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RESEARCH ARTICLE

Evolution during seed production for ecological restoration? A molecular analysis of 19 species finds only minor genomic changes

Malte Conrady[1,2] | Christian Lampei[1] | Oliver Bossdorf[3] | Walter Durka[4,5] | Anna Bucharova[1,2]

[1]Institute of Landscape Ecology, University of Münster, Münster, Germany

[2]Department of Biology, Philipps-University Marburg, Marburg, Germany

[3]Plant Evolutionary Ecology, Institute of Evolution & Ecology, University of Tübingen, Tübingen, Germany

[4]Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle, Germany

[5]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Correspondence
Malte Conrady
Email: malte.conrady@uni-muenster.de

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Abstract

1. A growing number of restoration projects require large amounts of seeds. As harvesting natural populations cannot cover the demand, wild plants are often propagated in large-scale monocultures. There are concerns that this cultivation process may cause genetic drift and unintended selection, altering the genetic properties of the cultivated populations and reducing their genetic diversity. Such changes could reduce the pre-existing adaptation of restored populations and limit their adaptability to environmental change.
2. We used single nucleotide polymorphism (SNP) markers and a pool-sequencing approach to test for genetic differentiation and changes in gene diversity during cultivation in 19 wild grassland species, comparing source populations and up to four consecutive cultivation generations. We linked the magnitudes of genetic changes to the species' breeding systems and seed dormancy to understand the roles of these traits in genetic change.
3. Cultivation changed the genetic composition across cultivated generations only moderately. The genetic differentiation resulting from cultivation was much lower than the natural genetic differentiation between different source regions. The propagated generations harboured even higher gene diversity than wild-collected seeds. Genetic change was stronger in self-compatible than self-incompatible species, probably due to increased outcrossing in monocultures.
4. *Synthesis and applications*. Our study suggests that large-scale seed production maintains the genetic integrity of natural populations. Increased genetic diversity may even indicate increased adaptive potential of propagated seeds, which would make them especially suitable for ecological restoration. Yet, it remains to be tested whether these molecular patterns will be mirrored also by plant phenotypes. Further, we used seeds from Germany and Austria, where the seed production is regulated and certified, and we do not know yet whether other seed production systems perform equally well.

Walter Durka and Anna Bucharova shared authorship.

KEYWORDS
cultivation syndrome, ecosystem restoration, genotyping-by-sequencing, native plants, rapid evolution, seed increase, seed orchard, seed provenancing

1 | INTRODUCTION

Ecological restoration of degraded habitats is an indispensable tool for handling the current biodiversity crisis (www.decadeonrestoration.org; Díaz et al., 2019). Degraded terrestrial ecosystems frequently lack diaspores for regenerating new communities, and successful restoration often requires the introduction of seeds from other sources (Elzenga et al., 2019; Hölzel et al., 2012). With upscaling restoration, the demand for native seeds is increasing, and seed shortage has become a major obstacles of restoration projects (Merritt & Dixon, 2011; Nevill et al., 2018). Harvesting seeds from the wild is not sustainable because seeds are the basic means of plant reproduction, and their excessive removal may threaten population persistence (Meissen et al., 2015). Consequently, wild-collected seeds are often first propagated on farms, and farm-produced seeds are then used for restoration projects (Bucharova et al., 2019; Kiehl et al., 2014; Nevill et al., 2018).

Agricultural propagation of seeds sourced from wild populations aims to maintain the natural integrity of the collected seed (Bucharova et al., 2019; Espeland et al., 2017). This differs from plant cultivars commonly bred to obtain specific characteristics like rapid growth, seedling vigour or high seed production (Leger & Baughman, 2015). Yet, even seed propagation that does not intentionally select certain genotypes could affect the genetic integrity because the propagation process may cause genetic drift or unintended selection (Espeland et al., 2017). In the seedbeds, plants are often grown in monocultures, with additional watering, fertilization and sometimes protection from herbivores, relaxing natural selection by these factors. Machine harvesting and seed cleaning can further select seeds of specific characteristics like shape or weight (Espeland et al., 2017). The seeds are often propagated for multiple generations, with a subset of cultivated seeds used to establish the next generation (Bucharova et al., 2019). This may result in repeated genetic bottlenecks and genetic drift, that is random changes in allele frequency and loss of genetic variability. Populations may also randomly accumulate alleles that reduce adaptation to natural environments (Lau et al., 2019; Pertoldi et al., 2007). The loss of genetic variability would be particularly problematic because standing genetic variation is a prerequisite for rapid adaptation (Crowe & Parker, 2008). Restored populations with low genetic variability would have a reduced ability to adapt to changing environmental conditions (Barrett & Schluter, 2008).

The severity of propagation effects on a seed lot's genetic properties will depend on cultivation methods and life-history traits of the plants. For example, manual seed harvest likely causes smaller changes than mechanical harvest once per season because it samples a greater variety of phenologies and thus a larger proportion of genetic variability. The cultivation effects are expected to decrease with increasing size of the cultivated population because genetic drift is stronger in small populations (Frankham et al., 2014). Regarding life-history traits, species with strong seed dormancy likely change more during cultivation because dormant genotypes will contribute less to the gene pool of the next generation (Kettenring & Galatowitsch, 2007). Moreover, self-compatible species will likely change more because selection can act faster on them (Andersson & Ofori, 2013). Indeed, one of the few existing studies on cultivation effects in plants propagated for restoration (Nagel et al., 2019) found the strongest genetic changes in a self-pollinating species.

Although genetic changes during cultivation are intensely debated in the restoration literature (e.g. Basey et al., 2015; Espeland et al., 2017; Pedrini et al., 2020), there is surprisingly little empirical evidence for them. A substantial body of literature describes crop domestication (reviewed in Pickersgill, 2009; Kantar et al., 2017), but in contrast to crops, plants cultivated for restoration are not intentionally bred. Other studies documented evolutionary changes in ex situ cultivation in botanical gardens (Ensslin & Godefroid, 2019; Rauschkolb et al., 2019), but ex situ populations are usually very small, whereas the cultivation of plants for ecosystem restoration usually involves much larger populations. The few studies that focused specifically on the evolution of plants for ecological restoration worked with individual species and/or documented cultivation only across a single generation (Dyer et al., 2016; Kucera et al., 2022; Pizza et al., 2021; St. Clair et al., 2020). Only one previous study focused on multiple cultivation generations across multiple species, and it found rather minor cultivation effects which differed between species (Nagel et al., 2019).

