

Species and genetic diversity patterns show different responses to land use intensity in central European grasslands

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Editor: Gwen Iacona

Abstract

Aim: Empirical studies have often reported parallel patterns of genetic and species diversity, but the strength and generality of this association, as well as its origin, are still debated. Particularly in human-dominated landscapes with complex histories of land use histories, more complicated and partly diverging patterns have been observed. In this study, we examine whether species and genetic diversity correlate across grasslands with different levels of land use pressure and spatial differentiation in habitat quality and heterogeneity.

Location: We selected eight extensively used (grazed, unfertilized) dry grasslands and eight intensively used (mown, fertilized) hay meadows in southeastern Germany.

Methods: We used vegetation surveys and molecular markers of six widespread dry grassland and six hay meadow plant species to compare species and genetic alpha and beta diversity between the two grassland types.

Results: Species diversity patterns expectedly showed higher alpha diversity, stronger spatial structure and less turnover in dry grasslands than in hay meadows. Neither of the corresponding genetic diversity patterns showed the same significant trends.

Main conclusion: Our results question the idea that species and genetic diversity patterns will always show similar patterns. Likely, genetic and species diversity emerge partly from shared, partly from different processes, including the regional species pool, environmental heterogeneity, fragmentation and land use history. The practical conservation implication is that species and genetic diversity are not generally interchangeable. Looking at species and genetic patterns together, however, may eventually lead to a better understanding of the complex processes that shape the structure and dynamics of ecological communities.

KEYWORDS

dry grassland, genetic diversity, grazing, hay meadow, land use, mowing, species diversity, species genetic diversity correlation

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1 | INTRODUCTION

In recent years, there has been increasing interest in genetic diversity, both as a target for conservation in its own right (CBD; www.cbd.int/convention/text/), but also as an indicator of species diversity, population viability and gene flow or genetic connectivity (Fuller et al., 2013; Kahilainen et al., 2014; Leimu et al., 2006; Münzbergová et al., 2013; Taberlet et al., 2012). Previous studies have often reported a positive correlation of species and genetic diversity (Frey et al., 2015; He et al., 2008; Odat et al., 2009; Papadopoulou et al., 2011; Struebig et al., 2011; Wei & Jiang, 2012), while other studies found no or even negative relationships between the two patterns (Avolino & Smith, 2013; Odat et al., 2004; Puschas et al., 2008; Silvertown et al., 2009; Taberlet et al., 2012). Most of these studies analysed variation in genetic diversity of a single species (Avolino & Smith, 2013; He et al., 2008; Odat et al., 2004, 2009; Puschas et al., 2008; Silvertown et al., 2009; Wei & Jiang, 2012). Only a few studies considered a larger set of species (Frey et al., 2015; Papadopoulou et al., 2011; Taberlet et al., 2012), which arguably allows more direct inference about community-level genetic diversity.

If and under which conditions we would expect associations between genetic and species diversity is still not well understood. Unlike phylogenetic diversity metrics, which measure between-species genetic differentiation in a community and are thus naturally correlated with species diversity (Cadotte et al., 2010), measures of genetic diversity are calculated per species and are thus not trivially linked to species diversity. If associations between the two are found, one would presume that they occur because the same ecological processes are driving both genetic and species diversity.

Candidates for such processes are manifold—genetic diversity, similar to species diversity, is thought to be affected by various factors, including environmental conditions (Amos & Harwood, 1998), landscape structure and isolation (Aguilar et al., 2008; Honnay & Jacquemyn, 2007; Putz et al., 2015), population size (Ellegren & Galtier, 2016; Ouborg et al., 2006) and a species' biological traits (Hamrick & Godt, 1996; Nybom & Bartish, 2000; Reisch & Bernhardt-Römermann, 2014).

It has been argued (Vellend, 2005; Vellend et al., 2014) that of those, landscape structure is the most likely candidate to explain correlations between genetic and species diversity. Vellend et al. (2014) propose that species and genetic diversity both follow the principles of the equilibrium theory of island biogeography (MacArthur & Wilson, 1967) and the island model of population genetics (Wright, 1940). We would therefore expect that both levels of biodiversity should exhibit parallel patterns in metacommunities that are structured mainly by population size and isolation (Vellend, 2005), and empirical studies that have indeed often found support for these assumptions. For example, several studies have found positive correlations between genetic and species alpha diversity (Evanno et al., 2009; Odat et al., 2004, 2009; Papadopoulou et al., 2011; Struebig et al., 2011), which can be understood when assuming that both patterns are predominantly driven by barriers against gene flow (Odat et al., 2004, 2009).

