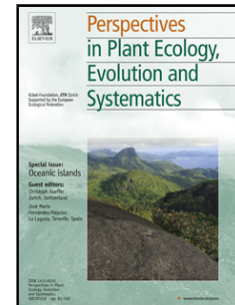


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- A novel approach combining landscape genetics with niche modeling.
- Alleles adaptive in the margin of the niche were also present in the niche center.
- The center of the niche contributes to the emergence of adaptive alleles.

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Combining Niche Modelling and Landscape Genetics to Study Local Adaptation: A Novel Approach Illustrated using Alpine Plants

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21

22 Abstract

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

32 In this paper, we propose and discuss a novel empirical approach that combines
33 landscape genetics with species niche modelling, to test whether alleles that confer local
34 adaptation are more likely to occur in either marginal or central populations of species niches.
35 We illustrate this new approach by using a published data set of 21 alpine plant species
36 genotyped with a total of 2,483 amplified fragment length polymorphisms (AFLP),
37 distributed over more than 1,733 sampling sites across the Alps. Based on the assumption that
38 alleles that were statistically associated with environmental variables were adaptive, we found
39 that adaptive alleles in the margin of a species niche were also present in the niche centre,
40 which suggests that adaptation originates in the niche centre.

41 These findings corroborate models of species range evolution, in which the centre of
42 the niche contributes to the emergence of novel adaptive alleles, which diffuse towards niche
43 margins and facilitate niche and range expansion through subsequent local adaptation.
44 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.

Glossary

Species distribution (or species range): the area encompassing all species occurrences.

Fitness: the ability to survive and reproduce in a given environment.

Adaptation: the increase in fitness associated with a genetic change.

Ecological niche: the environmental preferences of an organism, defined by its occurrence within the ecological space. Here, this term is synonymous with the 'realised environmental niche', which is a subset, realised in the field, of the 'fundamental (or physiological) niche'. The realised niche accounts for biotic interactions and dispersal limitations.

Maladapted alleles: alleles that hamper a population to reach its adaptive optimum.

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 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 (Figure 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 et al., 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 a species niche can provide insight into the mechanisms of niche evolution.

Here, we describe an original approach to describe the origin of alleles that are adaptive to niche margins, based on a combination of niche modelling and landscape genetics, and illustrate it with an empirical example based on an unprecedented genetic database of 21 common alpine plants from the European Alps. We then present our results in the light of

theoretical predictions drawn from a simulation model. Finally, we discuss our approach and suggest perspectives and potential improvements.

A new approach combining niche modelling and landscape genetics

Evolutionary events that occur at niche margins are the drivers of niche evolution. Here, we aim to introduce a framework that tests the two following scenarios concerning the origin of the alleles that are adaptive in the niche margin (Figure 1): (i) adaptive alleles emerge in the centre of a species niche and then potentially migrate towards the margin of the niche via dispersal (Bridle et al., 2009; Atkins and Travis, 2010); or (ii) adaptive genetic variation mostly emerges in isolated populations at the margin of the niche, disconnected from the flow of maladapted alleles coming from the centre of the niche. We focus here on *de novo* mutations and do not consider standing genetic variation. Our framework was developed in the context of the environmental space of the niche, and considers the geography of species ranges (for more details about niche-geography duality, see Colwell & Rangel, 2009; Guisan et al., 2014). In the following sections, we describe the main steps of our approach.

Modelling the niche for each species

To map the position of potentially adaptive alleles in the niche, the location of each sampled individual in the environmental space can be estimated using niche modelling (Thuiller and Guisan, 2005). In particular, the procedure of the outlying mean index (OMI; Dolédec et al., 2000) is appropriate for this purpose. The OMI was developed in a multi-species context to quantify the deviation of the species niche from the mean habitat conditions. Its main advantage is the absence of any assumption regarding the shape of

species responses to environmental gradients. The OMI has thus been widely used in the recent literature to quantify species niches in several contexts, ranging from biogeography to macroevolution (Boucher et al., 2012; Thuiller et al., 2004). The OMI can be interpreted as a species marginality value or, in other words, the environmental distance of each species from the centroid of overall environmental conditions. Here, instead of using the index to compare species, we chose to compute an equivalent of the OMI to compare populations within one species. We call this index OMIp, with "p" referring to "populations". The OMIp at the center of the niche equals zero. For each species, the OMIp can be used to map the occurrences of the potential adaptive alleles in the environmental space of the species niche. During this procedure, each allele has to be associated with the niche characteristics of the species to which it belongs, by performing an OMIp analysis for each species separately.

