with ongoing climate change, local provenancing has been increasingly criticized, because the plants are adapted to the past and current climate at the locality. As the climate changes, local adaptation is expected to lag behind (Anderson & Wadgymar, 2020). Some experts thus suggest to replace or supplement the local provenance by plants from populations that are adapted to predicted climate and thus, improve the performance of the restored population under climate change (Prober et al., 2015).

Throughout this provenancing debate, arguments mostly focused on plant performance. However, plants are the basis of most terrestrial ecosystems and there are myriads of other organisms that depend on them. Especially herbivores and pathogens differentiate among plant genotypes and some provenances support more herbivores than others (Crémieux et al., 2008; Field et al., 2019; Macel et al., 2017; Pearse et al., 2015; Sinclair et al., 2015). Moreover, there can be complex interaction patterns across trophic levels, so that herbivores are adapted to their local plant provenances (Garrido et al., 2012; Kalske et al., 2012; Runquist et al., 2020). The effect of plant provenance on herbivores can even cascade up to higher trophic levels (Bucharova et al., 2016). Therefore, the choice of plant provenance for restoration is likely to affect the structure of the food webs in the restored ecosystems.

In contrast to herbivores, the effect of plant provenance on pollinators is less known. Pollination is an important ecosystem service and many restoration efforts aim to promote pollinators in the landscape (Krinner et al., 2019; M’Gonigle et al., 2015; Nicholson et al., 2020). In this context, attention is paid to the selection of plant species that promote pollinators, but the variability within these plant species is largely ignored (M’Gonigle et al., 2017; Nichols et al., 2019; Williams & Lonsdorf, 2018). The effect of provenance on pollinators was mostly demonstrated in highly specialized plant-pollinator systems, for example, in orchids with one or few pollinators (Bobberg et al., 2014; Newman et al., 2012; Sun et al., 2014). Such specialized plants are rarely the target of large-scale restoration, because restoration mostly relies on common foundation species that tend to be generalists (Zelený & Chytrý, 2019).

Phenology differences between provenances are genetically determined, common and documented in many species, though the exact differences between provenances are species-dependent (Bucharova, Michalski, et al., 2017; Jones et al., 2001; Robson et al., 2013; Vander Mijnsbrugge et al., 2015; Wilkinson et al., 2017). In the restoration context, selecting earlier flowering provenances would imply earlier availability of flowers and higher flower abundance early in the season. When using multiple species for restoring plant communities, the provenance of the seed mixture will affect how the flower abundance and diversity of the restored community will vary through the season, because individual plant species will start and finish their flowering depending on the species-specific provenance effects. Such differences in flower abundance and diversity are likely to modulate how the plant community interacts with pollinators, and affect pollinator identity, abundance and diversity (Ebeling et al., 2008; Fründ et al., 2010; Fornoff et al., 2017). However, the effect of plant provenance on pollinators has been only rarely studied.

In this study, we focused on the effect of plant provenance on pollinators and flower visitors. We selected six insect-pollinated plant species that are an important component of species-rich seed mixtures for ecosystem restoration in Germany (Bucharova et al., 2019). For all six species, we obtained seeds from three provenances (Figure 1). We assembled small experimental plant communities that consisted of the same number of plants and the same provenances of these common species often vary in traits that may influence their interaction with pollinators, for example, in flowering phenology (Bucharova, Michalski, et al., 2017; Diaz & Merlo, 2008; Lyngdoh et al., 2012; Vander Mijnsbrugge et al., 2015).

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![FIGURE 1](https://example.com/figure1.jpg) Map of seed transfer zones in Germany with highlighted provenances used in the experiment. The star indicates the location of the common garden. After Bucharova et al. (2019)
species, but differed in provenance. We recorded plant phenology and observed pollinators and flower visitors. We hypothesized that (a) plant provenances differ in flowering phenology, which (b) results in differences in the diversity and total abundance of flowerers in the experimental plant communities, and subsequently (c) affects the interacting pollinators and flower visitors, ultimately leading to differences in plant–pollinator interaction networks between provenances.

