



## Conservation priorities differ at opposing species borders of a European orchid

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### ABSTRACT

How populations from different regions within the distribution of a species contribute to the adaptive potential and survival of that species has important implications for formulating conservation actions. We test assumptions of concepts on geographic population structure (e.g. central-marginal concept and 'rear edge versus leading edge' model) that could be used to inform conservation of plant species under climatic changes. We analyze a comprehensive dataset of demographic traits (e.g. population size, flowering,  $\delta^{13}\text{C}$  of plant leaves) of up to 32 sites of *Himantoglossum hircinum* (L.) Spreng. (Orchidaceae) located within six sub-regions of its European distribution range. Soil and climate parameters are employed as environmental predictors of variation in measured population traits. Climate is the main driver of demographic variability overriding central-marginal gradients that might be present. Warming of the climate at high latitudes paves the way for northward range expansion of species. Populations at the north and north-eastern range peripheries partly show exponential population growth and high genetic diversity and are likely to be the source of immigrants for colonization of newly suitable habitats as the climate continues to change. In recent times, populations at the southern range periphery have suffered from intensification of land use and decreasing rainfall, but in the case of Southern Italy are important because they contain genetically unique traits. Populations at both, 'leading' and 'rear', edges ought to be at the focus of conservation planning. Different conservation strategies are proposed at opposing species borders taking into account spatial variation in population needs on a geographic scale, projected population response to expected environmental changes and genetic characteristics.

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### 1. Introduction

Understanding the degree to which populations from different regions within the distribution of a species contribute to the long-term adaptive potential and survival of that species has important implications for formulating conservation actions (Thomas et al., 2008). Yet, sparse or patchy information on presence data for many species ('Wallacean shortfall', cf. Whittaker et al., 2005) as well as shortfalls in knowledge about local population trends, threats and responses to changes in climate (IPCC, 2007)

and land use (Sala et al., 2000) are a significant barrier for priority assessments (Kozłowski, 2008).

The position of a population within the overall distribution of a species is assumed to result in variation of population traits and genetic identity partly through density independent factors and also due to biogeographical history (Hewitt, 2004; Hampe and Petit, 2005). Geographical concepts on spatial variation in population structure and dynamics include the central-marginal concept (CMC, Hengeveld and Haeck, 1982; Kluth and Bruehlheide, 2005; also termed 'abundant centre model') and the 'rear edge versus leading edge' concept (RLEC, Hampe and Petit, 2005). The well-established CMC assumes a decrease in population growth rate, density and fitness from the centre to the margins of the range of a species (Hengeveld and Haeck, 1982; Brown, 1984; Gapare et al., 2005). These decreases have been linked to increasing environmental stress and decreasing availability of suitable habitat patches towards the range margins (Brussard, 1984), where

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species are presumed to be at their environmental distribution limit (Holt and Keitt, 2000). The formation of range boundaries of the species is thought to be mainly determined by particular climatic variables, such as low temperatures limiting the northward spread of the species and water availability being one of the limiting factors at the southern periphery (Woodward, 1996, 1997). Genetic consequences of the CMC include reduced gene flow and genetic diversity of populations at the range periphery (Giles and Goudet, 1997; Ellstrand and Hoffman, 1990) because populations are farther apart and swamping of the edge zone gene pool by pollen or seeds from core populations which significantly slow adaptation to edge habitats (Baack et al., 2006). A major consequence of this theory is that the emphasis of a management regime would be better placed on central populations to ensure optimal use of project resources, because management targets may become increasingly difficult to achieve towards the edge of a species range, as suggested from the research on insects at the pan-European level (Bourn and Thomas, 2002). However, evidence for the demographic assumptions (reviewed by Sagarin and Gaines (2002)) and the genetic implications (reviewed by Eckert et al. (2008)) of the CMC remains inconclusive and so conservation projects may not be based on these assumptions alone.

Recent findings stress the importance of populations at the range peripheries for species survival (Hampe and Petit, 2005; Pearson et al., 2009). Marginal rather than central populations may harbour much of the genetic diversity of a species shaped by past climate-driven range dynamics (Hewitt, 2004) and may contain genotypes evolved under variable, extreme and suboptimal conditions indicating specific adaptations (Channell and Lomolino, 2000). Hampe and Petit (2005) reviewed literature conducted across taxa and ecosystems and suggested that 'rear edge' populations (populations residing at the low-latitude margins of the distribution of species) may be disproportionately important as long-term stores for genetic diversity and foci of speciation. Conversely, Pearson et al. (2009) showed that small populations of the seaweed *Fucus serratus* at the southern periphery of its distribution are less resilient to abiotic stresses probably because of reduced fitness and lower adaptive capacity.