Here, we used molecular markers to study the effect of agricultural propagation on the genetic variation of 19 species of wild plants. We used seeds propagated in the German (Bucharova et al., 2019) and Austrian (Krautzer et al., 2020) seed production systems, where seeds collected from one or several wild populations are mixed and propagated for up to five consecutive generations. For each species, we obtained wild-collected seeds and seeds from one to four consecutive cultivation generations (Figure 1). We employed genotyping-by-sequencing of genome-wide anonymous markers to assess the effects of cultivation on the genetic properties of populations. We hypothesized that (a) genetic divergence from the wild population increases with the number of generations in cultivation, (b) genetic diversity decreases with the number of cultivation generations and (c) species characteristics predict part of the extent of genetic changes during cultivation.

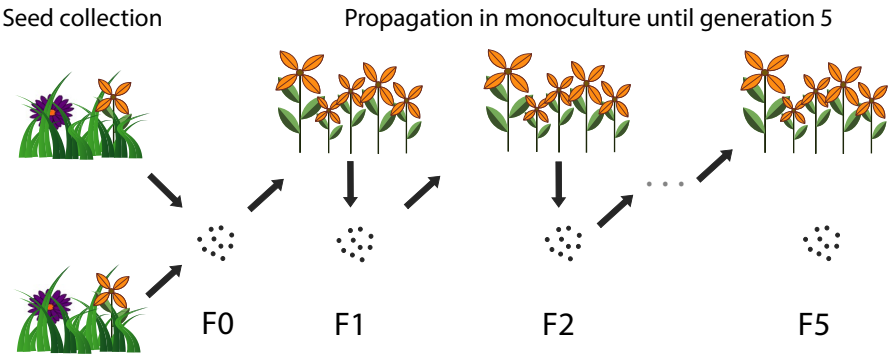

FIGURE 1 Schematic of the propagation of wild plant seed material for restoration. Seeds are collected from multiple natural populations and mixed (F0) by Producer 1. Producer 2 only uses one origin. The F0 seeds are used to establish the first generation in cultivation (F1). These cultivated seeds are available for restoration projects, and a small part is used to establish the next cultivated generation. After five cultivated generations (F5), new seeds must be collected from the wild

2 | MATERIALS AND METHODS

2.1 | Seed material

We obtained seeds of grassland plants from two producers of seeds for ecological restoration, one in Austria and one in Germany, which we call Producer 1 and Producer 2 throughout this paper. The propagation process starts with seed collection in the wild. Producer 1 bases its propagation on a mixture of seeds from multiple wild populations, whereas Producer 2 bases its propagation on seeds from only one population. The wild-collected seeds (F0) thus consist of a mixture of five populations in Producer 1 or of a single population in Producer 2. The F0 seeds are often first germinated in a greenhouse to produce plugs which are then planted into a field. When a farm propagates multiple cultivation lines of the same species, the fields must be separated by at least 500 m (more for grasses) to minimize gene flow between them (Prasse et al., 2010). The seeds of the first cultivated generation (F1) are used to establish the next cultivation (F2, Figure 1). The F2 seeds are mostly sold, but some are kept to establish the F3 generation. The procedure is repeated until F5 (Figure 1). Then new seeds must be collected from the wild to prevent suspected loss of genetic diversity and potential adaptation to the propagation environment. The seeds are usually mechanically harvested using agricultural machinery.

For our study, we obtained wild-collected and cultivated seeds of 19 different plant species. Because the seed producers stored the seeds from both the wild collection and almost every consecutive generation in cultivation, we were able to test for genetic changes during the cultivation process from generation to generation, up to the fourth cultivated generation. Four species were provided by both producers and one from one producer but two different regions (Table 1). In total, we obtained 24 independent cultivation lines (19 species, five of them from two regions), resulting in 83 accessions. To gain material for the genetic analysis, we raised seedlings on a seeding substrate and sampled leaves from 18 random individuals per species and generation.

2.2 | Molecular analysis

Because of the large sample size, we used a population pool approach (Futschik & Schlötterer, 2010), with 18 individuals per generation and cultivation line pooled into one sample. We used a reduced-representation sequencing approach for SNP (single nucleotide polymorphism) detection and genotyping and followed the ddRAD protocol (Peterson et al., 2012) with slight deviations (see Appendix).

After demultiplexing reads with process_radtags from the Stacks 2.0 pipeline (Catchen et al., 2013; Rochette et al., 2019), we used the dDocent 2.6.0 pipeline (O'Leary et al., 2018; Puritz et al., 2014) for contig assembly, SNP detection and assessment of allelic read counts for each cultivation line. SNP filtering of the resulting VCF file with vcftools removed indels, kept only biallelic loci with minimum Phred-scores of 30 and only one SNP per contig. For comparability of genetic diversity between generations (not biased by sequencing depths), we further filtered the data using R. We used only markers with a minor allele frequency ≥0.05 and genotypes with a minimum read depth of 36. We corrected for unequal sequencing depth of the same locus across pools of the same cultivation line by rarefaction, that is drawing the minimum number of reads from each pool to assess allelic read counts. Pools with <500 SNPs were removed (Table 1) (see Table S2 and supplemental R code for details). The final datasets consisted of 657–9,721 (average 5,137) biallelic SNP loci per pool across the 19 species and 24 cultivation lines, with between 0% and 14.6% missing data (Table S2).

2.3 | Data analysis

All analyses were performed in R (R Development Core Team, 2020). First, we tested whether the genetic differentiation between the wild-collected and cultivated plants increased with the number of generations in cultivation. We calculated the pairwise genetic differentiation F_{ST} for each cultivation line between the plants from the

TABLE 1 Species, seed sources included in the experiment and self-incompatibility. F0 are wild-collected seeds, and F1–F4 are consecutive generations in cultivation. The generations in parentheses were excluded from the data analyses because of insufficient SNP data and/or sampling depth (see text). SC, self-compatible; SI, self-incompatible (see Table S1 for references)

Species	Family	Producer 1	Producer 2	Self-compatibility
Achillea millefolium	Asteraceae	F0–F2	F0; F3; F4	SI
Anthoxanthum odoratum	Poaceae		F0–F2	SI
Centaurea jacea	Asteraceae	F0–F3		SI
Centaurea scabiosa	Asteraceae	F0–F2	F0; F1; (F2); F3	SI
Crepis biennis	Asteraceae	F0–F2; (F3)		NA
Cynosurus cristatus	Poaceae		F0–F2	SI
Dianthus carthusianorum	Caryophyllaceae		F0–F4	SC
Galium verum	Rubiaceae		F0–F2	SI
Leontodon hispidus	Asteraceae	F0–F2		SI
Leucanthemum ircutianum	Asteraceae	F0–F3	F0–F2; F4	SI
Lotus corniculatus	Fabaceae	F0–F3	F0; F1	SC
Lychnis flos-cuculi	Caryophyllaceae		F0–F2	SC
Ranunculus acris	Ranunculaceae	F0–F3		SI
Rumex acetosa region R6	Polygonaceae	F0; (F1); F2		SI
Rumex acetosa region R16	Polygonaceae	F0–F2		SI
Salvia pratensis	Lamiaceae		F0; F1; F3	SC
Silene dioica	Caryophyllaceae	F0–F3		SI
Silene vulgaris	Caryophyllaceae	F0–F3		SC
Trifolium pratense	Fabaceae	F0–F3		SI
Veronica teucrium	Plantaginaceae		F0–F2	SI

wild-collected seeds and each consecutive generation in cultivation using the R package POOLFSTAT (Hivert et al., 2018). We then centred the F_{ST} within each cultivation line by subtracting the cultivation line mean from each F_{ST} value to allow cross-species comparison. We related the centred F_{ST} to the generation number (continuous variable), producer identity and their interaction as explanatory variables, and cultivation line as a random factor in a linear mixed-effects model using the package LME4 (Bates et al., 2015). Only cultivation lines with ≥3 generations were included because a minimum of three F_{ST} values was required for meaningful centring (two cultivation lines excluded, see Table 1).