The equilibrium conditions assumed in this explanation, however, are the exception rather than the norm in many areas of the world, in particular in cultural landscapes that harbour the bulk of Europe's threatened species. Previous studies have often found different patterns of species and genetic diversity in such landscapes, which has been explained by different temporal responses to the availability of suitable habitats (Puschas et al., 2008). A key class of habitats in this context are grassland ecosystems, which cover about one-third of the agriculturally used area of Europe (Isselstein et al., 2005) and belong, therefore, to the most important elements of the European landscape. They were and are heavily transformed by human land use, resulting in species pools that have likely not yet returned to equilibrium, and that often show significant spatial differentiation in habitat quality and heterogeneity. All this makes them an interesting system to test the proposition that spatial habitat structure leads to parallel patterns in genetic and species diversity.

Regarding species diversity, previous research has stressed that grassland diversity patterns seem to be strongly determined by management (Gaujour et al., 2012). Extensively used grazed and unfertilized dry grasslands are among the most species-rich ecosystems worldwide with up to 105 species on 16 m² (Wilson et al., 2012), whereas intensively managed mown and fertilized hay meadows often only contain about 20 species on 16 m² (Gilhaus et al., 2017). The relationship between-species diversity and land use intensity by fertilization, mowing and/or grazing has been illustrated by numerous studies (Foley et al., 2005; Hodgson et al., 2005; Klaus et al., 2011, 2013; Klimek et al., 2007; Socher et al., 2012; Zechmeister et al., 2003). Fertilizer application, frequent mowing or grazing, and increased levels of atmospheric nitrogen deposition since the middle of the 20th century caused a general loss of species richness and shifts in species and functional composition of European grasslands (Diekmann et al., 2014; Huber et al., 2017; Klimek et al., 2007; Rook et al., 2004; Socher et al., 2012; Wesche et al., 2012).

For genetic diversity, the situation is less clear, also because the impact of grassland management on genetic diversity has been studied less frequently, and existing studies mostly focus on single species (Kloss et al., 2011; Last et al., 2014; Nakahama et al., 2016). It has been reported that mowing and fertilization reduce genetic diversity (Kölliker et al., 1998; Last et al., 2014). Grazing, in contrast, seems to have a positive effect due to the generation of habitat heterogeneity via trampling, litter removal and nutrient input by excrements, which promotes sexual reproduction and creates niches for different genotypes (Peng et al., 2015; Rudmann-Maurer et al., 2007; Völler et al., 2013). Several studies have demonstrated an impact of land use on genetic differentiation, mostly due to limited gene flow among populations because of differences in flowering and fruiting phenology resulting from different times for grazing or mowing (Reisch & Poschod, 2009; Völler et al., 2013). However, the impact of land use on genetic diversity may be obscured by intensive gene flow among grasslands, which buffers potential effects of genetic drift and erosion caused by land use (Kloss et al., 2011; Odat et al., 2004). This means that present gene flow among hay meadows may increase genetic

diversity and buffer the negative impacts of mowing. Moreover, dry grasslands were formerly more frequent than hay meadows, but currently the opposite is true. Recent research suggested that historic drivers dominate the pattern (Reisch et al., 2017). A few of these studies, however, are suitable to directly compare patterns of genetic and species diversity, either because they did not report species diversity on the same sites, or because most studies of genetic diversity consider for only one species per habitat type (Reisch & Schmid, 2019).

The aim of the present study is to contrast patterns of species and genetic alpha and beta diversity between extensively used, grazed, unfertilized dry grasslands and intensively used, mown and fertilized hay meadows in south eastern Germany, to explore to what extent both measures show parallel patterns, and to test if those patterns are compatible with our expectations about drivers of genetic and species diversity that have been discussed in our introduction. To this end, we calculated genetic and species alpha and beta diversity measures for 12 species in 16 populations (8 in extensively used dry grasslands and 8 in intensively used hay meadows), and compare to which extent those indicators show similar signals.

