

Patterns of genetic variation in European plant species depend on altitude

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Abstract

Aim: High mountain regions exhibit a much stronger environmental heterogeneity and a more complex glacial history than lowland regions. In this study, we compared the genetic variation of plant species occurring in different altitudinal zones. We tested the assumption that environmental and historic differences among high mountain regions and lowlands result in different patterns of genetic diversity and differentiation.

Location: Central Europe and the European Alps.

Methods: We first compiled a data set on genetic variation of 179 plant species occurring in Central Europe and the European Alps measured by AFLPs from the literature. Then, we compared genetic diversity and differentiation between species occurring in the lowland, montane, subalpine and alpine vegetation zone with the help of linear models. Geographic distance among sampled populations, plant frequency and three plant traits (life span, mating system and pollination mode) were included into the models, to account for their potential effects on level of genetic variation.

Results: Our analysis revealed different patterns of genetic variation in plant species occurring in the alpine and non-alpine zone. Genetic differentiation was significantly higher among populations of species from the alpine than subalpine, montane or lowland zone. In contrast, genetic diversity was significantly lower within populations from the alpine zone compared to the other zones.

Main conclusions: We argue that the observed pattern of genetic variation most likely results from restricted gene flow, both past and present, among spatially and environmentally isolated populations in alpine habitats.

KEYWORDS

AFLP, alpine plant species, Alps, genetic differentiation, genetic diversity, mountain plant, topography

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1 | INTRODUCTION

High mountain regions belong to the most species-rich areas worldwide (Körner, 2004, 2014). For instance, European mountain ecosystems harbour about a third to half of the total continental flora (Theurillat, 1995). Currently, these cold-adapted biodiversity hotspots are strongly threatened by the global change including climate warming, nitrogen eutrophication and land use change (Körner, 2014; Molau, 2004). Modelling studies indicate that 30%–55% of all European alpine plant species will lose more than 80% of their suitable habitat by 2070–2100 due to the effects of climate change (Engler et al., 2011). High mountain regions such as the European Alps are, therefore, threatened hotspots of biodiversity, deserving full conservation attention (Körner, 2004).

The unusually high level of species richness in high mountain regions compared to lowlands is considered as an effect of two main reasons. Firstly, high mountain regions display an extreme topographic complexity, which is assumed to be linked with environmental heterogeneity (Irl et al., 2017). Topographic complexity is a strong driver of species richness (Coblentz & Riitters, 2004; Irl et al., 2015; Stein et al., 2014); different exposure and inclination of mountain slopes with specific microclimate in combination with different geological substrates and soils and the related nutrient and water availability form a multitude of different microhabitats containing characteristic and locally adapted species (Körner, 2004). This process of ecological speciation is additionally intensified by geographic speciation due to reduced connectivity among isolated mountain regions (Smyčka et al., 2017). In other words, high mountain plants are often strongly isolated (García-Fernández et al., 2012), which may increase the rate of speciation (Steinbauer et al., 2016). Therefore, high mountain ecosystems are often rich in endemic species (Hughes & Atchinson, 2015; Noroozi et al., 2018). Contrastingly, non-alpine regions, such as the Central European lowlands, are topographically, climatically and geologically less heterogeneous. The lower level of complexity and the stronger impact of human activity all together result in a lower number of microhabitats per unit of area and consequently species richness decreases in Central Europe from the south to the north (Mutke et al., 2010).

Secondly, the high level of species richness reflects the complex history of the mountain regions. In the Northern Hemisphere, high mountain areas have been strongly affected by glaciations (Smyčka et al., 2017). The present flora of the European Alps has been shaped by the repeated expansion and retraction of alpine glaciers, confining species to numerous glacial refugia at the border of the high mountains regions during the cold periods and allowing recolonization from these refugia during the warmer interglacial periods (Schönswetter et al., 2005; Stehlik, 2003). Isolation during long-term persistence in glacial refugia promoted speciation (Steinbauer et al., 2016) and resulted in the level of endemic species, which can be observed in refugial areas today (Tribisch, 2004). In contrast, the Central European lowlands have been much more drastically affected by the glaciations during Pleistocene. The temperate forests