To provide context for the magnitude of genetic differentiation caused by the cultivation process, we compared it to the natural genetic differentiation between populations. Specifically, we compared the absolute values of genetic differentiation (F_{ST}) between the wild plants and the last cultivated generation within a cultivation line with the F_{ST} between wild plants of the same species coming from two different regions using a linear mixed-effects model (Bates et al., 2015) with F_{ST} as a response variable, wild versus cultivated population as an explanatory variable and species as a random factor. This was possible in five species for which the F0 was available from two different regions, either from two seed producers or, in one species, from two regions from the same producer (Table 1). The geographical distance between the regions ranged from 130 km to 560 km, with a mean of 380 km. For this analysis, the above-described SNP filtering steps were carried out per species and not per cultivation line.

Second, we focused on the effect of cultivation on the genetic diversity within cultivated generations, estimated as expected heterozygosity H_e. We hypothesized that genetic diversity would decrease with increasing generations in cultivation. To test this hypothesis, we calculated H_e, using the unbiased estimator of Nei and Roychoudhury (1974), for each cultivation line and generation, taking allelic read counts as allele frequencies. We centred the H_e values per cultivation line to ensure comparability across species. We related H_e to the number of generations in cultivation, producer identity and their interaction as fixed explanatory variables, and cultivation line as a random factor in a linear mixed-effects model (Bates et al., 2015). When we visually inspected the data, H_e did not appear to change continuously across generations, but it showed an abrupt change between the wild plants and the first cultivated generation. Therefore, we treated the generations in cultivation as a categorical variable in this model.

Next, we assessed how the different seed sourcing strategies of the two seed producers affected genetic diversity (H_e). As Producer 1 mixes seeds from multiple wild populations, while Producer 2 uses seeds from only one population, we expected the seeds from Producer 1 to harbour higher genetic diversity. We tested this only for species where data from both seed producers were available (Table 1) and related the absolute H_e values in each cultivation line and generation to species identity, generation and producer identity in the statistical models. The species and generation were included in the model to adjust for species identity and temporal trends across generations. For this analysis, the above-described SNP filtering

steps were carried out per species and not per cultivation line to assure that the same SNP markers were used between producers.

Finally, we tested whether the magnitudes of genetic differentiation and changes in genetic diversity caused by cultivation depended on species traits. We focused on two specific traits for which we expected an effect, and that varied among our study species: seed dormancy and self-compatibility. We obtained the data on self-compatibility from the BIOLFLOR database (Kühn et al., 2004) and additional literature (Table S1). Seed dormancy was estimated in a germination trial as the proportion of viable but non-germinating seeds in a sample of the wild-collected (F0) seed (Table S1). Other potentially relevant characteristics like harvest type (mechanic or hand) or harvest frequency could not be used because we had this information only for seeds from Producer 1, where all except one species were mechanically harvested once per year. As response variables in these analyses, we used the genetic change between the wild and the first cultivated generation because these two generations were available for most cultivation lines (Table 1). As a measure of genetic differentiation, we used the absolute F_{ST} value between F0 and F1. Changes in genetic diversity were quantified as $\Delta H_e = (H_{eF1} - H_{eF0})/H_{eF0}$, thus standardizing values across cultivation lines. A positive value indicated a gain, whereas a negative value indicated a loss of genetic diversity. We related these F_{ST} and ΔH_e values to the plant traits in bivariate linear models with the F_{ST} or ΔH_e as response variable and self-compatibility and seed dormancy as explanatory variables.

3 | RESULTS

The mean pairwise genetic differentiation between wild-collected seeds and seeds from the last generations across all cultivation lines of the 19 species was $F_{ST} = 0.034$ (range 0.002–0.071). When analysed across all cultivation lines, F_{ST} significantly increased with the number of generations a population underwent cultivation (Table 2a, Figure 2a). The response of F_{ST} differed between the seeds from the two producers (Figure 2a): while there was an increase in the material from Producer 1, we found no changes in F_{ST} in the seed material from Producer 2. In the five species for which seeds from different regions were available, the absolute values of F_{ST} between wild-collected seeds and the last cultivated generation were much smaller (mean $F_{ST} = 0.015$, range 0.001–0.028) than the F_{ST} between wild populations from different regions (mean $F_{ST} = 0.056$, range 0.016–0.143, Figure 2b; Table 2b.)

The mean expected heterozygosity in our data was $H_e = 0.303$ (range 0.282–0.337), and it was significantly lower in wild-collected seeds (F0) than in generations F1, F2 and F3 (Table 2a; Figure 3a). Only the H_e in the last cultivated generation F4 did not significantly differ from wild seeds, probably because of the small sample size. While the effect of cultivation on H_e did not differ between the two seed producers (Table 2a), the seeds from Producer 1 harboured a higher average H_e than the seeds from Producer 2 (Table 2c; Figure 3b).

The genetic differentiation (F_{ST}) between wild-collected seeds (F0) and the first cultivated generation (F1) was significantly higher in self-compatible species compared to self-incompatible species (Figure 4a), with a similar, albeit not statistically significant, trend in genetic diversity ΔH_e (Figure 4c). Seed dormancy was unrelated to genetic differentiation and genetic diversity (Figure 4b,d, Table 2d.)

4 | DISCUSSION

Seed propagation for restoration is indispensable to cover the rising demand for native seeds. Still, the propagation process could change the genetic properties of cultivated plants and impoverish their genetic diversity (Espeland et al., 2017). We used molecular markers to test for such effects in 19 species cultivated by two different seed producers. We found that cultivated populations genetically differed from the wild-collected seeds, and this differentiation increased with the number of generations in cultivation. Yet, the absolute size of the genetic differentiation due to cultivation was much smaller than that between natural populations from different geographic regions. The genetic diversity of cultivated seeds was even higher than that in wild collections, suggesting that cultivation, as done in Germany and Austria, does not compromise the genetic quality of seed material.