2 | MATERIALS AND METHODS

2.1 | Selection of plants and experimental garden

We chose six insect-pollinated plant species: *Centaurea jacea, Galium album, Hypochaeris radicata, Knautia arvensis, Lotus corniculatus* and *Silene vulgaris*; abbreviated by the genus name further on. All species were insect pollinated. We obtained the seeds from specialized seed producers that produce seeds for restoration according to the regional admixture provenancing (Bucharova et al., 2019; Nagel et al., 2019), Rieger-Hofmann GmbH and Saaten Zeller GmbH & Co KG. In these systems, seeds are collected from multiple populations within a given region, so called seed transfer zone, mixed and propagated on farms to produce regionally adapted, yet genetically diverse seed lots.

For all six species, we selected three provenances that span the geographic and climatic variability in Germany: a western, an eastern and a southern provenance (Figure 1). The western provenance, representing the regional provenance of our experiment, has an oceanic climate with relatively low seasonal differences, a mean annual temperature of 8–10°C and an annual precipitation of 700–800 mm. The southern provenance is slightly colder and wetter (6–8°C mean annual temperature, 700–1,000 mm annual precipitation), and has a continental climate with larger differences between seasons. The eastern provenance also has a continental climate, the same mean annual temperature as the western provenance (8–10°C), but receives considerably less precipitation of 450–550 mm per year (Deutscher Wetterdienst, 2020, www.dwd.de).

We carried out this experiment in 2019 in a common garden in Münster, Germany (Figure 1). The summer of 2019 was 2.4°C warmer with only 63% of the precipitation compared with the long-term mean (Deutscher Wetterdienst, 2020, www.dwd.de). The experimental garden was located in an abandoned botanical garden, a neglected area covered by a variety of habitats ranging from open grasslands to dense shrubs. It provides abundant and diverse flower resources and also nesting opportunities for pollinators.

2.2 | Establishing experimental plant communities

We sowed seeds of all six plant species and three provenances to seeding trays in March 2019 and kept the trays in a cold greenhouse. When the seedlings developed the first true leaves, we transplanted them to planting trays. After 4–6 weeks, depending on the species, we transplanted all small plants to 1.5-L pots filled with standard potting substrate and transferred them to the common garden. Using potted plants allowed each plant to grow in standardized conditions, and avoid confounding effects of mortality due to direct competition between the plants. We arranged sets of individual potted plants (one specimen of each species) all originating from the same provenance in small patches side-by-side. In the case that any of the experimental plants died, we replaced it with a back-up plant from the same species and provenance. In this way, we established small experimental plant communities that had the very same species composition and the same plant abundances, but they differed from each other in provenance. These experimental communities were replicated nine times for each of the three provenances, resulting in 27 experimental communities and 162 plants in total (Figure S1). The position of each species in the experimental community, and the arrangement of experimental communities within the experiment were selected at random. The diameter of each experimental community was approximately 70 cm, and the communities were 150 cm apart. We watered the plants as needed.

Shortly after transfer to the common garden, the experiment experienced a set-back due to massive herbivory by wild rabbits. After we fenced the whole experiment, we cut all plants to a height of 2 cm to standardize the above-ground defoliation. All plants regenerated within a few weeks, yet, this event delayed the flowering of all plants.

2.3 | Data collection

We recorded phenology during the whole experiment. We visited the plants every week and recorded whether individual plants did flower or not.

We observed pollinators at three dates: on July 31, August 14 and August 28, henceforth called early, mid and late observation. The early observation took place 1 week after all experimental communities produced at least one flower. At each observation date, we recorded the number of flowering units per plant in all the experimental communities. The flowering units were defined either as individual flowers (in *Silene*) or whole inflorescences (all other species), depending on the visually distinct entity in a given species. We call all flowering units ‘flowers’ in the further text.

