



Anticipating extinctions of glacial relict populations in mountain refugia



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ABSTRACT

Glacial relict populations at the rear-edge of species' distributions are expected to respond dramatically to climate warming, yet very few studies have compared their conservation status in current refugia. Here we combine population genetics with species distribution modelling to assess patterns and causes of extinction or persistence in two cold-adapted species, *Salix hastata* and *Juncus balticus*, which survived post-glacial retractions in calcareous fens of the Iberian Peninsula. In both species, we detected extremely-low genetic diversity and clonal strategies in red-listed populations of the most marginal region (Cantabrian Range), but high genetic diversity linked with sexual reproduction in populations from a less marginal region of the rear edge (Pyrenees). Genetic patterns were partially explained by past and present species' climatic niches, more remarkably in the arctic-alpine *S. hastata* than in the boreo-atlantic *J. balticus*, suggesting different biogeographic history but similar sensitivity to global change. Our results show different magnitudes of extinction debt in regional populations that have survived in mountain refugia since the Last Glacial Maximum. Functional extinction of the most marginal populations can be explained by postglacial climate change and the historical decline of mire habitats. In contrast with the current trend of predicting future effects of climate change, we highlight that glacial relict populations might be currently going into extinction in climatically marginal regions. These populations can provide valuable information about the processes involved in species extinctions, improving our capacity to anticipate the effect of global change across regions and habitats.

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1. Introduction

Understanding how species respond to climate change is a major challenge for biodiversity and conservation (Malcolm et al., 2006; Maclean and Wilson, 2011). Research on this topic has been mainly focused on predicting species distributions in future climatic scenarios (Thomas et al., 2004; Bellard et al., 2012). However, new perspectives in conservation biology suggest that many species might be more resilient to climate change than anticipated by model predictions (Hof et al., 2011). This question can be only addressed by considering the ability of populations to respond to changes in terms of persistence, adaptation or extinction (Davis et al., 2005; Chevin et al., 2010). Adaptation may be considered a form of persistence (Hoffmann and Sgrò, 2011), therefore assessing the chance of persistence versus extinction on extant populations is a crucial issue for predicting the effects of climate change (Fordham et al., 2012).

To accurately predict extinctions we need empirical information on the processes related to population decline in different habitat contexts

(Willis and Bhagwat, 2009; Fordham et al., 2012). On this regard, climate relicts are good models for studying species whose populations persisted or became extinct in different regions after climate change (Gavin et al., 2014). Particularly, glacial relicts are remnants of cold-adapted species that experienced strong postglacial retractions and left behind populations in enclaves under relatively benign conditions (Hampe and Jump, 2011; Woolbright et al., 2014). It has been widely demonstrated that these retractions resulted in extinctions of plant species in not-suitable regions during the postglacial period that followed the Last Glacial Maximum (LGM, circa 21,000 years ago) (Svenning, 2003; Puşcaş et al., 2008; Rubiales et al., 2008). Although past extinctions are difficult to confirm because many species cannot be tracked in the fossil record, biological processes that anticipate local extinctions might be still happening in marginal populations of cold-adapted species. Understanding the processes behind persistence or extinction in these populations is important for addressing conservation actions, but also for anticipating the effects of contemporary climate warming on cold-adapted species.

As projected by environmental niche models, it may be expected that climatic differences among regions will affect unequally the ability of glacial relict populations to persist over space and time (Engler et al., 2011). In southern European mountains, glacial relicts correspond to rear-edge populations, i.e. those residing at the low-latitude margins

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of species distribution ranges (Hampe and Petit, 2005). Reduction of suitable habitat and related stochastic processes have high impacts on these populations, resulting in genetic differentiation with high between-region diversity and low within-population diversity (Hampe and Petit, 2005; Frankham et al., 2014). In general, local extinctions may be explained by the extinction vortex, a complex set of abiotic and biotic processes, such as habitat loss and inbreeding, driving small populations downward to disappearance (Brook et al., 2008). Although genetic data for narrowly distributed plants generally show low levels of variability, this information can be understood better when compared with other populations or congeners with similar life histories, supposedly free from extinction risk (Gitzendanner and Soltis, 2000). The evaluation of genetic diversity in glacial relict populations is critical for understanding extinctions in southern refugia in the northern hemisphere (Stewart et al., 2010), but so far very few studies have compared the genetic effects of long-term isolation in rear edge populations across regions.

In this study, we evaluated symptoms of extinction and persistence in glacial relict populations that survived in mire habitats of the Iberian Peninsula. Our study system comprised populations of two cold-adapted species, *Salix hastata* L. and *Juncus balticus* Wild, which are categorized under different threat levels in different regions. Both species are currently distributed in the arctic regions of northern Europe and North America and also in calcareous fens of temperate mountains, where macro-climatic conditions and local micro-niches produce abiotic refugia (Blanca et al., 1998; Lorite et al., 2007; Jiménez-Alfaro et al., 2014; Fernández-Pascual et al., 2015). These properties make calcareous fens important habitats for the persistence of relict species (Hájek et al., 2010), but also sensitive systems to changes in temperature and precipitation (Essl et al., 2012). We hypothesized that at least some of the Iberian populations of *Salix hastata* and *Juncus balticus* show processes linked to the extinction vortex, e.g. low number of individuals, low heterozygosity and high inbreeding depression, which eventually could result in local extinctions (Brook et al., 2008). We further hypothesized that this effect might be only happening in regions where the climatic conditions are currently unsuitable for the species, following an 'extinction debt' model by which local populations have persisted despite habitat conditions became unsuitable (Kuussaari et al., 2009). Thus, populations that have persisted in the regions with the lowest climatic suitability may show symptoms that the extinction debt is close to being paid. To address these hypotheses, we compared population genetic diversity in different mountain regions where the two species are categorized under different extinction risk. We also compared the climatic niche of the studied populations with the present-day species distribution in Europe, computing distribution models under current conditions and under past conditions represented by the LGM. Our ultimate goal was to assess possible causes of extinction or persistence in different regions at the rear-edge of the two species' distribution.

