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Research article

Reprint of: Disentangling drivers of plant endemism and diversification in the European Alps - a phylogenetic and spatially approach

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ABSTRACT

Plant endemism in the European Alps is clustered into particular geographic areas. Two contrasted and non exclusive hypotheses have been suggested to explain these hotspots of endemism: (i) those areas were glacial refugia, where endemism reflects survival-recolonisation dynamics since the onset of Pleistocene glaciations, (ii) those are high elevation mountain areas, where endemism was fostered by local speciation events due to geographic isolation and harsh environmental niches, or by low dispersal ability of inhabiting species.

Here, we quantitatively compared these two hypotheses using data of species distribution in the European Alps (IntraBioDiv database), species phylogenetic relationships, and species ecological and biological characteristics. We developed a spatially and phylogenetically explicit modeling framework to analyze spatial patterns of endemism and the phylogenetic structure of species assemblages. Moreover, we analyzed interrelations between species trait syndromes and endemism.

We found that high endemism occurrs in potential glacial refugia, but only those on calcareous bedrock, and also in areas with high elevation. Plant assemblages in calcareous refugia showed phylogenetic overdispersion − a signature of non-selective conservation forces, whereas those located in high mountain areas showed phylogenetic clustering − a signature of recent diversification and environmental filtering. Endemic species were either stress-tolerant, poorly dispersing species, or high elevation specialists with a wide distribution within the European Alps.

While both calcareous refugia and high-elevation hotspots harbour a large portion of plant endemism in the European Alps, the species they host have substantially different characteristics. Our results suggest that hotspots of endemism in calcareous refugia are more important for nature conservation planning, as they host many range restricted endemic species and rather isolated evolutionary lineages.

1. Introduction

Mountain ranges across the world are considered typical examples of endemic-rich regions (Hughes and Atchinson, 2015), but the evolutionary mechanisms and historical factors generating this high endemism are not fully understood. It was early recognized that mountains have a much richer endemic flora than the surrounding lowlands, and also that within mountain systems, there exist specific areas with exceptionally high endemism (de Candolle, 1875; Pawłowski, 1970). Such hotspots of endemism in alpine regions were observed mostly in putative glacial refugia (Pawlowski, 1970; Tribsch and Schönswetter, 2003; Feng et al., 2016) or in high-elevation areas (Aeschimann et al., 2011; Nagy and Grabherr 2009; Tribsch and Schönswetter, 2003). This suggests that their occurrence is coupled with specific evolutionary dynamics: such regions may exhibit lower extinction rates due to climatic stability and reduced glacial extent, or higher speciation rates and poorer dispersal ability of high-elevation species.

Hotspots of plant endemism in the European Alps (Alps hereafter) have traditionally been explained by the presence of refugia on the periphery of glacial cover during the ice age periods. These refugia are assumed to have promoted long term population persistence of many species during glacial periods, which left imprints in the population structure of survivor species (Alvarez et al., 2009; Schönswetter et al., 2005; Stehlik, 2003). The distribution of glacial refugia has also shaped contemporary species distributions and endemism patterns, since some survivors could not recolonize all adjacent regions after the retreat of glaciers (Dullinger et al., 2012). It is often assumed that refugia with different bedrocks hosted different pool of species, as the majority of

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plant endemics of the Alps show either a clear affinity or a strong intolerance to calcareous bedrock, with endemic flora of calcareous bedrock being generally richer (Schönswetter et al., 2005; Tribsch and Schönswetter, 2003). It is likely that species survival during glacial periods has generated particular patterns of endemism, and also left a particular phylogenetic signature in local floras. We can thus hypothesize that species surviving glacial cycles in refugia were drawn from a pool of "pre-glacial" species, whereas species occurring outside refugia were filtered for ability of fast recolonisation, resulting in relative phylogenetic overdispersion of species assemblages in glacial refugia. Here, we aim at quantitatively testing across the whole Alps whether the areas predicted as inhabitable during glacial periods *sensu* Schönswetter et al. (2005) match the above described patterns of endemism and phylogenetic structure, and whether patterns of endemism in these potential refugia are influenced by other factors, as is refugium bedrock, topography, or geographic region.

In addition to the influence of Pleistocene historical processes, patterns of plant diversity and endemism in the Alps may also be linked to the characteristics of high-elevation ecosystems, such as geographic insularity and availability of free but hostile niches. Indeed, it was observed that endemic diversity in the Alps grows with elevation (Aeschimann et al., 2011; Tribsch and Schönswetter, 2003). This pattern could be explained by two processes that are not mutually exclusive. First, increased speciation rate in high elevation ecosystems (documented on a global scale and reviewed in Hughes and Atchison, 2015) could induce higher endemism in certain plant clades. This may be due to heterogeneity or niches in high mountain environments and specific life histories of mountain species favouring sympatric speciation (Dixon et al., 2009; Roquet et al., 2013a, 2013b), or due to topographic obstacles in high mountain environments stimulating allopatric speciation (Boucher et al., 2016; Comes and Kadereit, 2003). Repeated speciation events in high-mountain floras could then induce a phylogenetic signature of radiating lineages, producing a phylogenetic clustering in local species assemblages. Second, increased plant endemism in high elevations may have resulted from a reduced dispersal potential itself. Adaptation to high-alpine environments may imply stress tolerance, long lifespan, and preference for vegetative spread (Körner, 2003) to the detriment of dispersal capabilities (i.e. insularity syndrome). High endemism in mountains resulting from increased speciation rates or decreased dispersal capacities of high-elevation species can thus be expected to result in specific signatures of phylogenetic clustering in local species assemblages or in the presence of particular trait syndromes that have improved survival in high mountain environments at the expense of dispersal potential. This has never been tested to date.