Detecting the potentially adaptive loci via landscape genetics

According to the seminal work of Endler (Endler, 1977, 1986) and the more recent landscape genetics literature (Holderegger et al., 2008; Manel et al., 2003, 2010a; Schoville et al., 2012), evidence for natural selection in the wild can be obtained from replicated clinal variation of allele frequencies along replicated and independent environmental gradients. Various correlative methods can be used to detect associations between adaptive loci and environmental variables (e.g. Coop et al., 2010; Frichot et al. 2013; Joost et al., 2007, 2013; Manel et al., 2010b; Poncet et al., 2010, Schoville et al., 2012). The study of the distribution of allele frequency for these loci along environmental gradients is informative for recognising the ecological conditions in which local adaptation can emerge in particular populations (e.g., Hancock, 2011; Jones et al., 2013; Manel et al., 2012).

In our approach, we considered that all markers that were significantly associated with one or more environmental variables (temperature, precipitation, etc.), were potentially

adaptive alleles. These alleles were either located within a gene or were linked to a gene encoding phenotype(s) (or involved in regulation pathways of phenotypes) that improved fitness in a particular environment (Holderegger et al., 2008; Stinchcombe et al., 2008). The probability of the presence of a single allele (e.g., amplified fragment length polymorphism (AFLP)) in each sampling site can be modelled as a binomial process with a logistic regression (e.g., Joost et al., 2007). We used refinements to a logistic regression model to consider spatial autocorrelation within locations: the generalized estimating equation (GEE, Poncet et al., 2010; see also Dormann et al., 2007 for a review on regression methods accounting for spatial autocorrelation).

When testing for significant associations between allele presence and environmental variables, the logistic regression model might detect only alleles that are highly represented either at low values or at high values of the environmental variables, and consequently, our approach will detect alleles that are adaptive in only one of the margins of the environmental gradient. Alleles that are detected as potentially adaptive are thus likely to be under directional natural selection along the environmental niche gradient. In the future, the quadratic effect of environmental variables with logistic regression could also be used to detect alleles that are locally adaptive in the centre or at other locations within the environmental gradient.

Determining the adaptive alleles

Although alleles detected as putatively adaptive can be either directly located within the adaptive genes or linked to the genomic regions under selection (Nosil et al., 2009; Stinchcombe et al., 2008), regression-based approaches used to detect putative adaptive alleles are correlative and prone to confounding effects, mainly due to demographic history. As a consequence, complementary steps are required, to prove that the detected alleles are

really adaptive and improve **fitness** (Storz et al., 2010). These additional steps require the association of genetic data (allele frequency or occurrences), with phenotypic data (e.g., leaf size, flowering period, etc.) – or fitness-related traits (e.g., survival, number of offspring, etc.) – to confirm the influence of potentially adaptive alleles on individual fitness (Qi et al., 2013). Linking genetic variation to phenotypic and fitness differences can be achieved either through measurements in the field or through controlled laboratory experiments (e.g., reciprocal transplant studies, quantitative trait locus mapping and genome-wide association studies; Rogers and Bernatchez, 2005; Fournier-Level et al., 2011; Schoville et al., 2012). This task is easier for model species, for which an annotated reference genome is available (Fumagalli et al., 2011; Hancock et al., 2011).

This step is particularly delicate when analysing individuals genotyped with traditional AFLP markers, because it necessitates the sequencing of the individual with the allele potentially under selection. Due to recent advances in sequencing technologies, large-scale single nucleotide polymorphism (SNP) and phenotype databases are becoming increasingly available. Next Generation Sequencing (NGS) technologies arguably represent an important potential for the endeavour of understanding the population context of local adaptation and niche evolution in non-model species (see Perspectives section).

Mapping the adaptive alleles in the ecological niche

Once the OMip and the presence of the potentially adaptive alleles have been inferred for each sampling site, it is then possible to estimate the range of the OMip of each allele by calculating the following metrics: the minimum and maximum OMip of adaptive allele occurrences and the range of the OMip for each adaptive allele. The same metrics were derived for neutral alleles. If adaptive alleles come from the centre of the niche, we would expect a widespread occurrence in the niche. In contrast, if adaptive alleles originate in the

margin, the occurrence of adaptive alleles should remain restricted to species niche margins (Figure 1), because directional gene flow is presumed to be much higher from the centre of the niche to the margin than the other way around (Hendry et al., 2001; Bridle and Vines, 2007; Kawecki, 2008; Holt, 2009). Thus, different scenarios of niche evolution can be disentangled by comparing these metrics between adaptive and neutral alleles, owing to theoretical expectations that can be derived from simple simulations.