Subsequently, we observed flower visitors and pollinators. Not all insects that visit flowers transfer pollen, but we did not distinguish between legitimate pollinators and other visitors. However, we call all observed insects ‘pollinators’ in the further text for the sake of simplicity. To determine pollinators, we screened pollinators present in the experimental garden in the week before the first pollinator observations. We developed a classification key that allowed us to obtain as detailed information on the taxonomic status as possible when observing the insects sitting on the flowers without catchment. We divided the pollinators into six main groups: hoverflies, flies, honeybees, other wild bees, bumblebees and wasps. Some of
these groups were further divided into easily recognizable morphospecies. We did not observe any butterflies or beetles. In total, we identified 11 pollinator morphospecies (Figure 2; Figure S2).

To record pollinators, we observed each experimental community replicate for 15 min in two distinct 7.5-min sections, an early and a late one, to avoid the confounding effect of daytime and experimental community identity. The two sections were randomly assigned to two independent observers. All observations were conducted in stable conditions during dry weather, between 10 a.m. and 2 p.m. Within the 15 min, we recorded all observed flower-pollinator interactions, noting the plant species and the pollinator morphospecies. We defined individual flower-pollinator interactions as follows: when a pollinator visited several flowers at the same plant individually, we counted this as independent interactions, because the pollinator had to either fly or crawl over vegetative parts to get from one flower to another.

2.4 | Data analysis

We conducted five steps in our analyses. In the first two steps we focused on plants. We analysed whether plants of the three provenances differed in phenology, and consequently, whether the plant provenance did affect the flower diversity of the experimental communities. In the third and fourth step, we focused on the pollinators. We analysed the plant-pollinator network and tested whether the provenance identity of the experimental plant communities affected the number and diversity of flower-pollinator interactions. In the

![Diagram](A) All realized plant-pollinator interactions. (B) Pollinator interactions with provenance as the lower trophic level. Southern provenance attracted in total two times more pollinators than the other two provenances. The size of the boxes represents the relative abundance with which a particular pollinator or plant participated in plant-pollinator interactions.
fifth step, we connected the data on flower resources and pollinators to test whether the effect of plant provenance on pollinators was mediated by the diversity of flower resources. All these steps are detailed below. The analyses were made in \( \kappa \) (R Development Core Team, 2020).

First, we focused on plant phenology on the level of individual plants (each plant used as a replicate). As many plants did not start to flower over the course of the whole experiment, we analysed the data on phenology in two steps, first using flowering probability with all plants, and second flowering time only with plants that did flower. For flowering probability during the experiment, we related flowering (binary response yes/no) to plant species, provenance and the interaction term of these two explanatory variables in a GLM with a binomial error distribution. Among provenances of each individual species, we compared the probability of flowering using post hoc pairwise chi-square comparisons. For flowering time, we related the onset of flowering of each individual plant to species, provenance and the interaction term of these two variables in a linear model with a Gaussian error distribution. We compared provenances using pairwise comparisons as provided in the \texttt{multcomp} package (Hothorn et al., 2008). We further used the \texttt{effects} package to obtain fitted values and confidence intervals for visualization (Fox & Weisberg, 2014).