2 | METHODS

2.1 | Study sites

We selected eight extensively used, grazed, unfertilized dry grasslands and eight intensively used, mown and fertilized hay meadows in the valley of the river Laber on the Franconian Alb near Regensburg (Figure 1; Supplementary Material S1, Table S1.1). Dry grasslands and hay meadows were paired in a blocked design to avoid spatial pseudoreplication. The climate in this region is subcontinental with an annual precipitation of 649 mm and a mean annual temperature of 7.4°C (BayKLIMFOR, 1996). Dry grasslands in the study region date back at least to the period of the Roman Empire (Poschlod & Baumann, 2010) and have been grazed frequently until the 1960s, as have most other grasslands in central Europe (Poschlod, 2015). At present, they are infrequently grazed about once a year. Hay meadows occurred for the first time at the end of the seventeenth century (Poschlod, 2015) in central Europe and are, therefore, much younger. In our study area, they are mown twice and fertilized once a year.

2.2 | Species diversity

To determine species diversity, we established ten plots with a size of 3x4 m at each study site. We recorded all grass and herb species occurring in the plots and calculated the mean species diversity of each study site (Supplementary Material S1, Table S1.1). Area and distance to the nearest dry grassland or hay meadow (as proxy for isolation) were calculated using GIS (Arc Info 10.0, Esri) based upon orthorectified aerial photographs.

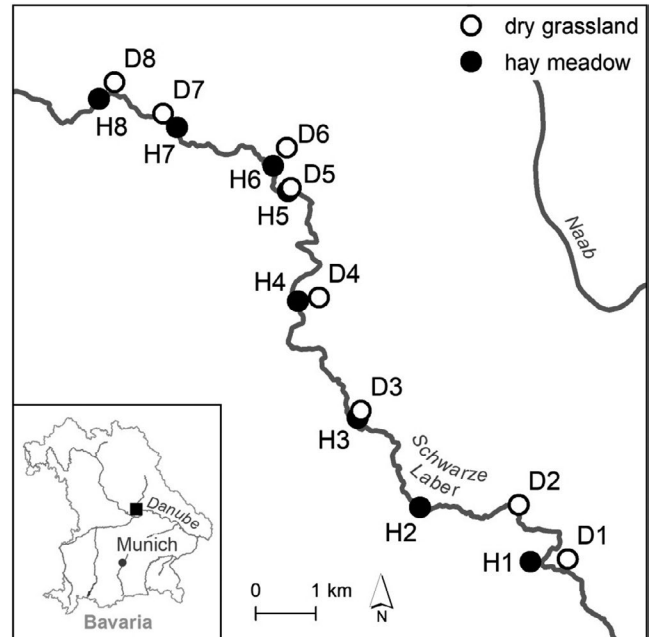


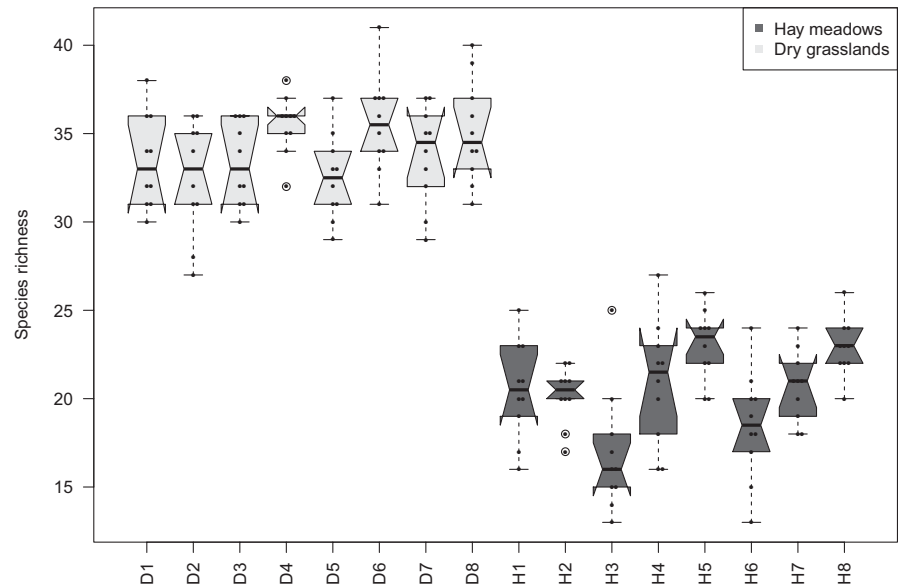
FIGURE 1 Geographic position of the selected dry grasslands and hay meadows in the valley of the river Laber on the Franconian Alb near Regensburg in southeast Germany