Theoretical predictions on the adaptive allele distribution in the ecological niche

To our knowledge, studies that have focused on the distribution of adaptive alleles across species niches are particularly scarce, probably due to the lack of clear theoretical predictions. To bridge this gap, we built a simple theoretical model that provides expectations about the distribution of adaptive (*vs.* neutral) alleles in the niche. This model predicts the expected shape of the curve depicting allele frequencies computed at every OMIp, according to the origin of the allele (centre or margin of the niche) and the strength of drift, selection and migration forces. We describe this model in detail and provide the R code in Supplementary material (S3 and File S2).

Application to alpine plants

Genetic sampling and environmental variables

We tested our approach with an extensive data set of 21 alpine plant species sampled and genotyped over the entire Alpine arc (2,483 AFLP markers in 1,733 sampling sites). These data are a subset of the original dataset of Gugerli et al. (2008), also previously analysed by Taberlet et al. (2012). The genetic database is available from DRYAD (Meirmans et al., 2011b). The plant species were collected and genotyped according to the methods

described by Gugerli et al. (2008; Table S1, Figure S1). At each location, three individuals were sampled for each species, if present. Fourteen monthly and annual environmental variables of temperature, precipitation, radiation, and topography (Zimmermann and Kienast, 1999) were used to characterise each sampling location (Manel et al., 2012). To circumvent multicollinearity among variables, we conducted a principal component analysis (PCA), to reduce the large number of environmental variables to a few uncorrelated axes. To select the number of informative axes, we used the screeplot method (Cattell, 1966) and confirmed that the axes explained a sufficiently high percentage of the variance of all environmental variables. Analyses were conducted using R 3.0.1, the R-package “ade4” (Dray and Dufour, 2009).

Identifying putative adaptive loci

To circumvent problems of model fitting, we only considered AFLP alleles with 10 occurrences (i.e., at least 10 presences and 10 absences). This pre-selection step eliminated 1,055 AFLP loci (not considered in the initial count, Table S3). Using this method improved model fitting and prevented the detection of alleles that had drifted to high local frequencies without the action of selection, as being potentially adaptive.

The probability of occurrence of each AFLP allele was then modelled as a binomial process as a function of the first axis of environmental PCA, separately for each species (script provided in Supplementary file S1). We accounted for spatial autocorrelation in the data resulting from the genetic relatedness of the three individuals sampled in each sampling location (e.g., Liang et al., 1986; Poncet et al., 2010), using GEEs (see Supplementary Material S1 for more details).

Determining the adaptive alleles

In the application we describe here, only dominant markers (AFLPs) were available. Because no phenotypic or genome-wide data were available, we chose a working hypothesis to determine the adaptive allele: given that a locally adapted population must have a higher fitness at its native site than any other populations introduced to that site (Savolainen et al., 2013), local adaptation can produce sharp shifts in allele frequencies at given sampling sites (Hancock et al., 2011). Previous studies have shown that alleles involved in local adaptation tend to be present in only few sites across the niche of a species (Fournier-Level et al., 2011) and to have a narrow distribution (Banta et al., 2012). We thus expected that such alleles occur at a high frequency in few populations of a given species. This is in line with the view that important adaptive changes for niche evolution take place in populations occurring at the margins of species niches (Lavergne et al., 2010).

As a consequence, we assumed that for the putative adaptive AFLP loci, i.e., those correlated with the environment, the rare state between the presence or the absence of each AFLP band in the whole niche space, was the one causing local adaptation (i.e., the one with the fewest occurrences in the whole niche gradient). This allowed us to locate alleles with adaptive relevance under marginal niche conditions, and thus to map them throughout species niches. This working assumption required transforming our data as follows: for each locus, if the band absence (value 0) was less frequent for the whole species, we replaced 0 by 1 and 1 by 0; if the band presence (value 1) was less frequent, data were not transformed. We applied this transformation to both putative adaptive and neutral loci, so that the comparison of their distribution within the niche space remained valid, and the results were independent of this transformation. We linked the presence of putative adaptive and neutral alleles to the environmental distance to the niche centre of each sampling site and then compared the resulting patterns of the OMIp ranges covered by adaptive and neutral alleles. Assuming that marginal populations tend to occur in the periphery of the species range, are probably less

connected and have small effective population sizes, it is expected that neutral loci show a trend towards low (or high) allele frequencies as the result of genetic drift. As a consequence, the rare state of the AFLP marker presence could be more (or less) frequent than expected by chance in the margin and thus, creates a conspicuously positive relationship between the presence of a putative adaptive allele and the distance to the niche centre. To address this issue, we compared “adaptive” and “neutral” allele frequency curves in the niche: if we detected an increase in the frequency of both adaptive alleles and neutral alleles near the margin, the relationship found was probably an artefact resulting from the data transformation. Conversely, if the frequency of adaptive alleles increased with the distance to the niche centre, whereas the frequency of neutral alleles remained stable, we can conclude that the trend detected is not an artifact and is probably due to pervasive local adaptation at the niche margins.