4.1 | Genetic differentiation

The genetic differentiation between wild and cultivated plants increased with the time the populations had spent in cultivation. Yet, this effect was rather small compared to the natural genetic differentiation between regions. The few previous studies that used molecular markers to analyse cultivation effects on plant material propagated for ecosystem restoration also reported no or only minor genetic differentiation through cultivation in the majority of species (Nagel et al., 2019). In contrast, theoretical studies expected cultivated plants to substantially genetically differentiate from wild plants due to genetic drift and unintended selection (Espeland et al., 2017; Pedrini et al., 2020). This discrepancy between theoretical expectations and real data has multiple potential reasons. First, some expectations were based on data from plant breeding and ex situ collections in botanical gardens (Lauterbach et al., 2012). Yet, ex situ collections have often very small population sizes, where genetic differences can quickly arise by genetic drift (Ensslin & Godefroid, 2019; Rauschkolb et al., 2019). The propagation of plant material for ecological restoration typically involves large populations, where the effects of genetic drift are likely minimal. Second, we have been working with a system where the seed producers are aware of potential negative effects of cultivation on genetic properties and try to prevent them (Bucharova et al., 2019; Krautzer et al., 2020; Prasse et al., 2010). However, such regulations may not be present in all production systems (Jones, 2013; Pizza et al., 2021). Third, the material we studied involved at maximum four, but mostly two or three cultivated generations. As the genetic differentiation was increasing with the number of generations, cultivation for more generations may lead to a more substantial genetic differentiation. Fourth, we worked with reduced-representation

TABLE 2 Results of different statistical models relating genetic changes in 20 cultivated wild plants to different aspects of the cultivation process or species traits. (a) The effects of generations in cultivation and seed producer identity on genetic diversity in and genetic differentiation between wild-collected and cultivated plants (Figures 2a and 3a). Note that generation is a continuous variable in the model for genetic differentiation, but categorical in the model for genetic diversity (see Section 2 for details). (b) Comparison between the genetic differentiation within cultivation lines and the natural genetic differentiation between regions (Figure 2b), for the five species where cultivation lines were available from two different regions (see Table 1). (c) Testing for differences in genetic diversity between the two seed producers (Figure 3b). In contrast to the model in Table 2a, this analysis was carried out only with species available from both seed producers. (d) The results of models testing the effects of self-compatibility and seed dormancy on changes in genetic diversity (ΔH_e) and genetic differentiation (F_{ST}) between wild-collected seeds (F0) and the first cultivated generation (F1) (Figure 4a,b). In multivariate models, the terms are fitted sequentially. Significant values are in bold

(a)	Genetic differentiation (F_{ST})				Genetic diversity (H_e)			
Effect	**NumDF**	**DenDF**	***F***	***p***	**NumDF**	**DenDF**	***F***	**P**
Generation	1	50	4.53	**0.038**	4	71	7.40	**<0.001**
Producer	1	50	4.54	**0.038**	1	71	0.64	0.428
Generation × Producer	1	50	5.98	**0.018**	3	71	1.11	0.351

(b)	Genetic differentiation (F_{ST})			
Effect	**NumDF**	**DenDF**	***F***	**P**
Within cultivation line versus between regions	1	9	8.92	**0.015**

(c)	Genetic diversity (H_e)			
Effect	**NumDF**	**DenDF**	***F***	**P**
Species	1	19	5.94	**0.003**
Generation	1	19	0.23	0.639
Producer	1	19	26.51	**<0.001**

(d)	Genetic differentiation (F_{ST}) between F0 and F1				Change in genetic diversity (ΔH_e) between F0 and F1			
Effect	**NumDF**	**DenDF**	***F***	***p***	**NumDF**	**DenDF**	***F***	**P**
Self-compatibility	1	16	16.55	**<0.001**	1	16	1.98	0.180
Dormancy	1	16	0.02	0.892	1	16	0.26	0.618

molecular markers, an excellent tool to identify population history and signs of genetic drift, but suboptimal for detecting adaptation (Lowry et al., 2017). The low genetic differentiation detected in this study does not preclude selection at particular gene loci because adaptive traits may be coded by few genes not covered by our markers. Identifying loci under selection was outside the scope of our multispecies study as this would necessitate whole-genome sequence data and reference genomes which are unavailable for our study species. A more realistic option to detect selective changes would be growing and phenotyping the plants in a common environment.

We did detect—although on a low absolute level—increased genetic differentiation across generations in cultivations in the material from Producer 1 but not from Producer 2. The producers differ in how they source the wild seed: Producer 1 starts with seeds from usually five natural populations, Producer 2 starts only with seed from one population (Krautzer et al., 2020; RegioZert, 2019). Mixing seeds from multiple populations within a source region, as performed by Producer 1, increases genetic diversity (Boca et al., 2020). Higher gene diversity may provide a higher chance of evolution during cultivation. For example, the contribution of individual source populations to the gene pool of the seed lot can shift during the propagation process (Kucera et al., 2022; St. Clair et al., 2020). The observed stronger differentiation across generations in the material of Producer 1 is thus potentially caused by the more diverse starting material. However, diverse starting material also means a diverse seed lot, which is beneficial to restoration because it enhances adaptive potential and the chances of restoration success across environments through the portfolio effect (Crowe & Parker, 2008). The increase in genetic differentiation during cultivation in the seeds from Producer 1 likely does not mean that the production practice of this company is suboptimal, but rather that the benefits of enhanced genetic variability by population mixing is accompanied by an increased probability of minor evolutionary changes in response to the cultivation process. Still, the gradually increasing genetic differentiation indicates that the rule of restricting seed production to a maximum of five generations (Prasse et al., 2010) is justified.

4.2 | Genetic diversity

Genetic diversity was higher in the cultivated generations than in wild-collected seeds, in the seed material from both producers. This contrasts

