University of Sassari
Ph.D. School in Natural Sciences
Via Muroni 25, I-07100 Sassari, Italy

Dissertation for the Degree of Doctor of Philosophy in Environmental Biology
presented at Sassari University in 2016

XXVIII cycle

COMPARATIVE STUDIES OF ECOLOGICAL NICHE VARIATION AMONG CENTRAL AND PERIPHERAL POPULATIONS OF MEDITERRANEAN ENDEMIC PLANTS

Ph.D. Candidate: **M. Guillaume Papuga**

Director of the School: **Prof. Marco Curini Galletti**

Supervisor: ***Prof. Emmanuele Farris***

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Nota Bene: in the text, “Figure 1-2.” Refers to the second figure of chapter one.

SUMMARY

The Mediterranean basin is a biodiversity hotspot for plants and is characterized by its high richness and endemism. Species distribution patterns are often complex and disjunct due to the geological patchwork and climatic history. Thus, it represents a place of prime interest to test robustness of biogeographical hypotheses, which may in the end bring insights on mechanisms that drive plant diversity. Among them, the centre-periphery hypothesis (CPH) is a corner stone of biogeography and has stimulated an important amount of work through the past 50 years. Here we show that empirical evidences have brought little support to it as a general rule, suggesting that complex eco-evolutionary mechanisms shape range wide variation of genetic and demographic characteristics. While the CPH relies on the assumption of a concordance between geographic periphery and ecological marginality, this PhD thesis proposes a new framework that supports the need of a precise evaluation of species history, geography and ecology in order to investigate genetic and demographic variation.

In this perspective, we set up a comparative study of 11 Mediterranean vasculat plants to investigate changes in the micro-ecological niche between central and peripheral populations of species reaching their northern limit in southern France. Despite growing in similar broad habitat, we showed that several shifts appeared when analyzing fine scale ecological characteristics, which emphasized the ecological originality of peripheral population. Those peripheral populations subsist in cooler and wetter climate compared to their mean central relatives, but cannot be considered marginal regarding the global climatic niche of each species. Several species presented similar distribution patterns on restricted areas in France, and we discuss ecological and historical drivers of their distribution, in particular their persistence at the periphery of their range during Pleistocene glaciations. This historical perspective was also fundamental to explain range wide patterns of floral polymorphism observed in more widely distributed species (i.e. *Narcissus dubius*).

Due to their spatial isolation and ecological originality, peripheral isolates have a high evolutionary potential, which emphasizes their conservation value. Here we show that understanding fine scale ecological characteristics and distribution history is essential to shed light on processes driving plant diversity in the Mediterranean.

KEY WORDS: Mediterranean plant, ecological niche, centre-periphery hypothesis, range limit, ecological marginality, glacial refugia, rear leading edge, climatic transition, floral polymorphism

RIASSUNTO

Il Bacino Mediterraneo è un *hotspot* di biodiversità vegetale ed è caratterizzato da elevata ricchezza specifica e alto tasso di endemismi. I pattern distributivi sono spesso complessi e presentano areali disgiunti, a causa della complessa storia geologica e climatica del bacino. Perciò, esso rappresenta un'area di primario interesse per testare ipotesi biogeografiche, che potrebbero in ultima analisi fare luce sui meccanismi che condizionano la diversità ed evoluzione delle piante mediterranee. Tra queste, la cosiddetta "*centre-periphery hypothesis*" (CPH) è una pietra angolare della biogeografia ed ha stimolato un'enorme quantità di lavori scientifici negli ultimi 50 anni. In questo lavoro dimostriamo come le evidenze empiriche hanno supportato solo debolmente questa ipotesi come regola generale, suggerendo che complessi meccanismi eco-evolutivi plasmano la variazione delle caratteristiche demografiche e genetiche all'interno delle aree distributive delle specie. Mentre la CPH si basa sull'assunto di una concordanza tra la periferia biogeografica e la marginalità ecologica, questa tesi dottorale propone un nuovo punto di vista che si basa sulla necessità di una precisa valutazione della storia, geografia ed ecologia delle specie per investigare in maniera appropriata le variazioni genetiche e demografiche.

In questa prospettiva, è stato impostato uno studio comparativo di 11 piante vascolari mediterranee per verificare differenze nella nicchia micro-ecologica tra le popolazioni centrali e periferiche di specie che hanno il loro limite distributivo settentrionale nella Francia meridionale (popolazioni periferiche) e il centro della loro distribuzione nelle penisole iberica e/o italiana (popolazioni centrali). Sebbene crescano negli stessi habitat, sono state evidenziate diverse variazioni grazie alle analisi di dettaglio delle caratteristiche ecologiche, che hanno enfatizzato l'originalità ecologica delle popolazioni periferiche. Queste persistono in climi più freschi e umidi rispetto alle popolazioni conspecifiche localizzate al centro dell'areale, ma non possono essere considerate marginali riguardo alla nicchia climatica globale di ciascuna specie in studio. Diverse specie presentano una distribuzione simile su piccole aree in Francia, e pertanto in questa sede si è ritenuto interessante discutere e approfondire i fattori storici ed ecologici che determinano questi pattern distributivi assai simili tra specie diverse, in particolare la loro persistenza alla periferia del loro areale durante le glaciazioni pleistoceniche. Anche questa prospettiva storica è stata fondamentale per spiegare variazioni del polimorfismo fiorale osservate in tutto l'areale di specie a distribuzione più ampia come il *Narcissus dubius*.

Grazie al loro isolamento spaziale e originalità ecologica, le popolazioni periferiche hanno un alto potenziale evolutivo, che incrementa il loro valore conservazionistico. In questa ricerca dimostriamo che la comprensione delle caratteristiche ecologiche a scala di dettaglio e della storia distributiva è essenziale per fare luce sui processi che determinano la diversità vegetale nel Mediterraneo.

PAROLE CHIAVE: centre-periphery hypothesis, limite di areale, limite distributivo meridionale, marginalità ecologica, nicchia ecologica, piante vascolari mediterranee, polimorfismo fiorale, rifugi glaciali, transizione climatica.

INTRODUCTION

The existence of range limits - geographical boundaries where populations of a species cannot (or have not) establish further - is the outcome of an interactive range of processes that have fascinated ecologists for a long time. Such range limits provide the opportunity to explore questions on processes existing between organisms, their life history traits, and their interactions with their surrounding environment.

Individual fitness and population demographic parameters can vary across the range, from places where they perform best to boundaries where populations may struggle to survive. This idea of a gradual decline in fitness gave birth to the so-called “centre – periphery hypothesis” (CPH), early in the 1980’s (Hengeveld & Haeck 1982; Brown 1984). This general framework has been declined into several hypotheses that relate to three main patterns of trait variation across a species range: 1) changes in the spatial genetic structure of populations, 2) variation in demographic parameters, and 3) variation in abundance and occurrence of populations. Trait variations are related to differences in the ecological characteristics of the habitat occupied by a species that are supposed to delimit species’ range.

As empirical data have accumulated on geographical patterns, the CPH has appeared to be rather more complex than first predicted. The interplay between metapopulation dynamics, ecological constraints and historical processes of range contraction and expansion have played a major role in shaping trait variation as species reach their range limits. Moreover, ecological and evolutionary processes may act differently regarding traits that are considered. Therefore, the need to disentangle those processes is important to better understand the mechanisms that drive population variation across a species range.

Also, there has been rather an amalgam between ecological marginality and geographical periphery in attempts to explain mechanisms driving CPH patterns. Indeed, this issue has received much criticism (Soulé 1973; Hardie & Hutchings 2010), and it remains unclear about whether ecological niche differences occur as species reach their range limits. This constitutes a major issue for our understanding of spatial patterns of trait variation in peripheral populations.

The CPH has been subject to much empirical investigation, although there is much bias towards studies that have focused on the northern edge of temperate taxa distributions in the northern hemisphere (Eckert, Samis & Lougheed 2008). This restriction to a particular case where temperate species face colder climates, and places that they have recolonized quite recently limits our comprehension of the underlying processes. Therefore, there is a need to diversify empirical studies to get clearer insights on the hypothesis. In this context, the Mediterranean climate region represents a setting of prime importance to understand the underlying mechanisms, as most of them were less impacted by ice sheet during Pleistocene glaciations, which strongly influenced range contraction and extension (Blondel *et al.* 2010). The Mediterranean basin provides a large number of potential study species due to the high richness and endemism of its flora, with distribution ranging from rare to widespread taxa (Thompson 2005). Its complex spatial configuration, with several geographical and ecological barriers, induces disjunct distributions with the persistence of isolates throughout and beyond the principal range (Comes 2004). The relative stability of climatic conditions during last glaciations and the absence of a large permanent ice sheet have allowed the persistence of a wide variety of taxa, both Mediterranean and non-Mediterranean, in locally restricted areas across a large part of the region, making the

Mediterranean Basin the third most important biodiversity hot-spot for vascular plants in the world (Myers et al. 2000).

In this context, this thesis attempts to obtain insights on the CPH, in particular in respect to possible ecological niche variation among central and peripheral populations, of Mediterranean plant species. The objectives here relate to five main questions.

Question 1. What can we learn from the empirical literature dealing with the centre-periphery hypothesis, and what does it tell us regarding the importance of ecological niche in large-scale processes? The first aim of this work was thus to make a global review on what is known about the CPH. Despite an important amount of empirical tests realized in the last two decades all around the world, no synthesis of this work had been undertaken to provide a broad view of the degree to which the above hypothesis has been confirmed or refuted and the contemporary challenges and issues related to the central peripheral hypothesis. Through a wide analysis of the literature we made an update of what has been published on the topic until now, and attempted to clarify various aspects of the CPH, in particular any biases which may influence global patterns of genetics, ecology and demography in central and peripheral populations. We paid particular attention to the need to disentangle ecological, geographical and historical processes that shape species traits across their range.

Question 2. How do history, ecology and range structure interact to shape current patterns of ecological and genetic variation? How does such variation relate to possible reproductive traits variation? To answer these questions we studied variation in the expression of a floral polymorphism and the ecological niche of *Narcissus dubius*, a western Mediterranean endemic geophyte, in regards to its contemporary and historical distribution in potential refugia in the Mediterranean area. We investigated how past distribution and ecological conditions may have contributed to contemporary patterns of floral variations among central and peripheral populations.

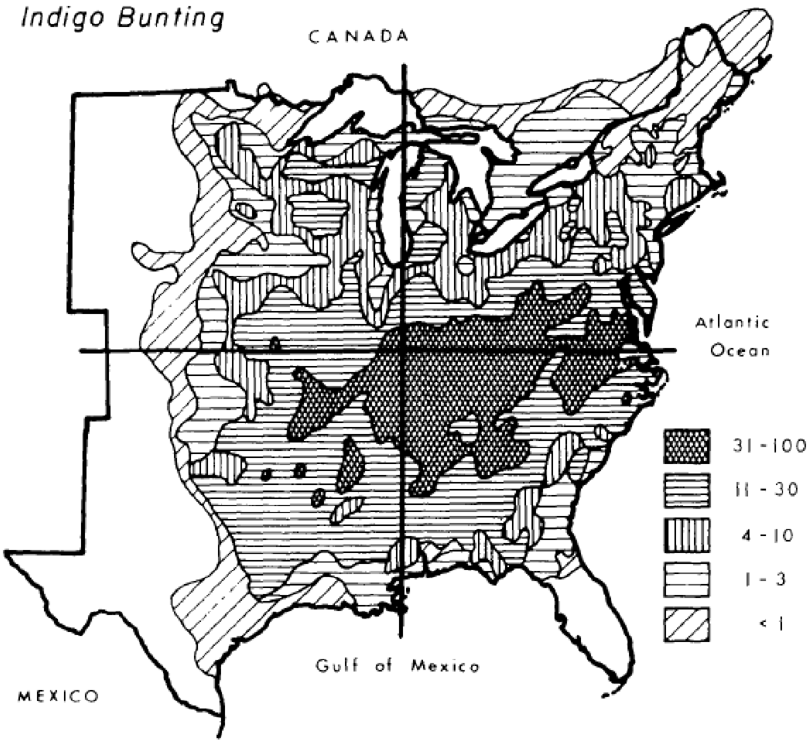
Question 3. Do species in a given region show similar patterns of ecological niche variation among central and peripheral populations? In particular: do micro-ecological features show repeated variation at the distribution limits? To answer these questions, we conducted a comparative analysis of variation in the ecological niche in central and peripheral populations of 11 Mediterranean plant species. This study represents a completely original cross taxa analysis of 11 species in their southern more central populations and their peripheral populations at the northern limits of their distribution in the Mediterranean climate region of France. Our emphasis here was on detecting any potential patterns of ecological originality where species persist at their northern distribution limit.

Question 4. How does the climatic niche vary across species range in a Mediterranean context? In particular, are peripheral populations climatically marginal regarding their entire climatic niche? To answer those questions we compared the climatic niche of 11 species previously studied in chapter 3 at their northern range limit in France, with populations located in the central part of their range. We also investigated whether other species shared a similar distribution pattern, and discuss the ecological drivers that limit species distribution.

Question 5. How do ecological factors interact across species range to shape local abundance? To answer this question we used data collected in chapter 3 and 4 and performed a global analysis to disentangle the impact of climatic variables, micro-ecological factors and position across the range on local abundance. We also proposed a new framework to investigate mechanisms that shape plant abundance.

Finally, we discuss those five questions together to bring insights on niche variation in a centre-periphery context. We conclude this thesis with a discussion on the place of peripheral isolates in conservation.

CHAPTER 1: Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm



Distribution of abundance of the Indigo Bunting, extracted from Brown 1984

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Setting the scene

Introduction

Biogeography is a science that seeks to understand patterns in the distribution of traits, species, communities and ecosystems in space and time (Brown & Lomolino 1998). It aspires to identify where species occur, how they perform at distinct locations and the spatial, ecological, historical factors that explain such variation in occurrence and performance. The discipline of biogeography thus provides a basis for the investigation of the processes that generate, maintain, and threaten biodiversity (Gaston 2000, 2003).

The “centre-periphery hypothesis” (hereafter the CPH) is a major biogeographical paradigm that aims to explain the variation in demographic, genetic and ecological characteristics of species across their distribution ranges, and ultimately, the causes of their range limits (Gaston 2009a; Sexton *et al.* 2009). Based on the assumption that the range of a species is a geographical representation of its ecological niche, the CPH postulates that environmental conditions are optimal near the center of the range and harsher at the periphery (Brown 1984). It also holds as a major tenet that populations are more isolated and less abundant near the range limits of a species (Hengeveld & Haeck 1982; Brown 1984). Ecological marginality, lower demographic performance and higher isolation are in turn predicted to cause a decrease in genetic diversity within populations (Soulé 1973; Lawton 1993) and an increase in genetic differentiation among populations (Da Cunha, Burla & Dobzhansky 1950; Mayr 1963; Eckert *et al.* 2008).

Many biogeographic studies have produced results that adhere to the predictions of the CPH, which has become a sort of “general principle” for several authors (Hengeveld & Haeck 1982; Guo *et al.* 2005; Eckert *et al.* 2008; de Oliveira *et al.* 2009) and has frequently been used to test ecological and evolutionary hypotheses (Holt & Keitt 2005; Sagarin, Gaines & Gaylord 2006). Conservation scientists have also used ideas of the CPH to assess the pertinence of conservation priorities (Lesica & Allendorf 1995; Gibson, Van Der Marel & Starzomski 2009; Thompson, Gaudeul & Debussche 2010; Rehm *et al.* 2015). In the last 15 years, there has been a series of attempts to assess the validity of the CPH for genetic and demographic features (Sagarin & Gaines 2002; Eckert *et al.* 2008; Sexton *et al.* 2009; Abeli *et al.* 2014). Although genetic diversity and differentiation appear to frequently follow predictions of the CPH (Eckert *et al.* 2008), abundance and other demographic vital rates (e.g. survival, fecundity) do not generally follow the expected pattern (Channell & Lomolino 2000; Sagarin & Gaines 2002; Sexton *et al.* 2009; Abeli *et al.* 2014). However, whether there actually is deterioration in environmental conditions towards the periphery of species ranges is frequently overlooked. This is despite the fact that the CPH could not stand if geographically peripheral populations were proven not to be ecologically marginal (Soulé 1973; Chardon *et al.* 2014). In addition, given that environmental conditions and species ranges change over time, populations currently considered to be ecologically or geographically central may have been marginal in the past, and vice-versa. For this reason, historical centre-periphery gradients, considering stable refuge areas (rear edge) as the “center” and recently colonized areas (leading edge) as the “periphery”, may provide a more accurate context in which to analyze patterns of genetic variation (Cain 1944; Hampe & Petit 2005; Carnaval *et al.* 2009) and/or demographic performance (Adams 1902; Hampe & Petit 2005).

The concepts of geographic centrality, ecological marginality, and center of origin have all been used in the CPH literature (Brown 1984; Hampe & Petit 2005; Kawecki 2008), but the interactions between geographical, ecological, and historical gradients have been rarely studied. At the same time, lumping different gradients into the general category of centre-periphery gradients might lead to misconceptions of the factors affecting the distribution of genetic variation and demographic performance (Pironon *et al.* 2015). Furthermore, the CPH assumes that genetic and demographic features are interdependent, and thus that they show the same centre-periphery pattern of variation (Carson 1959; Brussard 1984; Eckert *et al.* 2008). However, this assumption is contradicted by the fact that the CPH has been validated previously for genetic variation (Eckert *et al.* 2008) but not for spatial patterns of demographic rates (Sagarin & Gaines 2002; Sexton *et al.* 2009; Abeli *et al.* 2014). Merging species' information for the different components of the CPH would help clarify such incoherence. Finally, it has been proposed that the CPH might only be valid for some particular organisms, or in a subset of biogeographical regions, or at certain spatial scales, but very few studies have attempted to address this issue (Sagarin *et al.* 2006; Eckert *et al.* 2008).

Despite the common framework shared by the studies we review here, the naming of the hypothesis is variable. For the 248 papers that we selected, 168 (67%) did not explicitly name the hypothesis, although their aim was in fact to test some of its predictions. In the remaining 33%, three names were most commonly used: the abundant-centre (47%), the central-marginal (24%), and the centre-periphery (15%) hypotheses. In addition, several authors used various other terms to name the hypothesis (e.g. core-periphery, Carson's, Brown's hypothesis, etc.).

In a seminal publication, Brown (1984) introduced the "abundant-centre" hypothesis. Although it refers explicitly to abundance patterns, it has been invoked to underlie variation in other parameters in a centre-periphery context. In our study, we restrict usage of this term to the specific domain of abundance. The word « margin » has been used to refer to both ecological marginality (Soule, 1973; Farris & Schaal, 1983) and geographical marginality (Arana et al., 2010; Doudová-Kochánková et al., 2012). The latter is confusing because geographical and ecological gradients are not necessarily concordant (Soule, 1973; Pironon et al., 2015, see further discussion in IV.1.). For clarity, we prescribe the use of the term "centre-periphery hypothesis" when studying the geographical distribution of genetic and demographic performance, and restrict the use of "central-marginal" gradients to strictly ecological considerations (Shreeve, Dennis, & Pullin, 1996; Hardie & Hutchings, 2010).

Box 1-1. The centre-periphery hypothesis, a polymorphic concept.

In this paper, we first trace the long and complex history of the CPH by reviewing pioneer theoretical and empirical studies. Second, we test the validity of the CPH by updating the results of previous partial reviews, and linking the genetic and demographic patterns into a single overall analysis. This analysis aims to tackle a range of taxonomic, biogeographic, and methodological issues that had been raised in previous reviews. In addition, our study also differs from previous reviews in that 1) we evaluate whether the first assumption of the hypothesis is always checked and verified (i.e. environmental conditions become more marginal towards the range periphery), and 2) we attempt to disentangle the relative effects of geographical, ecological and historical centre-periphery gradients on the distribution of genetic variation and demographic performance. This critical assessment of the CPH allows us to better understand geographic patterns and the causes of species range limits, as well as the relative conservation value and vulnerability of central and peripheral populations.

History of the "centre-periphery hypothesis"

The pioneers (1900-1950)

The analysis of variation in species' properties across the geographical range has a long history. Right from the early days of such work, there has been a marked dichotomy between two lines of inquiry, one concerning the general performance of populations or individuals, and the other concerning genetic variation.

The idea that species become rarer and perform worse at their range margins due to less optimal environmental conditions can be found in the scientific literature since at least the 19th century. For instance, (Darwin, 1859, pp. 69-78) discussed ”the rigour of the climate […] on the confines of the geographical range” of taxa, and noted that “some species [were] gradually getting rarer and rarer, and finally disappearing” along geographical gradients. The basis for the study of geographic distribution limits was also being laid at that time (Wallace

1876). Specific interest in the issue of geographic variation in species' demographic performance across regions arose in the early 20th century. (Adams 1902) first proposed that species' abundance would be highest in their historical centers of origin. Simultaneously, other authors suggested that the centers of species' abundance could be defined by optimum ecological conditions, mainly climate (Cowles 1901; Transeau 1903, 1905; Shelford 1911). For example, (Cowles, 1901, p. 83) claimed that "each species varies in habitat in different regions, and […] in general a species can grow in the largest number of plant societies at its center of distribution, since there the climatic conditions favor it most highly". Similarly, (Transeau, 1905, p. 877) stated that species were most abundant in the centers of distributions, where "the complex of climatic factors most favorable to the development of this type of vegetation is […] localized and that as we depart from such centers we find conditions more and more unfavorable". Additionally, it was acknowledged that species had great difficulties in establishing beyond their required environmental conditions, with only "accidental" occurrences outside of a species' range (Grinnell 1922). Beyond abundance, some studies also found a lower individual performance in marginal populations of both animal and plant taxa, especially in terms of reproductive output (Salisbury 1926; Filipjev 1929). However, these pioneer studies were, not surprisingly, plagued with difficulties that hampered the production of meaningful conclusions, such as a frequent focus on vegetation units or communities rather than single species (but see Gleason, 1926) and scarce or, at best incomplete, data across the range of a given species (Griggs 1914; Salisbury 1926).

The interest in variation of species' genetic characteristics across their ranges also arose early in the 20th century, albeit slightly later and rather independently of demographic studies. The investigation of genetic patterns was first framed in a historical context of species' migrations and dispersal rather than in a static geographical perspective. Before intraspecific studies emerged, Adams (1902) had predicted higher species richness in the historical centers of origin of taxonomic clades. Later, several authors noted differences across species ranges in the abundance of varieties and genetic polymorphism. (Vavilov, 1926, p. 175) stated that "the basic centers of origin of cultivated plants appear, as a rule, to be found where a striking diversity of types is accumulated", and (Turrill, 1939, p. 230) observed that "towards the margins of their migrations species are less polymorphic" referring to wild plants. Notably, both authors acknowledged the existence of exceptions due to disturbing factors like geographical barriers.

To explain these patterns, it was proposed that species would suffer random losses in allele diversity in the course of colonization events or range expansion (Reinig 1938). At this time, the historical centers of species origin, associated with increased polymorphism, were explicitly differentiated from the centers of highest abundance (and highest individual size), which were in turn related to climatic favorability (Cain 1944). There were also early mentions of the existence of "marked variational forms" (i.e., greater genetic differentiation) in the geographic periphery of species' distributions, especially at the rear edge due to environmental stress (Good 1931). Of course these pioneer studies were based on observations of phenotypic variation, due to the lack of appropriate genetic tools at that time.

Towards the formulation of hypotheses (1950-1990)

- Demography

Ordination studies of vegetation in the 1950's and 1960's provided the first detailed data on intraspecific variation in abundance (Curtis & McIntosh 1951; Whittaker 1956, 1960; Monk 1965). With exceptions, these studies revealed that bell-shaped curves of abundance were very common along environmental gradients (Austin, 1976). This discipline, however, was frequently focused on the relative abundance of individuals of each species within the communities, and analyzed environmental or geographical gradients of local extent rather than across whole distribution ranges.

In the early 1980's, data on species' distribution and abundance were increasingly available in the form of atlases, flora and more conventional studies, which allowed the first general assessments of the CPH in different taxonomic groups. Two influential papers (Hengeveld & Haeck 1982; Brown 1984) proposed that patterns of higher abundance of individuals in range centers could be a general phenomenon. Haeck & Hengeveld (1981) attributed this pattern to an optimum-response surface, in which environmental conditions approach physiological optimum in the range centre. Brown (1984) proposed a more mathematical explanation in which the effects of multiple, independently varying environmental factors define the ecological niche with a bell-shaped curve. Although these authors acknowledged the underlying influence of the environment, they clearly emphasized the existence of a geographical pattern, unlike previous studies. Since then, much research has been carried out on animal and plant species to test what has become known as the "abundant-center hypothesis" (Carter & Prince, 1985; Caughley *et al.*, 1988; Carey, Watkinson, & Gerard, 1995; Curnutt, Pimm, & Maurer, 1996; Blackburn, Kevin. J. Gaston, *et al.*, 1999).

In addition to changes in abundance, many authors began reporting, mostly on insect taxa, higher extinction risk and demographic variability in populations at range edges due to poor environmental conditions (Birch, 1957; Nicholson, 1958; Richards, 1961; Whittaker, 1971; but see Grant & Antonovics, 1978). This could be explained by a higher susceptibility of peripheral populations to density-independent factors (Gaston 1990). However, higher demographic variability was also predicted for central (larger) populations (May 1981). Despite a growing consensus for central populations to have higher abundance and population growth rates (Mayr 1963; Soulé 1973), some authors showed that not all vital rates decline towards range margins, even when abundance is greatest at the center (Maurer & Brown 1989). Hence, the expected CPH pattern was demonstrated for some but not all demographic properties even within a given species.

- Genetic variation

Advances in genetics stimulated the analysis of patterns in genetic variation across species ranges in the 1950's, especially on Drosophila species. Interestingly, although geographical peripherality and ecological marginality were commonly associated, at that time authors emphasized the ecological status of populations rather than their geographical location to explain genetic patterns. A general pattern of a reduced chromosomal polymorphism in marginal populations began to emerge (Da Cunha *et al.* 1950; Townsend Jr 1952; Carson 1955; Goldschmidt 1956; Stalker 1964). Cunha *et al.* (1950) highlighted the role of habitat diversity in promoting genetic variation, whereas Carson (1955, 1959) argued that selection in more fluctuating peripheral populations would favor chromosomal monomorphism, which allows higher flexibility for recombination. Likewise, most early studies on allelic diversity in animals suggested higher polymorphism in central populations (reviewed in Mayr, 1963; Soule, 1973). These authors discussed the relative influence of stochastic processes, induced by spatial isolation and reduced gene flow, and strong selection, in marginal locations. However, some animals, such as Drosophila species, showed no reduction in allelic diversity in marginal populations (Soulé 1973), a result that was attributed to a homogenizing effect of high connectivity among populations of vagile taxa. In addition, some authors highlighted the potential differences in centre-periphery patterns between the commonly measured neutral markers, more affected by stochastic processes, and traits that better reflect the action of natural selection (Brussard 1984). Finally, besides trends in within-population genetic diversity, evolutionary biologists began to exhibit more interest in the possibility of greater genetic differentiation among peripheral populations (in more isolated areas with less gene flow) (Mayr *et al.* 1954; Brown 1957; Mayr 1963).

Thus, unlike pioneer studies prior to the 1950's, later papers primarily stressed contemporary rather than historical factors as drivers of genetic variation in different parts of a species range. In addition, the second half of the 20th century witnessed initial attempts to link genetic and demographic patterns by proposing that higher abundance in central populations would determine differences in inbreeding coefficients, isolation by distance, and the influence of density-dependence on selection (e.g. Haldane, 1956; Carson, 1959; Mayr, 1963). However, the generality of such postulates was limited; detailed information on both demographic and genetic patterns was only collected for Drosophila species, in which range-wide genetic variation could be explained by the potential roles of differences in selective regimes, abundance patterns and historical events (Brussard 1984).