2.3 | Genetic diversity

Dry grasslands and hay meadows have different species pools. As too few species occur in both grassland ecosystems, we selected six perennial, outcrossing, widespread and according to our assessment ecologically comparable plant species for each habitat type (approximately 15 individuals per population; Supplementary Material S1, Table S1.2). We collected leaf material of *Plantago lanceolata*, *Galium mollugo*, *Ranunculus acris*, *Trifolium repens*, *Trifolium pratense* and *Trifolium dubium* from hay meadows, and *Teucrium chamaedrys*, *Galium verum*, *Hippocrepis comosa*, *Dianthus carthusianorum*, *Plantago media* and *Medicago lupulina* from dry grasslands. We assessed the frequency of the study species on the study sites as proportion of occurrence in ten plots with a size of one m² (Supplementary Material S1, Table S1.3) and later interpreted this frequency as a proxy for population size.

Leaf material was placed in plastic bags in the field and stored in a laboratory freezer at -20°C until molecular analysis. In total, 1,446 individuals from 96 populations were analysed. Following (Reisch & Kellermeier, 2007), DNA for molecular analyses was isolated from dry leaf material using the CTAB-based method (Rogers & Bendich, 1994) and diluted with water to a concentration of 7.8 ng/μl. DNA solutions were then used to analyse Amplified Fragment Length Polymorphisms (protocol see Bylebyl et al., 2008; Reisch, 2008). After screening 30 primer combinations, three primer combinations per species were chosen for AFLP analysis (Supplementary Material S1, Table S1.4). The EcoRI primers were labelled with different fluorescent dyes. The resulting PCR products were separated using capillary gel electrophoresis (GeXP, Beckmann Coulter). Fragments were checked with the GeXP software (Beckman Coulter) and

FIGURE 2 Species richness of the studied dry grasslands and hay meadows. Notches depict nonparametric estimates of the 95% CI of the median for each box. Small points show the raw data for each group



analysed using the software Bionumerics 4.6 (Applied Maths, Kortrijk, Belgium). Only those fragments that showed clear and distinct bands were used for further analyses. Samples with weak banding patterns or PCR artefacts were repeated. The percentage of polymorphic loci per species ranged from 77.6 to 98.0 (Table S1.4). To confirm the reproducibility of molecular analyses, we used 10% of all analysed samples to estimate the genotyping error rate (Bonin et al., 2004), which was 3.8%.

AFLP bands were then transformed into a binary (0/1) matrix and analysed via analysis of molecular variance (AMOVA) for each species. AMOVA compares the pairwise squared Euclidian distance among molecular phenotypes, which are defined by the differences in discrete band states. From the AMOVA, we obtained pairwise genetic distances (Φ_{PT}) among the studied populations of each species and their levels of significance, as well as genetic diversity of each population (Table S1.5, see Fischer & Matthies, 1998). We used AMOVA sums of squares divided by $n-1$ to determine sample size independent levels of genetic diversity as described previously (Fischer & Matthies, 1998; Listl et al., 2017; Reisch et al., 2003). There are alternative metrics for genetic diversity, in particular gene diversity (H). An additional analysis of differences using H is provided in Supplementary Material S2.

2.4 | Statistical analysis

To identify factors influencing species and genetic alpha diversity, we used linear mixed and generalized linear mixed models from the R packages lme4 and lmerTest (Bates et al., 2015; Kuznetsova et al., 2016). For species alpha diversity (species richness), we considered habitat type, size and isolation of the population as explanatory variables. For genetic alpha diversity (measured as sums of squares/ $n-1$), we considered the same factors, plus frequency of the target species in the population and the interaction between frequency and habitat type.

Species beta diversity was quantified by multivariate homogeneity of groups' dispersion (Anderson, 2006; Anderson et al., 2006), implemented in the R package vegan (Oksanen et al., 2017). For the analysis of genetic beta diversity, we used a t test to test whether Φ_{PT} values (measuring genetic differentiation between populations) differed between habitat groups.

For the spatial analysis, we used Mantel tests from package vegan, to test for an association between-species Bray-Curtis dissimilarity and Φ_{PT} among populations with geographic distance.