We thus argue that patterns of endemism in the Alps could be explained both by local survival-recolonization dynamics following glaciations, and by dynamics of speciation and dispersal in high-elevation ecosystems. In this paper: (i) We quantitatively compare the relative importance of potential glacial refugia on different bedrocks on one side, and elevation on the other side, for patterns of plant endemism in the Alps. To do this, we use two measures of endemism, namely the proportion of endemic species and range size of endemic species, using a grid-based species occurrence data in the Alps (IntraBioDiv; Gugerli et al., 2008). (ii) We test whether the phylogenetic structure (richness-standardized phylogenetic diversity; Faith, 1992) of species assemblages differs between those different types of hotspots, according to hypothesized evolutionary processes. Importantly, we developed here a novel method based on Bayesian imperfect detection framework in order to overcome difficulties when calculating community phylogenetic indices from non-completely resolved phylogenies (Molina-Venegas and Roquet, 2014; Rangel et al., 2015). (iii) To shed more light on processes forming endemism in high elevations, we explore how endemism and range size of endemics are related to species elevational optimum (Landolt et al., 2010), ecological and functional characteristics related to high elevation adaptations and evolutionary distinctiveness of species (Isaac et al., 2007).

2. Methods

2.1. Study region

We focus on the European Alps, which corresponds to the great mountain range system stretching from south-eastern France to Slovenia. The tree line in the European Alps lies at cca. 2000 m a. s. l and upper limits of vascular plant occurrence lie in 3500–4500 m a.s.l., differing by region (Ozenda and Borel, 2003; Tribsch and Schönswetter, 2003). The European Alps belong to one of the coldest biomes on the planet at its highest elevations (Körner, 2011); nevertheless, this region appears to be relatively species rich, with a fairly high rate of plant endemism (about 13%; Aeschimann et al., 2004; Pawlowski, 1970). The Alps thus constitute a well known hotspot of biodiversity in Europe (Väre et al., 2003).

2.2. Species distribution and environmental data

Species distribution data originate from the mapping of the flora across the Alps produced by the IntraBioDiv consortium (IBD; Gugerli et al., 2008). This dataset contains census and expert based presences and absences of all plant species occurring above the tree line on a regular grid with cells of 20′ longitude and 12′ latitude (ca. 25 × 22 km). This grid was used for all subsequent spatial analyses. The restriction of the species pool to species occurring clearly above the treeline may be considered problematic for example for interpreting species richness across the dataset (but see Taberlet et al., 2012). Nevertheless, while investigating evolutionary processes, such restriction removes potential noise generated by lowland species that likely have reduced evolutionary histories related to mountains. We also excluded gymnosperms and ferns, because some of our working hypotheses may not be extended to them, trait definition for angiosperms are not easily applicable to those groups and sampling efforts for ferns was low compared to angiosperms.

To quantify which grid cells might serve as glacial refugia during glacial cycles, we overlaid the IBD grid with distribution of potential siliceous and calcareous refugia based on combination paleoclimatic model with geological data (adapted from Schönswetter et al., 2005) and estimated whether each grid cell contained calcareous, siliceous, none, or both types of potential refugia. The potential refugia, adapted from Schönswetter et al. (2005), are estimated for maximum of the last glacial period (110,000–12,000 years before present), but they can also be considered a proxy information for distribution of refugia in previous glacial periods. These potential refugia are mostly peripheral (along southwestern, southern, eastern and northern borders of the Alps), likely favouring isolation of plant populations for thousands of years (Schönswetter et al., 2005). The calcareous refugia are the ones lying on limestone or dolomitic bedrock, whereas siliceous refugia lie on variety of acidic bedrocks like granite or gneiss. Larger coherent areas of bedrock types not falling into these two categories are relatively rare within the Alps (Schonswetter et al., 2005; Tribsch and Schönswetter 2003). To separate the effect of refugia from the effect of bedrock itself, we also estimated whether each grid cell contained calcareous (limestone or dolomite) or siliceous bedrock (granite, diorite or gneiss) based on dominant parent material map (PARMADO) from European Soil database (resolution 1 × 1 km). To quantify the topography of grid cells, we calculated their mean elevation and their difference between highest and lowest elevation (elevation range, hereafter) based on Global digital elevation model by US Geological Survey (resolution 30″ × 30″, cca 1 × 1 km). All calculations were performed using the statistical environment R (R Core Team, 2016) and the R libraries raster (Hijmans, 2016), rgdal (Bivand et al., 2016) and spatialEco (Evans, 2016). All data used for our analyses are accessible in Dryad repository under accession number (to be completed after attribution of doi).

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