Many studies were carried out across the distribution ranges of different animals and plants from the end of the 1960's, most of them showing higher genetic diversity in the center of the distribution, although some studies showed no pattern or indeed the opposite to that predicted by the CPH (e.g. Prakash, 1973; Tigerstedt, 1973; Yeh & Layton, 1979). In addition, an interest emerged in analyzing the genetic consequences of pole-ward migrations since the last glaciation, with most studies illustrating a decline in genetic variation in northern range-limit populations in the northern hemisphere (e.g. Dessauer & Nevo, 1969; Highton & Webster, 1976; Schwaegerle & Schaal, 1979).

Evaluation and refinement of hypotheses (into the 21st century)

From the 1990's onwards, an ever-increasing number of CPH tests have been conducted on a wide array of organisms, traits and continents, at different spatial scales, and using a high diversity of methodological approaches (Fig. 1, Appendix S1). A large number of studies have examined patterns of demographic performance across species ranges. Contrary to expectations, several initial reviews found no general support for the CPH for demographic parameters such as abundance, individual vital rates or population growth rates (Sagarin & Gaines 2002; Sexton *et al.* 2009; Abeli *et al.* 2014), although a tendency for higher demographic variability in peripheral situations was detected (Sexton *et al.* 2009). Several recent studies have also challenged the view that species' geographical range limits match their ecological niche boundaries (Chardon *et al.* 2014; Hargreaves, Samis & Eckert 2014). Such observations therefore stress the need to disentangle centre-periphery gradients associated with either geographic peripherality or ecological marginality.

In addition, the last 20 years have been marked by the arguments of several authors for a less static view of the CPH by considering that the distribution of species' demographic performance may reflect their temporal range dynamics, from post-glacial recolonization events to contemporary extinction/colonization dynamics after environmental change (Hampe & Petit 2005). For instance, species have been found to be more resilient to range contractions in the periphery of their distribution than in the centre, due to lower anthropogenic effects (Channell & Lomolino 2000). However, very few studies have compared demographic rates of rear and leading edge populations (Hampe & Petit, 2005; but see Purves, 2009; Pironon *et al.*, 2015).

The most comprehensive reviews of the CPH in relation to patterns of genetic variation in plants and animals have shown a general trend for lower genetic diversity within populations and higher differentiation among populations in the periphery (Johannesson & Andre 2006; Eckert *et al.* 2008). However, these patterns are far from being universal, and the authors have pointed out strong taxonomical, biogeographical and sampling-related biases in the available studies. Also, strong selection pressure in marginal areas due to stressful and fluctuating conditions could lead to the appearance of novel adaptations and confer greater evolutionary potential, and thus conservation interest, especially in the context of global warming (Safriel, Volis & Karr 1994; Lesica & Allendorf 1995). Moreover, as for demographic patterns, recent studies call for independent analyses of the roles of geography and ecology in shaping range-wide patterns of genetic variation (Lira-Noriega & Manthey 2014; Sexton, Hangartner & Hoffmann 2014).

Historical effects on genetic variation have also received much recent attention, with numerous studies focusing on peripheral populations that represent recent colonization events. In general, such leading-edge populations show lower genetic variation than central populations (Hewitt 1996, 2000). On the other hand, some authors have pinpointed the relevance of frequently overlooked rear-edge populations, which might show unique genetic properties due to their persistence in stressful or exceptional conditions, or due to their older history (Hewitt 1996; Hampe & Petit 2005). Guo (2012) emphasized the importance of evaluating central-peripheral and latitudinal gradients together, considering both historical and contemporary events, to understand biological patterns across ranges, as highlighted several decades ago by Cain (1943).

Global survey and meta-analyses

Paper selection

To compile a representative dataset of articles that have tested the CPH, we selected publications according to a standardized sampling method. First, we extracted all studies cited in the main text and supplementary information of four comprehensive literature reviews of the CPH: Sagarin & Gaines (2002) for abundant-centre patterns, Sexton *et al.* (2009) for demographic vital rates; Abeli *et al.* (2014) for plant populations' performance and abundance; and Eckert *et al.* (2008) for genetic diversity and differentiation. We then used the ISI Web of Knowledge database to select all papers that have since cited at least one of these reviews. Finally, we made a search on the ISI Web of Knowledge browser using as keywords the centre ("cent*" or "core") with periphery ("marg*" or "peripher*" or "edge" or "limit*" or "satellite") and link word "AND". We restricted our research to the first 250 articles in the field "ecology". This search was performed on June 30, 2014; papers published after this date have not been included in our study. We obtained a total list of 1260 papers that we filtered to retain original articles that explicitly compared central and peripheral populations based on empirical data and in which we could extract species-level results supported by statistical tests. This resulted in a final pool of 248 papers (Fig. 1A, Appendix S1), 131 of which had been analyzed in one or more of the four previous reviews, and 117 of which are novel to our review.

Data collection

Results of the 248 studies were sorted into several broad categories (abundance, population performance, size, ecological niche, and genetic variation), that each contains a set of parameters.

“Abundance” patterns were studied at two scales: population occupancy at a regional scale (or population frequency in a given area) and abundance of individuals (number or density) in a population. “Population performance” was assessed in relation to the demography of the populations: survival, growth, fecundity, recruitment, and the overall population growth rate. “Size” covered morphometric measures of individuals. Size was often considered as proxy for growth, hence, we examined the results for size and performance together. We also extracted results concerning the spatial or temporal variability of all the parameters of the categories “Abundance”, “Population performance”, and “Size”. Population occupancy was the only parameter for which we found no study on variability. The “Genetic variation” category included measures of three parameters: within-population diversity, among-population differentiation, and inbreeding.

Finally, in addition to these categories, we regrouped all articles that focused on the “ecological niche”. Two parameters were considered: the mean ecological niche that captured variation in mean conditions between central and peripheral populations and differences in the ecological niche breadth (variability among sites within central and peripheral groups of populations). Results for this category are presented separately in section IV.1.

In each article, we extracted results at a species level and assessed whether a given parameter was significantly higher in central (C) or peripheral (P) populations or not significantly different between the two geographic groups of populations (N). A wide variety of indexes have been used to describe each parameter; therefore, when several indexes were used for a single parameter (e.g. genetic diversity estimated by the number of alleles per locus and heterozygosity), we discarded non-significant indexes, and assigned one value of C or P per parameter only if indexes associated with significant statistical tests were all higher in central or peripheral populations. If no difference was statistically significant or if significant trends were detected in opposite directions, we considered the result as being null (N). Thus, the total number of tests of the CPH represents the number of parameter comparisons for all species in the 248 articles.

The CPH has been tested on a large panel of organisms, with a wide variety of sampling protocols. Therefore, we also extracted methodological information from studied publications. We first aimed to quantify spatial aspects of sampling schemes to assess their impact on the validation of the CPH. We examined three main sampling characteristics. The first was the relative position of peripheral populations within the species range or "Degree of isolation" between peripheral populations and the central part of the distribution. Here, tests were allocated to one of three classes: intermediate (peripheral populations located between the centre and the edge of the range), absolute (peripheral populations at the edge of the range) and beyond (peripheral populations isolated beyond the edge of a continuous range). A second sampling effect involves the "Spatial extent" of the study area (i.e. the largest distance between two studied populations). Again, we allocated studies to one of three classes: small-scale studies (< 200km between the two most distant populations), regional-scale studies (200 - 2000km) and continental-scale studies (> 2000km). These classes were adapted from Pearson & Dawson (2003). The third sampling characteristic is “Range cover” which assesses the proportion of a species distribution that has been sampled in the study using four percentage classes (0-10% / 10-25% / 25-50% / 50-100%). When not provided directly by the authors in the main text, the extent of species’ distributions was extracted from external sources (supplementary information, atlases, internet). Finally, study species were classified by kingdom (plant or animal), and by the biogeographical regions they inhabit (following USDA http://www.nrcs.usda.gov).

Statistical analyses

Our analysis is based on frequency comparisons using Chi-square tests of homogeneity. We also conducted binomial tests on the numbers of tests that validated the CPH for each parameter. First, we tested whether the hypothesis was validated for more than half of the tests (hypothesized probability of success of 0.5; i.e. C>P+N for comparisons of mean parameters, P>C+N for comparisons of genetic differentiation and parameters’ variability). If this deviation was not significant, we investigated whether the hypothesis was validated for more than one third of the tests (hypothesized probability of success of 0.33; i.e. C>P or C>N for comparisons of mean parameters, and P>C or P>N for comparisons of genetic differentiation and parameters’ variability).

We used a Principal Component Analysis (PCA) to investigate correlations among the three main sampling characteristics and limit potential redundancy. Given that these variables are semi-quantitative, we recoded them on an ordinal scale before performing the analysis. “Spatial extent” and “Range cover” were highly correlated and well summarized by the first axis of the PCA (54% of variability explained; later named "Scale") while the second axis was driven by the "Degree of isolation" (32% of variation explained; later named "Isolation"). We therefore used coordinates of each study on these axes as synthetic variables. Then, we fitted a Generalized Linear Model (GLM) for binomial data with validation of the hypothesis (yes or no) as a response variable and "Scale" and "Isolation" as explanatory variables.

All analyses were performed using the software R (R development Core Team 2010) and the ade4 package for multivariate analysis (Dray & Dufour 2007).

The "centre-periphery hypothesis": an overview

Multiple approaches

Our database contained 248 papers published between 1968 and 2014 in 89 different journals representing a wide range of current impact factors (from <1 to 31) (Fig. 1A, Appendix S1). Genetic variation was the most studied category with 135 papers representing 301 tests (Fig. 1B). Abundance and population performance were examined in 76 papers (176 tests), and 82 papers (262 tests) respectively. Differences in size and environmental conditions have been the least often investigated in 54 papers (95 tests) and 42 papers (96 tests) respectively. No study conjointly analyzed genetic variation, population performance and abundance patterns. Most of these empirical studies have been conducted in North America and Europe (83% of the articles, Fig. 1C). This over-representation of temperate areas may strongly impact results and limit any global interpretation of trends, which highlights the necessity of analyzing its potential bias.

Most papers studying the "centre-periphery hypothesis" (CPH) considered a geographical centre-periphery gradient. However, other non-geographical interpretations of central-peripheral gradients were commonly used (Fig. 1D) including ecological gradients with peripheral populations in different (or marginal) conditions (Hargrove & Rotenberry 2011; Pouget *et al.* 2013), and temporal gradients with peripheral areas containing younger (more recently founded) populations (e.g. Tollefsrud *et al.*, 2009; Gassert *et al.*, 2013). This approach was explicitly used when precise data on past distribution were available, for example in relation to post-glacial (Cwynar & MacDonald 1987; Hoban *et al.* 2010; Jadwiszczak *et al.* 2011), or recent (Mandak 2005) colonization. Finally, some authors described a centre-periphery pattern based on the size and/or the density of the population (e.g. Van Rossum & Prentice, 2004; Lemke & Porembski, 2013).

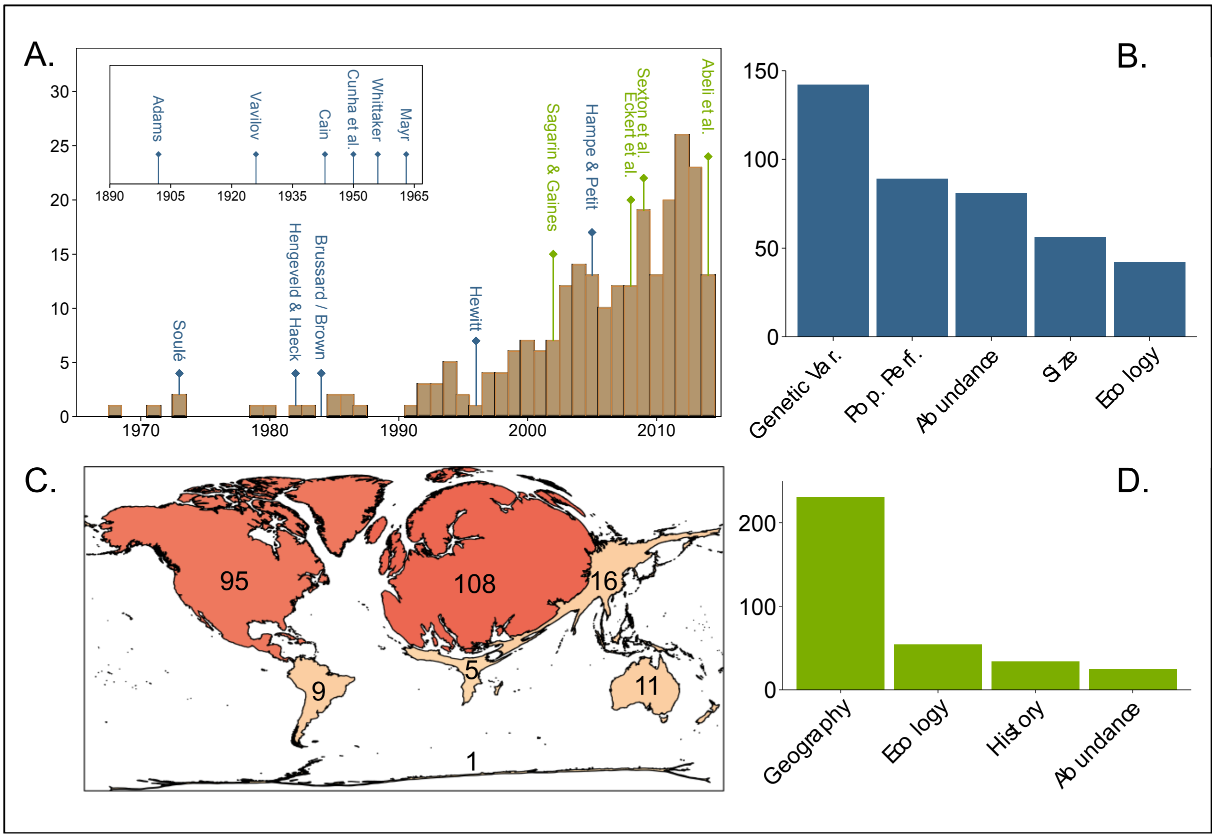


Figure 1-1. An overview of the CPH empirical literature.
A. The number of studies testing the CPH since 1968 with important review papers (green arrows) and major conceptual papers (blue arrows); B. The number of studies testing the CPH on different groups of species characteristics; C. Choropleth map representing the number of studies conducted on each continent; D. The number of studies that adopt different definitions of centre-periphery.

General results

To analyze the number of tests that show significant differences between central and peripheral populations for different parameters, we retained studies with a geographical centre-periphery approach and discarded articles whose centre-periphery pattern solely relied on population abundance or ecological gradients. This restricted the number of articles to 234, representing 804 tests of the CPH.

Abundance

The abundant-centre hypothesis (an offshoot of the general CPH) is based on two assumptions: environmental variables are spatially correlated throughout the range, and abundance peaks where environmental conditions are best, i.e. in central populations (Brown 1984; Sagarin *et al.* 2006).

We found that population occupancy showed a strong trend towards lower values in peripheral populations (81% of studied tests). However, this significant trend is based on only 21 tests in 15 papers (Table 1). Besides, we noticed that several studies considered this pattern as a fact and defined their centre-periphery sampling scheme based on this criterion. For example, some genetic studies oppose large and continuous central populations to small and scattered peripheral populations (Jones & Gliddon 1999; Van Rossum *et al.* 2003; Medrano & Herrera 2008), although they did not measure population size, density or fragmentation.

69 out of 135 tests (51%) focusing on the abundance of individuals reported higher abundance in the central part of the distribution, though the trend is weaker than for

occupancy patterns (Table 1). This result contrasts with Sagarin & Gaines (2002) who found weaker support for the hypothesis, but whose study gave a high importance to a relatively low number of papers (145 tests extracted from 22 papers, 39% of validation). In particular, the study by Blackburn *et al.* (1999) alone represented 44% of the total number of considered tests, and did not support the CPH. This paper was not included in our study, as we were not able to identify central and peripheral areas of the ranges of the different species considered.

Different results for population occupancy and abundance of individuals may be due to differences in the factors shaping those patterns (Lawton 1993; Hoffman & Blows 1994; Gaston 1996; Thuiller 2013), which may act over different scales (Gilbert 1980; Gilman 2005; Boulangeat, Gravel & Thuiller 2012). The strong spatial organization of occupancy patterns may be primarily driven by climatic factors which act over a large scale and are often spatially autocorrelated (Thuiller, Araüjo & Lavorel 2004). This is supported by recent cross-taxa empirical analysis for both plants (Boucher-Lalonde, Morin & Currie 2012) and animals (Boucher-Lalonde, Morin & Currie 2014). In contrast, variables linked to the abundance of individuals could operate at more local scale (Pearson & Dawson 2003; Elmendorf & Moore 2008) and exhibit low spatial structure (Caughley *et al.* 1988; Lawton 1993). For example, Gilman (2005) highlighted the importance of water temperature, tides, wave force and biotic interactions to shape the local abundance pattern of an intertidal limpet (Collisella scabra Gould). The spatial layering of these ecological factors Pearson & Dawson (2003) might explain range-wide clumped distributions of abundance of individuals observed in some taxa (see Brown, Mehlman, & Stevens, 1995), and lead to the low general support for a large scale decrease of abundance of individuals toward the periphery. However, species might respond differently to these ecological factors due to their diversity of life-history characteristics (Gaston 2003).

Spatial and temporal variation in abundance of individuals is also predicted to be higher at the periphery under the CPH (Curnutt *et al.* 1996; Sagarin *et al.* 2006). This can be explained, for example, by spatial patterns of habitat quality and their effect on source-sink models of colonization, assuming that populations collapse after establishing in low quality habitat (Lawton 1993; Curnutt *et al.* 1996; Vucetich & Waite 2003). Another possible explanation is the higher susceptibility of populations to density-independent factors in the periphery (Gaston 1990). Here, we only analyzed 19 tests, and these exhibited no significant trend (Table 1), although only one study showed higher variability in the range centre (Law 1994). Thus, the lack of information regarding variability remains an important gap in our understanding of range dynamics, and the possible occurrence of source-sink dynamics in peripheral populations (Pulliam 1988, 2000; Curnutt *et al.* 1996).

Population performance

Vital rates associated with population performance are predicted to decrease toward the range periphery, and to become more variable (Sagarin *et al.* 2006; Sexton *et al.* 2009). Lower fitness of peripheral populations could cause higher extinction probability and limit further colonization, creating stable range limits (Hardie & Hutchings 2010; Abeli *et al.* 2014). However, for five parameters (survival, growth, fecundity, recruitment, and overall population growth rate), we found no consistent patterns that support this hypothesis: each vital rate was equally likely to be higher in the centre, the periphery, or to exhibit no difference (Table 1). This conclusion confirms results obtained by Sexton *et al.* (2009) and

Abeli *et al.* (2014). Range-wide studies of reproductive performance have reached similar conclusions, emphasizing the important role of local environmental conditions on demographic rates, which might blur their geographical distributions (Garcia, Goni & Guzmán 2010; Villellas *et al.* 2012; Granado-Yela *et al.* 2013).

Very few studies evaluated the impact of abundance on population performance in a centre-periphery context. Some reported higher performance in larger populations, through higher fecundity and recruitment (Lemke & Porembski 2013), or higher survival (Rodríguez & Delibes 2002), whereas others found no differences in demographic rates between small and large populations (Berg, Becker & Matthies 2005; Lester, Gaines & Kinlan 2007). Although many cases of the positive effects of large population size have been highlighted (Reed 2005), the association between species fitness and abundance is not unidirectional; negative density-dependence effects can also occur (Johnson *et al.* 2012), and some species have been shown to perform well at low population size (García, 2008). Moreover, density-dependence effects might not always impact all demographic rates and/or overall population growth rate (Kolb, Dahlgren & Ehrlén 2010), and their intensity might vary across a species range (Williams, Ives, & Applegate, 2003). The presence, direction and intensity or the absence of density-dependence is just one of the many ecological factors influencing demographic rates and could contribute to why these rates do not always follow a centre-periphery pattern.

Individual size may also be lower in peripheral populations if they occur in less-optimal ecological conditions (Meiri *et al.*, 2009). However, in the studies we reviewed, there was no clear evidence of smaller individuals in peripheral populations: 55% of species showed no differences across their range (Table 1). Other biogeographical theories have tried to link organism size to their position in the range, among which Bergmann's rule predicts an increase in body size of endothermic animals with higher latitudes, in order to limit energetic loss(Blackburn, Gaston, & Loder, 1999; Meiri, 2011). This linear increase is different from the hump shaped scenario proposed by the CPH, which suggests that the size of individuals might be driven by different mechanisms. In this context, criticisms have been raised against the use of latitude as a proxy for harsher/colder environmental conditions (Blackburn, Gaston, *et al.*, 1999), which points to the need for a direct estimate of the ecological drivers.

Finally, four articles (Siikamaki & Lammi 1998; González-Guzmán & Mehlman 2001; Kark *et al.* 2004; Vaupel & Matthies 2012) dealt with the topic of developmental instability due to strong directional selection or high inbreeding in peripheral isolates (Levin 1970). However, we detected no difference in instability (measured as fluctuating asymmetry) between central and peripheral populations. Thus, no global pattern of higher stress toward range edges appeared in these studies (Parsons 1990).

Genetic variation

Several hypotheses have been proposed regarding the spatial organization of genetic variation in the different parts of a species range (Safriel *et al.* 1994; Hardie & Hutchings 2010). The first prediction of the CPH is that within-population genetic diversity is lower in peripheral than in central populations. In our dataset, 83 out of 175 tests (47%) showed this pattern (Table 1), which did not differ from a random expectation. This contrasts with results obtained by a previous review (Eckert *et al.* 2008), in which the CPH was upheld in 65% of 68 studies. This may be due to the fact that in our dataset we found a significant difference among temporal subsets of the data (3*2 χ^2=35.54, df= 2, P < 0.001); the pre-2008 literature validated the CPH at a rate of 69.8% (44 / 63 tests) while only 34.8% (39 / 112 tests) of post-2008 studies validated the CPH. Thus, it is likely that recent studies integrated Eckert *et al*'s (2008) conclusion for the need to use a more representative sampling methodology to assess trends across a greater proportion of the range, or better identify the relative position of the populations within the whole species' range (e.g. Diniz-Filho *et al.*, 2009; Dixon, Herlihy, & Busch, 2013). Additionally, most of the studies reviewed by Eckert et al., (2008) were conducted at the leading edge of temperate species distributions, hence, they recommended that other peripheral areas be examined in order to evaluate the general validity of the CPH and disentangle the potential confounding effects of historical drivers from ongoing contemporary processes. As they stated (page 1171), "relatively few studies exhibited consistent geographical patterns in population genetic diversity towards different range edges [when comparing] different studies", illustrating a potential weakness of tests of the CPH predictions. The post-2008 shift to more representative sampling is exemplified by the study of Lira-Noriega & Manthey (2014). The authors collected genetic data from the literature spanning most of the ranges of 40 plants and animals of different biogeographical origins, and computed distances to the centroids of the species distributions. They found little global support for the CPH.

In parallel, genetic differentiation is predicted to be higher among peripheral populations than among central populations (Mayr, 1963; Eckert *et al.*, 2008). 33 out of 74 tests (45%) showed this pattern (Table 1). This relationship was not different from a random expectation, and a large number of tests found no differences. Again, this result contrasts with Eckert's observations of higher differentiation among peripheral populations for 70% of studies (40 studies out of 57), although the validation rate in Eckert and collaborators' study decreased to 42% (n=26) when their test was restricted to publications that made statistical analysis of differentiation values. Again, we found less support for the hypothesis in publications since 2008 (χ^2= 8.5, df = 2, p = 0.01), Methodological issues may add some confusion to the interpretation of population differentiation across species range, because measures used to quantify it may be biased by differences in genetic richness and distances among populations for central and peripheral populations (Eckert et al., 2008). The low validation rate we detected indicates that empirical evidence does not globally support a higher differentiation among populations at range limits. Environmental differences (Lesica & Allendorf 1995; Sexton *et al.* 2014 p. 20) and metapopulation dynamics (Hampe & Petit, 2005) may be more important determinants of any such patterns (Endler 1973).

Our study provides empirical evidence for an association between within-population genetic diversity and among-population differentiation. Specifically, tests that exhibited significantly lower within-population diversity in peripheral populations had a higher probability of also showing an increase in genetic differentiation (χ^2= 35.54, df = 4, P < 0.001). Genetically depauperate peripheral populations may thus be more prone to drift and consequent genetic divergence (Eckert *et al.* 2008; Leonardi *et al.* 2012).

Finally, following the assumption of lower census and effective population size at range limits (Vucetich & Waite, 2003), inbreeding is predicted to be higher in peripheral populations. Our results did not deviate from random expectation, with 15 out of 31 tests (48%) reporting higher inbreeding in peripheral populations (Table 1). Thus, this underlines the fact that centre-periphery patterns did not coincide with patterns of effective population size variation across the range (Frankham 2007), as the results of abundance of individuals and actual population size suggest (see results above).

Finally, 22 tests used other approaches (for example karyology Medail *et al.*, 2002; Rivero-Guerra, 2008) that we did not analyze quantitatively due to their heterogeneity.

Table 1-1. The numbers of studies (a total of 248 sampled papers) and tests (a total of 813 tests) that exhibit significant or non-significant differences between central and peripheral populations for the different groups of species' parameters.

N_{centre} represents the number of tests that report significantly higher parameter values in geographically central populations; $N_{periphery}$ is the number of tests that report higher parameter values in peripheral populations; and $N_{no\ diff}$ is the number of tests that did not find significant differences between central and peripheral populations. Note that the CPH predicts higher values in genetic diversity, abundance and population performance parameters in central than in peripheral populations, but the opposite for variability of these parameters and genetic differentiation. Significance level of binomial tests is indicated as: *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$ (in black for a hypothesized probability of success of 0.5, and in grey for a probability of 0.33; see Methods for further details).

		$N_{articles}$	N_{test}	N_{centre}	$N_{no\ diff}$	$N_{periphery}$	Validation (%)	Significance level
Genetic	Diversity	120	175	83	82	10	47	***
	Differentiation	68	74	6	35	33	45	*
	Inbreeding	31	31	2	14	15	48	
Abundance	Population occupancy	15	21	17	4	0	81	**
	Abundance of individuals	70	136	69	59	8	51	***
Abundance Variability	Abundance of individuals	9	19	1	9	9	47	
Population Performance	Population Growth Rate	12	34	11	19	4	32	
	Growth	15	35	9	20	6	26	
	Survival	33	56	13	36	7	23	
	Fecundity	54	58	25	21	12	43	
	Recruitment	33	60	14	27	19	23	
Population Performance Variability	Population Growth Rate	5	7	3	1	3	43	
	Growth	1	1	0	1	0	0	
	Survival	3	3	2	1	0	0	
	Fecundity	3	3	1	1	1	33	
	Recruitment	5	5	0	3	2	40	
Size		47	82	20	45	17	24	
Size variability		8	13	8	4	1	62	

Plant – animal differences

Spatial patterns of genetic and demographic parameter variation are strongly linked to the life history characteristics of organisms, such as competitive or dispersal abilities (Gaston, 2003). Our dataset is composed of a large diversity of organisms including annual plants (N = 31), perennial plants (N = 171), birds (N = 65), mammals (N = 38), insects (N = 33), fishes (N = 13), amphibians (N = 10), reptiles (N = 6) and marine invertebrates (N = 44) (Appendix S1). Therefore, genetic variation, abundance, and population performance patterns may exhibit strong differences among groups (Gaston, 2003). To investigate this issue, we tested whether kingdom (plant or animal) influenced rates of validation of the CPH.