have been widely replaced by a cold steppe (Lang, 1994), and many species were pushed back to south-eastern and south-western European refugia (Hewitt, 2000; Schmitt & Hewitt, 2004). Although cryptic refugia have been demonstrated for several European grassland plant species (Leipold et al., 2017; Tausch et al., 2017) and the survival in suitable Central European habitats cannot be fully excluded, vegetation extremely differed from today, since large parts of the Central European lowlands were covered by an ice sheet or dominated by permafrost soil (Lang, 1994). Therefore, the most populations of non-alpine plant species are expected to have reimmigrated post-glacially to Central Europe (Lang, 1994).

Environmental heterogeneity and glacial history have, however, not only shaped the species diversity of alpine and non-alpine regions but have also an impact on genetic variation, an essential component of biodiversity (Heywood & Watson, 1995). Also, it is an indispensable prerequisite for the successful conservation of species and ecosystem diversity, since intraspecific variation provides the basis for any evolutionary change (Pauls et al., 2013). It has been shown that environmental heterogeneity increases genetic diversity (Rudmann-Maurer et al., 2007) and differentiation (Linhart & Grant, 1996). Furthermore, it has been demonstrated that restricted gene flow may cause increased genetic differentiation among populations located in high mountain microhabitats due to mismatch in flowering caused by differing snowmelt timing (Cortés & Wheeler, 2018; Hirao & Kudo, 2008; Shimono et al., 2009; Yamagishi et al., 2005). Moreover, habitat heterogeneity may also lead to increased genetic diversity due to fine-scale selection of genotypes adapted to the local environmental conditions (Parisod & Christin, 2008). The effects of this process may, however, be mitigated by smaller population sizes of high mountain species, since habitat availability is limited in high mountains regions and genetic diversity often correlates positively with population size (Leimu et al., 2006).

Genetic variation depends also strongly on the complex history of mountain regions. The long-term isolation of species in refugial areas during glaciations disrupted gene flow among populations located in different refugia and promoted genetic differentiation (Reisch et al., 2003; Schönswetter et al., 2005; Windmaißer et al., 2016). Furthermore, the repeated expansion and contraction of the distribution ranges of mountain species had also an impact on genetic diversity, since consecutive bottlenecks and founder effects often decreased genetic diversity, especially in formerly glaciated areas (Brochmann et al., 2003).

In the recent two decades, a great progress has been made in understanding drivers of the genetic variation in alpine plants, often in the context of phylogeography or population biology (Gabel et al., 2017; Hirao & Kudo, 2004; Schönswetter & Tribisch, 2005). Specifically, it has been suggested that levels of genetic differentiation increase with increasing altitude (Till-Bottraud & Gaudeul, 2002) and a few studies have already provided evidence for this assumption (DeChaine & Martin, 2005; Hahn et al., 2012). Yet, the question whether non-alpine and alpine species differ in their patterns of genetic variation remains to be tested as comparative studies including a larger number of species from both groups are generally lacking.

To close this gap, we employed a comparative approach by conducting a synthesis study of published literature on genetic variation of European species with different distributional patterns along elevational gradient. Our aim was to test the assumption that environmental and historic differences among high mountain regions and lowlands result in varying patterns of genetic diversity and differentiation in different altitudinal zones. Specifically, we expected lower levels of diversity within populations of alpine plant species due to limited habitat availability and smaller population sizes in high mountain areas. In contrast, we anticipated stronger genetic differentiation among populations of alpine plant species, due to historic and present isolation processes in the highly fragmented high mountain landscape.

2 | MATERIALS AND METHODS

2.1 | Data collection

We first compiled a data set with published data on the genetic variation of European plant species using amplified fragment length polymorphisms (AFLPs) in the web of knowledge by Thomson Reuters (search date 29.1.2018) with the keywords 'AFLP' and 'plant'. By doing so, we identified 136 studies published between 1998 and 2018 and extracted data on genetic variation of 156 different plant species (Table S1). Additionally, we included unpublished data of 15 species from our laboratory and of 8 species from a manuscript in preparation. Our compilation comprised, therefore, finally data from a total of 179 plant species.