Correlating the OMip of sampling sites to putative adaptive allele occurrence

The mean environment for all 14 climatic variables and the OMip were computed for each sampling location (separately for each species). To simplify the computation of allele frequency for each OMip, we split the whole OMip gradient into 10 evenly distributed classes. It is a common expectation that the ecological niche is characterised by more individuals in the centre than in the margin (Holt, 2009). We accounted for this demographic asymmetry by weighting the number of detected alleles (potentially adaptive or neutral) by the number of individuals present in each class of OMip. To obtain allele frequencies per OMip class, we also divided the number of potentially adaptive alleles by the number of loci studied in each OMip class.

Results and discussion

We analysed the results with respect to only the first two axes of the PCA applied to the 14 environmental variables (Table S1). Indeed, these axes explained approximately 60% of the variation in species occurrences along climatic gradients, thus, we assumed that they adequately captured the range of environmental variation that drives most climatic niche divergence in the study species. The first axis was mainly associated with temperature variables ($r = 0.96$) and altitude ($r = -0.89$), and the second axis with precipitation ($r = -0.88$) and soil humidity variables ($r = 0.52$; Table S2). The GEEs were applied to each AFLP locus, with the PCA axes as explanatory variables. We thus identified 93 loci (6.5% of the total) as putatively adaptive in 19 species (given the Bonferroni threshold $P < 0.05/\text{number of loci}$ studied for each species, Table S3; for more details see the Supplementary Material). The number of putative adaptive loci varied between species, with only one in *Trifolium alpinum* and 27 loci in *Arabis alpina*. No putative adaptive loci were detected for two species (*Luzula alpinopilosa* and *Gentiana nivalis*; see Table S3, and discussion in the Supplementary Material S2).

The shape of the niche, as described by the histogram of OMIP values of all individuals, followed a Gaussian curve that was skewed towards smaller values, indicating a maximum density of individuals towards the centre of species niches (Figure 2a). The decrease in density of individuals around null or nearly null OMIP values, was due to the statistical difficulty of sampling populations that occurred exactly in the centre of species niches. Consistent with much empirical evidence suggesting that a greater population size and genetic diversity occurs towards central niche conditions (Eckert et al., 2008; Sexton et al., 2009), more neutral and putative adaptive alleles were detected in the statistical centre of species niches, where individual density was greater.

The relative frequency of adaptive alleles per OMIP class was positively correlated with the distance to the niche centre ($P < 0.05$, adjusted $R^2 = 0.356$; Figure 2c), whereas the

frequency of neutral alleles was not ($P > 0.05$, adjusted $R^2 = -0.105$; Figure 2e). The absence of a relationship between OMip and the frequency of neutral alleles confirmed that our approach of considering the rare allele as adaptive did not create a conspicuous relationship between allele frequencies and the distance to the niche centre. Logistic regressions implemented with GEE tend to yield significant results for alleles that are abundant either in the lower or the upper margins of the environmental gradient, we thus expected such an increase in adaptive allele frequencies in the niche margin. A higher selective pressure in marginal environments can favour the fixation of these adaptive alleles, despite gene swamping from central populations (Hendry et al., 2001; Bridle and Vines, 2007; Bridle et al. 2009).

Notably, we found that putative adaptive alleles were distributed not only in the margin, but also in the centre of the niche (Figure 3): the minimum boundary of their OMip range was never detected above a score of 15. Most of the alleles present at the higher end of the margin (OMip > 60) were also present in the very centre of the niche (OMip < 10). This result invalidates the scenario in which alleles adapted to marginal conditions tend to originate only at the margin. The results rather suggest that gene flow from the centre to the margin are a major factor in shaping the distribution of adaptive alleles within the niche space (validation of the green scenario in Figure 1). Most alleles that are adaptive to marginal niche conditions might thus tend to emerge in the centre of species niches and then migrate towards marginal populations, suggesting that migration can help adaptation in the margin (Bridle et al., 2009).