Second, we focused on the provenance effect on flower abundance and flower diversity of the experimental communities, expressed by the Shannon index. As flower abundance and diversity were correlated \( (r = 0.56) \), we used only flower diversity for the analyses and results presented below. The results using flower abundance largely mirrored the results using flower diversity (Table S1; Figure S3). In this and subsequent analyses, a single value per experimental community was one replicate. We used linear mixed effects models and related flower diversity per experimental community to provenance, date of observation and their interaction as fixed factors, using the identity of the experimental community as a random factor to account for repeated observations. All mixed effects models (lmm and glmm) here and later were computed with the \texttt{mixed} package \citep{blme}. Third, we visualized all observed flower–pollinator interactions using the \texttt{bipartite} package \citep{bipartite}. Across all plants and species in the experiment, we used a chi-squared test to test whether the number of interactions per pollinator morpho species differed among plant provenances. Further, using a null model approach (function: \texttt{vaznull} \citep{vaznull}), we tested if pollinators preferably visited certain provenances by comparing their observed choice of provenance to what would be expected at random. To this end, we computed the specialization index \( H^2 \) for our observed interactions and compared it with the distribution of \( H^2 \) of 1,000 simulated pollinator-provenance networks (i.e. random provenance choices) with the same number of interactions. The specialization index \( H^2 \) ranges between 0 and 1 and takes on high values when a network is specialized, that is, when the pollinator interactions were not evenly distributed among provenances.

Fourth, we analysed the effect of provenance identity on the number of plant–pollinator interactions and the diversity of pollinators, essentially the number of pollinator taxa (a single value per experimental community was one replicate). Since the number of observations, and thus the number of plant–pollinator interactions, was often low per experimental community, we did not calculate the Shannon index but used the number of pollinator taxa (i.e. mor- phospecies richness) as a surrogate of insect diversity. We related this pollinator diversity and the number of interactions as response variables to provenance, observation date and their interaction term as explanatory variables in a generalized linear mixed effects model with a Poisson error distribution using experimental community as random block effect. To account for overdispersion we added an observation-level random effect (i.e. with a unique level for each data point) to the model with the number of interactions as response variable \citep{harrison14}.

Fifth, we connected the data on pollinators and flowers per experimental community and we tested whether flower diversity (expressed as Shannon index, see above) affects the number of plant–pollinator interactions and the pollinator diversity (i.e. the number of pollinator taxa, see above). We related the pollinator diversity and the number of plant–pollinator interactions as response variables to flower diversity, date of observation and their interaction and provenance as explanatory variables in a GLMM with a Poisson error distribution and the experimental community as random block effect. In a second step, we added provenance as an explanatory variable to this model, to analyse if provenance had an additional effect on top of the flower diversity effect \( (i.e. \text{if provenance explained any variability when fitted after flower diversity and date}), \) or if the provenance effect was driven by the flower diversity effect. Again, an observation-level effect was used to account for overdispersion \citep{harrison14}.

3 | RESULTS

3.1 | Plant phenology and flower diversity

Plant provenance affected both probability of flowering during the experiment and flowering time (Figure 3; Table 1A; Figure S4). This effect was especially strong in two species, \textit{Galium} and \textit{Centaurea}, with the southern provenance flowering more frequently than the other two provenances (Figure 3A,B). In these species, the southern provenance also flowered relatively early in comparison to the western provenance (Figure 3B, Table 1A). In \textit{Hypochaeris}, flowering time followed a similar trend, but the effects were not significant (Figure 3A).

The phenological differences resulted in a different flower diversity among provenances at a given date, with the experimental communities of southern provenance showing a twofold higher flower diversity than the experimental communities of the other two provenances. This effect was consistent across observation dates (Figure 4A,B; Table 1B).
In total, we observed 737 flower–pollinator interactions. The majority (>85%) of all interactions took place with three plant species only: Lotus, Hypochaeris and Centaurea (265, 264 and 108 interactions respectively). In contrast, flowers of the other three species, namely Galium, Silene and Knautia, were visited much less frequently (35, 33 and 32 interactions respectively). The two most common insects with the majority of interactions were bumblebees (morphospecies Bombus lapidarius, L 1758; 309 interactions), and honeybees (Apis mellifera, L 1758; 286 interactions). Bumblebees preferably interacted with Lotus, whereas honeybees preferentially interacted with both species from the family Asteraceae—Centaurea and Hypochaeris (Figure 2A).