In the study presented here, information on the geographic structure of demographic and genetic traits of populations of *Himantoglossum hircinum* (L.) Spreng. (Orchidaceae) have been used to test the assumptions of both the CMC and RLEC and consequently discuss the implications for formulating conservation measures. Detailed knowledge on life history (Carey and Farrell, 2002), climatic drivers of population dynamics (Pfeifer et al., 2006a,b), and distribution of *H. hircinum* makes the species a suitable model system for this task. Furthermore, *H. hircinum* is one of few species, where recent, climate-induced range shifts have apparently taken place demonstrated by the earlier onset of flowering and increases in abundance and population numbers at the species north and north-eastern range margins (Good, 1936; Carey, 1999; Carey et al., 2002; Pfeifer et al., 2006a), while decline in abundance and extinctions were observed along its southern range margin. Recent genetic diversity assessment showed that, contrary to expectations, genetic diversity of peripheral populations is not necessarily reduced (Pfeifer et al., 2009). Furthermore, the species is emblematic, being one of the tallest and hence most reliably recorded orchid species in Europe. At the northern range margins it tends to occur on threatened and highly diverse habitat patches. Both of these factors mark it out as a flagship for studying conservation requirements of communities rich in plant species originating from the Submediterranean–Subatlantic bio-geographic element (Preston and Hill, 1997) of the European flora and could act as an indicator of their response to climatic changes.

We analyse demographic traits of populations of *H. hircinum* for several central and peripheral regions within the distribution of

the species. Geographical structuring of habitat quality is assessed by investigating site-specific environmental traits (soil, climate, management). Plant stress is known to alter the  $^{13}\text{C}/^{12}\text{C}$  ratio (hereafter called  $\delta^{13}\text{C}$ ) in the plant tissue due to variation in photosynthetic capacity and stomatal conductance (Farquhar and Richards, 1984; Rundel et al., 1988) and this measure has been used in the work presented here to be an indicator of plant stress. Note that foliar carbon isotope variation is not related with plant stress per se, but with water use efficiency (WUE), and some studies have shown strong links between rainfall patterns and foliar  $\delta^{13}\text{C}$  variation (Stewart et al., 1995). Thereby, low WUE results in greater discrimination against  $^{13}\text{C}$  so that  $\delta^{13}\text{C}$  can be used as indicator of long-term water stress in individual plant species (Caldeira et al., 2001). Patterns of genetic traits, analysed in Pfeifer et al. (2009), are discussed in the light of geographical concepts and their implications for conservation planning.

We addressed four questions by the study presented below: (1) Do demographic traits (population size, number of flowering plants, flower production) vary between regions within the species geographical range? (2) Is habitat quality (e.g. soil attributes and climatic parameters) reduced at the periphery of the distribution of the species? (3) Is habitat quality reflected in demographic traits and physiology of the plants? (4) Do 'rear edge' populations differ from 'expanding edge' populations/core populations in their demographic traits and genetic structure and should they consequently be at the centre of attention for any conservation measures?

## 2. Materials and methods

### 2.1. Study area and study species

Thirty-two populations of *H. hircinum* (L.) Spreng. located across the European distribution range of the species (Fig. 1) were studied. *H. hircinum* is a Submediterranean Subatlantic distributed orchid species that perennates via tubers. Leaves emerge from below-ground tubers in autumn and grow over the winter months; plants start to develop inflorescences in late April (Carey and Farrell, 2002). Population growth rate, transition probabilities between life stages and flowering probability of *H. hircinum* populations at the north-eastern margin of its range have been shown to be strongly governed by variability in weather (Pfeifer et al., 2006a,b). Flowering takes place between May and July. Plants are pollinated by generalist insects (but especially solitary bees), seeds can fly very long distances but conversely some often remain lodged in the capsules, which are dropped beside the parent plant after maturation. The species is generally encountered in open habitats. While occurring more commonly within its assumed distribution centre (France), populations become increasingly isolated towards the range periphery often being bound to certain habitat types. The study covered five central sites, seven sites at the northern range periphery, a number of sites along a gradient towards the eastern range margin, and seven sites at the southern range periphery of its distribution (Fig. 1). Four populations located in the mountains in northern Spain were grouped as Atlantic sites because of the likely influence, climatically, of the Atlantic on population dynamics.

### 2.2. Collection and analyses of demographic data

Table 1 lists in detail, the measurements carried out at individual sites. Population size ( $N_{est}$ ) was estimated as number of plants in a population, in March 2007 and/or March 2008. In case of a high number of recruits, plants were counted in randomly located subplots and final population size was estimated by up-scaling to the area covered by the population. This is likely to underestimate real

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