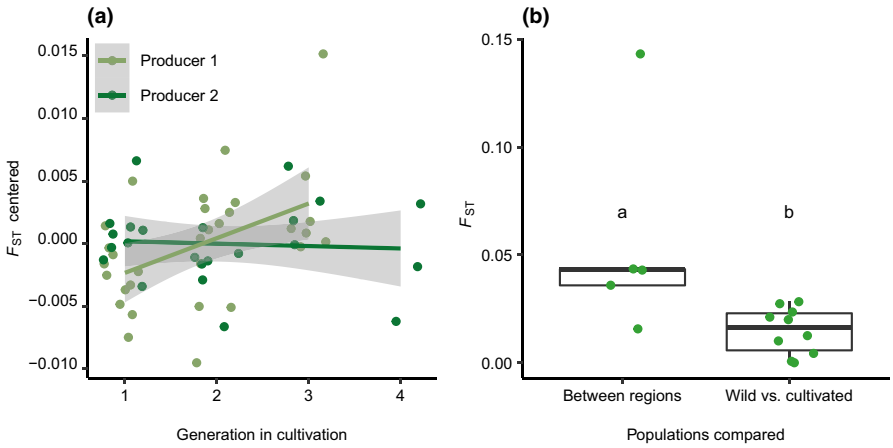

FIGURE 2 (a) The relationship between pairwise F_{ST} (centred to account for differences between species) between wild-collected seeds (F0) and later generations in cultivation across 19 wild plant species. Each point represents one generation of one independent cultivation line. The shaded area is the 95% confidence interval for predictions from a linear mixed-effects model, Producer 1: $F_{1,29} = 7.44$, $p = 0.011$ and Producer 2: $F_{1,21} = 0.09$, $p = 0.774$. For the full model results, see Table 2a. (b) Comparison of pairwise F_{ST} values between wild-collected seeds from the same species from two different regions (between regions), and between wild-collected seeds and the respective last generation in cultivation (wild vs. cultivated) for five species that were available from two regions; (see Table 2b for the model results). Each point represents a generation of an independent cultivation line. Letters above boxplots indicate significant differences ($P < 0.05$)

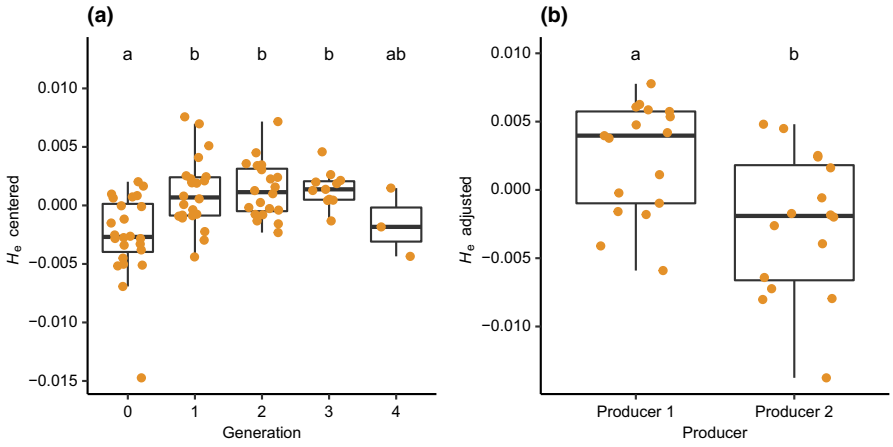

FIGURE 3 Effects of cultivation on genetic diversity. (a) Changes in gene diversity (H_e), centred within cultivation lines, across generations in cultivation (see Table 2a for model results). (b) Comparison of gene diversity between the two seed producers, based on four species available from both producers (see Table 2c for model results). In (b) gene diversity was adjusted for species identity and generation in cultivation. Each point represents a generation of an independent cultivation line. Letters above boxplots indicate significant differences ($P< 0.05$)

with the common expectations that genetic diversity should decline because of genetic drift and repeated bottlenecks (Breed et al., 2018; Espeland et al., 2017; Kantar et al., 2017), as well as with data from ex situ cultivations, where genetic diversity often rapidly declines (Ensslin et al., 2018; Lauterbach et al., 2012). However, as pointed out above, ex situ cultivations have small population sizes, making them extremely vulnerable to genetic drift and loss of variability. The propagation of seeds for restoration typically involves large populations, and the effect of drift is therefore much more limited (Frankham et al., 2014). Increased genetic diversity could in principle result from introgression from other cultivation fields of the same or related species, but this seems unlikely because seed producers keep a safety distance (depending on species, but at least 500 m) between cultivation fields of crossable species (Prasse et al., 2010). The most likely reason for the observed increase of genetic diversity seems enhanced outcrossing under cultivation. Under natural conditions, individuals that grow in close proximity have a higher chance of being closely related (Turner et al., 1982; Vekemans & Hardy, 2004; Zeng et al., 2012), which enhances mating between relatives due to limited distances of pollen dispersal (Kunin, 1993; Turner et al., 1982; Zeng et al., 2012). During all steps of seed propagation, however, seeds from individual plants are mixed, and neighbours are unlikely to be close relatives, even more so if multiple source populations are included. This, together with high population densities under cultivation, promotes outcrossing (Tong et al., 2020). As a result, cultivated seed lots likely contain more heterozygotes and thus harbour more genetic variability than wild-collected seeds.

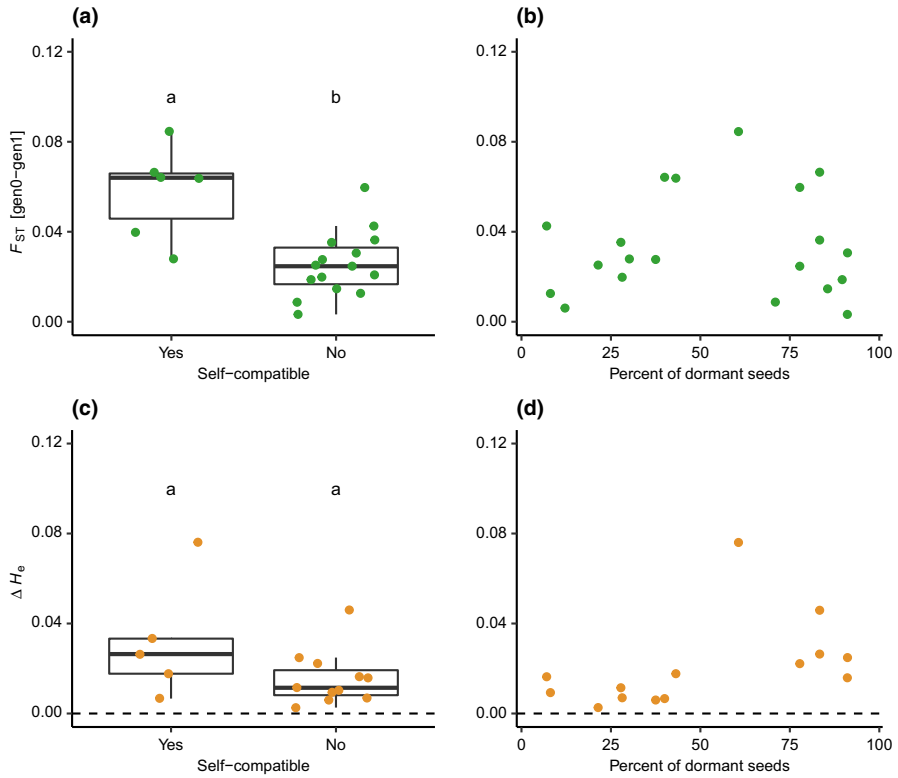

FIGURE 4 Relationships between the self-compatibility and seed dormancy of plants, and the observed magnitudes of genetic changes during cultivation, specifically genetic differentiation (panels a and b) and changes in genetic diversity (panels c and d) between wild-collected seeds (F0) and the first generation in cultivation (F1). Each point represents a species. The letters above boxplots indicate significant differences ($p<0.05$). For the full model results, see Table 2d

4.3 | Species traits and genetic changes

The magnitudes of genetic changes due to cultivation, estimated as the differences between wild seeds and the first cultivated generation, were significantly higher in self-compatible species than in obligate outcrossers for genetic differentiation and, as a trend, for genetic diversity. Wild populations of self-compatible species typically contain more homozygotes (Charlesworth, 2006) than populations of outcrossing species. Consequently, enhanced outcrossing during cultivation means a stronger change for self-compatible species than for outcrossers. These results support our interpretation above that increased outcrossing in the large and homogenized cultivated populations may be a major driver of genetic changes during cultivation.