Across all plants and species, plants of the southern provenance interacted with pollinators two times as often as the eastern and western provenance (yielding 369, 189 and 189 respectively; Figure 2B). Notably, while in the eastern provenance bumblebees accounted for 60% of all interactions, their share was lower in the western and southern provenance (Figure 2B). This indicates that pollinators differentiated between the provenances, which was further supported by a moderate specialization index $H^2_{uni} / var = 0.1$ for the network calculated across all monitoring dates. The index was significantly higher than zero ($p < 0.001$, Figure S5), which means that insects visited one of the provenances more often than would be expected if the visits were random (Figure 2B).

Accordingly, the provenance identity of the plant experimental communities affected the diversity of pollinators (expressed as the number of pollinator taxa), with the southern provenance interacting with more taxa than the western or eastern provenance (Figure 4A; Table 1B). The number of interactions was on average also the highest in the experimental communities of the southern provenance, but this effect depended on the date of observation (Figure 4B; Table 1B; Figure S6). Experimental communities with higher flower diversity interacted with more pollinator taxa and had a higher number of interactions (Figure 4A,B; Table 1C). The slope of these relationships differed between observation dates, but overall, the effect remained positive (Figure 4A,B; Table 1C; Figure S6). When we added provenance to this model, it had no significant effect, indicating that the provenance effect was mediated by flower diversity.

### 3.2 | Pollinators

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### 4 | DISCUSSION

We tested the effect of within-species population differentiation on the pollinator diversity and the frequency of flower visitation...
**TABLE 1** Results of (A) the model testing the effect of provenance, species and their interactions on plant phenology. (B) Model testing the effect of provenance, observation date and their interaction on flower diversity, pollinator diversity and number of flower–pollinator interactions. (C) Model testing the effect of flower diversity, observation date and their interaction on pollinator diversity and number of flower–pollinator interactions. Provenance was added to the model (C) after testing for significance of the other terms. All models are with type III sum of squares; significant values are in bold.

(A) **Plant phenology**

|                          | df | $\chi^2$ | p       | Resid df | F    | p     |
|--------------------------|----|----------|---------|-----------|------|-------|
| Species                  | 5  | 44.9     | <0.001  |           |      |       |
| Provenance               | 2  | 19.65    | <0.001  |           |      |       |
| Species x Provenance     | 10 | 13.62    | 0.191   |           |      |       |

(B) **Flower and insect diversity**

|                      | df | $\chi^2$ | p       | $\chi^2$ | p   | $\chi^2$ | p   |
|----------------------|----|----------|---------|----------|-----|----------|-----|
| Provenance           | 2  | 45.07    | <0.001  | 12.41    | 0.001 | 12.61    | 0.002 |
| Observation date     | 2  | 10.11    | 0.006   | 0.54     | 0.764 | 14.00    | <0.001 |
| Provenance x Observation date | 4  | 7.35    | 0.118   | 6.63     | 0.156 | 12.35    | 0.015 |

(C) **Effect of flower diversity on pollinators**

|                               | df | $\chi^2$ | p       | $\chi^2$ | p   | $\chi^2$ | p   |
|-------------------------------|----|----------|---------|----------|-----|----------|-----|
| Flower diversity              | 1  | 9.37     | 0.002   | 7.48     | 0.006 |         |     |
| Observation date              | 2  | 6.43     | 0.040   | 8.16     | 0.017 |         |     |
| Flower diversity x Observation date | 2  | 7.40    | 0.025   | 6.27     | 0.043 |         |     |
| Provenance                    | 2  | 1.08     | 0.583   | 0.061    | 0.970 |         |     |

**FIGURE 4** The relationship between flower diversity and (A) pollinator diversity, expressed as the number of taxa, and (B) pollinator abundance. Horizontal boxplots show the provenance effect on flower diversity, the same for A and B. Vertical boxplots show provenance effect on (A) pollinator diversity and (B) number of interactions. Note logarithmic y-axis in (B). Letters indicate significant differences. For model results, see Table 1B,C.
by pollinators and flower visitors (further pollinators for simplicity) in experimental plant communities that consisted of the very same plant species, but differed in their provenance identity. We recorded the plant phenology, the number of flowers and observed the pollinators. We showed that plant phenology differed between plant provenances, a pattern that resulted in differences in flower diversity among experimental communities of individual provenances. In consequence, the identity of plant provenance had a profound effect on the frequency of flower–pollinator interactions as well as on pollinator diversity. Among plant provenances, the southern identity interacted two times as often with pollinators and attracted two times as many species as each of the other two provenances.