Code and detailed results for all analyses are provided in Supplementary Material S2. See also section "Data availability statement."

3 | RESULTS

3.1 | Comparison of species and genetic alpha diversity

Species alpha diversity (average local species richness per 12 m², details see methods) was significantly higher in dry grasslands than in hay meadows. (Figure 2, effect of vegetation type was significant in a multiple linear regression after correcting for possible confounders, see Table 1). Isolation and habitat area (as a proxy of population size) did not have a significant effect on species richness (Table 1).

Habitat effects on genetic alpha diversity (measured as sum of AMOVA squares divided by $n-1$, $SSWP/n-1$) were visually much less pronounced (Figure 3) and statistically not significant in a multiple linear regression after correcting for the fixed effects area, isolation and frequency, as well as species and plot by random effects (Table 1). Moreover, none of the other secondary explanatory variables (area, isolation, frequency) showed significant correlations with genetic diversity either. The apparent correlation between genetic diversity and frequency in Figure 3 (which is significant without correcting for the effects of the other predictors) occurs because of

	Species alpha diversity			Genetic alpha diversity		
	Estimate	SE	p-Value	Estimate	SE	p-Value
Intercept	3.02	0.027	***	18.47	3.38	***
Habitat = hay meadow	0.49	0.039	***	5.42	4.79	n.s.
Area	-0.003	0.016	n.s.	0.22	0.31	n.s.
Isolation	0.02	0.018	n.s.	0.24	0.32	n.s.
Frequency	Not included			-0.19	0.60	n.s.
Habitat*frequency	Not included			1.14	0.82	n.s.