For within-population genetic diversity, a marginally significant difference (χ^2=5.9, df=2, P = 0.053) appeared between the two groups: 54% of tests conducted on plants validated the CPH (54 out of 100 tests), while only 39% (29 out of 75 tests) fit this model for tests conducted on animals (Table 2). However, when restricting our analysis to single species articles, both animal and plant-based tests presented a validation rate of 56%. The differential pattern was mainly driven by one multi-species article (Lira-Noriega & Manthey 2014), which validated the CPH for 4 plant species out of 13, and for only 1 out of 25 tests on animals.

For population performance parameters, no significant differences were detected between plants and animals (Appendix S2). Yet, for the size of individuals, animals showed a stronger trend toward the absence of pattern (N) across their range (χ^2=6.7, *df* = 2, $p < 0.05$).

For the abundance of individuals, the CPH was validated for animals but not for plants (χ^2= 22, *df* = 2, $p < 0.001$) (Table 2). This difference suggests that life history traits affect geographic patterns of variation in abundance. Svensson (1992) first proposed that the abundant-centre hypothesis would be valid for animals, but not necessarily for plants, based on the sparse observations available at that time (Carter & Prince 1981; Woods & Davis 1989) and without providing any theoretical explanation. In general, local ecological constraints may strongly impact organisms with a sessile life form such as plants for which abundance will be dependent on micro-ecological factors (Chapin *et al.* 1987; Lammi, Siikamäki & Mustajärvi 1999; Lönn & Prentice 2002; Nielsen *et al.* 2005). These variables tend to exhibit little geographic autocorrelation (Gilman, 2005), and therefore can blur geographic variation in abundance. In contrast, for vagile animals, individual requirements in terms of metabolic rate (Root 1988) and distribution of resources (Schluter & Repasky, 1991) can be major drivers of abundance patterns. These environmental processes strongly rely on climate, and thus are more coarsely spatially structured. In addition, resource limitation generates competition in mobile animals promoting long-distance dispersal to new potentially suitable sites (Curnutt *et al.* 1996), with vagrant individuals frequently observed out of their range (Grinnell 1922). Hence source-sink dynamics will be more common and spatially structured than in plants (Hoffman & Blows 1994; Pulliam 2000; Guo *et al.* 2005). Such sites are considered as being “outside” of the fundamental ecological niche, but tend to enlarge the realized niche (Pulliam 2000) and lead individuals to face harsh conditions (Hargreaves *et al.* 2014). This empirical evidence regarding differences between animals and plants for the CPH fits the predictions proposed by the spatial source-sink theoretical model of Guo *et al.* (2005). Ultimately, understanding abundance patterns and especially the structure and density of sink populations toward range edges could be a key to understand species range limit (Sexton *et al.* 2009).

Table 1-2. The numbers of tests that exhibit significant or non-significant differences in genetic diversity and abundance of individuals between central and peripheral populations for different groups of organisms.

	Genetic diversity					
	N test	N centre	N no diff	N periphery	Validation (%)	Significance level
Animal	75	29	43	3	39	
Amphibian	9	5	3	1	56	
Bird	26	11	15	0	42	
Fish	3	2	1	0	67	
Insect	16	1	14	1	6	
Mammal	8	3	5	0	38	
Marine Invertebrate	7	3	3	1	43	
Reptile	4	4	0	0	100	*
Other	2	0	2	0	0	
Plant	100	54	39	7	54	***
Annual	12	9	2	1	75	
Perennial	88	45	37	6	51	***

	Abundance of individuals					
	N test	N centre	N no diff	N periphery	Validation (%)	Significance level
Animal	92	55	37	0	60	*
Amphibian	2	1	1	0	50	
Bird	36	29	7	0	81	***
Fish	8	2	6	0	25	
Insect	7	4	3	0	57	
Mammal	4	1	3	0	25	
Marine Invertebrate	30	15	15	0	50	*
Reptile	1	1	0	0	100	
Other	4	2	2	0	50	
Plant	44	14	22	8	32	
Annual	6	3	1	2	50	
Perennial	37	11	20	6	30	

N_{centre} represents the number of tests that report significantly higher parameter values in geographically central populations; $N_{periphery}$ is the number of tests that report higher parameter values in peripheral populations; and $N_{no\ diff}$ is the number of tests that did not find significant differences between central and peripheral populations. Significance level of binomial tests is indicated as: *** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05 (in black for a hypothesized probability of success of 0.5, and in grey for a probability of 0.33). Differences between plants and animals in other parameters are shown in Appendix 2.

Limitations associated with sampling methods

Several authors have discussed the importance of methodological biases in studies testing the CPH, especially the failure to adequately sample central and peripheral parts of a species range (Eckert *et al.* 2008). As a result, this may hinder generalization about the validity of the CPH (Sagarin & Gaines 2002). Indeed, the shape and size of species ranges can vary dramatically among taxa and thus affect the expression of variation in demographic and genetic characteristics (Gaston, 2003). Thus, we analyze two spatial parameters. First, geographic isolation of peripheral populations is supposed to limit colonization events and consequently slow down metapopulation dynamics (Gilpin & Hanski 1991) and affect genetic patterns across species' ranges (Hastings and Harrison 1994). In our database, only 11% of all tests considered a periphery beyond the main range; 42% sampled peripheral populations at the very edge of the range, while 45% considered populations clearly located within the main range of the species as peripheral populations. Second, the majority of species distribution ranges exceed individual dispersal abilities, hence populations in different parts of the range are fairly isolated from one another, at least on a short term (Wright 1943; Hardy & Vekemans 1999). Therefore, range size may condition the frequency of interactions among populations, and the representativeness of the sample in terms of the global distribution of the species may affect its power to capture such processes. In our pool of papers, 28% of all tests considered less than 10% of the range of the species, and 26% studied 10 - 50% of the range. Hence, only 44% of all tests were conducted over more than 50% of the species' ranges. Most studies (56%) thus identify peripheral populations that others would consider as central. The strong correlation that we found between "representativeness" and "spatial extent of the study" showed that studies carried out at a larger scale tend to be more representative of the global range extent of species, and advocate the use of a single variable “scale” that synthesizes both measures.

Regarding abundance of individuals, we found that the variable “scale” had a significant positive impact on the validation rate of the CPH. Thus, studies that encompassed more than 50% of a species distribution and that were conducted at a large scale (continental) were more likely to detect a reduced abundance of individuals in peripheral populations, as envisioned previously by Sagarin *et al*. (2006). Choosing representative central and peripheral populations might thus increase the probability of sampling less optimal ecological conditions at the periphery of a species distribution (Sagarin & Gaines 2002). However, this result may also be over-influenced by a small number of studies on multiple bird species (representing a high number of tests), that showed a pattern that strongly supports the CPH and that had a more range-wide sampling than studies of plants (for plant-animal comparison, χ^2=5.03, df=2, P = 0.08). Thus, the pattern should be interpreted with caution, and large scale studies should be applied to plant to disentangle the effect of organism and scale at which studies are conducted. It is also worth noticing that spatial isolation has no impact on abundance patterns, which highlights that peripheral isolates might occur in suitable environmental conditions allowing to establish viable populations.

For population performance, the absence of any impact of the variables “scale” and “isolation” reinforces their relative independence from the extent of the geographical gradient (Table 3). However, studies with larger sampling schemes were more likely to exhibit an absence of difference (N) in recruitment across the range. This is in accordance with previous results that emphasized the importance of local variables that exhibit little spatial structure (Connolly, Menge & Roughgarden 2001; Granado-Yela *et al.* 2013; Ibáñez & McCarthy-Neumann 2014).

For genetic diversity, we found a strong positive impact of peripheral isolation on the validation rate of the CPH, which highlighted the importance of current range structure on genetic diversity (Table 3) (Holt 2003; Leonardi *et al.* 2012). Indeed, this validation rate decreased from 70% (N_{test} = 35) to 61% (N_{test} =61) to 42% (N_{test} = 83) when considering peripheral isolates out of the range, absolute peripheries and intermediate peripheries. Peripheral isolation will slow down metapopulation dynamics and limit gene flow among populations (Holt & Keitt 2000; Holt 2003; Böhme *et al.* 2007). In addition, studies that used population size to define their centre-periphery gradient brought evidences for a positive impact of population size on genetic diversity: 10 out of 14 tests found a higher genetic diversity in larger populations (e.g. Lammi, Siikamäki, & Mustajärvi, 1999; Dostálek, Münzbergová, & Plačková, 2014), whereas four of them did not find differences (e.g. Michalski & Durka, 2007). Besides the impact of isolation, a nearly significant effect of scale indicated a greater decrease of genetic diversity when considering larger spatial scales. This suggests that there is a trend for genetic diversity to decrease gradually from the centre to the periphery that requires sampling wide enough to capture it. This can be interpreted as the footprint of repeated founder event following post-glacial range expansion (e.g. Cwynar & MacDonald, 1987; Dudaniec *et al.*, 2012), which have an impact on large scale patterns, and might be strongly dependent on species history (Petit *et al.* 2003). As a result, genetic diversity will be shaped by both contemporary factors and historical events, the relative importance of which may be species specific (Hampe & Petit 2005; Kropf 2012).

Genetic differentiation was strongly linked to the physical isolation of peripheral populations (Table 3). This observation suggests that gene flow among populations decreases toward the range edge depending on peripheral isolation (Leonardi *et al.* 2012; Wang, Glor & Losos 2013). However, the absence of any effect of the variable scale pinpoints the relative independence from the spatial extent of the study (Table 3). This indicates that genetic differentiation does not follow a “simple” isolation by distance process, in which gene flow is inversely proportional to distance among populations (Sexton *et al.* 2014).

Table 1-3. Generalized linear model (GLM) of the correlation between the CPH validation and "scale" and "isolation" variables.
"Scale" represents the spatial extent of the sampling scheme, while "isolation" describes the position of peripheral populations in relation to the species range. Parameters studied in less than 30 tests were discarded from the analysis. Significance level indicated by: *** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05.

		Scale				Isolation			
		Chi-square	Degree of freedom	P-value	Significance level	Chi-square	Degree of freedom	P-value	Significance level
Genetic	Diversity	3,1	1	0,077		14,0	1	0,000	**
	Differentiation	1,1	1	0,299		5,4	1	0,020	*
	Inbreeding	1,8	1	0,179		0,5	1	0,484	
Demography	Population Growth Rate	0,4	1	0,520		0,2	1	0,622	
	Growth	0,2	1	0,646		0,1	1	0,733	
	Survival	1,8	1	0,182		0,2	1	0,693	
	Fecundity	2,6	1	0,108		0,1	1	0,745	
	Recruitment	6,6	1	0,010	*	0,7	1	0,414	
	Size	2,0	1	0,160		1,1	1	0,295	
Abundance	Abundance of individuals	10,1	1	0,001	**	0,1	1	0,731	

Geographically peripheral or ecologically marginal?

Are peripheral populations ecologically marginal?

A major tenet of the CPH is that a species distribution is a geographical representation of its ecological niche with environmental conditions optimal at the range centre and poorer at the periphery (Brown 1984; Hoffman & Blows 1994; Holt & Keitt 2000). However, it has been argued that "not all marginal populations are peripherally located and not all peripheral populations are ecologically marginal" (Soulé, 1973; see also Hardie & Hutchings, 2010). This assumption is often overlooked when testing the CPH: only 17% (42 studies) of our pool of 248 papers quantitatively evaluated environmental conditions (biotic and/or abiotic) in central and peripheral locations (Fig. 1B).

Of these 42 studies (82 tests), 34 (81%) compared environmental variables (i.e. ecological niche) in central and peripheral populations; five papers compared spatial or temporal variation of these variables (i.e. ecological niche breadth), and only three considered measures of both ecological niche and ecological niche breadth. In general, the authors considered a wide variety of environmental variables: 17 studies (40%) examined abiotic variables (e.g. climate, soil properties), 16 (39%) considered biotic variables (e.g. mutualism, predation, competition), and 9 studies (21%) examined both biotic and abiotic niche dimensions. Overall, we found that 62% of the 82 tests on the ecological niche reported different environmental conditions between central and peripheral populations (the "Different" bar in Fig. 2). Although this result is highly dependent on the choice of the environmental variable, it supports the notion that species encounter different ecological conditions at their range limits. This is not surprising given the low probability of finding exactly the same conditions in two different areas.

In the 82 tests, 57 provided data that allowed us to examine whether the environment is more optimal in central populations compared to peripheral populations (the “Optimal” bar in Fig. 2): i.e. presence or absence of natural enemies (e.g. Briers, 2003), pollinators (e.g. Lemke & Porembski, 2013), habitat suitability (e.g. Diniz-Filho *et al.*, 2009), or food availability (e.g. Gilman, 2006). Despite the fact that environmental conditions are different in central and peripheral populations, there is no evidence that environmental quality is systematically lower at the periphery of a species’ distribution (Fig. 2). For instance, Lira-Noriega & Manthey (2014) found positive correlations between distances from populations to species’ geographic range centers and climatic niche centroids in only 16 out of their 37 tests (43%). These results are in line with previous studies that showed that the different dimensions of a species ecological niche were not distributed continuously in space but rather discretely (Poulin & Dick 2007; Hidas, Ayre & Minchinton 2010; Baldanzi *et al.* 2013), and that the conditions at the geographical range limits did not always match with the conditions at the limit of the species niche (Chardon *et al.* 2014; Hargreaves *et al.* 2014). In a study of 11 Mediterranean plant species, Papuga et al. (unpublished manuscript) also show multiple ecological differences between central and peripheral populations. But again, there is no evidence that such differences involve a change in habitat quality.

Our results thus reject the hypothesis that geographical and ecological gradients are systematically associated with one another and that peripheral populations are always ecologically marginal. Ecologically optimal sites can be found across most species’ ranges (Poulin & Dick 2007). In addition, peripheral populations might preferentially occupy the sites where the environment is locally favorable for the species (Lennon *et al.* 2002; Thompson *et al.* 2010), even though such locations are less common near the range limits. However, little is known about whether the availability of high quality sites generally increases towards the centre of the range (González-Guzmán & Mehlman 2001; Murphy, VanDerWal & Lovett-Doust 2006). The presence of such geographical structure might depend mainly on the relative influence of highly spatially autocorrelated variables, such as climate. Further comparative studies on the distribution of spatial and temporal variation in species ecological niche, in particular niche breadth, are now needed.

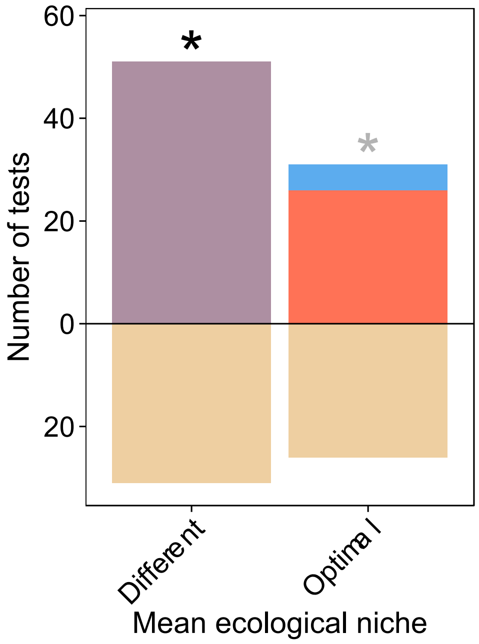


Figure 1-2. Relationship between species' geographical range and their ecological niche.
The "Different" bar represents the number of species that exhibit either significant differences between geographically central and peripheral populations in terms of environmental conditions (purple), or that do not exhibit any difference (beige). From these 82 tests, we extracted the 57 tests that explicitly qualify environmental conditions in terms of species preferences. The "Optimal" bar represents the number of these tests that exhibit optimal environmental conditions in the range centre (in red), at the periphery (in blue), or no difference between the centre and the periphery (in beige). Significance level of binomial tests is indicated as: *** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05 (in black for a hypothesized probability of success of 0.5, and in grey for a probability of 0.33).

Ecological marginality and genetic and demographic variation

We have shown that the literature does not illustrate a strict and consistent concordance between geographical and ecological gradients. Hence, it is important to test whether the variation in different parameters in different parts of a geographic range are actually associated with spatial variation in ecological conditions. In our pool of 248 studies, only 54 (22%) measured ecological conditions at different sites (geographically central/peripheral or not) and simultaneously assessed one or other of the above categories of species' parameters (genetic diversity, abundance, population performance, size). 21 out of these 54 papers clearly identified environmental conditions of higher and lower suitability for the species (e.g. Lönn & Prentice, 2002; Gilman, 2006; Lira-Noriega & Manthey, 2014), whereas 33 just considered ecological gradients without indications as to species preferences (e.g. Howes & Lougheed, 2008; Stanton-Geddes, Shaw, & Tiffin, 2012). To have a sufficiently high sample size of studies, we therefore focused on whether species perform differently in regions that currently present clear ecological differences (without analyzing whether such differences involve enhanced performance in more favorable conditions). For the same reason, we also considered only four broad categories of parameters (Genetic diversity, Abundance, Population performance, Size) (Fig. 3). When a paper studied different biological parameters on the same species (e.g. survival and fecundity in the "Population performance" category), we considered these tests separately. Finally, it is also worth noting that we only focused on the literature related to the CPH and that many other studies have focused on responses of different genetic or demographic features across environmental gradients (e.g. Doak & Morris, 2010; Manel *et al.*, 2012). Future reviews or meta-analyses of these studies could help refine our conclusions.

First, we found that 62% of species did not exhibit any difference in genetic diversity between populations occurring in different environmental conditions (Fig. 3). Some studies observed differences in genetic diversity across climatic gradients (e.g. Howes & Lougheed, 2008; Moeller, Geber, & Tiffin, 2011) and some did not (e.g. Shulgina *et al.*, 2006; Diniz-Filho *et al.*, 2009). Other articles found differences across habitats (e.g. Shumaker & Babble, 1980; Hamilton & Eckert, 2007) and others did not (e.g. Van Rossum *et al.*, 2003). However, a recent meta-analysis showed that the distance to climatic niche centroids better explained the distribution of the genetic diversity of 40 plant and animal species than the distance to their geographic range centers (Lira-Noriega & Manthey, 2014). That said, the authors argued that current ecological conditions may not directly affect within-population genetic diversity, but rather through indirect effects such as changes in effective population size, gene flow, or population stability. Here, the temporal dynamics of ecological conditions might have a greater impact than current static conditions. For instance, many studies have shown that current spatial patterns of genetic variation have been shaped by past climate change via changes in species occurrence and/or abundance (Hewitt, 2000; Carnaval *et al.*, 2009; Excoffier, Foll, & Petit, 2009; Hoban *et al.*, 2010; Pironon *et al.*, 2015; see further discussion in section V). However, contemporary effects of environmental isolation might directly shape distributional patterns of genetic variation for some species presenting relatively stable distributions over time (e.g. some Mediterranean, tropical, or small range species not less impacted by glaciations) (Ortego *et al.* 2012; Sexton *et al.* 2014).

In contrast, ecological gradients may be related to differences in abundance, demographic rates and size (Fig. 3). Indeed, most studies reported associations between these parameters and climate (e.g. Crozier, 2004), or habitat type (e.g. Stanton-Geddes *et al.*, 2012; Huntsman

& Petty, 2014). Moreover, several studies that were able to identify species preferences reported enhanced performance in areas less disturbed by humans (Fuller *et al.* 2009), with optimal substrate conditions (Lönn & Prentice, 2002), or presenting higher food supply (Gilman, 2006). In addition, several recent meta-analyses have found higher plant and animal species abundances at the centre of their climatic niche and have thus tried to affirm the validity of the abundant-centre model (VanDerWal *et al.* 2009; Oliver *et al.* 2012; Martínez-Meyer *et al.* 2013; Van Couwenberghe *et al.* 2013).

If ecological conditions are distributed discretely (rather than continuously) in geographical space (see above), demographic performance might follow a multimodal distribution (rather than a simple gradient), as proposed by the “local-oasis model” (Poulin & Dick, 2007) and described by other studies (Murphy *et al.* 2006; Baldanzi *et al.* 2013). However, we previously exposed that population occupancy better matched the CPH predictions than the abundance of individuals, which in turn provides more support for the CPH than other demographic rates (e.g. survival, growth) (see section III.2.). The relative influence of geographical and ecological gradients may thus be scale-dependent: the impact of geography might decrease from broad (i.e. population occupancy) to fine scale (i.e. demographic rates), whereas the effect of local ecological conditions might increase (Hoffmann & Blows, 1994). Although more studies are needed to confirm such trends, population occupancy may be related to a decreasing availability of optimal sites from the range centre to the periphery, whereas the abundance of individuals and other demographic rates may be high in optimal sites found both at the centre and the periphery of the species range (see above). Finally, the different components of demographic performance (abundance and other vital rates) could be influenced by different ecological factors (e.g.

climate, habitat, biotic interactions), and these relationships may vary among species (Pironon *et al.* 2015; Villellas *et al.* 2015). Some recent studies have proposed the concept of "demographic compensation" by demonstrating that vital rates of one species might often follow opposing patterns along geographical and/or environmental gradients (Doak & Morris 2010; Villellas *et al.* 2015). All in all, there remains the important and challenging task to identify which ecological niche dimensions better predict the distribution of these components for different species (Boulangeat *et al.* 2012; Ehrlén & Morris 2015).

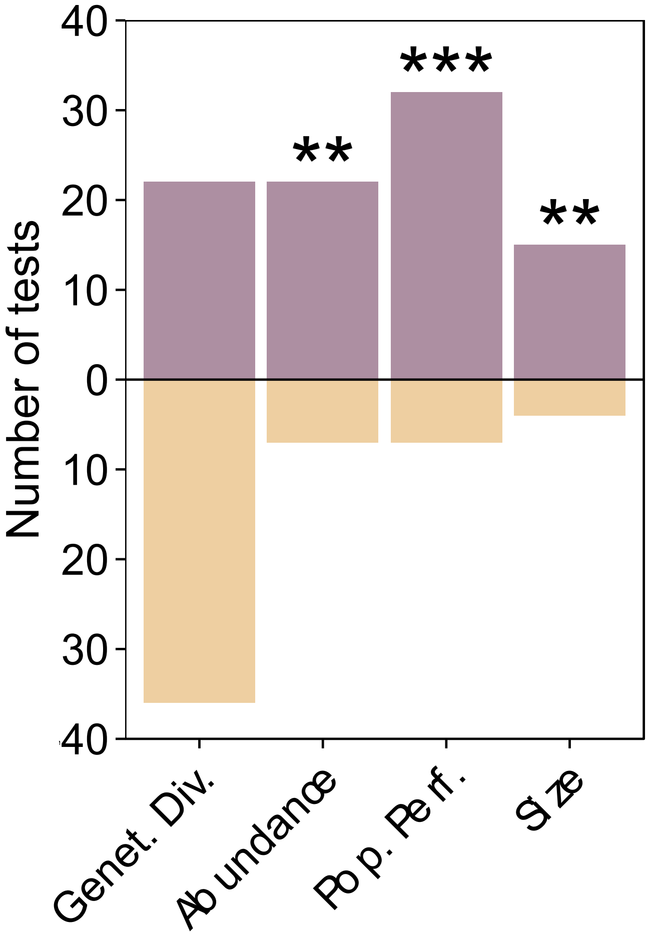


Figure 1-3. Testing how different ecological conditions discriminate between high and low values of genetic diversity, abundance, population performance, and size of individuals.
The number of tests that report significant differences in any parameter under different ecological conditions is represented in purple, whereas the number of tests with no difference is represented in beige. "Population performance" is composed of papers studying population growth rate, survival, growth, fecundity, and/or recruitment. Significance level of binomial tests is indicated as: *** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$ (for a hypothesized probability of success of 0.5).

Centre-periphery or rear-leading edge?

Disentangling the dichotomy

There is much debate concerning whether geographic patterns of variation in species characteristics are driven by the current shape of their range (i.e. contemporary connectivity among populations) (Johansson, Primmer & Merilae 2006) or by historical processes associated with past environmental change such as post-glacial recolonization and/or human activities (Hewitt 2000; Channell & Lomolino 2000; Excoffier *et al.* 2009). Disentangling the relative impacts of contemporary and historical drivers is thus important, and there is a growing interest in the documentation of rear- versus leading-edge effects that provide a more dynamic explanation for patterns otherwise attributed to a static contemporary centre-periphery contrast (Hampe & Petit 2005; Eckert *et al.* 2008; Pironon *et al.* 2015).

In our pool of 248 papers, we have very little information on the past distributions of most of the studied species. For this reason, we first used the proxy “latitude/altitude” to define what may have been historical central and peripheral parts of the species’ ranges. Many species have in fact been shown to follow latitudinal/altitudinal gradients when contracting or expanding their ranges during the alternation of glacial cycles, particularly temperate species (Hewitt, 2000). Moreover, considering both central-peripheral and latitudinal gradients together has been shown to be of particular importance for understanding patterns of genetic diversity across current species distributions (Guo 2012). We thus make the assumption that all species present older and more stable populations at low latitude/altitude and younger populations at high latitude/altitude (Hampe & Petit, 2005).

To study this issue, we discarded studies monitoring populations on longitudinal, ecological, or abundance-related gradients. In each of the 220 remaining studies (565 tests), we examined whether the genetic or demographic parameters under consideration showed two potential trends. First, we examined whether species showed either an increase (“P” in Fig. 4), a decrease (“C”), or no significant change (“N”) from the current range centre (i.e. mid-latitude/altitude) towards the actual range periphery (i.e. higher and/or lower latitudes/altitudes). Second, we examined whether species showed either an increase (“H” in Fig. 4), a decrease (“L”), or no significant change (“N”) from the historical range centre (i.e. low latitude/altitude) towards the periphery (i.e. high latitude/altitude). These comparisons allowed us to identify nine different scenarios and the percentage of tests validating each of them (Fig. 4). Obviously, all of the 220 studies did not intend to test for such latitudinal/altitudinal relationships, so this information results from our reinterpretation of trends clearly exposed in each paper.

First, the scenario of no variation across the range (“N-N”, lower-right scenario in Fig. 4A) is always overrepresented because, unlike other scenarios, it combines both range-wide studies and articles studying only one range periphery. Then, we found that, whatever the genetic/demographic parameter considered, most studies were conducted at only one range periphery (four upper-left scenarios in Fig. 4A), and especially at the high latitude/altitude periphery (upper-left and middle scenarios in Fig. 4A). It is thus not possible to discriminate in those studies the potential contributions of historical and contemporary causes of current geographic patterns. These results therefore expose the need for more range-wide conjoint studies of spatial genetic variation and demographic performance.

Also, the results confirm our finding that the geographical structure of species ranges is more closely associated with genetic variation and population occupancy than with the abundance of individuals and the different components of population performance (Table 1, Fig. 4). While there is mainly no difference in the size of individuals between central and peripheral populations, or between low and high latitude/altitude populations ("N-N" scenario in Fig. 4), demographic rates (survival, growth, fecundity, and recruitment) respond in many different directions. Indeed, it is unlikely that historical range shifts impact current individual size and demographic rates (Pironon *et al.* 2015), except for cases of very recent changes in species distribution, e.g. invasive species (Kilkenny & Galloway 2013).