The percentage of dormant seeds in the source population was unrelated to the magnitudes of genetic changes. This surprised us. The loss of dormancy is among the best-documented evolutionary processes during domestication of wild plants (Purugganan, 2019) because genotypes with dormant seeds do not germinate readily after seeding, and thus do not produce any seeds that could be harvested. We expected that as dormant genotypes would get lost under cultivation in some species, these would experience more pronounced genetic changes. However, the loss of dormant genotypes would be a result of selection. We possibly did not detect this effect due to methodic constraints because reduced-representation sequencing is suboptimal for identifying signatures of selection, which often affects only a small part of the genome and easily escapes detection (Lowry et al., 2017; Mckinney et al., 2017).

While our study provides valuable insight into potential propagation effects and suggests how species traits may affect genetic change during seed production, the latter results should be interpreted with caution. For most species we had only one cultivation line, and we are thus not able to dissect between cultivation line-specific and species-specific patterns. Further, our study included only 19 species representing a narrow trait spectrum. To understand which species are more prone to genetic change during cultivation, we need to study more cultivation lines of more species representing a wider range of traits and production methods.

4.4 | Implication for practice

Agricultural propagation of native plants for ecosystem restoration is mandatory to ensure a sufficient number of seeds for achieving the ambitious targets set by The UN Decade for Ecosystem Restoration (Merritt & Dixon, 2011). Yet, there have been concerns that propagation in production fields may compromise the genetic composition of wild seed and reduce their genetic diversity (Espeland et al., 2017). Our results suggest that these concerns may be, to a certain degree, unwarranted, at least in the highly regulated seed production systems of Germany and Austria.

We detected genetic differentiation between wild and cultivated plants across species, but it was much smaller than the differentiation between wild populations of different regions. As genetic differentiation gradually increased throughout the three to five studied cultivation generations, it is possible that after additional generations the seeds could become substantially different from the original seed sources (Pizza et al., 2021). We also cannot exclude selection on particular phenotypic traits due to

cultivation and harvesting conditions. A cap on the maximum number of generations, for example five in the seed production we studied (Prasse et al., 2010) or in the Yellow Tag certification system in the United States (Young et al., 2003), therefore seems reasonable.

We found that genetic diversity during cultivation even increased, probably as a result of enhanced outcrossing and sometimes mixing multiple source populations in the production fields. This makes such farm-produced seeds especially suitable for restoration because higher genetic diversity enhances adaptive potential and restoration success across different environments through the portfolio effect (Crowe & Parker, 2008).

In summary, we show that the propagation of native seeds for ecosystem restoration only moderately changes the genetic composition of the cultivated seed lots and that genetic diversity is not only maintained but even increased. Yet, our approach did not allow to identify adaptive genetic variability and possible effects of unintended selection (e.g. Nagel et al., 2019) as well as the potential fitness consequences of maternal effects (e.g. Espeland & Hammond, 2013). Future research should attempt to close this gap through common-garden studies and transplant experiments that test for changes in phenotypes and examine the adaptive significance of genetic changes.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.B., O.B. and W.D. conceived the idea; M.C. performed the laboratory analysis with support from W.D.; M.C. analysed the data with support from W.D., C.L. and A.B.; M.C. wrote the first draft with significant input from A.B. and C.L. All authors critically revised the manuscript.

DATA AVAILABILITY STATEMENT

Raw sequence data have been deposited in the European Nucleotide Archive (ENA, https://www.ebi.ac.uk/ena) under project accession number PRJEB47978 and individual sample accessions ERS7671398 - ERS7671620. SNP data in vcf format and the SNP filtering R code are available via Dryad Digital Repository https://doi.org/10.5061/dryad.8pk0p2npw (Conrady et al., 2022).

ORCID

Malte Conrady https://orcid.org/0000-0003-2661-3967
Christian Lampei https://orcid.org/0000-0003-2866-2869
Oliver Bossdorf https://orcid.org/0000-0001-7504-6511
Walter Durka https://orcid.org/0000-0002-6611-2246
Anna Bucharova https://orcid.org/0000-0002-5468-5426

REFERENCES

Andersson, S., & Ofori, J. K. (2013). Effects of mating system on adaptive potential for leaf morphology in *Crepis tectorum* (Asteraceae). *Annals of Botany*, *112*(5), 947–955. https://doi.org/10.1093/aob/mct158

Barrett, R. D. H., & Schluter, D. (2008). Adaptation from standing genetic variation. *Trends in Ecology & Evolution*, *23*(1), 38–44. https://doi.org/10.1016/j.tree.2007.09.008

Basey, A. C., Fant, J. B., & Kramer, A. T. (2015). Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. *Native Plants Journal*, *16*(1), 37–53. https://doi.org/10.3368/npj.16.1.37

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Boca, S. M., Huang, L., & Rosenberg, N. A. (2020). On the heterozygosity of an admixed population. *Journal of Mathematical Biology*, *81*(6–7), 1217–1250. https://doi.org/10.1007/s00285-020-01531-9

Breed, M. F., Harrison, P. A., Bischoff, A., Durruty, P., Gellie, N. J. C., Gonzales, E. K., Havens, K., Karmann, M., Kilkenny, F. F., Krauss, S. L., Lowe, A. J., Marques, P., Nevill, P. G., Vitt, P. L., & Bucharova, A. (2018). Priority actions to improve provenance decision-making. *BioScience*, *68*(7), 510–516. https://doi.org/10.1093/biosci/biy050

Bucharova, A., Bossdorf, O., Hölzel, N., Kollmann, J., Prasse, R., & Durka, W. (2019). Mix and match: Regional admixture provenancing strikes a balance among different seed-sourcing strategies for ecological restoration. *Conservation Genetics*, *20*(1), 7–17. https://doi.org/10.1007/s10592-018-1067-6

Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., & Cresko, W. A. (2013). Stacks: An analysis tool set for population genomics. *Molecular Ecology*, *22*(11), 3124–3140. https://doi.org/10.1111/mec.12354