TABLE 1 Regression table for predictors of species and genetic alpha diversity

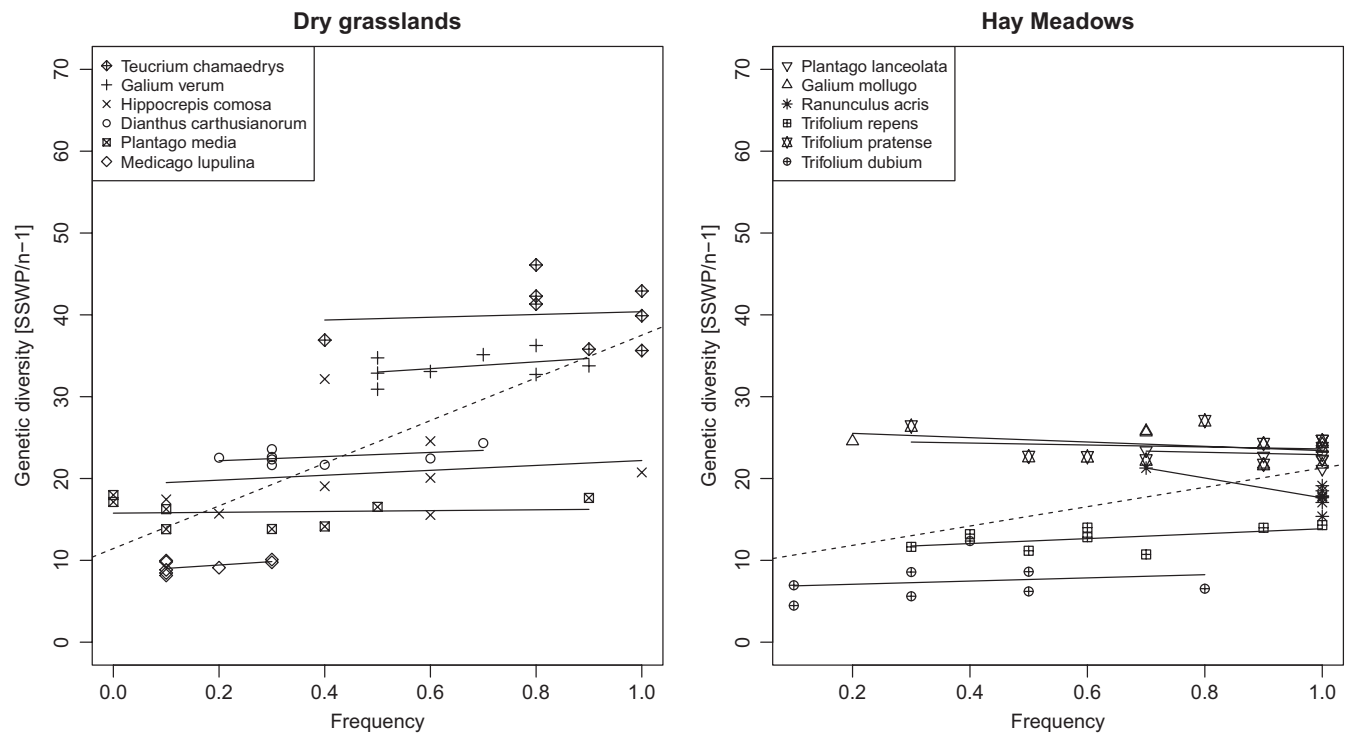


FIGURE 3 Genetic alpha diversity (measured in SSWP/n-1) for the 6 species each in the dry grasslands and hay meadows against the frequency (FR) of plots in which the species was found. The dashed line in each plot shows a linear regression estimate across all species and populations, the solid lines show linear regression estimates per species. The comparison (and Table 1) suggests that genetic diversity differs little within species, and apparent correlations between FR and genetic diversity occur because of a confounding of FR with species

a confounding between-species identity and frequency—as soon as species identity is included in the statistical model, differences in genetic diversity are preferably explained by species identity, with no further significant effects of the other variables (see Supplementary Material S2).

The confounding between frequency and species occurs because species with a higher mean frequency also tended to have a higher mean genetic diversity, in particular in dry grasslands (Figure 1). However, these correlations were not significant at the species level (see Supplementary Material S2). It should be noted, however, that we had only six replicates (species) per habitat, meaning that we had low power to detect such effects if it exists.

3.2 | Comparison of species and genetic beta diversity and spatial patterns

Species beta diversity (measured as multivariate homogeneity of group dispersion, see methods) was significantly higher in hay meadows. Community similarity was significantly correlated to distance in dry grasslands, but not in hay meadows (Mantel Tests, see Supplementary Material S2).

Genetic beta diversity (measured as genetic differentiation between sites, Φ_{PT}) was not significantly different between hay meadows and dry grasslands (*t* test, see Supplementary Material S2). Mantel tests showed a significant spatial effect on genetic similarity

for four of the six hay meadow species and for three of the six dry grassland species.

4 | DISCUSSION

The aim of this study was to compare patterns of species and genetic diversity in dry grasslands and hay meadows. Our main findings are that both alpha and beta patterns differ between genetic and species diversity. For species diversity, we generally find higher diversity, stronger spatial structure, and lower turnover in dry grasslands, while the same differences are largely absent or negligible in genetic diversity patterns. For reasons explained in more detail below, we conjecture that species diversity patterns are more strongly driven by habitat heterogeneity, age and fragmentation, while genetic patterns may be diluted by gene flow due to historical management and various historical contingencies, for example the historic reversal of habitat area managed as dry grasslands and hay meadows.

4.1 | Species diversity patterns

We observed higher species alpha diversity in extensively grazed and unfertilized dry grasslands, characterized by lower land use intensity. There are several possible explanations for this pattern: some previous studies link species alpha diversity to land use intensity (Isselstein et al., 2005), and in particular to the application of fertilizers, which results in a loss of less competitive plant species (Klaus et al., 2011, 2013; Klimek et al., 2007). Another explanation is that hay meadows are typically mown, while dry grasslands are grazed. Mowing tends to reduce species alpha diversity (Socher et al., 2012; Zechmeister et al., 2003), because it impedes seed production (Nakahama et al., 2016) and seedling establishment (Gaujour et al., 2012) when applied during flowering and fruiting periods. Grazing, in contrast, tends to have positive effects on species alpha diversity as it increases grassland heterogeneity. Finally, the dry grasslands located in our study region go back until the time of the Roman Empire (Poschlod & Baumann, 2010), whereas hay meadows occurred for the first time at the end of the seventeenth century (Poschlod, 2015) in this region. We conjecture that this temporal continuity may have contributed to increased levels of species alpha diversity in dry grasslands (Hájková et al., 2011).