Only 19 tests investigated the distribution of population occupancy, and most of these studies were conducted in the higher latitude/altitude range half, which impedes the detection of any differences between centre-periphery and rear-leading edge effects. On the other hand, more cases of "no variation" across the range were registered for the abundance of individuals. Again, most of the papers only studied one half of the range (at high latitude/altitude) but, when a pattern was found at low latitude/altitude or across the whole range, it seemed to provide more support for the CPH than the rear-leading edge interpretation ("Abundance" in Fig. 4B). The long-term dynamics of species ranges are therefore very unlikely to have an effect on current species abundance, contrary to original predictions (Adams, 1902). As suggested by other studies (Cowles 1901; Transeau 1903; Martínez-Meyer *et al.* 2013; Van Couwenberghe *et al.* 2013) and our previous results (see section IV.2.), the contemporary distribution of ecological conditions seems to have a stronger impact.

Finally, within-population genetic diversity decreases from the centre towards the high latitude/altitude edge of many species, and genetic differentiation frequently increases (Fig. 4) especially when the former is the case (see section III.2.c.). However, although the CPH seems slightly more validated than the rear-leading edge hypothesis (“Genetic diversity” and “Genetic differentiation” in Fig. 4B), what shapes the distribution of genetic rates across the whole species range and towards low latitude/altitude remains rather unclear. Rear edge populations are probably impacted by different environmental factors than leading edge populations, by potentially undergoing a stronger effect from local environmental factors such as biotic interactions, and a less limiting effect of regional climate (Schemske *et al.* 2009; Louthan, Doak & Angert 2015; Cunningham *et al.* 2015). Moreover, rear edge populations have generally been more stable over short (Parmesan *et al.* 1999), and long-term (Hewitt, 2000) periods, which might contribute to their higher genetic diversity (Hampe & Petit, 2005). Nevertheless, little is known regarding the impact of current and past habitat fragmentation on the genetic structure of rear edge populations (but see Sexton, Strauss, & Rice, 2011, Sexton *et al.*, 2014). As highlighted previously by Hampe & Petit (2005), “the rear edge matters” and more investigations on rear edge populations (and on the whole species range, from the rear to the leading edge) would help to understand how species can cope with future climate and land use change, as well as to refine the predictions of the CPH.

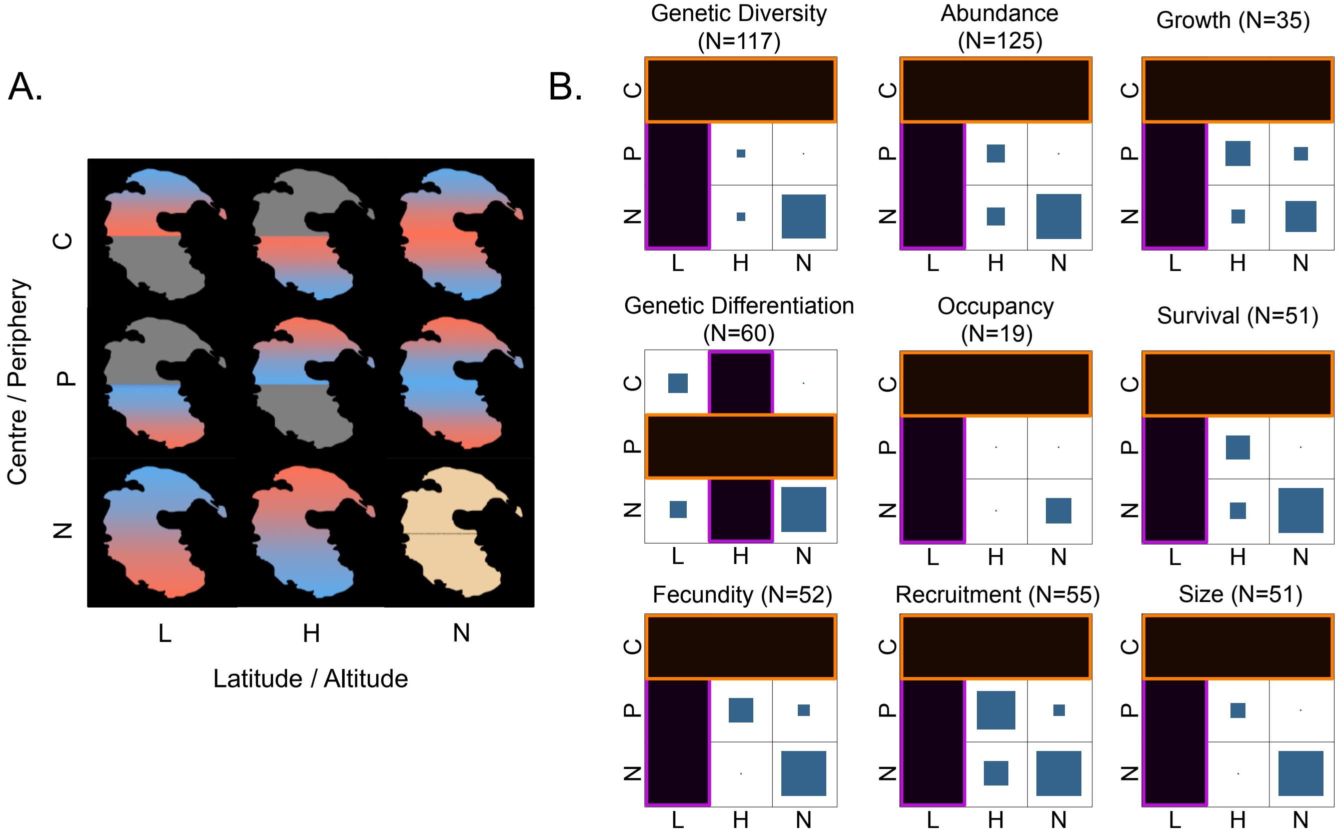


Figure 1-4. The dichotomy between Centre-Periphery and Rear-Leading Edge hypotheses. For each test (N=565), we evaluated whether values of each parameter were higher at the geographical range centre ("C"), the periphery ("P"), or if there was no difference between centre and periphery ("N"), and whether it was higher at low ("L"), high ("H"), or if there was no difference between low and high latitudes/altitudes ("N"). The 9 different scenarios encountered are represented in Figure 5.A. where the distribution of any parameter is represented across a virtual range (using the Pangaea continent as an example). Higher values in any parameter are represented in red, lower values in blue, and no differences between regions in beige. Some scenarios, to be plausible, required that half of the range was not sampled (in grey), and thus represent incomplete centre-periphery and/or rear-leading edge patterns. Finally, we represented the proportion of tests validating each of the 9 scenarios for each trait in Figure 5.B. The size of the squares is proportional to the percentage of studies validating each scenario. The tests that support the centre-periphery hypothesis are highlighted in orange, whereas the tests supporting the rear-leading edge hypothesis are highlighted in purple.

Historical range dynamics

We extracted from our pool of papers the 22 studies (22 tests) that purposefully tested for differences in genetic diversity between clearly identified refugia and areas of post glacial recolonization (Fig. 5). Evidence for historical range shifts were obtained in relation to the known past distribution of the ice sheet (e.g. Dolan, 1994; Hoban *et al.*, 2010; Stone *et al.*, 2012), climatic reconstructions of species distributions at the Last Glacial Maximum (LGM) (e.g. Fuchs *et al.*, 2013; Gassert *et al.*, 2013), or through fossil dating (e.g. Cwynar & MacDonald, 1987). 16 of the 22 selected tests (73%) showed lower genetic diversity in potentially younger, recolonizing populations relative to potentially older populations (refugia). Although there is no perfect match, the latitudinal/altitudinal gradient tends to follow the direction of species recolonization after glaciations, at least for temperate species. This is not pertinent for species that may have had high- or mid-latitude refugia, such as tropical species (Nunes, Norris & Knowlton 2009; Fuchs *et al.* 2013).

Another interesting result here is that the CPH is only confirmed for 9 out of the 22 tests (41%; Fig. 5). Centre-periphery and rear-leading edge gradients are therefore not always concordant, and the latter, when clearly identified and not only based on a latitudinal proxy, appears to represent a major driver of the geographic structure of genetic diversity in many species. Although our analysis is based on a relatively small number of studies (22), several recent papers have also supported this view (Diniz-Filho *et al.* 2015; Pironon *et al.* 2015; Roberts & Hamann 2015; Duncan *et al.* 2015). However, we cannot conclude that contemporary geography of species ranges has no effect and that history acts alone (see section III.4.). In fact, both historical and contemporary factors no doubt act to shape spatial patterns of genetic diversity (Guo, 2012).

Regarding genetic differentiation, only 14 tests can be used for such analysis, which prevent us from making general conclusions. However, seven of these tests found lower differentiation among populations in areas that once served as refugia ("glaciation"), and only two reported lower differentiation among central populations ("centre/periphery"). Overall, our study highlights the need for more systematic studies disentangling the relative effects of contemporary and historical factors on the distribution of species' genetic variation. Past refugial areas are not always located at the centre of current species' ranges, hence the importance of prudence when making tests of the CPH in a historical context.

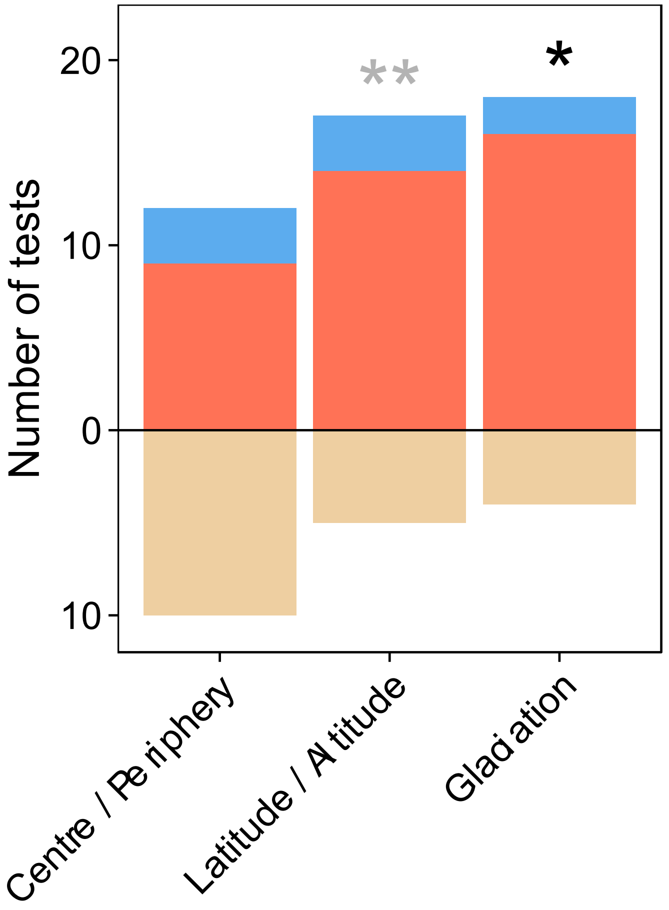


Figure 1-5. Impact of glaciations on the distribution of species genetic diversity.
Here, we only considered studies that purposefully tested for differences in genetic diversity between clearly identified refugia and areas of post-glacial recolonization. The "glaciation" bar represents the number of tests that reported higher genetic diversity in refuge areas (red), at the recolonization front (blue), or no difference among regions (beige). The "latitude/altitude" bar represents the number of tests that reported higher genetic diversity at lower latitude/altitude (red),

at higher latitude/altitude (blue), or no difference between low and high latitude/altitude (beige). The “centre/periphery” bar represents the number of tests that reported higher genetic diversity at the geographical range centre (red), at the periphery (blue), or no difference between centre and periphery (beige). Significance level of binomial tests is indicated as: *** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05 (in black for a hypothesized probability of success of 0.5, and in grey for a probability of 0.33).

The effect of species chorology

Finally, we classified all species into one of four chorological classes based on the bioregions they inhabit: boreal/tundra, temperate, Mediterranean, and tropical. Again, we evaluated whether species features responded to a centre-periphery (longitudinal studies were included this time to increase sample size) or a latitudinal/altitudinal gradient. Studies considering non-geographical centre-periphery gradients were discarded, as well as those considering marine species (too few for reliable comparisons). The number of studies analyzing population occupancy and performance was too low to allow for comparisons, so we focused on the study of abundance of individuals and genetic parameters. For genetic differentiation and abundance of individuals, we did not find any significant differences among biogeographical groups (Appendix S3). Although sample sizes were very low for some regions, this result confirmed that the CPH is invalidated globally for these parameters. Irrespective of the species’ chorology, historical processes (past range shifts) do not appear to have driven current patterns in species abundance, and the causes of the distribution of genetic differentiation still remain unclear. In contrast, we found different distribution patterns for genetic variation for species of different biogeographic origins (Fig. 6).

Many temperate species have expanded or shifted their ranges from low to high latitudes since the LGM (Hewitt, 2000), and their genetic diversity reflects past range shifts (Fig. 5), therefore we would expect latitudinal/altitudinal gradients to provide a higher confirmation rate than a simple central-peripheral gradient. However, 31 out of 64 tests (48%) conducted on temperate species found a centre-periphery distribution of genetic diversity, and a very similar proportion found a latitudinal/altitudinal pattern (24 tests out of 45; 53%). As we saw previously, most of these studies have been conducted at the high latitude/altitude range limit and we are therefore not able to disentangle centre-periphery from rear-leading edge effects (Fig. 4). In addition, latitude might not always reflect the effects of range history, even in the case of temperate species. For instance, many North American species have followed east-west routes of recolonization (Williams *et al.* 2004), which might affect the relevance of a latitudinal proxy. Moreover, within-population genetic diversity of many temperate taxa has been shown to reach maximum values at intermediate latitudes, due to the admixture of divergent lineages coming from distinct low-latitude macrorefugia (Petit *et al.* 2003) or cryptic high latitude refugia (Stewart & Lister 2001). Although genetic diversity of temperate species often follows latitudinal gradients, this pattern cannot be generalized and will depend on how each species distribution has been impacted by past environmental changes.

Boreal/Tundra species exhibited a similar CPH validation rate (50%) to that of temperate species, but their genetic diversity was less likely to follow a latitudinal/altitudinal gradient (validation rate of only 29%). The distribution of boreal/tundra species has not been impacted by glaciations in the same way as temperate species'. Indeed, many of them might have subsisted in macrorefugia (e.g. Beringia refugium) or cryptic localized refugia (e.g. nunataks) at very high latitudes/altitudes (Abbott *et al.* 2000; Shafer *et al.* 2010), or may no longer have a rear edge at low latitude (Williams et al., 2004). Populations of higher genetic diversity might therefore be located at the crossroads of different recolonization routes, often (but not always) positioned at the centre of the current range of the species.

Finally, very few studies (<20 tests) have been conducted on Mediterranean or tropical species. Only 7 tests out of 18 (39%) validated the CPH for Mediterranean taxa, whereas 11 out of 19 tests (58%) validated the CPH for tropical species. Latitude/altitude do not seem to explain better the distribution of genetic diversity of these taxa, especially for tropical species, for which only one test out of 14 found higher values at low latitude/altitude. Mediterranean and tropical species are particularly interesting because their historical ranges have been impacted very differently than temperate or boreal/tundra taxa. Indeed, the ice sheet never arrived at such low latitudes during peak glaciation, so the impact on their historical ranges will not have been to the extent observed for temperate species (Ortego *et al.* 2012). Nevertheless, climate and topography have changed through time in these regions (Fauquette *et al.* 2006; Claussen *et al.* 2013) and the genetic legacy of ice ages can be detected in tropical and subtropical species, but not particularly on gradients of latitude (Diadema *et al.* 2005; Carnaval *et al.* 2009; Fuchs *et al.* 2013). Genetic diversity in these species does not follow systematic central-peripheral or latitudinal patterns, but rather reflects the specific localized temporal dynamics of suitable environmental conditions. More investigations should be conducted on these particular biogeographical groups (e.g. Diniz-Filho *et al.*, 2015; Papuga *et al.*, 2015) if we are to reduce the overrepresentation of studies conducted at the northern range limit of temperate taxa – as highlighted previously (Eckert *et al.* 2008).

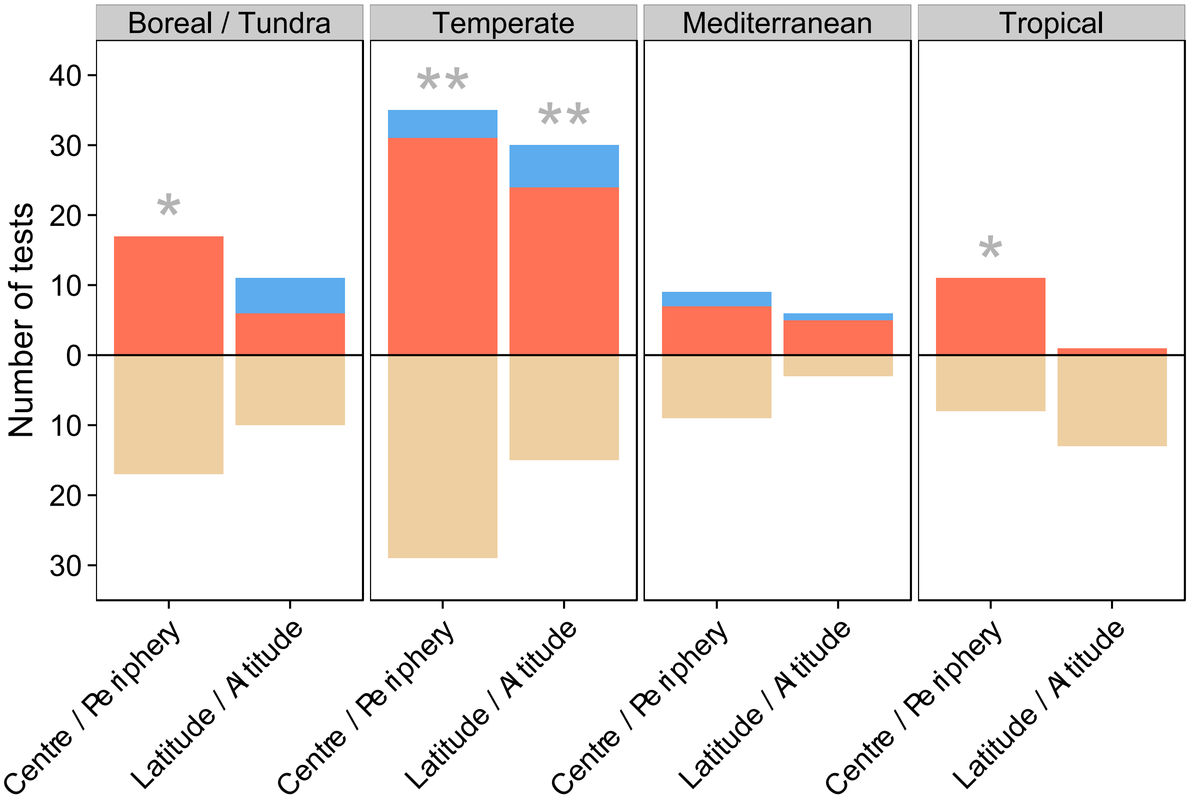


Figure 1-6. Distribution of genetic diversity according to species biogeographic origins.
The "centre/periphery" bar represents the number of tests that reported higher genetic diversity at the geographical range centre (red), at the periphery (blue), or no difference between centre and periphery (beige). The "latitude/altitude" bar represents the number of tests that reported higher genetic diversity at lower latitude/altitude (red), at higher latitude/altitude (blue), or no difference between low and high latitude/altitude (beige). Significance level of binomial tests is indicated as: *** P ≤ 0.001; ** P ≤ 0.01; * P ≤ 0.05 (in grey for a hypothesized probability of success of 0.33).

A new multifaceted framework

Our results showed that the relative position of populations within their current geographic ranges is not sufficient to explain the distribution of variation in genetic and demographic variation. Therefore, the CPH cannot be considered a general rule and needs to be reframed in relation to potential effects of the interactions between geographical and ecological, contemporary and historical, and demographic and genetic factors. Based on our review of the literature, we propose a new basis for future work (Fig. 7).

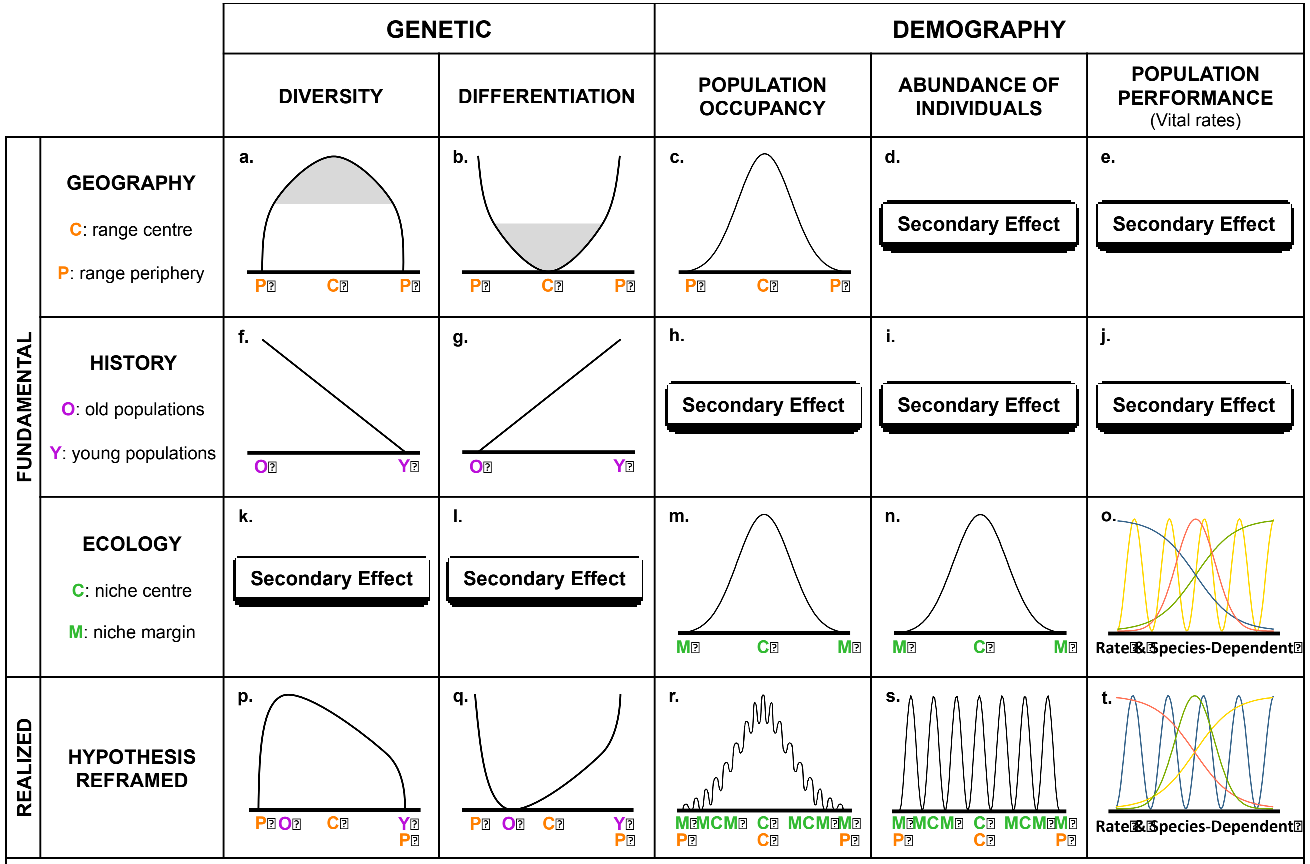
Although few studies investigated spatial patterns of population occupancy, most of them found decreasing numbers of populations (increasing isolation) from the centre towards the periphery of species ranges, as predicted by the CPH (Fig. 7c). On the contrary, a large quantity of data presented empirical evidence that other demographic and morphological parameters (e.g. abundance of individuals, survival, fecundity, size of individuals) do not follow the geographical predictions of the CPH (Fig 7d-e). Yet, most demographic rates have been found to vary across ecological gradients, emphasizing that ecological and geographical marginality gradients do not always go hand in hand. Species' abundance often decreased from optimal/central environmental conditions towards less optimal/marginal conditions (Fig. 7n). Many species' vital rates also followed ecological marginality gradients, but these rates can also be sensitive to density-dependence or stochastic effects. Moreover, the distribution of these rates across environmental gradients seems species and rate-dependent, as each species and vital rate might respond to different niche axes, and optimal conditions for each species and vital rate may have different positions along these axes (Fig. 7o). Finally, the long-term dynamics of species ranges may not primarily influence the distribution of current species' demographic performance (Fig. 7h-j), and short-term effects (e.g. ongoing global change) could potentially reshape it.

We therefore propose that the geographical variation in species' occupancy might be the consequence of the interaction between geographical and ecological central-marginal gradients, and may follow broad patterns of one or a few spatially auto-correlated environmental variables (e.g. climate). As these variables do not always track geographical gradients, we expect them to induce a slight deviation from the gradual central-peripheral pattern expected by the CPH (Fig. 7r). On the other hand, given that the abundance of individuals can follow local ecological conditions, and that these conditions are not always of lower quality in peripheral sites, we expect abundance to fluctuate across the range according to the distribution of high quality sites, without following any geographic centre-periphery gradient (Fig. 7s). Even though marginal conditions may be more frequent in the periphery, populations could persist in favourable environments both in the centre and the periphery of the range, which will translate into lower population occupancy in the periphery but similar abundance of individuals. However, the effective distribution of abundance seems more geographically-structured for vagile than sessile organisms due to their dependence on more spatially-autocorrelated environmental variables. It might therefore follow the distribution pattern of population occupancy (Fig. 7r) and the original predictions of the CPH (see section III.3.). Finally, we propose that the different vital rates of a species might not systematically show the same geographical pattern, and might depend on the spatial configuration of their particular environmental requirements and/or of the other vital rates (Fig. 7t).

Our results highlight the impact of spatial isolation in shaping geographical patterns of species' genetic variation. Peripheral isolates may incur genetic drift and lower gene flow, and consequently harbor lower genetic diversity and higher differentiation (Fig. 7a-b). However, we did not find a consistent pattern of gradually decreasing genetic diversity and increasing differentiation within species' geographic ranges, from the centre towards the periphery. Although genetic diversity and differentiation decrease and increase respectively at the range margins, the highest values of genetic diversity and lowest values of differentiation are not always located at the current geographic range centre. For many species, genetic diversity might instead decrease gradually from past refugial areas (characterized by high environmental stability over glaciation cycles) towards more recently colonized areas through multiple founder events (Fig. 7f-g). The temporal dynamics of environmental conditions and its consequences on species' geographic ranges might therefore have a stronger impact on the broad distribution of genetic variation than current static environmental conditions (Fig. 7k-l).

We therefore propose that within-population genetic diversity could in general reach its optimum in refugial areas (or in admixture zones for species having multiple scattered refugia), decrease gradually towards more recently founded populations, and finally decrease abruptly in isolated populations located at both rear and leading edges of the geographical range (Fig. 7p). For genetic differentiation, the opposite pattern may occur (Fig. 7q).

This framework does not pretend to predict the distribution of genetic and demographic variation of all species. What it proposes is to emphasize the need to adopt an integrated approach in order to improve our understanding of the geographic distribution of species' genetic and demographic parameters, and reframe the oversimplifying CPH. Identifying further limits of this framework will help to refine predictions of the distribution of genetic and demographic performance, and ultimately to prioritize areas of conservation interest, especially in the context of global change.