Charlesworth, D. (2006). Evolution of plant breeding systems. *Current Biology*, *16*(17), 726–735. https://doi.org/10.1016/j.cub.2006.07.068

Conrady, M., Lampei, C., Bossdorf, O., Durka, W., & Bucharova, A. (2022). VCF files of common grassland plants from wild collected seeds of 19 common European grassland species with up to 4 consecutive generations grown in monoculture for seed production for restoration. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.8pk0p2npw

Crowe, K. A., & Parker, W. H. (2008). Using portfolio theory to guide reforestation and restoration under climate change scenarios. *Climatic Change*, *89*(3–4), 355–370. https://doi.org/10.1007/s10584-007-9373-x

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., … Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*(6471). https://doi.org/10.1126/science.aax3100

Dyer, A. R., Knapp, E. E., & Rice, K. J. (2016). Unintentional selection and genetic changes in native perennial grass populations during commercial seed production. *Ecological Restoration*, *34*(1), 39–48. https://doi.org/10.3368/er.34.1.39

Elzenga, J. T. M., Bekker, R. M., & Pritchard, H. W. (2019). Maximising the use of native seeds in restoration projects. *Plant Biology*, *21*(3), 377–379. https://doi.org/10.1111/plb.12984

Ensslin, A., & Godefroid, S. (2019). How the cultivation of wild plants in botanic gardens can change their genetic and phenotypic status and what this means for their conservation value. *Sibbaldia: The International Journal of Botanic Garden Horticulture*, (17), 51–70. https://doi.org/10.24823/Sibbaldia.2019.267

Ensslin, A., Van de Vyver, A., Vanderborght, T., & Godefroid, S. (2018). Ex situ cultivation entails high risk of seed dormancy loss on short-lived wild plant species. *Journal of Applied Ecology*, *55*(3), 1145–1154. https://doi.org/10.1111/1365-2664.13057

Espeland, E. K., Emery, N. C., Mercer, K. L., Woolbright, S. A., Kettenring, K. M., Gepts, P., & Etterson, J. R. (2017). Evolution of plant materials for ecological restoration: Insights from the applied and basic literature. *Journal of Applied Ecology*, *54*(1), 102–115. https://doi.org/10.1111/1365-2664.12739

Espeland, E. K., & Hammond, D. (2013). Maternal effects on growth and competitive ability in a commonly used restoration species. *Native Plants Journal*, *14*(3), 231–242. https://doi.org/10.3368/npj.14.3.231

Frankham, R., Bradshaw, C. J. A., & Brook, B. W. (2014). Genetics in conservation management: Revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation*, *170*, 56–63. https://doi.org/10.1016/j.biocon.2013.12.036

Futschik, A., & Schlötterer, C. (2010). The next generation of molecular markers from massively parallel sequencing of pooled DNA samples. *Genetics*, *186*(1), 207–218. https://doi.org/10.1534/genetics.110.114397

Hivert, V., Leblois, R., Petit, E. J., Gautier, M., & Vitalis, R. (2018). Measuring genetic differentiation from pool-seq data. *Genetics*, *210*(1), 315–330. https://doi.org/10.1534/genetics.118.300900

Hölzel, N., Buisson, E., & Dutoit, T. (2012). Species introduction – A major topic in vegetation restoration. *Applied Vegetation Science*, *15*(2), 161–165. https://doi.org/10.1111/j.1654-109x.2012.01189.x

Jones, T. A. (2013). Ecologically appropriate plant materials for restoration applications. *BioScience*, *63*(3), 211–219. https://doi.org/10.1525/bio.2013.63.3.9

Kantar, M. B., Nashoba, A. R., Anderson, J. E., Blackman, B. K., & Rieseberg, L. H. (2017). The genetics and genomics of plant domestication. *BioScience*, *67*(11), 971–982. https://doi.org/10.1093/biosci/bix114

Kettenring, K. M., & Galatowitsch, S. M. (2007). Tools for Carex revegetation in freshwater wetlands: Understanding dormancy loss and germination temperature requirements. *Plant Ecology*, *193*(2), 157–169. https://doi.org/10.1007/s11258-006-9255-8

Kiehl, K., Kirmer, A., Shaw, N., & Tischew, S. (2014). *Guidelines for native seed production and grassland restoration*. Cambridge Scholars Publishing. Retrieved from https://www.cambridgescholars.com/product/978-1-4438-5900-4

Krautzer, B., Graiss, W., & Blaschka, A. (2020). Prüfrichtlinie für die Zertifizierung und den Vertrieb von regionalen Wildgräsern und Wildkräutern nach "Gumpensteiner Herkunftszertifikat". *Bundesministerium für Nachhaltigkeit und Tourismus*, 1–18. Retrieved from https://gzert.at/assets/downloads/G-Zert-Richtlinie-Web.pdf

Kucera, K. F., Fant, J. B., Jensen, S., Landeen, M., Orr, E., & Kramer, A. T. (2022). Genetic variation and structure change when producing and using mixed-source seed lots for restoration. *Restoration Ecology*, *30*(3). https://doi.org/10.1111/rec.13521

Kühn, I., Durka, W., & Klotz, S. (2004). BiolFlor - a new plant-trait database as a tool for plant invasion ecology. *Diversity and Distributions*, *10*(5–6), 363–365. https://doi.org/10.1111/j.1366-9516.2004.00106.x

Kunin, W. E. (1993). Sex and the single mustard: Population density and pollinator behavior effects on seed-set. *Ecology*, *74*(7), 2145–2160. https://doi.org/10.2307/1940859

Lau, J. A., Magnoli, S. M., Zirbel, C. R., & Brudvig, L. A. (2019). The limits to adaptation in restored ecosystems and how management can help overcome them. *Annals of the Missouri Botanical Garden*, *104*(3), 441–454. https://doi.org/10.3417/2019430

Lauterbach, D., Burkart, M., & Gemeinholzer, B. (2012). Rapid genetic differentiation between ex situ and their in situ source populations: An example of the endangered *Silene otites* (Caryophyllaceae). *Botanical Journal of the Linnean Society*, *168*(1), 64–75. https://doi.org/10.1111/j.1095-8339.2011.01185.x

Leger, E. A., & Baughman, O. W. (2015). What seeds to plant in the great basin? Comparing traits prioritized in native plant cultivars and releases with those that promote survival in the field. *Natural Areas Journal*, *35*(1), 54–68. https://doi.org/10.3375/043.035.0108

Lowry, D. B., Hoban, S., Kelley, J. L., Lotterhos, K. E., Reed, L. K., Antolin, M. F., & Storfer, A. (2017). Breaking RAD: An evaluation of the utility of restriction site-associated DNA sequencing for genome scans of adaptation. *Molecular Ecology Resources*, *17*(2), 142–152. https://doi.org/10.1111/1755-0998.12635