Using information from *Flora alpina* (Aeschmann et al., 2004), species were assigned to four vegetation zones (lowland, montane, subalpine and alpine zone) according to their altitudinal distribution. Plant species occurring along a larger gradient were assigned to several zones. From previous studies, it is known that study design, species-specific spatial parameters and life history traits affect patterns of genetic variation (Reisch & Bernhardt-Römermann, 2014). We included in our study, therefore, also data on the maximum distance between populations, the frequency of the plant species, as well as their life span, mating system and pollination (Table S2), which are known to have the most notable effect on genetic diversity and differentiation (Reisch & Bernhardt-Römermann, 2014). Information on the maximum distance between populations was obtained from the publications. Data on life history traits were taken from the population biology databases BioPop (Poschlod et al., 2003) and BioFlor (Klotz, et al., 2002) and pertinent Floras (Oberdorfer, 2001; Seybold, 2006).

From the selected publications, we then extracted data on the genetic variation of the studied plant species. In these publications, numerous statistical methods were applied to analyse AFLP data. We restricted our compilation to the most common estimators of genetic variation (Table S2). For this reason, we calculated mean Nei's Gene Diversity ($H = 1 - \sum(p_i)^2$) per population, which is equivalent with expected heterozygosity, to characterize genetic diversity

within populations. Furthermore, we took Φ_{ST} and F_{ST} values (these are comparable) from the selected publications, which derive from analyses of molecular variance (AMOVAs) and serve as estimators for genetic differentiation among populations.

2.2 | Data analysis

Linear models were used to estimate differences in genetic variation among species from the different altitudinal zones. In two regressions set up, we used the genetic variation measures (H and Φ_{ST}) as dependent variables and occurrence (lowland, montane, subalpine, alpine) as an explanatory categorical variable. Lowland was set up as a reference group. As described above, we included into the models also maximum distance between populations (numeric variable; in km), the frequency of the plant species (numeric variable; 1—rare species, 6—frequent species), life span (categorical variable; annual and perennial), mating system (numeric variable; 0—self-compatible; 0.5—mixed; 1—self-incompatible) and pollination mode (categorical variable; wind- and insect-pollinated).

All numerical variables were scaled to zero mean and unit variance prior to analyses. The H -values were sqrt-transformed to improve the normality of the residuals. The full model was reduced via backward selection of the least significant variables until we achieved the minimal adequate model (Crawley, 2007). Model assumptions were met in all the cases. All statistical calculations were performed in R software version 3.6.0 (R-Core-Development-Team, 2018).

3 | RESULTS AND DISCUSSION

The minimal adequate model revealed significantly higher levels of genetic differentiation among populations (Φ_{ST}) of species from the alpine (0.36) than from the lowland (0.26), montane (0.24) and subalpine (0.26) zone (Table 1; Figure 1a). Geographic distance and frequency had a positive effect on Φ_{ST} values and genetic differentiation was significantly higher in annual than in perennial species (Table 1; Table S2), which confirms the patterns of genetic differentiation demonstrated in previous studies (Hamrick & Godt, 1996; Nybom & Bartish, 2000; Reisch & Bernhardt-Römermann, 2014).

As previously described, genetic differentiation depends strongly on gene flow via pollen and seed dispersal (Slatkin, 1987). Generally, pollen dispersal is limited to only few kilometres (Kwak et al., 1998; Matter et al., 2013). Nevertheless, differences in flowering time may cause considerable genetic differentiation among populations located in environmentally differing microhabitats (Cortés & Wheeler, 2018; Hirao & Kudo, 2008; Shimono et al., 2009; Yamagishi et al., 2005) due to restricted pollination. Hence, stronger environmental heterogeneity in alpine habitats constitutes an important factor generating stronger differentiation among populations of plant species in the alpine zone. Seed dispersal may, in contrast, also bridge longer distances (Schönswetter & Tribsch, 2005), although the probability of seed dispersal strongly decreases with geographic