Conditions (if not respected, curves might be reshaped and factors considered as secondary might reach significance):

- The range must be continuous
- The species must have only one main refugial area
- The range must be stable on short-term
- The species range must have been impacted significantly by past environmental changes (e.g. glaciations)

Figure 1-7. A proposed multifaceted framework for the distribution of species genetic and demographic performance.
The "fundamental" row represents the potential effects of geographical, historical, and ecological gradients on the different parameters. The "realized" row represents the potential effective distribution of genetic variation and demographic performance in space, according to the combined effects of geography, history, and ecology. Uncertainty is represented in grey. In the "population performance" column, each vital rate (e.g. survival, growth, fecundity…) is represented by a different color. In this column, no letter is displayed on the axes, as niche centres and margins for demographic rates and species .may have different locations.

Conclusions

1) Our review shows that although the “centre-periphery hypothesis” (CPH) has not been confirmed as a general rule common to all species, it has, after more than a century of study, thought and discussion, stimulated an immense interest in the understanding of the complex factors shaping the distribution of variation in species genetic and demographic performance.

2) We show here that in addition to the relative position of populations within geographic range, which alone cannot explain the distribution of genetic and demographic variation in all species, the relative effects and possible interactions between geographical, ecological, and historical gradients should be examined.

3) The distribution of genetic diversity may reflect both historical and contemporary factors associated with post-glacial range dynamics and spatial and ecological isolation. For many temperate species, a latitudinal gradient often confounds central-peripheral and rear-leading edge effects. Conducting more studies at the rear edge, as well as across the whole ranges of species within other biogeographic regions (i.e. tropical, Mediterranean, desertic, boreal), would be most helpful here.

4) Genetic differentiation seems to follow the opposite pattern of genetic diversity, with highest values in peripheral isolates and lowest ones in refugial areas. However, this pattern remains rather unclear due to methodological issues. More systematic and standardized studies are needed. Moreover, it now seems particularly important to disentangle the relative effects of geographical and environmental isolation.

5) Overall, species abundance does not follow the CPH. Ecological conditions should not be assumed to systematically follow geographical gradients, which may impinge on some

factors (population occupancy) but not others (abundance of individuals). Population occupancy may relate to a lower availability of ecologically suitable sites at the periphery of the range, whereas abundance within suitable sites may be more related to environmental quality.

6) In many cases, species demographic rates (i.e. population growth rate, survival, growth, fecundity, recruitment) do not follow the CPH. Local ecological, as well as density-dependent and stochastic effects might be more influential than the position of the populations within the range (each rate being impacted differently by these factors, and differently among species).

7) Finally, setting conservation priorities for populations simply according to their position within the range would not necessarily provide a representative selection of high-priority sites; the ecological, demographic, or genetic value of populations for conservation is not strictly related to geographic position.

CHAPTER 2: Range-wide variation in the ecological niche and floral polymorphism of the western Mediterranean geophyte Narcissus dubius Gouan

To be cited as:

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Introduction

Variation in the ecology and genetics of natural plant populations across a species' geographic range is crucial to our understanding of the factors that have shaped current distribution patterns (Gaston 2003) and the processes acting in expanding range limits (Thomas *et al.* 2001). The comparison of populations in the central part of a species distribution with those in peripheral or (peripherally) isolated parts of a species distribution has been a dominant theme in such work. Such studies provide an opportunity to examine variation in the adaptive and nonadaptive processes acting on populations across the range of widespread species.

There has been much interest in how levels of neutral genetic diversity within and among populations may vary from central to peripheral populations. Many studies have indeed shown how levels of genetic variability within populations may decline, despite possible increased differentiation among populations at range limits (Lönn & Prentice 2002; Persson *et al.* 2004; Hampe & Petit 2005; Eckstein *et al.* 2006; Eckert *et al.* 2008; Meeus, Honnay & Jacquemyn 2012). In parallel, the comparison with populations in the central part of a species distribution provides insights into how adaptive traits and population dynamics may vary at range limits in relation to differences in their size and isolation (Brown 1984; Sagarin & Gaines 2002; Herlihy & Eckert 2005; Angert 2006; Villellas *et al.* 2012). Floral polymorphisms have been particularly interesting here, because variability in the relative frequency of floral types and possible loss of the polymorphism are highly sensitive to variation in both natural selection pressures (Thompson, Barrett & Baker 2003) and nonadaptive stochastic processes (Barrett, Morgan & Husband 1989). Indeed, species with floral polymorphisms often show marked geo- graphic variation in morph ratios across their range, which may be related to variation in adaptive mechanisms linked to changes in pollinator composition (Arroyo & Dafni 1995; Barrett, Cole & Herrera 2004; Hodgins & Barrett 2008a; Pérez-Barrales & Arroyo 2010; Santos-Gally *et al.* 2013b) and selection on floral traits that facilitate selfing and associated reproductive assurance in parts of the range where pollination is limited (Eckert & Barrett 1993; Herlihy & Eckert 2005). But this pattern can also be the result of stochastic effects in colonizing populations or past bottlenecks (Couvet, Bonnemaison & Gouyon 1986; Barrett *et al.* 1989; Berjano *et al.* 2015).

There has been continued discussion of the idea that geographically peripheral populations may be ecologically marginal (Brown 1984; Abeli *et al.* 2014), although this has received much criticism (Soulé 1973; Kawecki 2008; Martínez-Meyer *et al.* 2013; Chardon *et al.* 2014; Lira-Noriega & Manthey 2014; Pironon *et al.* 2015). In this context, there has been increasing effort to compare the ecological characteristics of central and peripheral populations, either with an approach based on models of the macroniche, primarily based on broad climatic features of the region where populations occur (Diniz-Filho *et al.* 2009; Martínez-Meyer *et al.* 2013; Lira-Noriega & Manthey 2014), or by empirical investigation of the micro-ecological niche, where plants grow in terms of soil properties (Farris & Schaal 1983; Van Rossum & Prentice 2004; Duffy *et al.* 2009; Leuschner, Köckemann & Buschmann 2009; Wagner *et al.* 2011; Wasof *et al.* 2013), competition, community composition (Carter & Prince 1985; Alexander *et al.* 2007), herbivory (Bruelheide & Scheidel 1999; Stanton-Geddes, Tiffin & Shaw 2012b; Castilla, Alonso & Herrera 2013), and/or other biotic interactions (Zalewska-Gałosz, Nowak & Dajdok 2012). To date no general pattern of converging ecological features toward range margins has been identified

(Leuschner *et al.* 2009). The contemporary distribution of many western Mediterranean plants provides an ideal situation to conduct range-wide studies of variation in the genetics and ecology of natural plant populations. The Mediterranean region of southern France is particularly interesting here, in that it represents the northern and eastern or western range limits of many Mediterranean plant species (Jahandiez 1937; Quézel & Médail 2003; Noble & Diadema 2011, G. Papuga, unpublished data). The distribution of such species is related to an interactive combination of the geological and climatic histories of the region, which have imposed biogeographic barriers and created climatic conditions for changes in species distribution. They constitute evolutionary processes that are associated with diversification (Thompson *et al.* 2005). The onset of the Mediterranean climate in the Pliocene, followed by repeated glacial periods in the Pleistocene, has caused repeated range contractions, with persistence in distinct refugia (Carrión *et al.* 2003; López de Heredia *et al.* 2007; Médail & Diadema 2009) and subsequent expansion. As a result, the historical center from which species have spread may not always be the central part of the contemporary geographic range (Carnaval *et al.* 2009; Lira-Noriega & Manthey 2014). Hence, species history may contribute to the processes underlying contemporary patterns (Hampe & Petit 2005; Pironon *et al.* 2015).

In this article, we explore variation in a floral polymorphism and the ecological niche of central and peripheral populations of the Mediterranean geophyte, *Narcissus dubius* Gouan. Like many species of its genus, N. dubius shows a stigma-height polymorphism, with two morphs that have anthers at roughly the same height and stigmas that are either positioned below the anthers (short-styled S-morph) or level with or above the anthers (long-styled L-morph). Several Narcissus species show striking patterns of geographic variation in morph ratios across their range (see references above), and preliminary observations illustrate that this may also be the case for *N. dubius* (Baker, Thompson & Barrett 2000a; Thompson 2005). The species occurs across a broad climatic gradient in the Mediterranean region, from southern Catalonia to Provence in southeast France and into the Aragon region of central Spain.

This study has three objectives. First, to assess whether peripheral and central populations of *N. dubius* differ in ecological characteristics, we quantify the broad-scale habitat characteristics (climate parameters and altitude) or macroniche of natural populations and the fine-scaled ecological features of the precise environment in which plants grow (i.e., the micro- niche). To do so, we compiled a database of known populations and their broad habitat characteristics and performed an empirical investigation of the micro-niche in two groups of central populations and two groups of geographically peripheral populations (in Aragon to the northwest and in Provence to the northeast). Second, we investigated geographic variation in the floral polymorphism in two ways. We quantified the ratio of morphs in populations throughout the range of the species and assessed the proportion of dimorphic and monomorphic populations in central and peripheral groups. Then, for the L- morph, we quantified variability in stigma-anther separation within and among dimorphic (central) and monomorphic (peripheral) populations to assess any trend toward a floral biology that could facilitate selfing (i.e., reduced herkogamy). Third, given the importance of the Mediterranean region as a glacial refugium, we constructed historical projections of the possible distribution of *N. dubius* under the Last Glacial Maximum (LGM) to assess the probability that contemporary peripheral populations formed part of the recent historical distribution of the study species.

Material and methods

Study species distribution

To provide a precise distribution map and to select populations of *Narcissus dubius* for study, a geolocalized database of known population locations was compiled from four main sources: the Silene database of the Conservatoire Botanique National Méditerranéen de Porquerolles, France, with 401 locations; the IPE database of the Instituto Pirenaico de Ecologia, Jaca, Spain, with 39 locations; the Biodiversidad Valenciana database of the Valence community, Spain, with 208 locations; and the Anthos online database (http://www.anthos.es), with 80 locations. We also gathered personal data for 85 locations in northern Catalonia and France (J. D. Thompson, and see “Acknowledgments”). Only data with a resolution of !1 km^2 were used in our study, and the initial total of 813 occurrence points was carefully checked to remove duplicates, producing a final number of 363 occurrence points.

Narcissus dubius has a geographic range that extends from the Murcia province in southeastern Spain, where its distribution is limited by the Sistema Betica and Sistema Iberico mountains, to the southwestern corner of Provence in France (fig. 1). The species’ distribution is fairly continuous along the east coast of Spain, with large numbers of populations in the coastal hills in the province of Valencia and up into Catalonia. However, three notable features form a contemporary and possibly historical break in population continuity and a basis for the identification of either central or peripheral populations. The first concerns the Ebro valley, where the Puertos de Tortosa-Beceite (northeast of the Sistema Iberico) creates a major barrier with high-elevation mountains. Populations that are located from Caspe to Tudela in Aragon province thus occur at the northwestern distribution limit in Spain. A second break in population continuity is associated with both the physical and the ecological barrier imposed by both the non calcareous eastern tip of the Pyrenees and Albères mountains and the adjacent Roussillon coastal plain. Further north of this break, populations are spread in a lowland band around the Mediterranean to the southwestern corner of Provence, where the species reaches its distribution limits (fig. 1). Within this latter part of the distribution, there is a physical division across the delta of the Rhône valley (no populations are found there).

Based on these physical and ecological barriers, we distinguished four geographic groups of populations. In Spain, we distinguished central populations that occur in a continuous group of lowland populations close to the Mediterranean Sea (Catalonia, Valencia, and Alicante provinces) from those located in the more isolated inland part of the Ebro valley (Aragon) as peripheral populations. In France, central populations occur in a southwestern continuous group widespread across the lowland garrigues of Languedoc-Roussillon toward the Rhône valley. Peripheral populations are those that are present at the distribution limits of the species to the east and north of the extensive wetlands of the Camargue and at the confluence of two major river valleys (the Gardon and the Rhône). The distinction of these central and peripheral groups of populations is thus based on contemporary physical and ecological breaks in the distribution that may have played an important role regarding population isolation in recent history.

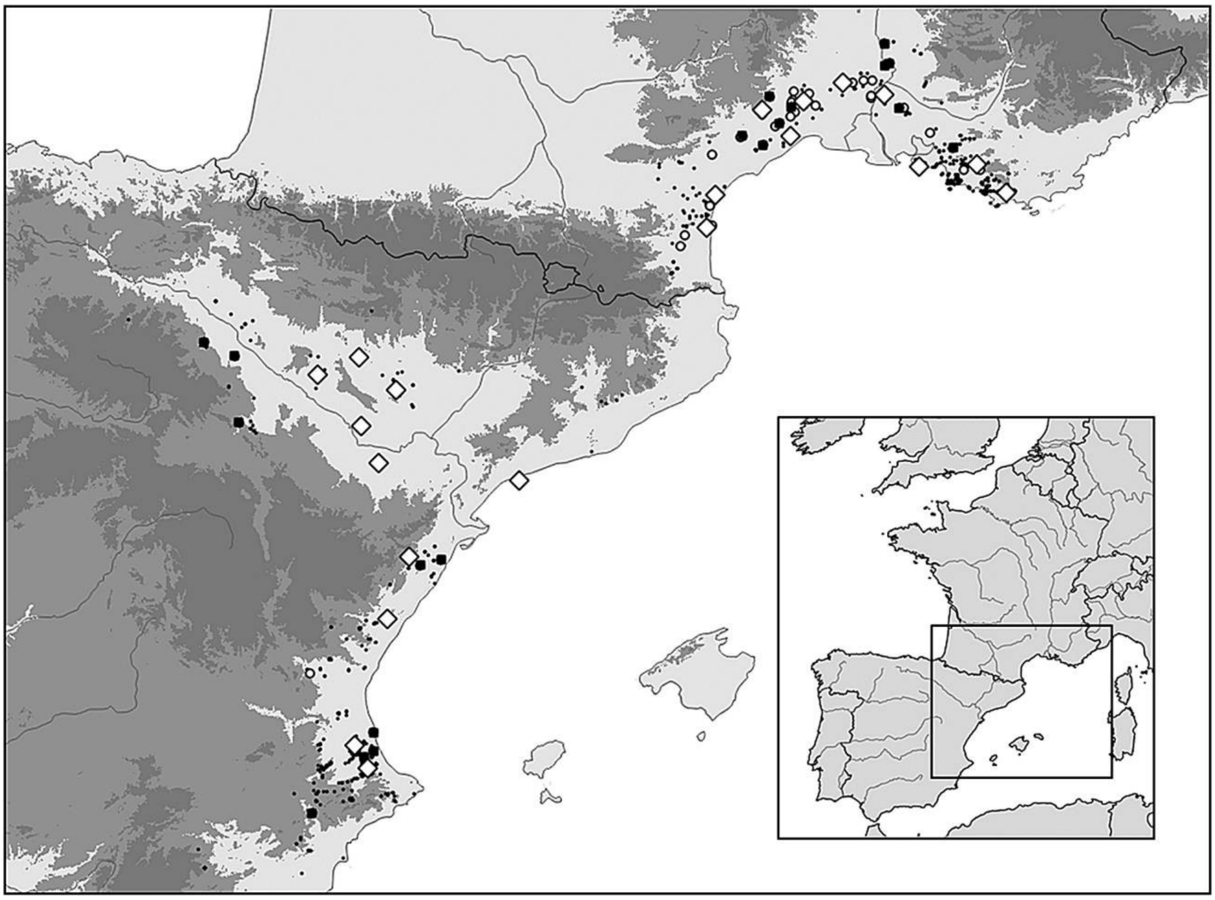


Figure 2-1 Distribution of the 363 locations of *Narcissus dubius* compiled from four different data sources.
Diamonds represent populations where the ecological niche, floral measures, and morph ratio were quantified; squares represent sites used for floral measures and morph ratio estimates; open circles represent sites where only morph ratio estimates were made; and filled circles represent locations that were used only to model the climatic niche of this species.

Modeling distribution patterns in relation to past and present climate

To study climatic characteristics of populations, we extracted annual mean temperature and precipitation, temperature seasonality, and precipitation of the driest month for the 363 locations of *N. dubius* populations from the WorldClim database (http://www.worldclim.org) at a 2.5 arc-minute resolution (Hijmans *et al.* 2005). These four variables were chosen in order to summarize the climatic conditions occupied by this species and to limit any multicollinearity among the 19 bio- climatic variables available in the WorldClim database and the altitude.

We carried out principal component analysis (PCA) of the four variables to characterize the climatic niche for the 363 locations. The distribution of *N. dubius* was modeled using four commonly used algorithms implemented in the biomod2 pack- age in R (Thuiller 2014): generalized additive model, generalized boosting model, random forest, and Maxent. These probabilistic models require information on species' absence (i.e. data that are rarely available), hence the need to assume a virtual or pseudoabsence, which can be generated by computer simulation. The number of points used, their method of selection, and the need to calculate mean values across simulations for such pseudoabsence are important to model accuracy (Chefaoui & Lobo 2008; Barbet-Massin *et al.* 2012). Following the recommendations of these authors, we randomly selected 1000 pseudoabsence points across the study area and repeated the modeling procedure 10 times with different subselections of pseudoabsences (Barbet-Massin *et al.* 2012). We calibrated the different models with 70% of the data and evaluated the results with the remaining 30%. We repeated this procedure five times to limit the impact of this random-splitting strategy. Model predictive accuracy was evaluated using the standard measures of the area under the receiver operating characteristic (ROC; Hanley & McNeil 1982) curve and the true skill statistics (TSS; Allouche, Tsoar & Kadmon 2006).

In order to get historical insights, we established a broad estimate of what might have been the distribution of *N. dubius* at the LGM and how climatic suitability might have changed across the species' distribution since the LGM. Although the species and its genus clearly predate this period (Santos-Gally, Vargas & Arroyo 2012), we have focused attention on the LGM because it is recognized as an important event that has dramatically modified species ranges in the recent past. Although the impact of the LGM can be assumed to be less for Mediterranean taxa than for more temperate taxa, it may have caused complex pat- terns of isolation in diverse microrefugia (Diadema *et al.* 2005; Rodríguez-Sánchez *et al.* 2009; Patsiou *et al.* 2014) rather than simply a major north-south contraction (Rodríguez-Sánchez *et al.* 2009; Alba-Sánchez *et al.* 2010; Besnard *et al.* 2013).

We projected the probability of occurrence in space and time on 2.5 arc-minute grids representing the climatic conditions at the current time and at the LGM (i.e., ~21,000 yr BP). These forecasts assume climate niche conservatism (Wiens & Graham 2005), for which there is now evidence (e.g. Martínez-Meyer & Peterson 2006). Past climate information was generated by the Palaeoclimate Modeling Intercomparison project (Braconnot *et al.* 2007) and was made available by WorldClim. We took into account the variability in the LGM climate projections by considering the output of two different global circulation models (MIROC3.2 and CCSM). According to Swets (1988) and the means of ROC and TSS scores obtained across our ensemble of models (mean ROC score: 0.911 +/- 0.016; mean TSS score: 0.719 +/- 0.034), we can assume that our species distribution models performed well. In order to summarize these forecasts and obtain a single map for each time period, we computed mean values across the different projections, weighted by their respective model predictive accuracy (i.e., TSS scores).

Due to the absence of fossil data for this species, we were not able to validate our historical projections with empirical evidence. Our interpretations are thus made with caution.

Ecological niche

The ecological niche was studied in terms of the broad vegetation type and the fine-scaled abiotic and biotic characteristics of patches where the species is abundant. This was done during peak flowering (March) in five randomly selected populations in each of the four geographical groups of populations (fig. 1). At each site, the range of broad habitat characteristics included the type of vegetation cover and the height of each biological type (Raunkiaer 1934) in the plant community (therophytes, hemicryptophytes, geophytes, chamephytes, and phanerophytes present in the phenological niche of the study species), slope, and elevation.

Fine-scaled ecological characteristics were studied in three quadrats (each 4 m^2) that were established in high-density patches, at least 5 m apart, in each population. For each quadrat, a soil sample was collected, dried at 40°C for 48 h, sieved at 2 mm, and stored before analysis. Conductivity, pH, and salinity were measured using a Eutech Cyberscan. After mixing 10 g of dry soil with 20 mL of water, we blended the solution for 20 min, separated phases using a centrifuge (10 min), and measured values in the supernatant at room temperature (ca. 20°C). The total amounts of carbon (C) and nitrogen (N) were determined using a ThermoFinnigan Flash EA 1112 series on 70 mg samples grinded with a crusher (3 min, frequency p 30). Water-retention potential is the percentage of water lost after drying a wet soil for 48 h at 40°C. Water-retention capacity was then calculated as the percentage of water remaining in previously 40°C dried soil by again drying the sample at 110°C for 5 h. Organic matter was estimated as the percentage of matter lost after burning a dried sample at 500°C for 5 h.

In each quadrat, 100 contact points were established with 20 by 20-cm divisions of the 4 m^2. We also estimated the mean height of each biological type. At each point, we recorded con- tact with one or more of the following elements: bedrock, blocks (>25 cm), stones (2.5–25 cm), gravel (0.5–2.5 cm), bare soil, lichen, moss, herbaceous litter, woody litter, and other plant species. Each contacted plant species was identified and attributed to a biological type (Raunkiaer 1934). We were interested in species only growing in the phenological niche of *N. dubius* and thus did not identify other species growing later in the spring. Preliminary observations of the data showed that bedrock, block, and stone had low values (making statistical analyses difficult for each parameter), and so we summed them at the quadrat level to make a composite substrate variable. When several components were touched at a given point, we constrained the value of each contact point to 1 so that the total cover per quadrat did not exceed 100. For each quadrat, we calculated species richness (the number of species touched during the contact point sampling) and the Shannon diversity index and its associated Hill number (Jost 2006). An important point here is that our aim is to identify the characteristics of the micro-niche where plants grow and when plants grow. This, of course, includes other species, which we detected in our study. We limit this to species present and growing only during the phenological cycle (niche) of *N. dubius*. These species are identified at the time of peak flowering of *N. dubius*. The many other species that may be present but in a different phenological niche are not quantified here.

All statistical analyses were performed using R 3.1.1 (R development Core Team 2010), integrating central and peripheral population groups in each country. We fitted a linear mixed effect model (with country and geographic group as fixed effects and population as a random factor) and carried out two-way analysis of deviance based on type 2 Wald χ^2 tests for mixed models. We corrected P-values following the Benjamini-Hochberg false discovery rate method (Benjamini & Hochberg 1995). We present P-values that fall between 0.05 and the corrected value as weakly significant and those that are less than the corrected threshold as highly significant. To quantify amounts of variation for each variable, we calculated the coefficient of variation between quadrats (within-population variation) and between populations (using mean values across quadrats) in each geographic group. Single-tailed Wilcoxon tests were carried out using the different traits to test for differences in within- and between-population variation among peripheral and central populations. Field studies and experimental laboratory analyses were conducted during spring 2013 and 2014.

Floral polymorphism

Narcissus dubius flowers in February and March. Plants usually bear 3–5 flowers, but this can range from 1 to 12, depending on plant size and location (Worley *et al.* 2000). Flowers show a stigma-height dimorphism; individual plants are either long-styled (L-morph) or short-styled (S-morph), and both have anthers at roughly the same height in the flower (Baker *et al.* 2000a). This species is primarily pollinated by hawk moths, flies, and solitary bees (Baker *et al.* 2000a). Individuals are self- compatible and exhibit no intramorph incompatibility (Baker, Thompson & Barrett 2000b).

In order to assess geographic variation in the presence of the two floral morphs, morph ratio counts were made through- out the range of the species in a total of 74 populations (figure 1; annex a). Population counts were made during spring 2013 or 2014.

In each population, we aimed to sample at least 75–100 flowers to determine the morph ratio. Plants were sampled more than 2 m apart to avoid resampling the same individual. If S-morph individuals were not found, sampling continued up to 200 flowers to check for an eventual very low frequency of S-morph individuals. The number of individuals was estimated visually to provide an indicator of population size in eight classes (with n = the number of individuals: n<10; 10<n<50; 50<n<100; 100<n<500; 500<n<1000; 1000<n<5000; 5000<n<10000; 10000<n). In 19 populations <75 flowers were sampled due to small population size. To quantify variation in the relative position of sex organs, seven populations were selected at random in each of the four geographic groups (fig. 1). In 2014, in each population, we measured flower length, stigma height, and the upper and lower extremity of both upper and lower anthers on 30 flowers, each from a different L-morph individual (fig. 2). These were fully developed mature flowers. Flowers of the S-morph were not measured and included in the analysis, because they were un- common or absent in many populations and do not show significant differences in flower size or anther position compared to the L-morph (Baker et al. 2000a). The only morph of interest to our question is the L-morph that occurs in dimorphic populations and alone in monomorphic populations.

First, we quantified the frequency of L-morph individuals for which the stigma is positioned above the upper anthers in each population. We then calculated stigma-anther separation, after correction for variation in flower size (following Baker *et al.* 2000a), as the distance from the top of the upper anther to the height of the stigma (fig. 2). This measure quantifies both stigma-anther separation (positive values indicative of herkogamy when the stigma is above the anthers) and how deep the style is within the top anther whorl (zero or negative values). To test for variation in stigma-anther separation, we fitted two linear mixed effect models (with country and geographic group as fixed factors and population as a random factor) and per- formed two-way analysis of deviance based on type 2 Wald χ^2 tests (Nelder & Baker 1972). A spatial autocorrelation analysis was also performed (app. B) to verify that there was no major spatial correlation among populations that would otherwise hinder our interpretations of spatial patterns.

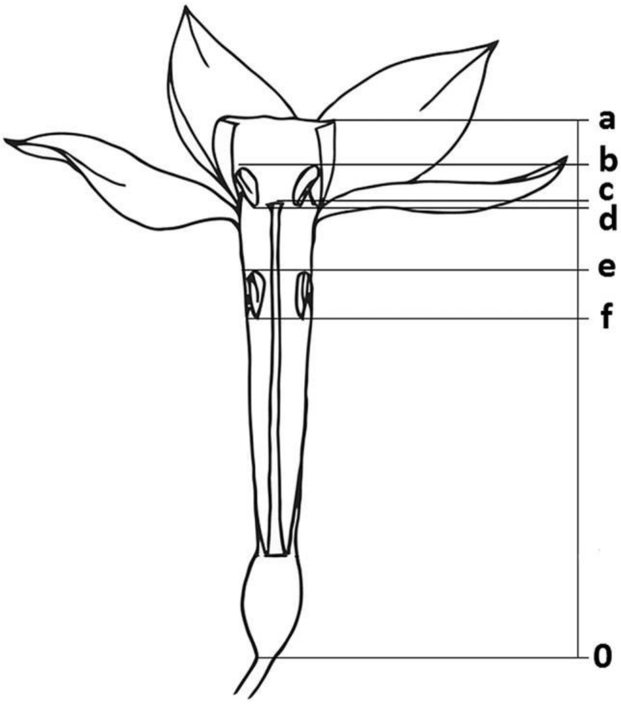


Figure 2-2.Floral measures made on flowers of the long-styled morph of *Narcissus dubius*.
All measures were made from the base of the ovule (O): corolla length (a), upper (b) and lower (d) extremity of the upper anther, stigma height (c), upper (e) and lower (f) extremity of the lower anther. Adapted from Arroyo and Dafni (1995).

Results

Climate analysis and projected past distribution

The projection of the first two axes of the PCA covers 87% of the variation of the whole data set (fig. 3; table 1). The first component is driven primarily by two variables: the precipitation of the driest month and the mean annual temperature. The second component is primarily the result of temperature seasonality and, to a lesser extent, annual precipitation.