We also found that neutral alleles tend to have a significantly smaller range of occurrence in the niche gradient than adaptive alleles: mean ranges of OMip scores were 35.3 for neutral and 43.5 for adaptive alleles, respectively (t -test, $P < 10^{-6}$, Figure 3). This is consistent with the prediction of our theoretical model that positive selection should increase

the local frequency of adaptive alleles (Supplementary Material S3, Figure S11), whereas the variation in the frequency of neutral alleles is less predictable due to overwhelming stochastic processes. Wide OMip ranges in adaptive alleles can also be explained by high gene flow from the centre to the margin of the niche (Figure 1). Wider OMip ranges for adaptive alleles than for neutral alleles were found for the majority of the species studied (Figure S9), including: *Androsace obtusifolia*, *Arabis alpina*, *Campanula barbata*, *Carex firma*, *Carex sempervirens*, *Cerastium uniflorum*, *Geum reptans*, *Gypsophila repens*, *Hedysarum hedysaroides*, *Hypochaeris uniflora* and *Juncus trifidus*. Only two species, namely *Ligusticum mutellinoides* and *Sesleria caerulea*, showed slightly wider OMip ranges for neutral than for adaptive alleles, with exceptionally large OMip ranges for neutral alleles. Previous studies have proposed that these species might possess good dispersal abilities (Table S4, Meirmans et al., 2011a), which might explain why all alleles tend to experience wide-ranging dispersal, regardless of their adaptive character.

Limitations

Although these results are based on a large spatial, environmental and genetic database of several species, this first application of our methodology is exploratory, and the results presented here are only applicable if local adaptation is associated with an increase in the frequency of the adaptive alleles and if adaptive alleles are assumed to be the variants with the fewest occurrences within niche space. Considering that rare alleles are adaptive might bias our results towards identifying alleles restricted to rare environments. Given that rare environments are more likely to be found in the niche margin, the data transformation might artificially increase adaptive allele frequencies in marginal conditions. However, there are two reasons why such a bias should be reduced: (i) we showed that the frequency of rare neutral alleles did not increase in the margin, thus providing a 'null' pattern to compare to adaptive

alleles (Figure 2e), (ii) most alleles detected as being adaptive were not restricted to the margin, but were also present in the centre of the niche (Figure 3). We relied on the assumption that rare alleles were adaptive, because phenotypic and fitness data were absent, which precludes the exploration of genome-wide associations with putative traits involved in local adaptation. The assumption that rare variants are locally adapted is thus not intrinsic to our method, but to our dataset. Further studies will not have to rely on this assumption, when phenotypic and genomic data become available to determine the individual fitness associated with adaptive alleles.

Here, we constructed the realised niche of the species from presence-only data points and used the realised niche as a proxy for estimating the fundamental niche, i.e., the true physiological tolerance of the species (see also "**Ecological niche**" definition in the glossary). This is an important assumption that can be potentially overcome by using a dataset that comprises the whole geographical range of each species (thus, also considering true absence data) and ideally, including data concerning species dispersal abilities and local biotic interactions.

In this study, we also considered that the allele frequency sampled along ecological gradients was representative of the real allele frequency in natural populations. This is a reasonable assumption with respect to the high number of sampled individuals and the large range of environmental conditions encompassed by our study design. Finally, the approach of computing allele frequencies in each class of OMIP permits the computation of allele frequencies in different populations with close positions in niche space but not necessarily in geographic space, which strongly reduces the potential biases introduced by demographic events and allele surfing on the detection of outlier alleles.

Overall, we acknowledge that the scenarios described in this article might not fully cover all the options encountered in reality. Although we are aware of some limitations of our data and approach, this publication as a forum article can help to stimulate research at the intersect between ecology, biogeography and population genomics.

Perspectives

Further studies describing the distribution of adaptive genetic variation within species niches will exploit recent developments of high-throughput NGS in non-model organisms. Indeed, the approach illustrated here might be greatly improved by genomic data obtained from restriction-site-associated DNA sequencing (RAD-seq), RNA sequencing (RNA-seq, also called, whole transcriptome shotgun sequencing, WTSS), DNA sequencing (DNA-seq) or genotyping by sequencing (GBS). These technologies generate sequences for a large number of loci. For species with a reasonable genome size, DNA-seq might also allow *de novo* whole-genome assembly (Schoville et al., 2012; Narum et al., 2013; Gagnaire et al., 2013; Brawand et al., 2014). Single nucleotide polymorphisms (SNPs) obtained with these sequencing methods provide more information than the dominant AFLP markers used here. When available, it will also become possible to match sequences potentially under selection with genomes of model organisms, with a reciprocal BLAST algorithm (for example, Altschul et al. 1990). Information about the function of the genes identified can also be obtained following gene ontology (GO) term enrichment techniques, especially when information on gene expression is available (with RNA-seq). In the absence of a reference organism genome (such as in Seeb et al., 2011), parts of the genome under selection might also be detected via other methods, such as genome-wide association study, if phenotypes are available (GWAS; Hoekstra, 2014), the study of the ratio between non-synonymous substitutions (under selection) and synonymous (neutral) substitutions in relation to climatic

variables (also referred to as the dN/dS ratio, e.g., Hancock et al., 2011), or via association tests between genomic regions and measures of population differentiation (under a F_{st} model, Brawand et al., 2014).