2. Materials and methods

2.1. Study species

Salix hastata L. (halberd willow, *Salicaceae*) is a dioecious shrub usually forming thickets up to 4 m in height. The species has a circumpolar distribution and mainly occurs in arctic and tundra environments of Eurasia and North America. In Europe, *Salix hastata* has an arctic-alpine distribution, widespread in Scandinavia but with a limited distribution in southern Europe (Fig. 1). The species occurs in wet habitats cleared after the snow melts in arctic regions (Sandvik and Odland, 2014) and in the margins of water springs and fens in the southern European mountains. We studied the unique populations known in the Cantabrian Range (Critically Endangered, without seed production) and the sole population of Sierra Nevada (Critically Endangered, with seed production) (Fig. 1, Table 1); and one "not at risk" population from the Pyrenees (with seed production) for comparison purposes.

Extinction risk follows the IUCN species categorization in Spain (Moreno, 2010).

Juncus balticus Wild. (baltic rush, *Juncaceae*) is a perennial species forming stems 25–80 cm tall characterized by a creeping long-noded rhizome. The species is widely distributed in coastal dunes, salt marshes and margins of calcium-rich mires in the northern hemisphere. In Europe, the species extends from Scandinavia to the Iberian Peninsula, but unlike other cold-adapted species, it is not present in Central European Mountains (Fig. 1). The populations of the Iberian Peninsula grow in mountain fens of the Cantabrian Range, the Iberian System and the Pyrenees (Snogerup et al., 2002). We studied the only four populations currently known in the Cantabrian Range (Table 1), which are infertile (without seed production) and categorized as Endangered (IUCN criteria, Robinson et al., 2008); and one "not at risk" population of the Pyrenees, where the species is fertile (with seed production) for comparison.

2.2. Field sampling and genetic analyses

Fresh material was collected in five populations of *Juncus balticus* and in three populations of *Salix hastata* (see Table 1), covering the whole distribution range of the two species in the Cantabrian Range and Sierra Nevada, where the species are supposed to be under extinction risk. Since the study populations show, in most cases, a continuous distribution that makes it difficult to distinguish between individuals, we defined a minimum distance of 3 m between plants to optimize the number of samples according to the occupied area. In each population, between 9 and 30 plants (Table 1) were sampled along the whole area of occupancy (AOO). In *Salix hastata* ten leaves per plant were collected, while in *Juncus balticus* each sample consisted of two stems; the number of samples was constant in *Salix hastata* (N = 20) but differed in *Juncus balticus* according to the AOO of the populations. Plant material was maintained dried with silica gel until DNA extraction in the laboratory.

The genetic structure and the frequency of clonal plants were analyzed by Inter-Simple Sequence Repeat (ISSR) markers. ISSRs are widely used in conservation genetics since they are reproducible and a relatively high number of markers can be scored per reaction (Godwin et al., 1997; Nagaoka and Ogiwara, 1997). Genomic DNA was extracted from approximately 0.2 g of dried tissue by using the DNeasy Plant Mini kit (Quiagen, Clifton Hill, Victoria, Australia). DNA was quantified using a NanoDrop spectrophotometer, diluted at a final concentration of 20 ng/μl and stored at –20 °C. ISSR amplifications were conducted with the primer set #9 from the University of British Columbia (UBC, University of British Columbia Nucleic Acid-Protein Service Unit). Following an initial screening of 40 primers, nine primers whose bands were highly reproducible were selected (UBC # 811, 812, 813, 817, 822, 824, 834, 850 and 860). PCR amplifications were carried out in a total volume of 25 μl reaction mixtures, containing 20 ng of DNA, 2.5 μl of PCR Buffer 10×, 5 μM of primer, 2 mM of each dNTP, 10 μg/ml of BSA, 1u of *Taq* DNA polymerase and distilled water. Amplifications were carried out using a thermocycler Gene Amp PCR System 9700 (California, USA), with an initial denaturation step of 7 min at 94 °C, followed by 45 cycles of 30 s at 94 °C (denaturation), 45 s at 52 °C (annealing), and 2 min at 72 °C (elongation), and a final period of 10 min at 72 °C. PCR products were separated in 2% agarose gels in TAE and visualized using the RedSafe™ Nucleic Acid Staining Solution. Agarose gels were photographed (Gene Genius, Syngene, Cambridge, UK) and the size of PCR products was estimated by comparing with commercial DNA ladders using the TotalLab software (Newcastle Upon Tyne, UK).

The presence/absence of ISSR bands were analyzed for each sample. The percentage of polymorphic loci was directly calculated from the data. Genetic differentiation among populations was first carried out by Analysis of the Molecular Variance (AMOVA) in GenAlEx v6.501 (Peakall and Smouse, 2012). The genetic relationships among individuals were estimated by computing Jaccard's genetic similarities

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