We used the s.class function from the ADE4 package to de- scribe climatic variation among populations where the ecological niche was characterized. The ellipses drawn include 78% of the data of the group. This allows us to identify the relative position of the four different population groups regarding the overall climatic niche of the species, whose center is represented by the intersection of the two axes (fig. 3). Central populations in France and Spain and peripheral populations in France occur in the same range of variation along axis 2. These three groups show a gradual decline in mean annual temperature and a higher mean precipitation of the driest month (i.e., a less marked Mediterranean climatic regime) toward peripheral and central populations in France, which differ from central populations in Spain (i.e., toward the left of axis 1). Peripheral populations in Spain are clearly distinct from all other populations (on axis 2) in terms of their higher seasonality: four of the five populations are beyond the gray circle representing the mean climatic niche of the species. This illustrates the more continental climatic regime of their location.

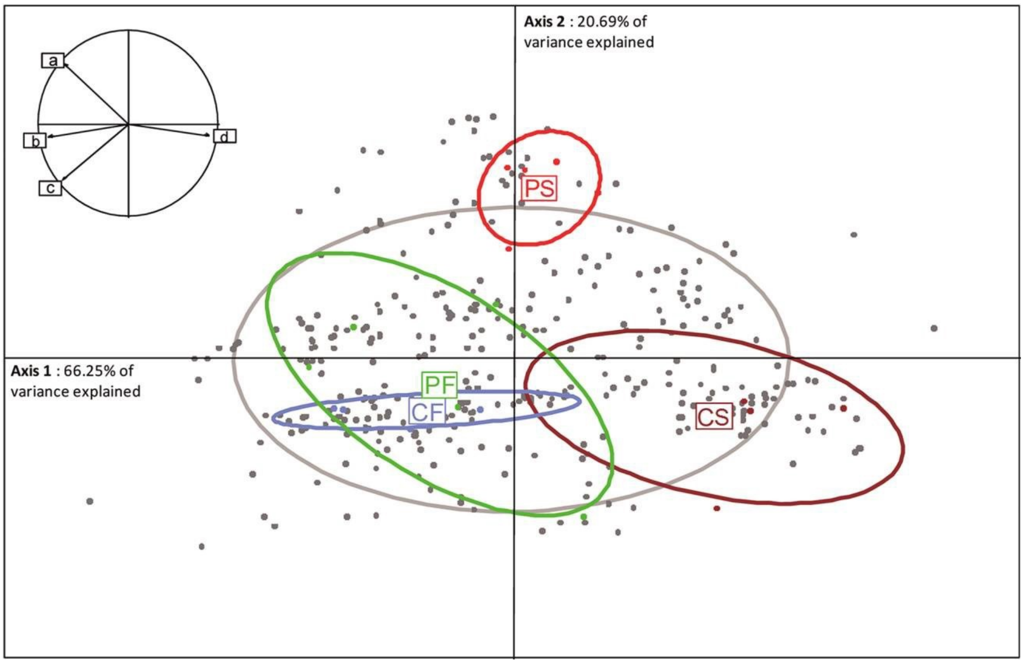


Figure 2-3. Principal component analysis of climate data for all known population locations (gray dots). The four climate variables are temper- ature seasonality (a), mean precipitation of the driest month (b), mean annual precipitation (c), and annual mean temperature (d). Ellipses were drawn with the ADE4 package to include 75% of each class variance. The gray ellipse represents all the locations, and the colored ellipses depict the position of the four geographical groups of populations. P is for peripheral populations, C is for central populations, F is for France, and S is for Spain.

Table 2-1. Results of the Principal Component Analysis

	Principal components			
	PC-1	PC-2	PC-3	PC-4
Eigenvalues:	2.6502	0.8276	0.2920	0.2303
Projected inertia (%)	66.256	20.689	7.299	5.756
Pearson *r* with				
BIO1	0.90	0.13	0.32	0.28
BIO4	0.72	0.65	0.025	0.26
BIO12	0.74	0.61	0.14	0.25
BIO14	0.89	0.14	0.41	0.14

Note: Variables are BIO1 mean annual temperature, BIO4 temperature seasonality, BIO12 mean annual precipitation and BIO14 mean precipitation of the driest month.

The current (fig. 4a) and historical (fig. 4b, 4c) projections of the probability of occurrence of *Narcissus dubius* populations based on current climate data and potential climate of the LGM were obtained using two simulation models (CCSM and MIROC). Differences in past climate predictions do not qualitatively change the results. In the area where central populations occur in Spain, large areas of suitable climate may have existed during the LGM. This was not the case for the area where peripheral populations now occur in Spain. In France, suitable potential climate probably existed as a belt spread above actual sea level around the Mediterranean coastal belt (fig. 1). For current emergent land, only two disjunct areas were climatically suitable for this species, one in the area occupied by peripheral populations north of Marseille and the other southwest of Narbonne in part of the area occupied by central populations.

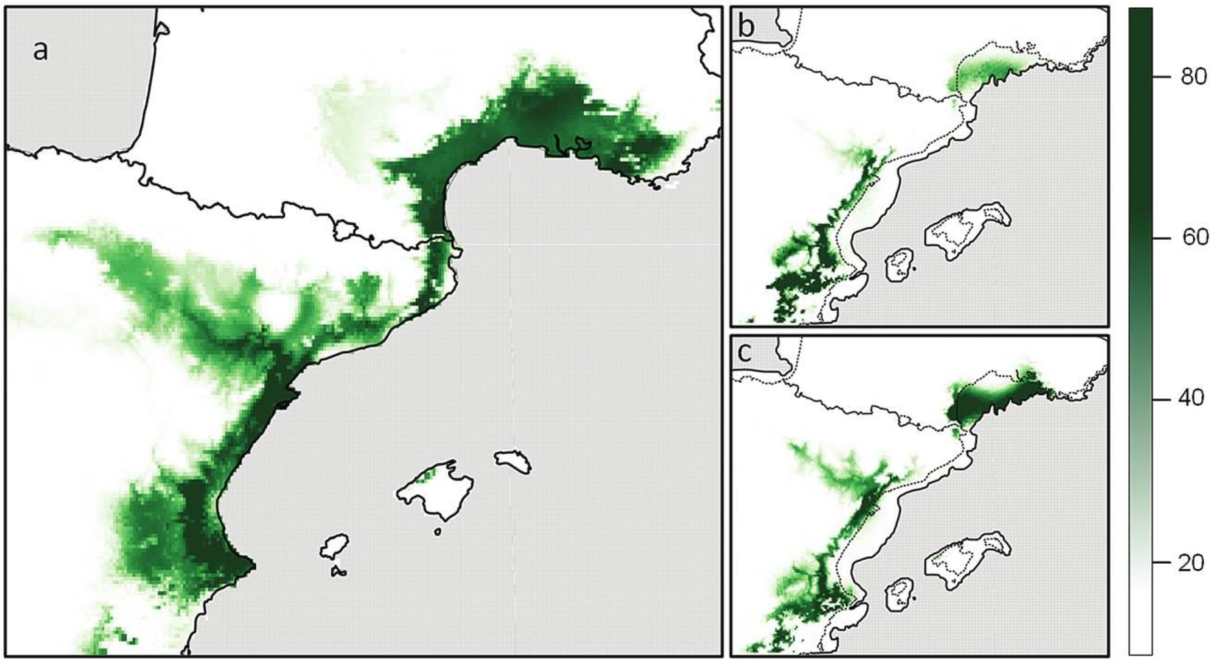


Figure 2-4. Modeled probability of occurrence of Narcissus dubius.
Contemporary distribution (a) and at the Last Glacial Maximum according to CCSM (b) and MIROC (c) climate models. For the two historical projections, historical sea level is drawn as a solid line, while the contemporary coastline is represented by a dotted line. The color scale represents the probability of climate suitability.

Microecological niche

Central and peripheral populations of *N. dubius* showed differences in the mean value of several abiotic and biotic components of the ecological niche (table 2). For the abiotic niche, the composite variable of substrate elements (combination of bedrock, blocks, and stones) showed a significantly lower cover in peripheral populations (fig. 5a), the cover of bare soil was significantly higher in peripheral populations (fig. 5b), and the C/N ratio (fig. 5c) was significantly lower in peripheral populations only in Spain. In general, soil properties varied significantly only between countries (table 2), all showing lower values in Spain, except for pH that was higher in Spain than in France.

For the biotic niche, we found that the cover of therophytes was significantly higher in peripheral populations (fig. 5d). The number of species per quadrat (fig. 5e) and the Hill's number associated with the Shannon diversity index (Jost 2006; fig. 5f) both showed a similar trend of increase in peripheral populations, although this trend was not statistically significant.

Table 2-2. Chi-square values and significance tests for the analysis of deviance of abiotic and biotic components of the ecological niche of Narcissus dubius in central (C) and peripheral (P) populations in Spain and southern France.

Niche component	Country	C vs P	Interaction
Soil analyses			
pH	10,4324**	0,4786	2,2314
Soil conductivity	6,5203**	1,804	1,7691
Water retention potential	10**	1,1525	3,8906
Water retention capacity	16,8847**	2,7819	1,1523
Organic matter	12,351**	1,1014	3,119
Carbon	12,233**	0,3362	1,2719
Nitrogen	3,8662**	0,3119	0,1619
C/N	7,1131**	8,0987**	15,0746**
Point contact cover data			
Mineral	1,0463	3,8934*	0,8522
Gravel	4,3522	0,4529	0,1567
Bare soil	2,3715	5,5124*	0,604
Litter	0,6645	0,3561	1,4115
Therophytes	0,0201	10,6814**	0,505
Hemicryptophytes	0,27	0,1146	0,1401
Geophytes	0,2151	0,7177	0
Chamephytes	2,4277	0,1384	0,0376
Phanerophytes	0,0754	0,4699	0,4021
Species data			
Species number	0,048	2,722	0,3583
Shannon diversity index	0,1008	3,1875	0,2525

Note. Ns : non-significant, * 0.05 > p > corrected significance level, ** p < Corrected significance level. Mineral cover is a combination of bedrock, blocks and stones. All tests are based on a single degree of freedom.

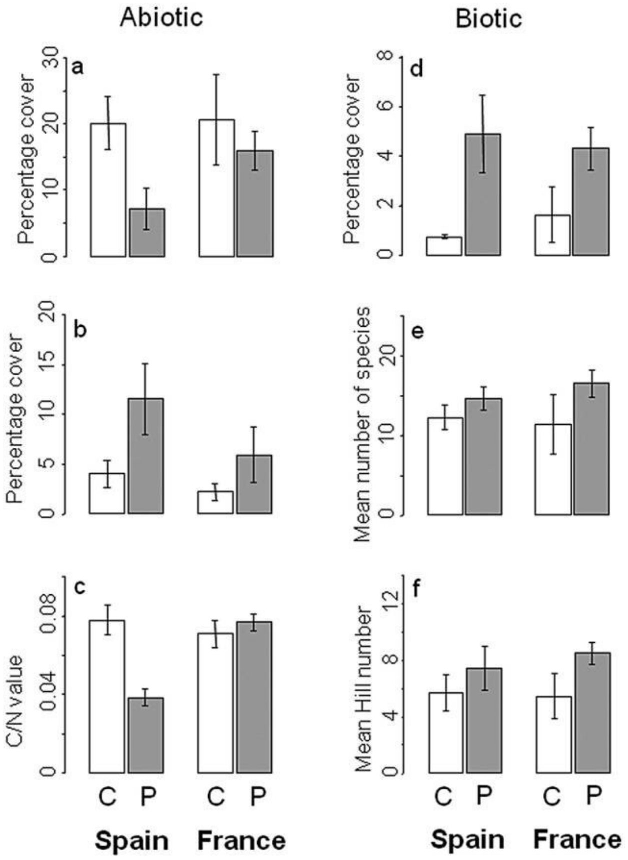


Figure 2-5. Mean values per quadrat of abiotic and biotic features of the ecological niche of Narcissus dubius that show significant variation among central and peripheral populations.
a, Percentage cover of mineral elements. b, Percentage cover of bare soil. c, Carbon/nitrogen ratio. d, Percentage cover of therophytes. e, Number of species. f, Hill number associated with the Shannon diversity index.

Ecological niche variation among quadrats (fig. 6a) showed no significant difference between central and peripheral populations (Wilcoxon test, *V* = 383, *p* = 0.2184), while variation among peripheral populations was significantly greater than that among central populations (Wilcoxon test, *V* = 204, *p* = 0.0218) (fig. 6b)

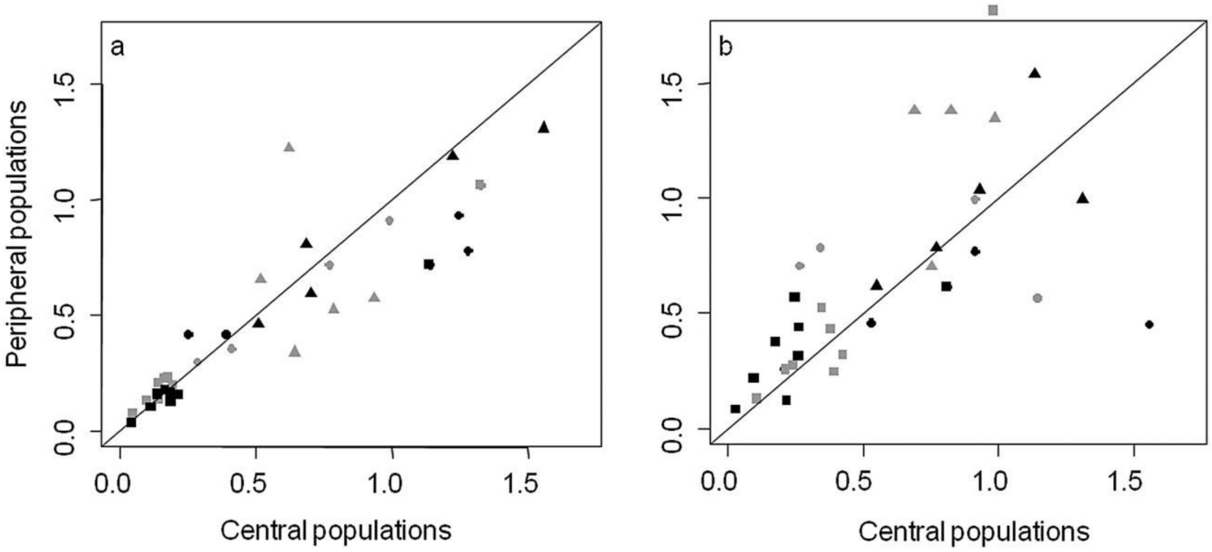


Figure 2-6. Ecological niche variability of central and peripheral populations of Narcissus dubius among quadrats within populations (a) and among populations (b).
Squares represent soil variables, triangles represent biotic count variables, and circles represent abiotic count variables. Values on the two axes are standardized values of the coefficient of variation. For a point that falls on the bisector, trait variability is identical. Points to the left of the bisector signify greater variability among peripheral populations; points to the right of the bisector signify greater variability among central populations.

Floral polymorphism

A total of 74 populations were sampled to assess morph ratio variation (fig. 7). In the central group of populations in the Languedoc-Roussillon region of southern France (n = 30 populations, for a total number of 3753 individuals), *N. dubius* populations are in majority dimorphic but with a consistently L-morph-biased ratio (80%–95%). Only three very small populations (n = 26, 26, and 66 flowering plants) were monomorphic, which is thus potentially an artifact of low sample size. In the peripheral group of populations, only the L-morph was observed in the 20 studied populations (3655 individuals). In Spain, a similar pattern was observed: 10 of the 14 central populations in the coastal hills (a total number of 1703 sampled individuals) were dimorphic, with an L-morph-biased ratio (75% - 99%). In contrast, seven of the nine peripheral populations were monomorphic for the L- morph. In the two dimorphic peripheral populations, only a single S-morph individual (in a total of 45 and 315 studied plants per population, respectively) was observed per population. Hence, in this peripheral group of populations, only two S-morph plants were observed in a total of 1944 sampled plants (figure 7). There was no significant correlation between population size and morph ratio in dimorphic populations ($R^2 = 0.014$, $P > 0.05$).

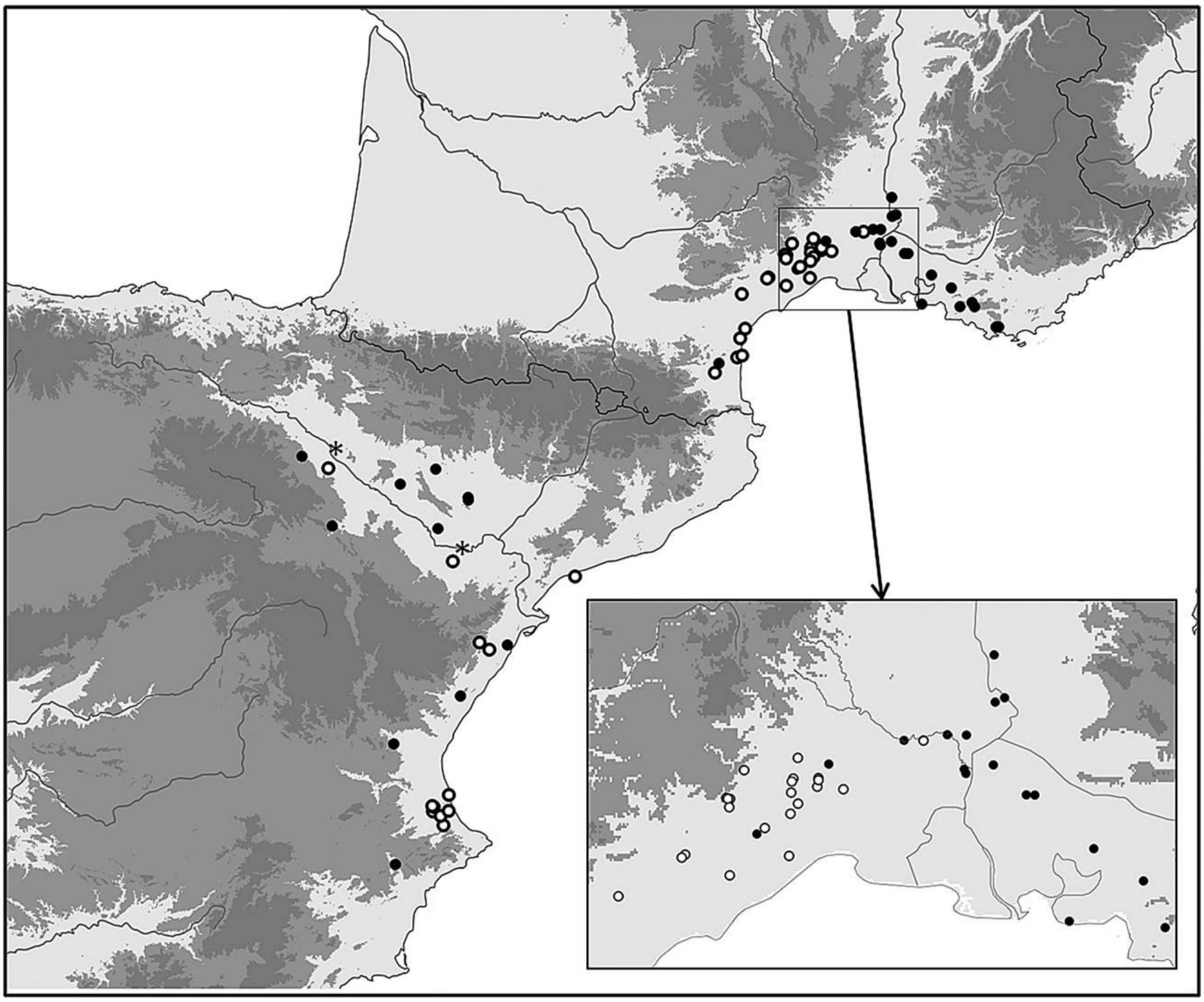


Figure 2-7. The distribution of monomorphic (filled circles) and dimorphic (open circles) populations of *Narcissus dubius* across its distribution in the western Mediterranean.
The two open circles with adjacent asterisks are peripheral populations in Spain with a single S-morph individual.

Floral traits of the L-morph showed several patterns of variation (figure 8; table 3) that accompany differences in the occurrence of dimorphic and monomorphic populations. The measures we made were standardized as described above to remove effects of correlated variation among traits (app. C). Corolla size showed significant differences among countries (P<0.001; figure 8a), with smaller flowers in France than in Spain and a significant country-by-geographical-group inter- action (P<0.01). Spanish peripheral populations had significantly larger flowers than central populations (P<0.001), whereas French peripheral populations had significantly smaller flowers than central populations (P<0.001). The frequency of individuals with stigmas above the anthers (figure 8b) was significantly higher (P<0.031) in both groups of central populations (19%) compared to in peripheral populations (8% and 10.5% for French and Spanish peripheral populations, respectively). Stigma-anther separation (figure 8c) showed a similar trend, with less stigma-anther separation in peripheral populations (P<0.002), particularly peripheral populations in France (fig. 8c).

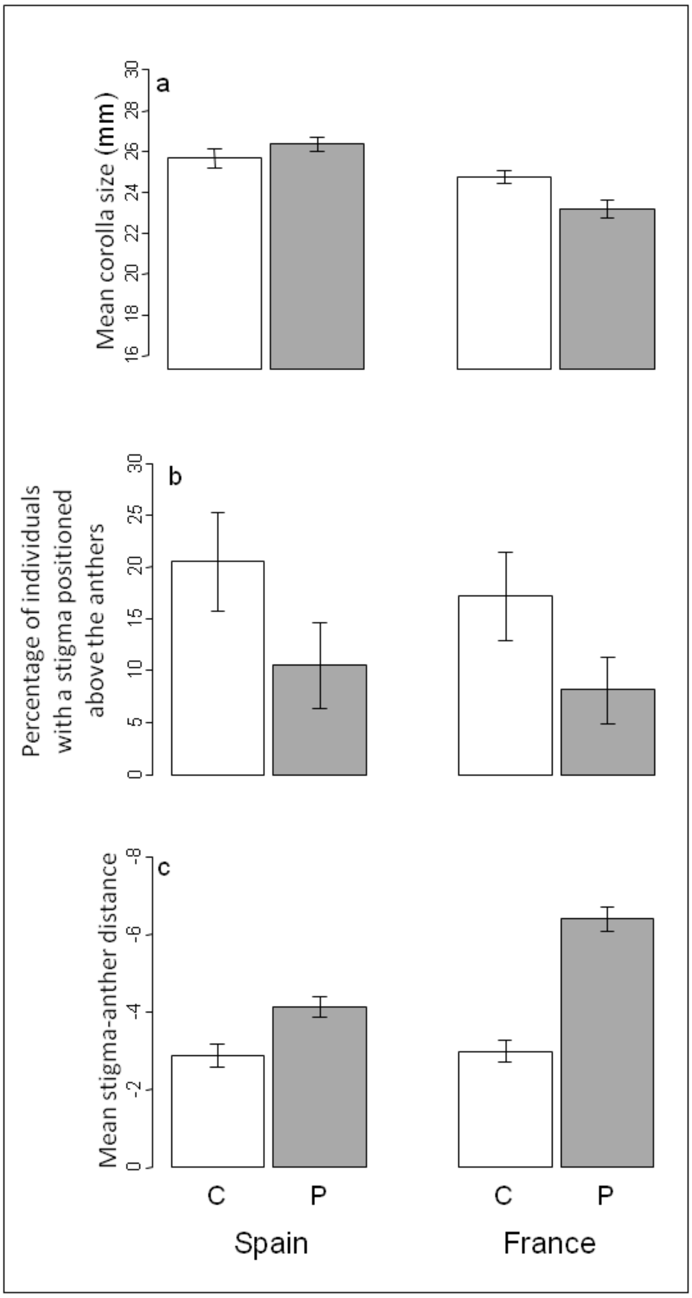


Figure 2-8. Floral biology of the long-styled morph of Narcissus dubius in central (C) and peripheral (P) populations in France and Spain.

a, Mean corolla size. b, Percentage of individuals with a stigma positioned above the anthers. c, Mean stigma-anther distance (i.e., the distance of the stigma to the upper tip of the upper anther).

Table 2-3. Chi-square values and significance tests for the analysis of deviance of corolla size and relative stigma anther separation and ANOVA table for frequency of individuals with stigma above the anthers for the long-styled morph of Narcissus dubius in central (C) and peripheral (P) populations in Spain and southern France.

Flower measure	Country	C vs P	Interaction
Analysis of Deviance table			
Corolla size	27,5721**	1,2298	8,6410**
Relative stigma-anther separation	2,4718	9,3771**	2,0394
ANOVA table			
Frequency of individuals with stigmas above the anthers	F = 0,4742	F = 5,2689**	F = 0,0132

Note. Ns : non-significant, * : 0.05 > p > corrected significance level, ** : p < Corrected significance level. All tests involve a single degree of freedom.

Discussion

This study provides an illustration of how the ecological niche and traits associated with a floral polymorphism vary among different parts of the range of a Mediterranean geophyte, with consistent patterns of change toward geographically peripheral populations. Climate-based historic projections of distribution changes associated with the LGM provide a historical context for the interpretation of these contemporary patterns.

Ecological niche variation

The ecological characteristics of the habitat occupied by populations of *Narcissus dubius* show a repeated pattern of variation between central and peripheral populations. In terms of the microecological niche (*i.e.* the precise ecological conditions where plants grow), peripheral populations occur in patches with a higher cover of bare soil and therophytes. Peripheral populations of *N. dubius* thus tend to occur in richer and more diverse vegetation, as therophyte communities of the Mediterranean flora are very diverse (Madon & Médail 1997; Blondel *et al.* 2010). In addition, peripheral populations in Aragon (Spanish periphery) have a very different macro-niche in terms of broad habitat characteristics; they occur in Mediterranean steppic grasslands that are very different from the rocky calcareous garrigues where this species occurs across the Mediterranean coastal belt of eastern Spain and southern France, especially regarding soils that are poorer in organic matter (and thus total carbon) and have lower water retention potential. These peripheral populations in Spain also occur in a more continental type of climatic regime.

Other studies have shown variable results in terms of the habitat characteristics of species in peripheral populations, with richer and more diverse vegetation in some (Jump & Woodward 2003) but not all (Lönn & Prentice 2002; Murphy *et al.* 2006; Mueller *et al.* 2011) cases. Variation in habitat quality also does not show a clear repeatable pattern of differences in studies of central and peripheral plant populations (Medail *et al.* 2002; Duffy *et al.* 2009). In our case, the consistent changes in the micro-ecological niche (i.e. more open habitats with a greater cover of annual plants in peripheral populations) might represent a shift toward less competitive and more disturbed ecological conditions at range limits (Grime 1988; Madon & Médail 1997). Verification of this hypothesis will require experimental investigation of the impact of ecological conditions on individual fitness and whether local adaptation and/or phenotypic plasticity are associated with ecological niche variation in different parts of the species' range (Holt & Keitt 2004; Pearman *et al.* 2008a).

Finally, in the comparison of ecological trait variation, interpopulation variability is higher among peripheral populations than among central populations. This is not an artifact of having sampled populations over greater distances for peripheral populations. The mean (± SE) distance among studied peripheral populations is 83 km (± 13.0) in France and 56 km (± 6.2) in Spain, and the mean distance among studied central populations is 70 km (± 11.8) in France and 145 km (± 25.1) in Spain. In fact, in Spain, the central populations we studied are farther apart than peripheral populations. Our results, thus, differ from findings in other studies that report a narrower, more specialized ecological niche in peripheral populations (Kavanagh & Kellman 1986; Svensson 1992; Rivero-Guerra 2008), although comparative analyses of several taxa have found little support for this trend (Leuschner *et al.* 2009; Wasof *et al.* 2013). In our study, the consistent ecological changes in populations in two distinct peripheral areas of the distribution of *N. dubius* provide evidence that niche shift in peripheral populations is not necessarily linked to reduced niche width and specialization.