TABLE 1 Estimated parameters for minimal adequate linear models and their significances showing the differences in genetic variation within (H) and among (Φ_{ST}) populations and spatial characteristics of plant species with different distributional patterns along altitudinal gradient and effects of geographic distances among study population, species frequency and life span (annual versus perennial)

Trait	Variable	Estimate	SE \pm	p-value
Φ_{ST}	Intercept	0.37	0.03	<.001
	Montane zone	0.01	0.03	.78
	Subalpine zone	0.04	0.04	.22
	Alpine zone	0.10	0.04	.03
	Geographic distance	0.12	0.02	<.001
	Frequency	0.04	0.01	.003
	Life span	-0.12	0.04	.001
H	Intercept	0.37	0.02	<.001
	Montane zone	-0.01	0.01	.65
	Subalpine zone	-0.02	0.02	.27
	Alpine zone	-0.05	0.02	.01
	Geographic distance	-0.05	0.01	<.001
	Frequency	-0.04	0.01	<.001
	Life span	0.06	0.02	<.001

Note: Abbreviation: SE, standard error.

H-values were square root-transformed to improve the normality of residuals. Significant p-values are shown in bold.

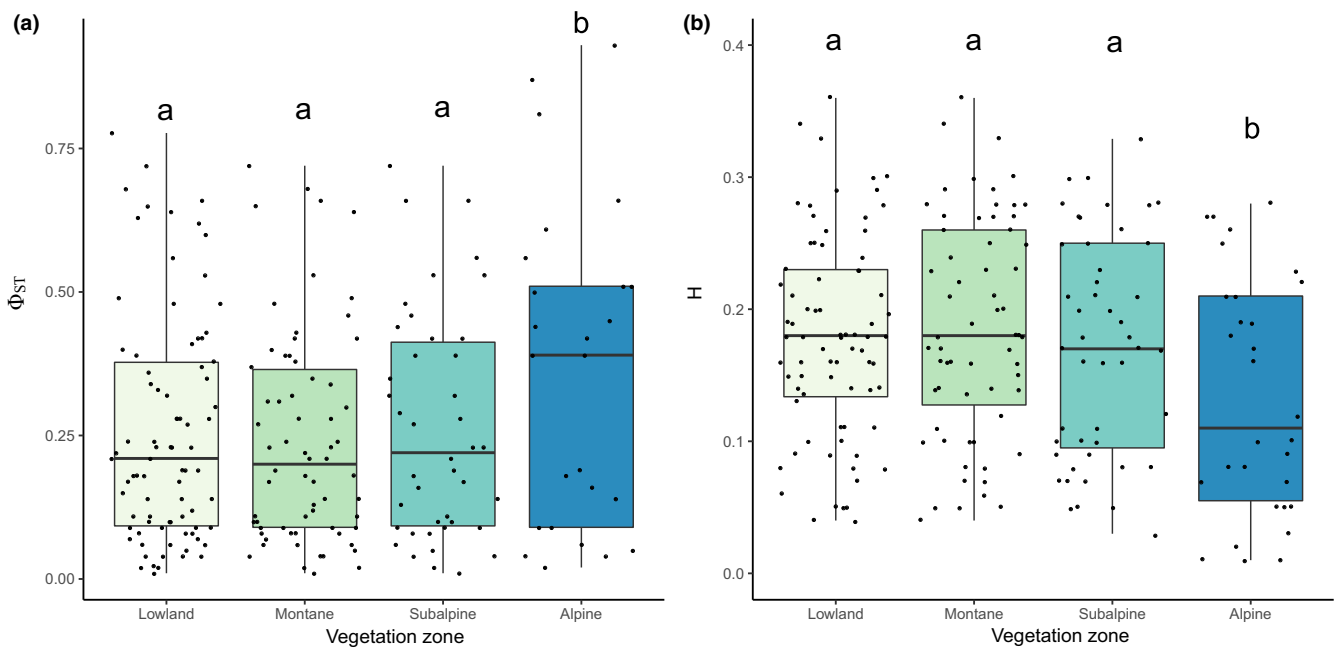


FIGURE 1 Genetic variation among (Φ_{ST}) and within (H) populations of plant species in different altitudinal zones. Letters indicate significant differences ($p < .05$) between the lowland (the control group) and either montane, or subalpine or alpine zone as estimated by linear models