Given this plethora of new tools, it is becoming feasible to study the spatial distribution of adaptive genetic variation in virtually any organism, without the extensive lead-in work required to identify candidates through traditional quantitative genetic studies (e.g., QTL studies) of laboratory or captive populations (Stinchcombe and Hoekstra, 2008; Lowry et al., 2010; Manel et al., 2010a; Sexton et al., 2011; Schoville et al., 2012; Joost et al., 2013). In the next decade, we thus expect an increasing number of studies using massive amounts of genetic data, to empirically test theoretical hypotheses regarding local adaptation and niche evolution from the field-based sampling design of non-model organisms.

Conclusion

On the basis of the analysis of a massive AFLP dataset gathered for 21 plant species distributed across the entire European Alps, this study provides an original empirical test of the classic theoretical hypotheses that link adaptive genetic variation and species climatic niches. Our results thus provide interesting insights into the population genomic processes of niche evolution. We suggest that alleles that are potentially adaptive in the margin of a species niche mainly emerge in near-central populations and then migrate towards niche margins, where they are positively selected, ultimately allowing niche expansion – or at least, stability in niche margins. Local adaptation thus rarely emerges in isolated populations at the margin of species niches, but is rather favoured by continued gene flow from central populations. These findings might have important implications concerning the spatial distribution of potential adaptive alleles and the importance of maintaining gene flow to favour future adaptations in the face of climate change. Overall, the existence of standing adaptive genetic

variation will allow species to track climate change and adapt to it, as long as sink habitats remain connected to source populations (Hampe and Petit, 2005; Kremer et al., 2012). Our results also suggest that adaptation might occur more rapidly if populations occurring near central niche conditions, which are generally larger populations, are confronted with the new unfavourable environmental conditions. Our approach will help to resolve future challenges in understanding the origins and dynamics of contemporary adaptation to changing climate. In particular, it might provide insights into determining optimal gene flow between central and marginal populations to allow species survival in a shifting climate (as in Alleaume-Benharira et al., 2006). Quantifying the relative contribution of different portions of a species niche (centre and margin) to the emergence and fixation of novel adaptive alleles, will also help to understand the demo-genetic processes that adjust species requirements to existing climatic conditions or enhance the colonisation of formerly inhospitable niche conditions (Kawecki, 2008). Finally, knowledge on the spatial location of reservoirs of adaptation to future climate conditions might be important for designing reserve networks (Mumby et al., 2011).

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657

658 Figures

659 **Figure 1. Theoretical predictions concerning the occurrence and frequency of adaptive**
660 **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 Figure 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.

Figure 2. Distributions of (a) the number of individuals, (b) the number of potentially adaptive alleles, (c) the frequency of the potentially adaptive alleles, (d) the number of neutral alleles and (e) the frequency of neutral alleles as a function of the distance to the niche centre, as captured by 10 classes of OMIp scores. The OMIp classes are evenly distributed between 0 and the maximum OMIp of each species. The results are jointly

presented for the 21 study species. Frequencies correspond to the number of potentially adaptive (or neutral) alleles weighted by the number of individuals and by the total number of loci for each class of OMip.

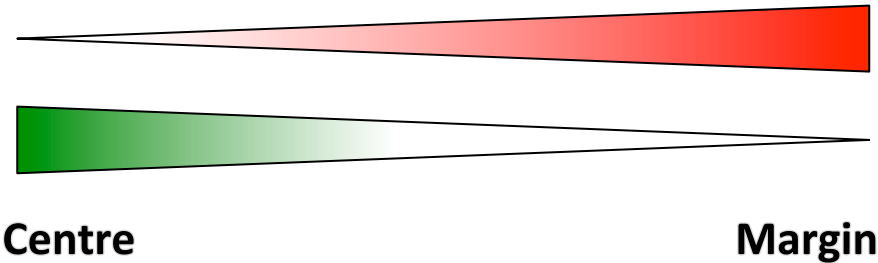
Figure 3. Histograms of the minimum OMip, maximum OMip, and OMip ranges of adaptive and neutral alleles occurring across species niches. These histograms are shown for (a) the 93 potentially adaptive alleles and (b) the 1,335 neutral alleles, jointly for all species.