4.1 | Plant phenology

Plants from the three provenances differed in phenology. Plants coming from the southern provenance (continental climate) flowered earlier and more often than plants from the other two provenances, especially, in comparison to the western provenance, which has an oceanic climate. This effect was significant in two out of six species. Such differences in phenology of provenances are common among plants. Bud burst, leaf flush, flowering phenology or senescence are important parts of plant adaptation to their environment and they are partly genetically underpinned (Bucharova, Michalski, et al., 2017; Cooper et al., 2019; Vander Mijnsbrugge et al., 2015; Vitasse et al., 2009; Zhang et al., 2019). Our results partly correspond to the fact that in temperate regions, plants from warmer and more continental origins typically show advanced phenology when compared to plants from northern origins and more oceanic climates (Jones et al., 2001; Robson et al., 2013; Vander Mijnsbrugge et al., 2015; Wilkinson et al., 2017).

However, attributing the phenology differences to climate at origin must be done with caution. We have watered the plants throughout the experiment, and it is possible that the provenance that has profited the most from the surplus of water started to flower earlier. Further, we only observed the phenology in the first year after germination in perennial plants, ignoring the possibility that the phenology in the year of establishment may differ from that in later years. Yet, phenology differences among provenances are highly genetically determined and they tend to be similar across the years (Jones et al., 2001; Liang, 2015). Further, the experiment also suffered from massive herbivory damage by wild rabbits, which almost completely removed above-ground biomass. The plants thus had to first regrow, and the observed difference in flowering could be caused by a faster regrowth of some provenances compared to others. Yet, this is rather unlikely. First, similar phenology differences among provenances as in the current study, but without herbivory damage, were observed in a previous study with a larger set of plants from the same ecosystem (Bucharova, Michalski, et al., 2017). Second, all the plants are characteristic species of human-managed grasslands, they are adapted to regular mowing and rapid regrowth is part of their survival strategy (Bucharova et al., 2020).

On the community level, the differences in flower phenology among provenances caused that experimental communities of the later flowering provenances lacked flowers of the species with delayed phenology (i.e. Centaurea and Gallium), especially during the first observation dates. This necessarily resulted in differences in flower abundance and diversity among provenances, with the early flowering southern provenance having on average a more than two-fold higher flower diversity.

4.2 | Pollinators and flower visitors

The differences among provenances in flower diversity resulted in differences in the number and diversity of flower–pollinator interactions. Specifically, experimental communities of plants from the earlier flowering provenance (i.e. southern) had higher flower diversity and consequently, their flowers interacted more frequently with pollinators and flower visitors, and the interacting insects were more diverse. Flower diversity is, in fact, a well-known predictor of pollinator diversity (Ebeling et al., 2008; Fründ et al., 2010; Fornoff et al., 2017). Yet, the evidence so far came from observations of communities that differed in plant species richness. Since we kept the plant diversity constant by harmonizing plant species identities and richness across provenances, we illustrate how important is the variability within plant species for the interaction with pollinators.

The effect of plant provenance on the diversity of interacting pollinators is likely underestimated in our study. We differentiated pollinators only to 11 morphospecies that were easy to identify when observing insects sitting on the flowers. These morphospecies likely comprise several true species that differ in seasonality. It is thus possible that, for example, hoverflies or wild bees interacting with flowers during the first observation belonged to a different species than individuals of the same morphospecies observed at the last observation date (Ball & Morris, 2015; Westrich (2018) for wild bees). Our estimate of provenance effect on pollinators is thus rather conservative.

