

## Forum

## Combining niche modelling and landscape genetics to study local adaptation: A novel approach illustrated using alpine plants

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## ABSTRACT

Understanding the factors that shape adaptive genetic variation across species niches has become of paramount importance in evolutionary ecology, especially to understand how adaptation to changing climate affects the geographic range of species. The distribution of adaptive alleles in the ecological niche is determined by the emergence of novel mutations, their fitness consequences and gene flow that connects populations across species niches. Striking demographical differences and source–sink dynamics of populations between the centre and the margin of the niche can play a major role in the emergence and spread of adaptive alleles. Although some theoretical predictions have long been proposed, the origin and distribution of adaptive alleles within species niches remain untested.

In this paper, we propose and discuss a novel empirical approach that combines landscape genetics with species niche modelling, to test whether alleles that confer local adaptation are more likely to occur in either marginal or central populations of species niches. We illustrate this new approach by using a published data set of 21 alpine plant species genotyped with a total of 2483 amplified fragment length polymorphisms (AFLP), distributed over more than 1733 sampling sites across the Alps. Based on the assumption that alleles that were statistically associated with environmental variables were adaptive, we found that adaptive alleles in the margin of a species niche were also present in the niche centre, which suggests that adaptation originates in the niche centre.

These findings corroborate models of species range evolution, in which the centre of the niche contributes to the emergence of novel adaptive alleles, which diffuse towards niche margins and facilitate niche and range expansion through subsequent local adaptation. Although these results need to be confirmed via fitness measurements in natural populations and functionally characterised genetic sequences, this study provides a first step towards understanding how adaptive genetic variation emerges and shapes species niches and geographic ranges along environmental gradients.

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## Introduction

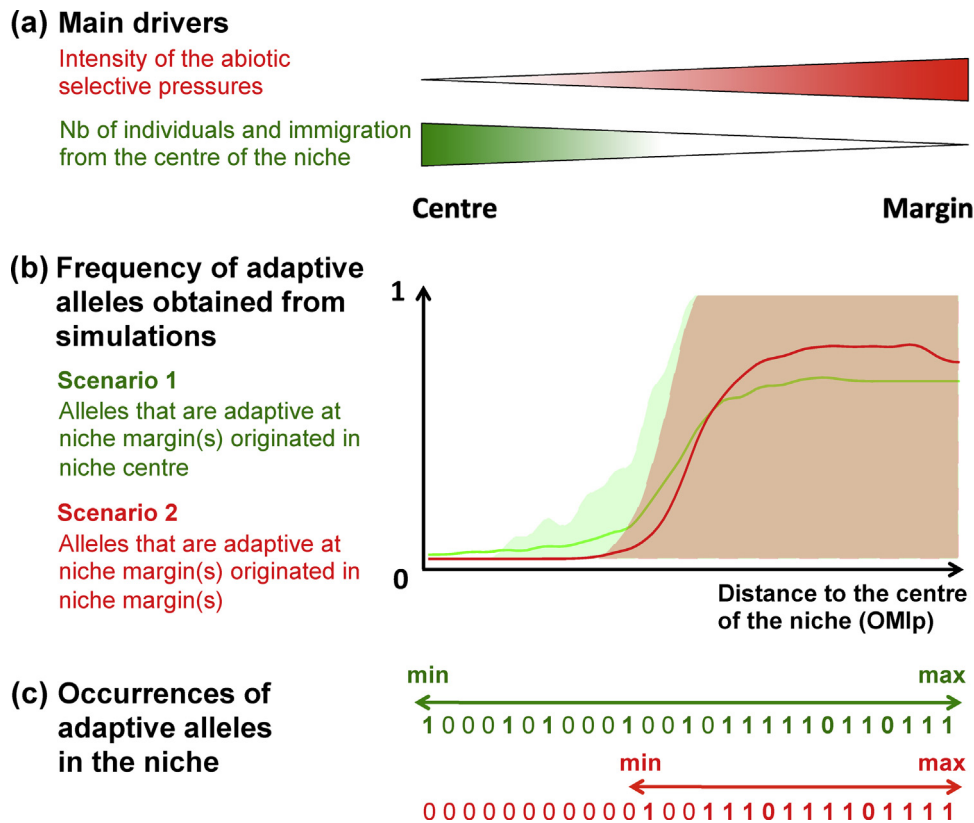
Understanding how species distributions will be modified by global changes has become an urgent task for ecologists (Parmesan, 2006). A first approach to study changes in species distributions is to model the realised ecological niche. Such models relate species occurrences to climatic variables and infer the future species distribution in response to climate change scenarios (Guisan and

Thuiller, 2005; Peterson et al., 2011). These approaches have been used for a long time, but they only rarely account for the adaptive potential of species (Banta et al., 2012; Lavergne et al., 2010). However, local adaptation constantly shapes species distributions (Lavergne et al., 2010; Manel and Holderegger, 2013; Pauls et al., 2013; Razgour et al., 2013) and provides an important way to cope with unfavourable conditions.