Figure 1

(a) Main drivers

Intensity of the abiotic selective pressures

Nb of individuals and immigration from the centre of the niche



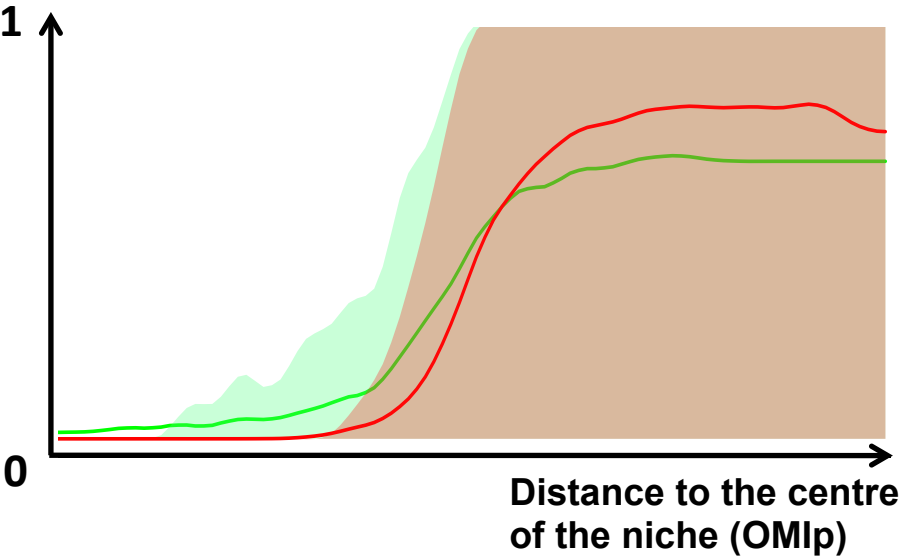
(b) Frequency of adaptive alleles obtained from simulations

Scenario 1

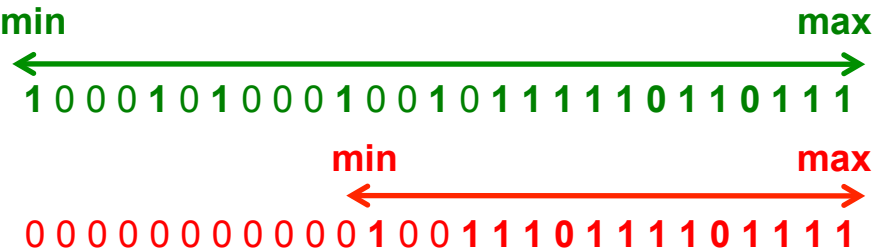
Alleles that are adaptive at niche margin(s) originated in niche centre

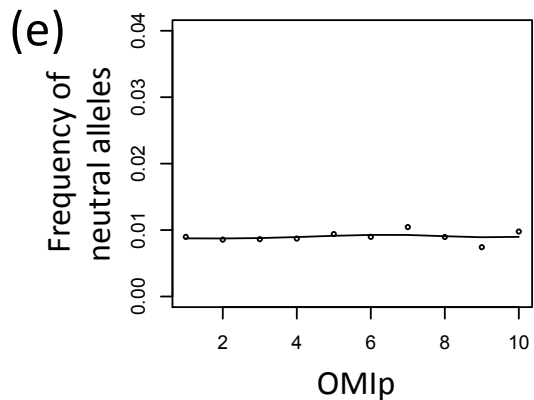
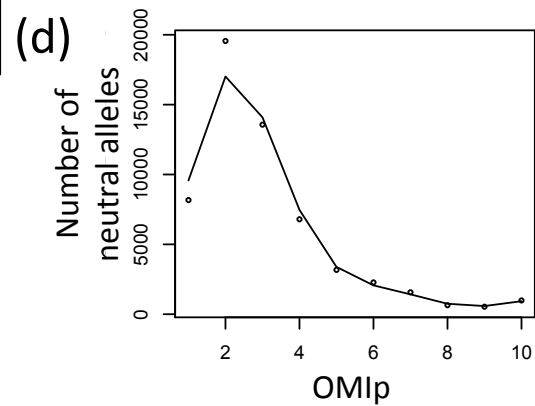
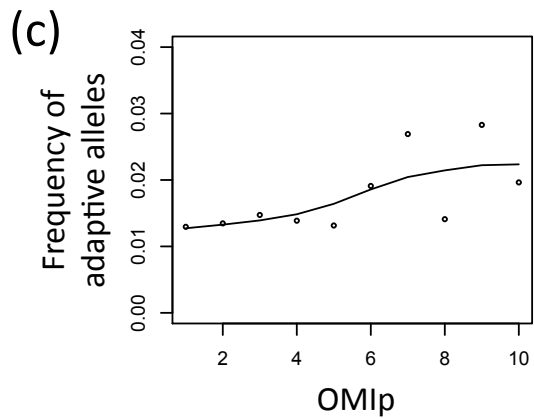
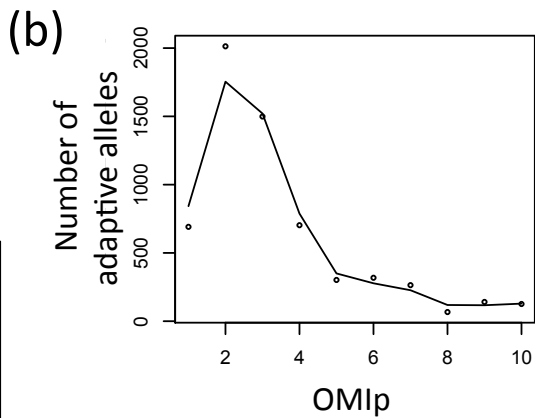
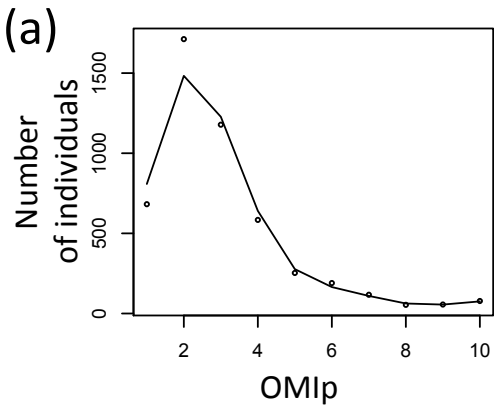
Scenario 2