Species turnover in our study was higher in hay meadows, and spatial effects were stronger in dry grassland. A possible explanation of this pattern could be that hay meadows have more pronounced environmental differences that are, however, often driven by management and therefore not strongly spatially autocorrelated. For example, soil fertility and humidity are typically less variable among dry grassland, which are located on dry and nutrient-poor slopes of the river valley, whereas hay meadows are located along the river under more variable environmental and hydrological conditions. Differences in environmental conditions (Kofos & Banaszuk, 2018) such as soil fertility (Klimek et al., 2007)

or humidity (Gaujour et al., 2012) are important predictors for species presence. Moreover, management differs more strongly in hay meadows. Especially the timing and frequency of mowing (Sullivan et al., 2018) can have strong effects on the occurrence of grassland species (Milberg et al., 2017). Overall, however, we interpret our findings as suggesting that community composition of hay meadows is more strongly driven by habitat filtering, while community composition of dry grasslands depends more strongly on a mix of dispersal and possibly spatially autocorrelated habitat diversity.

4.2 | Genetic diversity patterns

We observed no significant differences in genetic alpha diversity between dry grasslands and hay meadows, after accounting for species identity (Table 1). There seemed to be a tendency of more frequent species to have higher genetic diversity, especially in dry grasslands (Figure 3) and also a tendency of higher genetic diversity in dry grasslands (Figure 3), but none of these patterns were significant. We acknowledge that the sample size for comparisons between species was low ($n = 6$ for each habitat). On the other hand, also the magnitude of estimated effect sizes (Table 1, Figure 3) in relation to the between-species variability was clearly much smaller than for the comparison of species diversity (Figure 2). Based on this, we do not think that statistical power alone explains the lack of a signal. Rather, we interpret our data as suggesting that differences in genetic diversity between habitats, if they exist, are likely smaller than difference in species diversity. It is possible, however, that results would differ for rare or self-compatible plant species, which are less connected by gene flow.

There are various possible interpretations of these results. In our view, the most likely interpretation is that species diversity patterns are more strongly driven and maintained by habitat differences at the alpha and beta scale, while genetic patterns are more driven by historical and current fragmentation. This interpretation is supported by a previous study (Reisch & Schmid, 2019) that did not find a correlation between species and genetic alpha diversity within dry grasslands either. The authors conjecture that this pattern can be explained by the higher speed at which species compared to genetic alpha returns to equilibrium after disturbances (Lamy et al., 2013; Münzbergová et al., 2013; Vandepitte et al., 2007).

Our results differ from previous studies that reported negative effects of mowing on genetic alpha diversity (Kölliker et al., 1998; Last et al., 2014; Nakahama et al., 2016), while grazing often appeared to create positive impact on genetic alpha diversity (Peng et al., 2015; Rudmann-Maurer et al., 2007; Völler et al., 2013). Some authors have also suggested that stronger habitat heterogeneity in more intensively grazed habitats creates a small-scale mosaic of selection, increases genetic alpha diversity (Völler et al., 2013). However, previous studies also demonstrate intensive gene flow among grasslands, which may obscure such habitat effects (Kloss et al., 2011; Odat et al., 2004). Moreover, hay meadows are currently more common than dry grasslands at present, and one would expect a positive

relationship between population size and genetic diversity (Busch & Reisch, 2016; Gabel et al., 2017; Leimu & Mutikainen, 2005), but the reverse was true when going back centuries and millennia. These temporal changes may further obscure a possible effect of habitat, but also other predictors, such as area as a proxy of population size, on genetic diversity.

Genetic beta diversity was comparable in the two grassland types. This may appear surprising, because previous studies suggested that genetic differentiation is driven by mowing and grazing, especially via flowering phenology (Reisch & Poschlod, 2009; Rudmann-Maurer et al., 2008; Völler et al., 2013, 2017). These studies, however, looked at genetic differentiation within a single species that occurred both in mown and grazed habitat. So far, few studies have compared average genetic beta diversity of populations within mown and grazed habitats, like we do here (but see Rudmann-Maurer et al., 2008, who report a positive effect). For both habitats, we found comparable patterns of spatial genetic differentiation. We conjecture that this apparent similarity in gene flow explains the lack of differences in genetic beta diversity in our study. In general, one would expect gene flow to be promoted by grazing, which frequently transports seeds over large distances, but in our study area, geographic distance between study sites was low enough (500 m to 10 km) to still permit gene flow via pollination, and there are mowing practices that are suited to transport seeds between populations in hay meadows (Strykstra et al., 1997). These and other processes may have contributed to a high amount of gene flow and thus similar levels of genetic beta diversity among populations from both habitat types.