To date, the factors that drive the emergence of local adaptation are largely unknown (Schoville et al., 2012). The emergence of locally adapted genotypes depends on several processes (Kawecki, 2008): (i) the probability of a novel mutation emerging, (ii) the relative strength of selection and drift in populations where the mutation emerges, and (iii) the time for dispersal from the location

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**Fig. 1.** Theoretical predictions concerning the occurrence and frequency of adaptive alleles to marginal niche conditions (large distance to niche centre) across a species niche space. Our theoretical model predicts that the occurrence of an allele that is adaptive to marginal niche conditions should be more widespread across niche space if it emerged in the centre of the niche than at the margin. (a) Drivers of adaptive allele distribution across niche space (from central to marginal niche conditions). Green and red triangles display the relative influence of these two potential drivers: in green, more individuals promote the emergence of adaptive alleles in the centre of the niche, whereas in red, the strength of abiotic selective pressures fosters adaptation at the niche margins. (b) Allele frequencies across the niche gradient expected under our theoretical simulations, for alleles originating in the centre of the niche (green) or in the niche margin (red), and all alleles being under positive selection in marginal niche conditions (model outputs shown in Fig. S11, Cases 1 and 2, see supplementary material S3 for more details). Solid lines represent the mean of all simulations for the two alternative scenarios of origin location of adaptive alleles (green and red, respectively), whereas the shaded area of the same colours corresponds to the range of possible simulation outcomes between the 0.1 and the 0.9 quantiles. The distance to the centre of the niche is measured by the outlying mean index of a population (OMIp, see section 'Modelling the niche for each species' for more details). (c) Example of expected occurrence distributions of adaptive alleles as a function of distance to the niche centre for alleles originating in the centre of the niche (green) or in the niche margin (red). 0 and 1 refer to the absence and the presence of the adaptive allele, respectively. Note that allele frequency increases towards the niche margin, i.e., where it is adaptive, in both scenarios (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

where the mutation emerges to the environment where it confers a selective advantage (e.g., marginal vs. central populations in the niche). Depending where novel adaptive alleles emerge (i.e., in the centre or margin of a species niche), different distributions of adaptive alleles are expected within a species niche space (Fig. 1).

Determining the origin of adaptive mutations occurring in marginal populations helps to distinguish two different scenarios debated in the literature (Kawecki, 2008). In the first scenario, many adaptive alleles are expected to emerge in the centre of the species niche – due to larger effective population sizes and consequently, more mutations. These alleles then migrate towards the margin of the niche due to demographic asymmetry. Alleles surfing towards niche edges will then be sorted by natural selection and potentially contribute to adaptation to the local environmental conditions of the niche margins (e.g., Bridle et al., 2009; Atkins and Travis, 2010). In the second scenario, adaptive alleles emerge directly at the margin and become fixed when their selective advantage overcomes the effects of genetic drift – due to the small size of marginal populations. Moreover, as individuals in marginal sites can be far from their optimal fitness, more mutations might be expected to be favourable. In this scenario, adaptation can also be promoted by the significant isolation from gene flow of maladapted alleles coming from central populations (Bridle and Vines, 2007; Hendry et al., 2001).

Empirical tests of theoretical predictions concerning the emergence of adaptation in the field are rare (Hampe and Petit, 2005; Kawecki, 2008; Sexton et al., 2009). Until recently, the detection of local adaptation under field conditions was mainly based on reciprocal transplant experiments and phenotypic measurements in common garden experiments (Leimu and Fischer, 2008). Those studies were not designed to detect specific genes involved in adaptation, but recent advances in DNA sequencing technologies, combined with statistical methods of population genomics, are major tools to detect loci potentially under selection (Storz, 2005; Stapley et al., 2010; Tiffin and Ross-Ibarra, 2014). It is now possible to sequence thousands of genetic markers for hundreds of individuals at a sufficiently large geographic scale to cover entire species distributions (Banta et al., 2012). These improved genome scans allow the distribution of several loci in the environmental landscape to be simultaneously described (e.g., Hancock et al., 2011), and quantitative hypotheses about the spatial distribution of adaptive genes to be tested. Mapping the position of adaptive alleles across species niches can provide a novel and relevant approach to determine in which populations local adaptation is most prominent and how adaptive alleles might rescue populations in marginal niche conditions, i.e., away from the centre of a species niche. We propose that describing the distribution of these markers (potentially located in genome regions under selection) within

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