McKinney, G. J., Larson, W. A., Seeb, L. W., & Seeb, J. E. (2017). RADseq provides unprecedented insights into molecular ecology and evolutionary genetics: Comment on Breaking RAD by Lowry et al. (2016). *Molecular Ecology Resources*, *17*(3), 356–361. https://doi.org/10.1111/1755-0998.12649

Meissen, J. C., Galatowitsch, S. M., & Cornett, M. W. (2015). Risks of overharvesting seed from native tallgrass prairies. *Restoration Ecology*, *23*(6), 882–891. https://doi.org/10.1111/rec.12295

Merritt, D. J., & Dixon, K. W. (2011). Restoration seed banks – A matter of scale. *Science*, *332*(6028), 424–425. https://doi.org/10.1126/science.1203083

Nagel, R., Durka, W., Bossdorf, O., & Bucharova, A. (2019). Rapid evolution in native plants cultivated for ecological restoration: Not a general pattern. *Plant Biology*, *21*(3), 551–558. https://doi.org/10.1111/plb.12901

Nei, M., & Roychoudhury, A. K. (1974). Genic variation within and between the three major races of man, Caucasoids, Negroids, and Mongoloids. *The American Journal of Human Genetics*, *26*(4), 421–443.

Nevill, P. G., Cross, A. T., & Dixon, K. W. (2018). Ethical seed sourcing is a key issue in meeting global restoration targets. *Current Biology*, *28*(24), 1378–1379. https://doi.org/10.1016/j.cub.2018.11.015

O'Leary, S. J., Puritz, J. B., Willis, S. C., Hollenbeck, C. M., & Portnoy, D. S. (2018). These aren't the loci you'e looking for: Principles of effective SNP filtering for molecular ecologists. *Molecular Ecology*, *27*(16), 3193–3206. https://doi.org/10.1111/mec.14792

Pedrini, S., Gibson-Roy, P., Trivedi, C., Gálvez-Ramírez, C., Hardwick, K., Shaw, N., Frischie, S., Laverack, G., & Dixon, K. (2020). Collection and production of native seeds for ecological restoration. *Restoration Ecology*, *28*(S3), S228–S238. https://doi.org/10.1111/rec.13190

Pertoldi, C., Bijlsma, R., & Loeschcke, V. (2007). Conservation genetics in a globally changing environment: Present problems, paradoxes and future challenges. *Biodiversity and Conservation*, *16*(14), 4147–4163. https://doi.org/10.1007/s10531-007-9212-4

Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., & Hoekstra, H. E. (2012). Double digest RADseq: An inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS One*, *7*(5), e37135. https://doi.org/10.1371/journal.pone.0037135

Pickersgill, B. (2009). Domestication of plants revisited – Darwin to the present day. *Botanical Journal of the Linnean Society*, *161*(3), 203–212. https://doi.org/10.1111/j.1095-8339.2009.01007.x

Pizza, R., Espeland, E., & Etterson, J. (2021). Eight generations of native seed cultivation reduces plant fitness relative to the wild progenitor population. *Evolutionary Applications*, *14*(7), 1816–1829. https://doi.org/10.1111/eva.13243

Prasse, R., Kunzmann, D., & Schröder, R. (2010). *Development and practical implementation of minimal requirements for the verification of origin of native seeds of herbaceous plants*. Deutsche Bundesstiftung Umwelt, Hannover, Germany. Final Report of the Research Project (DBU FKZ: 23931). Retrieved from https://www.dbu.de/OPAC/ab/DBU-Abschlussbericht-AZ-23931.pdf

Puritz, J. B., Hollenbeck, C. M., & Gold, J. R. (2014). dDocent: A RADseq, variant-calling pipeline designed for population genomics of non-model organisms. *PeerJ*, *2*, e431. https://doi.org/10.7717/peerj.431

Purugganan, M. D. (2019). Evolutionary insights into the nature of plant domestication. *Current Biology*, *29*(14), R705–R714. https://doi.org/10.1016/j.cub.2019.05.053

R Development Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/

Rauschkolb, R., Szczeparska, L., Kehl, A., Bossdorf, O., & Scheepens, J. F. (2019). Plant populations of three threatened species experience

rapid evolution under ex situ cultivation. *Biodiversity and Conservation*, *28*(14), 3951–3969. https://doi.org/10.1007/s10531-019-01859-9

RegioZert®. (2019). *Regelwerk des Zertifizierungssystems RegioZert® zur Herkunfts- und Qualitätssicherung von gebietseigenem Saatgut Ein Konzept der BDP AG Regiosaatgut*. Retrieved from https://www.bdp-online.de/de/Branche/Saatguthandel/RegioZert/Autochthones_Saatgut___was_ist_das_/2019-08-22_Konzept_RegioZert_Stand_Aug_2019.pdf

Rochette, N. C., Rivera-Colón, A. G., & Catchen, J. M. (2019). Stacks 2: Analytical methods for paired-end sequencing improve RADseq-based population genomics. *Molecular Ecology*, *28*(21), 4737–4754. https://doi.org/10.1111/mec.15253

St. Clair, A. B., Dunwiddie, P. W., Fant, J. B., Kaye, T. N., & Kramer, A. T. (2020). Mixing source populations increases genetic diversity of restored rare plant populations. *Restoration Ecology*, *28*(3), 583–593. https://doi.org/10.1111/rec.13131

Tong, Y., Durka, W., Zhou, W., Zhou, L., Yu, D., & Dai, L. (2020). Ex situ conservation of *Pinus koraiensis* can preserve genetic diversity but homogenizes population structure. *Forest Ecology and Management*, *465*, 117820. https://doi.org/10.1016/j.foreco.2019.117820

Turner, M. E., Stephens, J. C., & Anderson, W. W. (1982). Homozygosity and patch structure in plant populations as a result of nearest-neighbor pollination. *Proceedings of the National Academy of Sciences*, *79*(1), 203–207. https://doi.org/10.1073/pnas.79.1.203

Vekemans, X., & Hardy, O. J. (2004). New insights from fine-scale spatial genetic structure analyses in plant populations. *Molecular Ecology*, *13*(4), 921–935. https://doi.org/10.1046/j.1365-294x.2004.02076.x

Young, S. A., Schrumpf, B., & Amberson, E. (2003). *The Aosca native plant connection*. Association of Official Seed Certifying Agencies (AOSCA). Retrieved from https://www.aosca.org/wp-content/uploads/Documents///AOSCANativePlantConnectionBrochure_AddressUpdated_27Mar2017.pdf

Zeng, X., Michalski, S. G., Fischer, M., & Durka, W. (2012). Species diversity and population density affect genetic structure and gene dispersal in a subtropical understory shrub. *Journal of Plant Ecology*, *5*(3), 270–278. https://doi.org/10.1093/jpe/rtr029

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