Loss of the floral polymorphism in peripheral populations

Narcissus dubius has a mating system in which both selfing and outcrossing occur (Baker *et al.* 2000a) and in which outcrossing can involve assortative (within-morph) and dissortative (between-morph) mating. A strong L-biased morph ratio is commonly observed in floral polymorphic *Narcissus* species (Dulberger 1964; Arroyo & Dafni 1995; Arroyo *et al.* 2002; Thompson, Cesaro & Arroyo 2012). This pattern is consistently observed in dimorphic populations across the range of *N. dubius*, for which the highest frequency of the S-morph does not exceed 25% of a population. We found no association between population size and morph ratio, which is consistent with previous results (Baker *et al.* 2000a). As shown by theoretical models (Baker *et al.* 2000b), a strong L-biased morph ratio in natural populations is likely to be due to a higher rate of assortative mating in the L-morph compared to in the S-morph. In *N. dubius*, this may be favored by the absence of reciprocity between anther position in the L-morph and stigma height of the S-morph, the self-compatibility of this species that allows for selfing (Baker *et al.* 2000a), and the reduced herkogamy of the L-morph that we report in monomorphic populations. Indeed, peripheral populations of *N. dubius* are almost exclusively monomorphic, lacking the S-morph. Occasionally, populations lack the S-morph in the central part of the range in both Spain and France. Such monomorphic central populations are either very small population patches (<50 individuals) or have incurred recent disturbance (fire).

Mechanisms that favor outcrossing can be heterogeneously distributed across the range of widespread species (Barrett 2001; Cheptou 2011), and as a result, many polymorphic species show changes in the relative frequency of morphs in different parts of their range (Weller 1986; Barrett & Richards 1990; Arroyo & Dafni 1995; Arroyo *et al.* 2002; Barrett *et al.* 2004; Thompson *et al.* 2012), sometimes with the loss of particular morphs (Shore & Barrett 1985; Barrett *et al.* 1989; Eckert, Manicacci & Barrett 1996; Hodgins & Barrett 2008a). In Narcissus papyraceus in southern Spain, northern peripheral populations show a loss of the S-morph (Arroyo *et al.* 2002) and lower levels of genetic diversity than central populations (Simón-Porcar, Picó & Arroyo 2015). The latter author found a significant correlation between genetic diversity and the frequency of the S-morph, which further confirms a trend toward reduced outcrossing in peripheral populations. This follows the central- peripheral model that predicts lower genetic diversity at the edge of the distribution (Eckert *et al.* 2008; Sexton *et al.* 2009). Unlike in N. papyraceus, where peripheral populations are often smaller than central populations (Arroyo *et al.* 2002), the monomorphic peripheral populations of *N. dubius* are mostly large and fairly abundant within the region where they occur, particularly in Provence. This occurrence of monomorphic populations could be due to selection that favors assortative mating and/or selfing or be a consequence of stochastic forces acting in peripheral populations.

The loss of the S-morph and reduced stigma-anther separation in peripheral populations may be linked to pollinator- induced selection that enhances assortative mating and/or self-fertilization (Belaoussoff & Shore 1995; Baker *et al.* 2000b; Herlihy & Eckert 2004). Indeed, reduced herkogamy may permit reproductive assurance in the absence of pollinators (Lloyd & Schoen 1992; Affre & Thompson 1999; Moeller 2006). Changes in pollinators and reduced pollination service have been documented in other Mediterranean Narcissus species in relation to changes in morph abundance, particularly a relative loss of long-tongued pollinators that assure the reproduction of the S-morph (Arroyo & Dafni 1995; Pérez-Barrales & Arroyo 2010; Santos-Gally *et al.* 2013b). *Narcissus dubius* is visited by a range of generalist pollinators in southern France (J. D. Thompson, personal observations), including long-tongued Lepidoptera, primarily Macroglossum stellatarum, and short- and long-tongued bees (mostly *Apies* and *Anthophora*). We have no evidence for any variation in composition among central and peripheral populations, and because the widespread distribution of the long-tongued pollinators covers the peripheral group of populations in France, it is therefore unlikely that the loss of the long-tongued pollinators causes a pollinator-based shift toward increased assortative mating and selection for selfing in peripheral populations. This will, however, require further investigation for confirmation.

In floral polymorphic species, morph ratio variation has also been found to be linked to the spatial and temporal dynamics of populations, which may lead to modifications in the genetic assemblage of colonizing populations and randomly cause a decline in the abundance or loss of particular morphs (Barrett *et al.* 1989; Eckert & Barrett 1992; Husband & Barrett 1992; Hodgins & Barrett 2008a; Berjano *et al.* 2015). The loss of the S-morph in peripheral populations of our study species could thus also result from stochastic events associated with historical processes of range contraction and spread

Insights from the recent history of *N. dubius*

Our historical projections of the distribution of *N. dubius* at the LGM provide insights into this potential role of stochastic variation during periods of range contraction and expansion of *N. dubius* populations. Although this timescale does not allow us to fully cover the species' history due to its probable ancient origin (Santos-Gally *et al.* 2012), the LGM has been found to be a major cause of contemporary patterns in many species (Hewitt 1999; Rodríguez-Sánchez *et al.* 2009; Alba-Sánchez *et al.* 2010). Nevertheless, we interpret historical projections with prudence, given the absence of palaeoecological and phylogeographical data for this taxon (Gavin *et al.* 2014) and the fact that nonanalogous climatic conditions between the current time and the LGM may influence the results (Pearman *et al.* 2008b; Veloz *et al.* 2012).

Suitable climatic conditions for the persistence of *N. dubius* during the LGM probably existed in the coastal hills of south- east Spain (1000-m elevation). This area has been identified as a potential LGM refugia for other Mediterranean plants (Carrión *et al.* 2003; Médail & Diadema 2009) and, during previous Pleistocene glaciations, for oceanic (Taberlet *et al.* 1998; Médail & Diadema 2009) and Mediterranean (Lumaret *et al.* 2002; Gómez & Lunt 2007; López de Heredia *et al.* 2007; Besnard *et al.* 2013) temperate species. At the LGM, the Ebro valley (current peripheral populations) appears to have been unsuitable for *N. dubius*. This area might have served as a refugium for temperate taxa, such as Corylus avellana L., now present only in a few shallow gorges in the Ebro valley (González-Sampériz, Valero-Garcés & Carrión 2004; Valero-Garcés *et al.* 2004), but not for more typical Mediterranean taxa, such as our study species (González-Sampériz *et al.* 2008). Since the LGM, an arid steppe habitat with a rather novel veg- etation type has developed in this area (Pérez-Collazos *et al.* 2009). *Narcissus dubius* may thus have spread from south-eastern refugia to colonize the Ebro valley since the LGM thanks to an adaptation to a more seasonal, continental-like climate. This colonization pathway has also been proposed for *Ferula loscosii* (Lange) Willk. (Pérez-Collazos *et al.* 2009), a species in which genetic homogeneity has been interpreted as a signal of recently founded populations. This interpretation may thus be applied to the almost complete loss of the S-morph in peripheral populations in this area. This loss may have occurred as a result of repeated founder effects and stochastic loss during colonization events or perhaps historical selection by pollinators. Given the already-low frequency of the S-morph in central populations, this loss may indeed occur fairly easily and thus repeatedly. An interesting point here is that *N. dubius* occurs in a clade with monomorphic species (Santos-Gally, Gonzalez-Voyer & Arroyo 2013a).

In southern France, it is not clear exactly where elements of the Mediterranean flora persisted during the LGM (Pons & Vernet 1971); the precise location of potential refugia is difficult, and hypotheses for their location should be interpreted cautiously. For *N. dubius*, LGM projection of potentially suit- able climate (fig. 4b, 4c) occurred in an area that is now either submerged or on and around the calcareous mountains of southwestern Provence and in the Languedoc-Roussillon region near Narbonne, where several low-elevation calcareous ranges were islands in recent history. These two areas have been historically isolated by a large barrier of unsuitable sandy and coastal areas and have several restricted endemic species (Fréville *et al.* 2004; Pouget *et al.* 2013) or disjunct endemic species whose populations are peripheral isolates of more southern Mediterranean species (sensu Thompson 1999, 2005; G. Papuga, unpublished data).

Hence, although the historical projections and current patterns for peripheral populations are less clear in southern France than in Spain, the possibility of persistence in different microrefugia in the coastal belt of southern France cannot be ruled out. Elsewhere, it has been proposed that, despite a globally unfavorable climate matrix, the Mediterranean Basin probably contained several microrefugia (Feliner 2011), even locally (Patsiou *et al.* 2014). Given the complete absence of the S-morph from all the contemporary peripheral populations (despite their size and abundance), their reduced flower size, and their reduced stigma- anther separation, it is possible that the S-morph might have been lost as a result of a bottleneck or selection during repeated range shifts (this species may disperse quite well; Santos-Gally *et al.* 2012) from a local refugium. As a result, the southern part of the Rhône valley (fig. 7, inset) may in fact represent an admixture zone where two colonization fronts have met, as observed for genetic diversity in *Quercus ilex* L. (Lumaret *et al.* 2002), and not only a simple separation between contemporary central and peripheral populations.

Conclusion

This comparison of the ecological niche and floral polymorphism in the different parts of the range of *N. dubius* in the western Mediterranean illustrates how diverse directions of colonization out of distinct microrefugia may have shaped contemporary patterns of variation. In eastern Spain, colonization toward Aragon has involved a shift in ecological conditions and an almost complete loss of the S-morph. In Mediterranean France, trait variation could reflect persistence and spread from different refugia and not a gradual shift from central to peripheral populations. We have now investigated a collaborative phylogeographic study of this species in order to test these possible interpretations for the historical evolution of contemporary patterns of ecological and genetic variation.

CHAPTER 3: Ecological niche differentiation in peripheral populations: a comparative analysis of Mediterranean plants at their northern range limits

To be cited as:

Papuga, G., Gauthier, P., Pons, V., Pironon, S., Farris, E. & Thompson, J.D. (submitted) Ecological niche differentiation in peripheral populations: a comparative analysis of Mediterranean plants at their northern range limits.

Introduction

There has been a long standing interest in the idea that populations close to species’ range limits may show fundamental differences in abundance, ecology and genetic variation compared to those in the central part of their distribution (Sagarin & Gaines 2002; Eckert, Samis & Lougheed 2008; Sexton *et al.* 2009, Pironon, Papuga et al., in prep). The exploration of this so-called “central-peripheral” hypothesis has provided a baseline for many studies on the factors that prevent species from colonizing areas beyond their current limits (Gaston 2009b; Sexton *et al.* 2009). Three main elements dominate this literature.

First, patterns of population and individual abundance in the different parts of a species range has led to the proposition of an “abundant center” hypothesis (Hengeveld & Haeck 1982; Brown 1984) which has been the subject of ongoing examination and debate (Sagarin *et al.* 2006). Second, individual fitness and population demography are proposed to decline toward range limits (Herlihy & Eckert 2005; Angert 2006; Villellas *et al.* 2012; Abeli *et al.* 2014), although empirical evidence remains rare (Pironon, Papuga et al., in prep). Third, many studies document lower levels of genetic variability within populations and often increased differentiation among populations at range limits (Lönn & Prentice 2002; Persson *et al.* 2004; Hampe & Petit 2005; Eckstein *et al.* 2006). Such variation includes examples of a loss of genetic polymorphism due to the absence of one or more floral morphs in peripheral populations (Hodgins & Barrett 2008b; Pérez-Barrales & Arroyo 2010; Papuga *et al.* 2015; Santos-Gally *et al.* 2015; Simón-Porcar *et al.* 2015). However, the occurrence of unique gene combinations in peripheral populations (Levin 1970, 1995; Lesica & Allendorf 1995; Petit, El Mousadik & Pons 1998) supports their conservation interest (Lesica & Allendorf 1995; Petit *et al.* 1998; Thompson *et al.* 2010).

Empirical tests of the central-peripheral hypothesis have often been made under the assumption of a concordance between geographic periphery and ecological marginality. However, there has been much debate concerning whether environmental conditions are indeed optimal near the center of the range, and more marginal towards the periphery (Levin 1970; Soulé 1973; Hardie & Hutchings 2010; Pironon *et al.* 2015) and the possibility of ecological niche differences between peripheral and central populations has received much less empirical attention than the above-mentioned topics (Papuga, Pironon et al unpublished ms).

The correct characterization of the ecological niche is a complicated task (Pulliam 2000). The diversity of environmental factors and the complexity of their interactions render the delimitation of a species niche a delicate issue. Many recent studies have focused on the climatic niche (Martínez-Meyer & Peterson 2006; Thuiller *et al.* 2008; Diniz-Filho *et al.* 2009; Lira-Noriega & Manthey 2014), however this provides only limited insights into our understanding of how fine-scaled population processes may vary at range limits (Pulliam 2000; Boulangeat *et al.* 2012). In addition, it has been increasingly recognized that broad habitat units or vegetation types are insufficient to describe the precise ecological niche of plants (Hall, Krausman & Morrison 1997), which requires explicit descriptions of the suite of habitat characters required by a species (Miller & Hobbs 2007). In this context, some authors have compared central and peripheral populations based on empirical investigation of the micro-ecological niche in which plants live, in terms of soil properties and other abiotic components of the environment (Farris & Schaal 1983; Van Rossum & Prentice 2004; Duffy *et al.* 2009; Leuschner *et al.* 2009; Wagner *et al.* 2011; Wasof *et al.* 2013; Papuga *et al.* 2015), competition and community composition (Carter & Prince 1985; Alexander *et al.*

2007) and biotic interactions (Bruelheide & Scheidel 1999; Zalewska-Gałosz *et al.* 2012; Stanton-Geddes *et al.* 2012b; Castilla *et al.* 2013). These single-species comparisons in different contexts do not show a general pattern of niche differences among central and peripheral populations.

The flora of the Mediterranean region of southern France provides a multitude of examples of range limits in western Mediterranean species (Jahandiez 1937; Quézel & Médail 2003; Noble & Diadema 2011) some with a semi-continuous distribution (Papuga *et al.* 2015) others in peripherally-isolated populations (Medail *et al.* 2002; Lhotte, Affre & Saatkamp 2014). These patterns are closely associated with the geological and climatic history of the region, particularly the onset of the Mediterranean climate in the Pliocene and repeated glacial periods in the Pleistocene (Thompson 1999; Carrión *et al.* 2003; Thompson *et al.* 2005; López de Heredia *et al.* 2007; Médail & Diadema 2009). They provide ideal situations for studies of whether ecological conditions vary across species' ranges within a single climatic region.

Based on a comparative analysis of 11 Mediterranean plant species in nine different families and with variable herbaceous growth forms, we test for a general pattern of variation in the ecological niche of peripheral populations (northern range limits in Mediterranean France central) compared to central populations (in continental Spain or Italy). To do so we address three objectives. First, we test whether species show consistent differences in their macro- and/or micro-ecological niche among central and peripheral populations. Second, we attempt to identify whether species share similar patterns of ecological niche variation across their range. Third, we test whether the ecological niche breadth is different in the peripheral part of the range compared to the central part of the species distributions.

Material and methods

Species and populations selection

In order to select species for a comparative analysis of niche variation among central and peripheral populations we followed a step-by-step procedure. First, we made a list of the 337 Mediterranean plant species (Annex 1) that are listed for protection in France, or present in the Red List of Flora for part of this region as being “endangered”. We based our selection on listed species because their distribution is solidly documented (not the case for more common specie) and also because of their conservation significance.

We immediately excluded from this list any species whose distribution in Mediterranean France is directly linked to recent human activities (e.g. species of horticultural importance such as *Chamaerops humilis*, or *Ampelodesmos mauritanica*) and species of trees, ferns, helophytes and aquatic plants whose study would require different sampling methods. We also excluded species whose taxonomic rank is under discussion or which are genetically heterogeneous (e.g. polyploidy complexes). This selection reduced the list to 186 species.

We then restricted our list to species that exhibit a clear central-peripheral type of distribution, with a central part of their range in the Iberian or Italian peninsula and/or North Africa and northern peripheral populations in the Mediterranean climate region of France, with at least five known populations in our database for this region (in order to make a correct study of variability of the ecological niche in these peripheral populations). We also excluded species for which populations in the central part of the distribution were very scattered and rare, making population localization extremely difficult. This produced a list of 48 species.

To make the study as general as possible we chose one species per family, except for the *Asteraceae* in which three species belonging to three different clades of this family and in two different biological group forms were selected. To facilitate field work and make a continuous study of several species in a given year - we chose species flowering at different moments of spring and autumn. This excluded several species from the French Riviera region which flower simultaneously. We included one non-protected species, *Narcissus dubius*, which was the subject of a previous study (Papuga *et al*. 2015). A final list of eleven species (Table 1) containing three therophyte species, three hemicryptophytes, three geophytes, and two chamephytes was thus obtained.

In order to select study populations for the 11 species, a geolocalized database of known population locations was compiled from four main sources: the *SILENE* database of the Conservatoire Botanique National Méditerranéen de Porquerolles (France); the *IPE* database of the Instituto Pirenaico de Ecologia (Jaca, Spain); the *Biodiversidad Valenciana* data base of Valence community (Spain) and the Spanish *Anthos* online database (http://www.anthos.es/). We also gathered personal data from colleagues in France, Spain and Italy. Only data with a resolution of < 1km^2 were used in our study. As a result we were able to construct a geographic distribution map for each of the 11 species in the western Mediterranean basin (Figure 1).

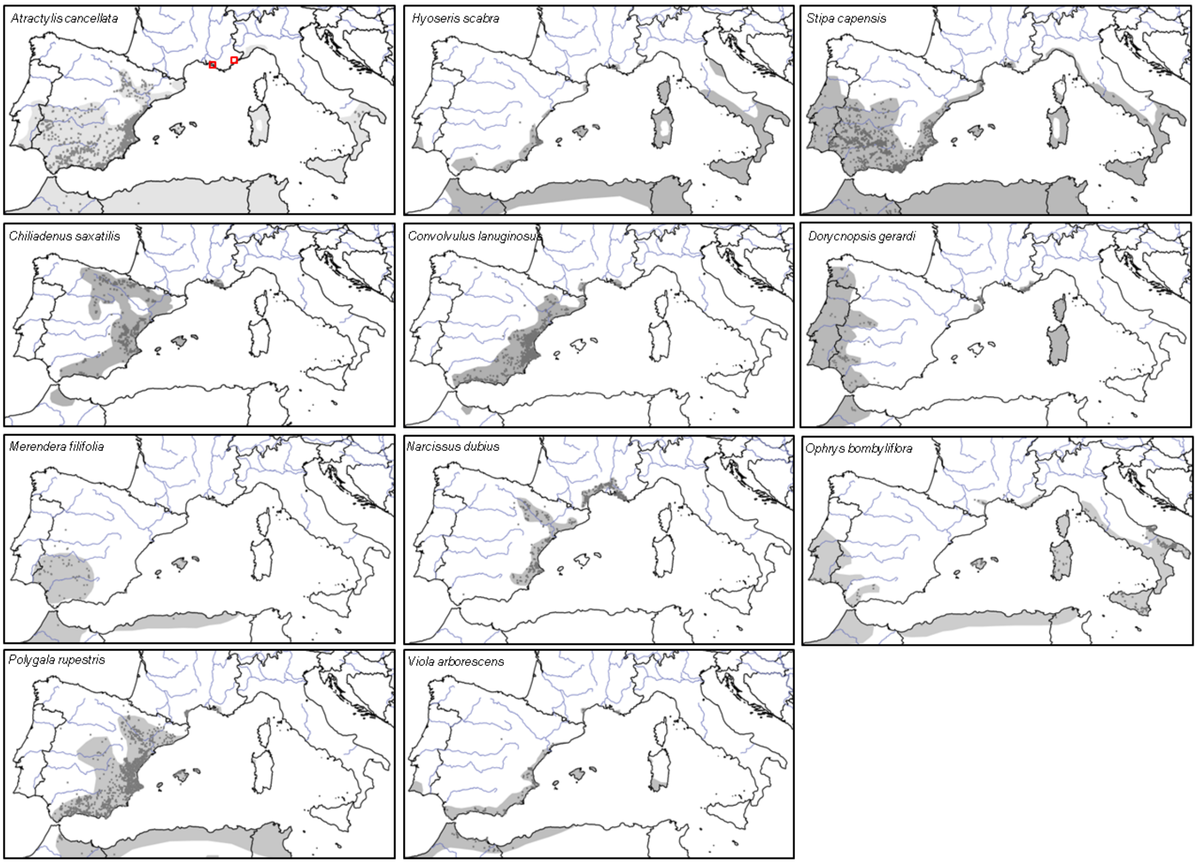


Figure 3-1. Distribution maps of the 11 studied species in the western Mediterranean basin.
Dark gray dots are locations contained in our database; grey areas represent the distribution of each species adapted from Bolos & Vigo (2000); red squares represent areas where peripheral isolates occur in southern France.

To compare central and peripheral populations of each species, we randomly chose five central and five peripheral populations in our database (Annex B). If a population could not be found in the field, we selected the closest known population for study. In southern France, populations were selected to cover the distribution range of the species and primarily to have populations from both the Languedoc-Roussillon region (to the west of the Rhône valley) and Provence (east of the Rhône valley). We attempted to have a similar as possible distance between the two most geographically distant populations in each of the two geographical groups of populations of a given species. This distance is of course highly variable among species (Table 1).

Table 3-1. List of studied species, their biological features and distances among sampled populations.
The nomenclature follows the most recent taxonomic referential of the Mediterranean Botanical Conservancy (http://silene.eu).

N°	Species	Family	Flowering month	Biological type	Quadrat size (m^2)	Mean and maximum distance among peripheral populations		Mean and maximum distance among central populations	
1	*Atractylis cancellata* L.	Asteraceae	Late spring	Therophyte	1	97	193	199	400
2	*Chiliadenus saxatilis (Lam.) Brullo*	Asteraceae	Autumn	Hemicryptophyte	4	32	60	87	172
3	*Convolvulus lanuginosus* Desr.	Convolvulaceae	Late spring	Hemicryptophyte	4	125	212	169	360
4	*Dorycnopsis gerardi* (L.) Boiss.	Fabaceae	Late spring	Hemicryptophyte	4	192	323	70	105
5	*Hyoseris scabra* L.	Asteraceae	Mid-spring	Therophyte	1	71	175	77	182
6	*Merendera filifolia* Cambess.	Colchicaceae	Autumn	Geophyte	1	1	3	105	185
7	*Narcissus dubius* Gouan	Amaryllidaceae	Early Spring	Geophyte	4	83	155	145	271
8	*Ophrys bombyliflora* Link	Orchidaceae	Mid Spring	Geophyte	1	12	25	142	266
9	*Polygala rupestris* Pourr.	Polygalaceae	Mid spring	Chamephyte	1	78	177	340	603
10	*Stipa capensis* Thunb.	Poaceae	Late spring	Therophyte	4	123	204	148	292
11	*Viola arborescens* L.	Violaceae	Autumn	Chamephyte	1	88	217	319	617

Field and data-base examination of the macro niche

For each population, the natural habitat was broadly described in terms of vegetation structure (e.g. forest, grassland, etc.), dominant species, topographical characteristics (e.g. crest, plain, slope, etc.) and type of substrate (e.g. calcareous, granitic, quaternary soil, etc.). Based on these field descriptions and notes, we assigned each population to a broad habitat type following the EUNIS classification (http://eunis.eea.europa.eu/habitats.jsp). Based on information in the above data bases we identified the “minimum” and “maximum” altitude values and the two limits which enclose 90% of altitude values (such that 5% of values fall below the “lower limit” and 5% above the “higher limit”) in the central and peripheral parts of the range of each species. We verified the results by comparing them with published data in *Flora Iberica* (Castroviejo 1986).

Field investigation of fine-scaled niche characteristics

Once a population was located in the field, an empirical investigation of its ecological niche was done at peak flowering in a part of a site where the species is most abundant (following Lavergne *et al.* 2004). Fine-scaled ecological characteristics were studied in three quadrats per population each either 1m^2 or 4m^2 depending on the size of individuals and the pattern of distribution of the species (table 1). Each quadrat was established in a randomly selected high-density patch, each patch at least 5m apart. For each quadrat, we measured the slope and its orientation, and visually estimated the mean height of each vegetation stratum (following Raunkiaer 1934).

A fine-scaled analysis of ecological characteristics was made with point contact data collected for each quadrat. Each quadrat was divided into 100 contact points (10*10cm grid for 1m² quadrats; 20*20cm grid for 4m² quadrats). At each point we recorded contact with one or more of the following elements: bedrock, blocks (>25cm), stones (2.5 – 25 cm), gravel (0.5 – 2.5 cm), bare soil, lichen, moss, herbaceous litter, woody litter and living plants. Each contacted plant species was identified. When several components were touched at a given point, we constrained the value of each contact point to 1, so that the total cover per quadrat could not exceed 100%. For each quadrat we calculated species richness (as the number of species touched during the contact point sampling), the cover of each biological type (Raunkiaer 1934) and the Hill number associated with the Shannon diversity index (Jost 2006) for the whole community (later named total diversity) and per biological type.

Field studies and experimental laboratory analyses were conducted during spring and autumn 2013 and in spring 2014. For each species central and peripheral populations were studied in the same year.

Soil analysis

We collected one soil sample per quadrat. Soils were dried at 40°C for 48h, sieved at 2mm and stored in a cool room prior to analysis. Conductivity (c) and pH (pH) were measured using an *Eutech Cyberscan*. After mixing 10g of dry soil with 20ml of water, we blended the solution during 20min, then separated phases using a centrifuge (10 minutes), and measured values in the supernatant at room temperature (circa 20°C). The total amount of carbon (C) and nitrogen (N) were determined using a *ThermoFinnigan Flash EA 1112 series*, on 70µg samples grinded with a crusher (3 minutes, f=30). Water retention potential (WRP) is the percentage of water lost after drying a wet soil during 48h at 40°. Water retention capacity (WRC) was then calculated as the percentage of water remaining in previously 40°C-dried soil, by drying again the sample at 110°C during 5 hours. Organic matter (OM) was estimated as the percentage of matter lost after burning a dried sample at 500°C during 5 hours. Soil samples from central and peripheral populations of a given species were analyzed at the same time and thus in the same "machine" sequence.

Statistical analyses

A preliminary Principal Component Analysis (PCA) allowed us to delete correlated redundant measures (data not shown). To identify ecological niche differences between central and peripheral populations, we first examined variation between mean population values for central and peripheral populations within each species with a Welsh two-sample t test. We also investigated differences between the two geographic groups of populations in terms of variation among their populations (niche breadth in a given region), and ran Ansari-Bradley tests to analyze levels of variation among paired samples. Both tests were chosen for their robustness to non-normal distribution patterns.

Following this, to provide a comparative analysis, we plotted the mean value (± standard error) of each species for each ecological variable in central and peripheral populations in relation to a bisector that represents a line of equality for central or peripheral populations (following Lavergne *et al.* 2004). Any significant variation can thus be depicted in terms of distance from the bisector. To statistically test this relationship we fitted a general mixed effect model, with the trait value as response variable and species and population as random factor with population nested within species and geographic location (central or peripheral) as a fixed factor. We carried out analysis of deviance based on type-2 Wald Chi-square tests for each analysis.