distance (Skarpaas et al., 2004). Isolation by distance is, therefore, of outstanding relevance for restricted gene flow among populations (Kuss et al., 2008). Gene flow among spatially isolated populations on closely located mountain peaks in the alpine zone may, however, be more strongly restricted than among lowland populations due to the steeper environmental gradients in high mountain regions. The complex and rugged topography seems to cause stronger spatial

isolation of populations which triggers genetic differentiation among populations of plant species in the alpine zone.

The gene flow limiting isolation may also have occurred in the past. The impact of former isolation on genetic variation among populations has clearly been demonstrated in numerous studies on the biogeography of alpine plant species, which survived glaciations in different, spatially isolated refugia (Petit et al., 2003; Slovák

et al., 2012; Windmaïßer et al., 2016). The present pattern of genetic variation often still reflects this historical isolation, and many alpine plant species consequently exhibit strong differentiation among populations. In contrast, genetic differentiation among populations is often low in formerly glaciated lowland areas of Europe (Petit et al., 2003). The observed stronger genetic differentiation of plant species from the alpine zone compared to plant species from the lowland, montane and subalpine zone may thus be a joint result of environmental heterogeneity in association with both historic and present isolation due to the complex landscape structure and history of high mountain regions.

Genetic diversity within populations of montane ($H_e = 0.19$) and subalpine ($H_e = 0.17$) plants was not substantially different from their lowland counterparts ($H_e = 0.18$), whereas this value was slightly, but significantly lower in alpine plants ($H_e = 0.13$; Table 1; Figure 1b). Furthermore, similarly to Φ_{ST} , geographic distance, frequency and life span significantly affected genetic diversity; however, the nature of these relationships were reverse to the former (Table 1; Table S2). The findings are, therefore, in line with the results of previous meta-studies on the drivers of genetic diversity (Hamrick & Godt, 1996; Nybom & Bartish, 2000; Reisch & Bernhardt-Römermann, 2014).

The most important reason for lower levels of genetic diversity in populations from the alpine zone may be population size, which is one of the most important determinants of genetic diversity. The positive relationship between both parameters is beyond doubt (Leimu et al., 2006). It can, however, be supposed that habitat availability and therefore population size decrease with increasing altitude (Gabel et al., 2017; Körner, 2004). Consequently, genetic diversity should be lower within populations from the alpine zone compared to populations from lower altitudes. The results of our study support this assumption. However, population size estimation is not trivial and very time-consuming (Reisch et al., 2018), so that detailed and comparable information, especially about alpine plant population sizes, is not accessible. Thus, further data are needed to verify the potential impact of population size on the genetic diversity of alpine and non-alpine plant populations.

4 | PERSPECTIVES AND CONCLUSIONS

Previous studies demonstrated a strong impact of life history traits on genetic variation. Particularly, it has been shown that genetic variation depends on life span, mating system and pollination type (Meirmans et al., 2011; Nybom & Bartish, 2000; Reisch & Bernhardt-Römermann, 2014; Thiel-Egenter et al., 2009). Our study revealed significant differences in patterns of genetic variation between plant species occurring in the alpine and non-alpine zones, but also confirmed the strong impact of geographic distance, and life history traits such as frequency or life span on the patterns of genetic variation. There are certainly differences in further life history traits between plant species occurring in the different altitudinal zones, which may affect genetic variation, such as dispersal

type (Thiel-Egenter et al., 2009), viability of seeds in the soil (Honnay et al., 2008), capacity for clonal propagation (Widén et al., 1994) and many others. It would have been desirable to include more detailed life history traits in our study, in particular concerning seed dispersal. However, such data are largely missing for alpine species in the existing data bases, such as TRY (Kattge et al., 2011) or LEDA (Kleyer et al., 2008), and additional experiments are therefore urgently needed for a more detailed analysis.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Tables S1,S2 of this article.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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