4.3 | Implications for management

The Convention on Biodiversity (CBD; www.cbd.int/convention/text/) calls for the protection of biodiversity at the level of ecosystems, including species and genes. In practice, however, conservation efforts have focused nearly exclusively on protecting species diversity. This was rarely seen as a problem, not least because many authors assumed that protecting species would automatically protect genetic diversity as well, for all the reasons discussed in the introduction of this paper (Kahilainen et al., 2014). Vice versa, some authors have suggested that genetic diversity of common species could be used as a proxy for the occurrence of endangered species and that molecular analyses may thus be an efficient approach to identify priority areas for conservation planning (Fuller et al., 2013). When species and genetic diversity patterns diverge, these assumptions will not hold. In the worst case, there could even be conflicts between the two goals of conserving species and genetic diversity (Kahilainen et al., 2014). Our results indicate that correlations between genetic and species diversity in human-dominated landscapes such as grasslands may be low, although we caution that this may be different for rare or self-compatible plant species with populations being less connected by gene flow. This study is therefore calling for more comprehensive

conservation approaches that explicitly consider both levels of biodiversity.

5 | CONCLUSIONS

In conclusion, our results highlight that expectations to find parallel patterns between genetic and species diversity (Vellend, 2005; Vellend et al., 2014), especially in island-like habitats such as mountain tops or islands in the ocean (Whitlock, 2014), will not always be fulfilled in human-dominated ecosystems that are characterized by temporally changing habitat boundaries (Huber et al., 2017; Reisch et al., 2017), as well as by variation in the dominating processes of community assembly.

We see these results by no means as discouraging the parallel study of species and genetic diversity. Rather, they highlight the complementary information that is contained in species and genetic diversity patterns. A complete theory of community ecology at the landscape scale should be able to explain the emergence of both patterns, because they are ultimately linked to the same ecological processes. Considering species and genetic diversity patterns in parallel may be of great use to advance our understanding of the mechanisms that structure biodiversity in complex dynamic landscapes. A challenge for such a research agenda is the still high costs to generate genetic information as well as the availability of models and theories that simultaneously predict species and genetic diversity based on the same processes.

Having sampled only six species per habitat type prevented additional analyses that would be interesting, in particular finding predictors that explain the differences in genetic diversity between species. Moreover, a limitation of null hypothesis significance tests they only allowed us to compare whether differences between habitats exist for genetic and species diversity, but not how large they are. With models that create quantitative expectations for effect sizes in genetic and species diversity, we could also compare the two patterns in magnitude. We hope that both challenges could be addressed in the future, as advanced sequencing technology and quantitative models combining ecological and genetic processes become increasingly available.

ACKNOWLEDGEMENTS

Special thanks go (in alphabetical order) to Lina Begemann, Dominik Fiegle, Christian Fink, Fridtjof Gilck, Marius Hausmann, Martina Kolb, Patricia Krickl, Theresa-Anna Lehmail, Tamara Löffler, Lena Marquardt, Kathrin Sagmeister and Lars Tappert for performing molecular analyses. We are also obliged to Petra Schitko for technical assistance in the laboratory, to Sabine Fischer for her help with GIS and to Peter Poschlod for his generous support. Open access funding enabled and organized by ProjektDEAL.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13199>.

DATA AVAILABILITY STATEMENT

Code and data to replicate the analyses presented in this article are available at <https://github.com/florianhartig/Reisch-Hartig-2021>. A persistent copy of the repository is available at <https://doi.org/10.5281/zenodo.4284718>.

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BIOSKETCH

Florian Hartig is mainly interested in the mechanisms that determine ecosystem functions and diversity patterns, at the community scale as well as at biogeographical and evolutionary scales; (Bayesian) statistical methodology, conservation biology and ecological theory in general. Christoph Reisch is working in the field of molecular ecology and conservation genetics. In his research, he focuses on the mechanisms creating and maintaining genetic variation in anthropogenic and natural ecosystems and the relationship between-species and genetic diversity.

Author contributions: CR conceived and designed the study. FH analysed the data. CR and FH wrote the manuscript. Both authors read and approved the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Reisch C, Hartig F. Species and genetic diversity patterns show different responses to land use intensity in central European grasslands. *Divers Distrib.* 2021;27:392–401. <https://doi.org/10.1111/ddi.13199>