Alleles that are adaptive at niche margin(s) originated in niche margin(s)



(c) Occurrences of adaptive alleles in the niche

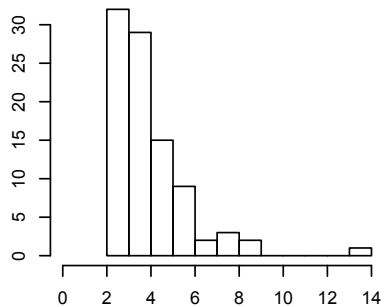




(a)

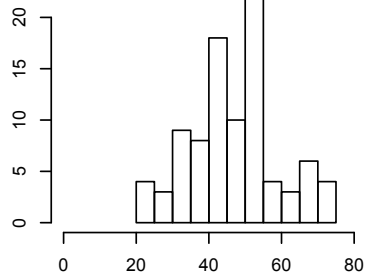
Number of
adaptive alleles

Minimum OMlp



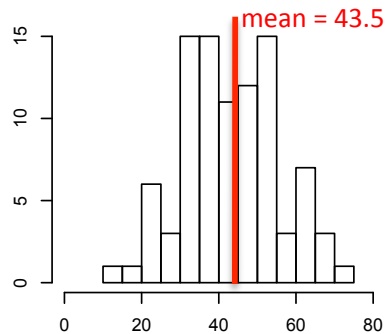
OMlp

Maximum OMlp



OMlp

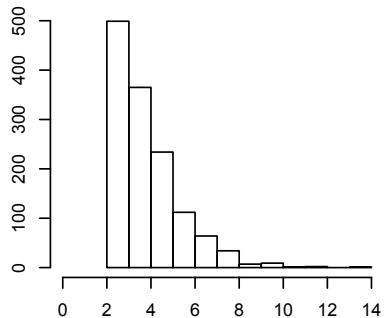
Range OMlp



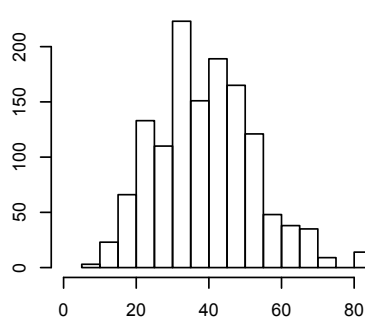
OMlp

(b)

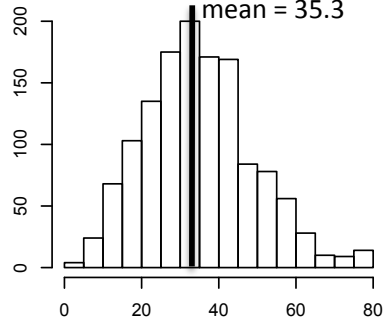
Number of
neutral alleles



OMlp



OMlp



OMlp