4.3 | Implications for ecosystem restoration

We have demonstrated that the provenance identity of plant experimental communities alters the diversity of flowers of these experimental communities which subsequently affects the frequency of flower–pollinator interactions and the diversity of interacting insects. The provenance selection for ecosystem restoration is intensively debated, especially in the context of ongoing climate change (Breed et al., 2013, 2018; Prober et al., 2015), but the arguments are mostly about plant performance. As ecological restoration aims to restore all components of ecosystems, ecosystem functions and services, the effect of provenance choice on interacting biota including herbivores and pollinators should not be neglected. This is especially the case in projects that aim on supporting pollinators in agricultural landscapes (Krimmer et al., 2019; M’Gonigle et al., 2015; Nicholson et al., 2020). In this context, attention is usually paid to the selection of particular
plant species that are beneficial to pollinators, but within-species variability of these plants is largely neglected (M’Gonigle et al., 2017; Nichols et al., 2019; Williams & Lonsdorf, 2018). We show that within-species variability may have a substantial impact on how flower resources are available throughout the season, potentially leading to a decoupling of plant–pollinator interactions. Such decoupling may shift the abundance and diversity of pollinator interactions, as generalist pollinators that collect pollen from multiple species will likely be less affected than species specialized on one or a few plants (Renner & Zohner, 2018; Visser & Gienapp, 2019). In consequence, the properties of the plant–pollinator interaction network will likely depend on the phenology of the provenance that was used for a given restoration project (Bartley et al., 2019).

Caution is needed when interpreting our results on the landscape level because of methodology. We used an experimental set-up in which we offered experimental communities of different provenance to pollinators within one garden and the pollinators were given the choice. In reality, restored habitats are usually seeded with one provenance and pollinators cannot choose. Yet, the selection of provenance will affect the availability of flower resources, which will subsequently influence the abundance and diversity of pollinators in the whole restored habitat (Fründ et al., 2010). Further, we used potted plants to establish the experimental communities, which reduced competition between plants. In restoration, plants are seeded or planted and they compete for resources. The competitive ability of individual plant species differs between provenances, but the provenance effect is not consistent across species (Bischoff et al., 2006). Competition at a restoration site thus could suppress or promote different species depending on the specific provenance, which would further increase differentiation between the communities (Weißhuhn et al., 2012). Consequently, in real restoration projects, the impact of the provenance selection on pollinators is potentially larger than shown in this study.

The highest pollinator diversity was not supported by the local provenance, but by a provenance from a different region. Shall we plant foreign provenances to support pollinators? The pollinators observed in our study were mostly generalists and thus, they profited from the earlier start of the flowering period (Iler et al., 2013). More specialized pollinators, however, may suffer because they are more sensitive to temporal decoupling from their forage plants (Kudo & Ida, 2013). Besides the consequences for pollinator interactions, plant phenology is also an important part of adaptation to local climatic conditions (Cooper et al., 2019; Robson et al., 2013), and the foreign provenances that differ in phenology may have reduced fitness because of, for example, frost damage.

In summary, our study provides proof of principle that provenance selection does affect pollinator abundance and diversity in the restored habitat. Yet, more research is needed to formulate conclusive recommendations on the choice of the optimal provenance. Specifically, we need more data on the adaptation of plants to their environment, on co-adaptation between the plants and local pollinators, optimally obtained from reciprocal transplant experiments (Bucharova, Durka, et al., 2017).

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AUTHORS’ CONTRIBUTIONS
A.B. conceived the idea; A.B., D.O., E.M. and J.M. designed the study; E.M., M.C. and J.M. conducted the experiment; A.B. and C.L. analysed the data; A.B. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.m905qvoX (Bucharova et al., 2021).

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