To compare global niche breadth in central and peripheral populations of each species, we calculated niche volumes for each group of populations using a Principal Component Analysis (PCA) on the whole set of micro-ecological niche variables available. We plotted the first two axes of the PCA for each species, drew two convex hulls including all central and all peripheral populations, and calculated their surface. We repeated this procedure three times on subsets of the total dataset, retaining only variables of soil, abiotic and biotic compartment, to refine overall trends. We plotted each series following the procedure described above. To assess the significance of each trend, we ran single-tailed Wilcoxon sign rank tests for pairwise data with the "greater" option to test whether the niche volume is greater in the center of the range.

To statistically tests cross-taxa differences in the mean altitude between central and peripheral populations, we fitted a linear mixed effect model with position (C or P) as a fixed factor, and species as a random factor. We also plotted the mean and the maximum altitude (which includes 95% of known locations) following the procedure described above.

All statistical analyses were performed using R:3.2.1 (R development Core Team 2010). We did not include any terms to control for spatial autocorrelation that can arise as a result of spatial structure of micro ecological niche variables (Dormann *et al.* 2007). We corrected *p*-values following the Benjamini-Hochberg false discovery rate method (Benjamini & Hochberg 1995). We present *p*-values that fall between 0.05 and the corrected value as weakly or marginally significant (*) and those that are less than the corrected threshold as highly significant (**).

Results

Field and data-base examination of the macro niche

The broad habitat (vegetation) type in which the sampled populations occur was in most species very similar for central and peripheral populations. Only one species, *Ophrys bombyliflora*, occurred in more vegetation types in central than in peripheral populations (Table 2). Nine out of eleven species were found in Mediterranean xeric grasslands on calcareous soils. Among them, annual species occurred primarily in Mediterranean annual communities on shallow soil, or in their degraded form qualified as subnitrophilous and dominated by tall annual grasses (*Avena spp.*). Hemicryptophytes and geophytes tended to occur in xeric grassland often dominated by *Brachypodium retusum*, while the two chamephytes also occur in cracks and fissures on rocky escarpments and cliff faces. Two species occurred in habitats different to the other species, namely *Dorycnopsis gerardi* which was found in land reclamations and post-agricultural fields on a more acid substrate, and *Chiliadenus saxatilis* which was found in calcareous cliffs within chasmophyte communities.

The minimum altitude and the lower limit of altitudinal distribution for 90% of all values of peripheral and central populations were close to sea level (Table 3). However, species were consistently found at higher mean altitude in their central range (analysis of deviation, $\chi^2=711$, $df = 1$, $p < 0.001$), with an altitudinal range amplitude ratio that was from 1.5 to 5 (depending on the species) in comparison with peripheral populations (Table 3, figure 2). This ratio is exceptionally high for *Merendera filifolia* due to its very restricted altitudinal amplitude in France, while being widely distributed from seal level to over 1130 m in the south of Spain.

Table 3-2. The different broad habitat types occupied by the 11 study species in five central (C) and five peripheral (P) populations.
The nomenclature follows the EUNIS referential (http://eunis.eea.europa.eu/habitats.jsp). Species are : (1) Atractylis cancellata, (2) Chiliadenus saxatilis, (3) Convolvulus lanuginosus, (4) Dorycnopsis gerardi, (5) Hyoseris scabra, (6) Merendera filifolia (7) Narcissus dubius (8) Ophrys bombyliflora, (9) Polygala rupestris, (10) Stipa capensis, (11) Viola arborescens.

		Species																					
EUNIS	Habitat	1		2		3		4		5		6		7		8		9		10		11	
		C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P	C	P
A2.5	Coastal saltmarshes and saline reedbeds																1						
E1.2A	Brachypodium phoenicoides swards															1							
E1.31	West Mediterranean xeric grassland											1	1			1							
E1.311	Retuse torgrass swards					1	1					1		1	1	1		1	1			1	1
E1.313	Mediterranean annual communities of shallow soils	1	1							1	1					1	1			1	1		
E1.61	Mediterranean subnitrophilous grass communities									1										1	1		
E5.12	Weed communities of recently abandoned urban and suburban constructions										1												
E5.15	Land reclamation forb fields							1	1														
F5.3	Pseudomaquis																	1	1				
G3.743	Provenço-Ligurian *Pinus halepensis* forests																					1	
H3.21	Tyrrheno-Adriatic eumediterranean calcicolous chasmophyte communities			1	1														1			1	1

Table 3-3. The altitudinal range of the 11 studied species based on population locations in severals databases for each species (see methods).
The “minimum” and “maximum” columns correspond to the lowest and highest altitude values respectively, “lower limit” and “higher limit” are two limits that exclude 5% of data points for altitudinal distribution of each species at low and high altitude respectively. Hence, 90% of the data points occur between these limits.

	Central Populations					Peripheral populations				
	Minimun	Lower limit	Median	Higher limit	Maximum	Minimun	Lower limit	Median	Higher limit	Maximum
Atractylis cancellata	0	40	283	822	2414	12	14	361	558	585
Chiliadenus saxatilis	0	201	822	1315	1879	0	76	313	656	861
Convolvulus lanuginosus	0	87	462	1021	2822	0	1	121	344	493
Dorycnopsis gerardi	0	40	411	988	1356	0	4	111	304	495
Hyoseris scabra	0	10	180	814	1019	0	0	21	301	409
Merendera filifolia	0	3	310	1130	1663	0	2	21	30	32
Narcissus dubius	0	69	397	902	1378	0	19	171	519	788
Ophrys bombyliflora	0	7	321	815	1109	0	2	47	189	291
Polygala rupestris	0	84	585	1127	1959	0	0	54	223	559
Stipa capensis	0	15	382	831	1895	0	2	48	392	553
Viola arborescens	0	0	150	719	923	0	0	45	219	326

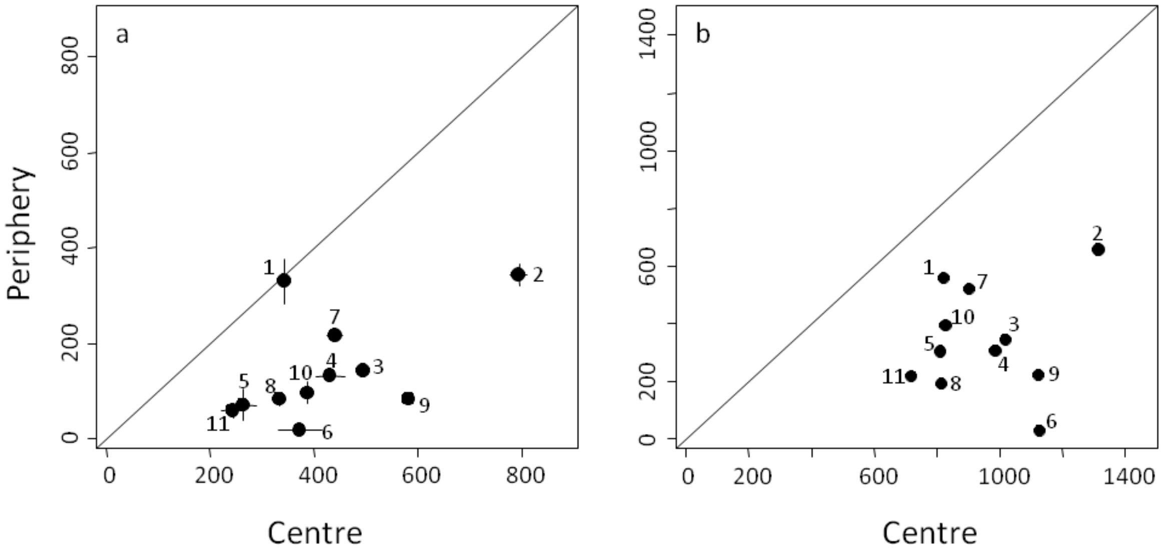


Figure 3-2. Mean (a) and range (b) altitude values (m) of central and peripheral populations of 11 Mediterranean plant species.
The bisector represents equal mean values for central and peripheral populations.

Field investigation of fine-scaled niche characteristics

Preliminary inspection of the data sets obtained for the different species showed that some variables were highly correlated with one another, and that some similar variables all showed very low frequencies in the point contact data set. Prior to analyses we thus removed several measures from the analysis. Nitrogen content, due to its high correlation with conductivity, and organic matter content and water retention potential, due to their high correlation with water retention capacity, were removed from the analysis. Block and bedrock had consistently low values so given their ecological similarity we summed them to have a single ("rock") variable. Likewise, point cover data for lichens and mosses were summed into a single variable for "cryptogam" cover and chamephytes and phanerophytes into a single variable for "woody species" cover. Number of species and the Hill number associated with the Shannon diversity index were strongly correlated, so we deleted the former variable due to its sensibility to rare species presence (Jost 2006).

Differences in mean ecological characteristics

The comparison of central and peripheral populations for each species showed significant differences for between five and ten of the 20 ecological parameters studied (table 4). On average, eight variables differed significantly per species (representing 40% of the variables investigated, see Table 4). Seven ecological characteristics showed very little variation, with no more than two species showing significant differences. These are mostly biotic characteristics (notably the cover of biological growth forms and diversity of woody plants and geophytes). On average, soil characteristics and abiotic cover variables (other than bare soil) showed the most significant differences among central and peripheral populations (from five to eight species). All species showed at least one significant difference for both the three soil characteristics and the five cover variables (Table 4). For biotic niche components, the total diversity of associated species and therophyte diversity showed significant differences for several species (seven and six respectively), as did total biotic cover and therophyte cover but to a lesser extent (four species). Despite the large number (5-10 traits) of observed significant differences for each species (Table 5) only comparisons of *Convolvulus lanuginosus* with *Hyoseris scabra, Merendera filifolia and Viola arborescens* showed five or six common differences respectively. The majority of common differences for all other species comparisons was less than five.

Table 3-4. Comparative analysis of trait difference between central (C) and peripheral (P) populations in eleven Mediterranean plant species.
Welch two sample t-tests are used for pairwise comparisons, and analysis of deviance based on χ^2 analyses is used for cross taxa analyses. The number of species (NSD) and traits (NTD) that show a significant difference are given in column and row sums respectively. The letter code with significance values refers to a higher value in either central or peripheral populations. Species are : (1) *Atractylis cancellata, (2) Chiliadenus saxatilis, (3) Convolvulus lanuginosus, (4) Dorycnopsis gerardi, (5) Hyoseris scabra, (6) Merendera filifolia (7) Narcissus dubius (8) Ophrys bombyliflora, (9) Polygala rupestris, (10) Stipa capensis, (11) Viola arborescens.*

Niche characteristic	Species											NSD	χ^2 analyses
	1	2	3	4	5	6	7	8	9	10	11		
S1.Water retention capacity	P**	P**	C**				P*				C*	5	0,19
S2. Conductivity			C**	C*	C*	P**	P**	C**	C*		C*	8	6,07*
S3. pH	C**			P**		P**	C**	C*		C**	P**	7	4,50*
A4. Rock	P**	P**	C*		C**				C**		C**	6	4,33*
A5. Stone			P**			P*		P*	P**		P*	5	11,91**
A7. Gravel		C**	P**	P*		C*	P**	P*				6	0,22
A8. Bare soil	C**								C*			2	2,22
A9. Litter	C**	C*	C*		P*	C*				P**	P*	7	0,01
A10. Slope		P**	C**		C**	C**	P**		C**		C*	7	1,94
B11. Total biotic cover		C*			P**			C**		C**		4	0,03
B12. Therophyte cover			P*		P**		P**			C**		4	0,65
B13. Hemicryptophyte cover	P**											1	0,00
B14. Geophyte cover	C*										P**	2	0,51
B15. Woody vegetation cover						P*						1	0,11
B19. Cryptogams cover							C*					1	0,69
B16. Total diversity	P**	C*		P**	P**		P**	C*		P**		7	3,98*
B17. Diversity of therophytes	P*		P*		P**	P*	P**			P**		6	22,30**
B18. Diversity of hemicryptophytes	P*		C**	P**		C*					C*	5	0,01
B19. Diversity of geophytes					C**			C**				2	6,41*
B20. Diversity of woody plants										P*		1	0,01
NTD	10	7	10	5	9	9	9	7	5	7	9		

* : 0.05 > *p* > corrected significance level, ** : *p* < Corrected significance level.

Although for most niche components there was no common pattern of higher values in either central or peripheral populations, seven ecological characteristics showed significant cross-taxa deviation from equal values in central and peripheral populations (Table 4). Visual inspection of the differences for abiotic and biotic niche components revealed that some of these traits showed a consistent pattern of differences between central and peripheral populations (Figure 3). For soil characteristics, there was a marked overall trend for species to occur on soils with low conductivity (Figure 3a) and a more basic pH (Figure 3b) in peripheral populations. For abiotic niche elements, there was a cross taxa trend of occurrence on less rocky but more stony habitats in peripheral populations (Figure 3c and 3d). Two species (*Atractylis cancellata* and *Chiliadenus saxatilis*) however showed a significant increase in rock cover in peripheral populations (table 4). Slope did not show a general trend across species, despite the fact that seven species show differences between central and peripheral populations (Table 4).

For biotic niche components, total biotic cover was highly conserved between central and peripheral populations (Table 4 & Figure 3f). Three groups of species showed broadly similar values in their central and peripheral populations: *Chiliadenus saxatilis* was the only species that colonizes habitats with very low vegetation cover (below 25%), a group of six species occured in habitats with vegetation cover between 35 to 50%, and a group of three species occupied dense vegetation with cover values that ranged from 65 to 80%. The cover of each growth form remained very similar between central and peripheral populations, and no global trend was observed across taxa (Table 4). Total species diversity, as quantified by the Hill number associated with Shannon's diversity index, showed a weakly significant cross taxa trend towards more diverse communities in peripheral populations (Figure 3e). This trend was significant for five species (Table 4), with the notable exception of *Ophrys bombyliflora* and *Chiliadenus saxatilis* which showed a weakly significant trend toward higher values in central populations. For the different biological growth forms this trend is highly significant for the diversity of therophytes (in six of the eleven species: Figure 2g). Diversity of geophytes showed a weak cross taxa trend toward higher diversity in central populations, mainly driven by two of the three target geophytes and *Hyoseris scabra* (Figure 2h). Finally, woody species diversity was similar for all species except *Stipa capensis*, while hemicryptophytes diversity differed for five species in opposite directions, resulting in no global trend.

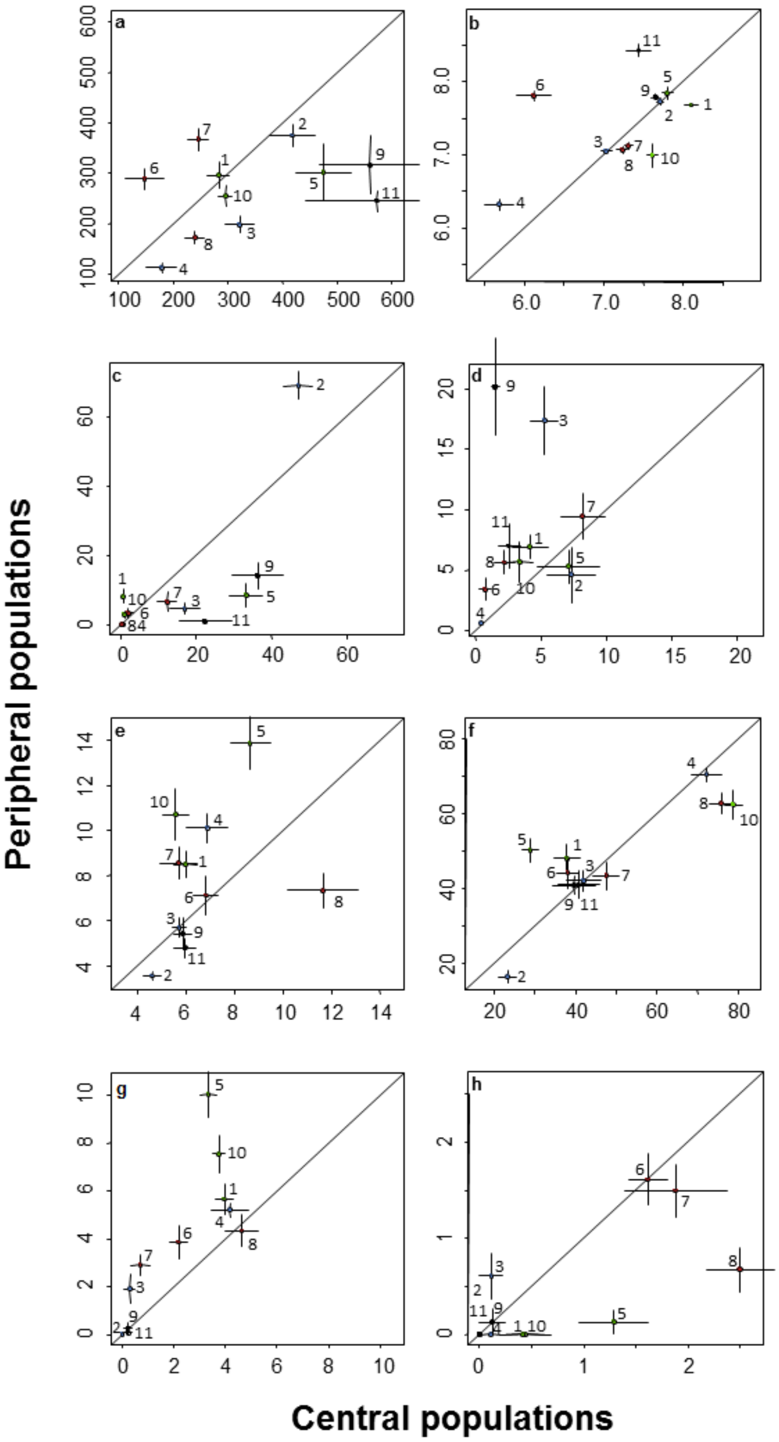


Figure 3-3. Soil characteristics, abiotic and biotic cover variables that show overall significant differences (Table 4) among central and peripheral populations of 11 Mediterranean plant species.

The bisector represents equal mean values for central and peripheral populations. Traits are (a) conductivity, (b) pH, (c) rock cover, (d) stone cover, (e) total diversity, (f) total biotic cover, (g) therophyte diversity, (h) geophyte diversity. Species number codes are shown in table 1.

Differences in niche breadth

When comparing levels of trait variability in central and in peripheral populations, we detected only weakly significant differences in 43 of the 220 tests (Table 5). The majority (N = 32) of these comparisons showed significantly greater variation among populations in the central part of their range than among peripheral populations. The maximum number of species with a significantly different niche breadth for a given trait was only four species, hence cross-taxa comparisons showed no significant overall trend for particular variables except for the cover of stones, slope and woody vegetation, that showed a weakly significant trend toward greater variability among central populations. Notwithstanding, six species showed several traits with mostly higher levels of variation among central populations, three species had a small number of trait differences and mostly higher variability among peripheral populations and two species showed little (one trait) or no differences for central and peripheral populations (Table 5). This resulted in a weakly significant overall trend towards smaller niche volume for peripheral populations (Figure 4a), despite the fact that the three therophyte species we studied showed the opposite trend (Wilcoxon test, V=55, p=0.0269, p-corrected=0.0537). When this global niche volume is segregated into different components, the edaphic niche (*e.g.* soil characteristics, figure 4b) showed a cross taxa trend towards a significantly wider niche in the central part of the distribution (Wilcoxon test, v=57, p=0.016, p-corrected=0.054), while biotic (figure 4c) and abiotic (figure 4d) niche components showed no such trend (Wilcoxon test, v = 51, p > 0.05 and Wilcoxon test, v = 46, p > 0.1, respectively).

Table 3-5. Comparative analysis of niche variability between central (C) and peripheral (P) populations in eleven Mediterranean plant species.
Ansari-Bradley tests are used for pairwise comparisons, and single tail Wilcoxon test are used to assess for a greater niche volume for central population. The number of species (NSD) and traits (NTD) that show a significant difference are given in column and row sums respectively. The letter code with significance values refers to a higher value in either central or peripheral populations. Species are : (1) *Atractylis cancellata, (2) Chiliadenus saxatilis, (3) Convolvulus lanuginosus, (4) Dorycnopsis gerardi, (5) Hyoseris scabra, (6) Merendera filifolia (7) Narcissus dubius (8) Ophrys bombyliflora, (9) Polygala rupestris, (10) Stipa capensis, (11) Viola arborescens.*

Niche characteristics	Species											NSD	*Wilcoxon test*	*Wilcoxon test*
	1	2	3	4	5	6	7	8	9	10	11		V	V
S1.Water retention capacity						C*		C*	C*		P*	4	55	Soil niche volume 57*
S2. Conductivity						C*					P*	2	43	
S3. pH				C*								1	50	
A4. Rock						C*		P*				2	21	Abiotic niche volume 46
A5. Stone											C*	1	56*	
A7. Gravel	C*				P*							2	52	
A8. Bare soil		C*			P*							2	17	
A9. Liter											C*	1	32	
A10. Slope								P*				1	9*	
B11. Total biotic cover			C						C*			2	43	Biotic niche volume 51
B12. Therophyte cover	P*	P*	C									3	26	
B13. Hemicryptophyte cover									C*		P*	2	38	
B14. Geophyte cover		C*							C*		C*	3	24	
B15. Woody vegetation cover						C*						1	57*	
B19. Cryptogams cover	C*			C*							C*	3	31	
B16. Total diversity		C*		C*		P*						3	37	
B17. Diversity of therophytes		C*	C*						C*		P*	4	28	
B18. Diversity of hemicryptophytes		C*										1	36	
B19. Diversity of geophytes		C*	C*	C*							C*	4	6	
B20. Diversity of woody plants										C*		1	41	
NTD	3	7	4	4	2	5	0	3	5	1	9			55*

Note. For Ansari Bradley test, significantly higher variation among central (C) or peripheral (P) populations are shown by their letter and either * : 0.05 > *p* > corrected significance level, ** : p < Corrected sign. level.

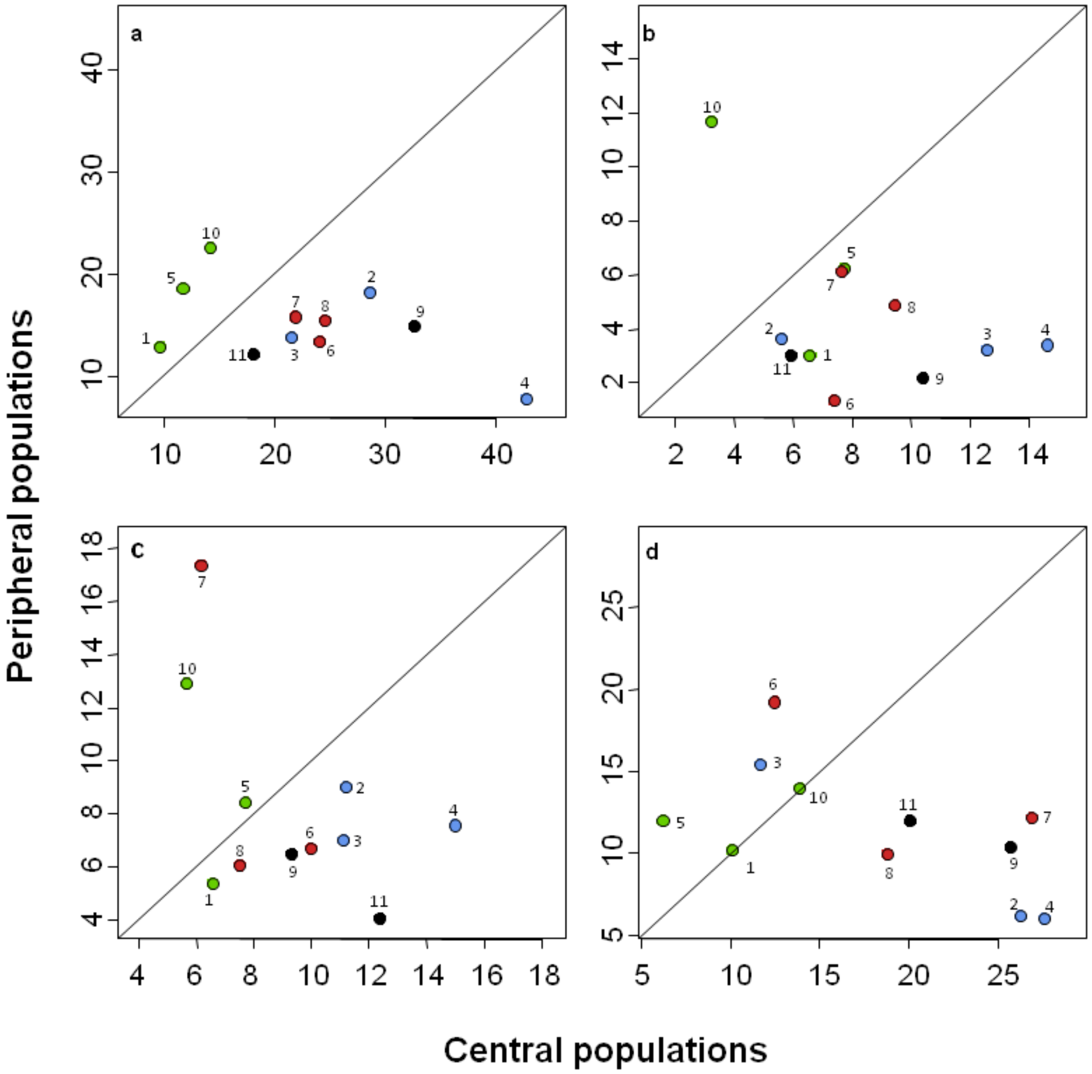


Figure 3-4. Comparison of levels of variation in niche components among central and among peripheral populations of 11 Mediterranean plant species.
The bisector represents equal mean values for central and peripheral populations; (a) Overall niche volume including biotic, abiotic and soil variables, (b) niche volume for soil characteristics, (c) niche volume for biotic characteristics, (d) niche volume for abiotic traits. Species number codes are shown in Table 1.

Discussion

In a novel comparative study of 11 plant species we provide evidence of marked ecological differences among central and peripheral populations and a trend towards a narrower niche breadth in peripheral populations. Whereas the species tend to occur in one main broad habitat type and across a single Mediterranean type climatic region, they show marked differences between central and peripheral populations in their fine-scaled ecological niche. The differences tend to be species-specific, illustrating the pertinence of a multi-species study. The ecological originality of peripheral populations and the fine-scaled nature of this variation have numerous implications for understanding the causes of distribution patterns and species diversification at range limits and the conservation significance of peripheral populations.

Ecological originality of peripheral populations

The broad habitat (vegetation) type in which species occur is remarkably similar in central and peripheral populations of all but one species (*Ophrys bombyliflora*) in our study. Indeed the cover of different biological forms is very similar in central and peripheral populations, especially the cover of hemicryptophytes (the main part of the vegetation cover) in communities where the perennial target species occur. In general our results illustrate that the type of vegetation in which species establish a population is relatively similar across their range and that broad habitat types are highly conserved. The main climatic regime is also the same across their range, i.e. a Mediterranean-type climate with a summer drought. The only difference between central and peripheral populations here is the occurrence of shorter summer-drought period and slightly cooler mean average temperatures in peripheral populations in southern France (e.g. Papuga *et al.* 2015).

In direct contrast, significant variation in the micro-ecological niche exists for several ecological characteristics in all the species studied, and all traits exhibit differences for at least one species. While some trends are shared, many changes are species-specific. Three groups of species which exhibit comparable niche shifts can be distinguished. The first group is composed of seven semi-open, rocky, grassland species: *Atractylis cancellata, Convolvulus* *lanuginosus, Hyoseris scabra, Merendera filifolia, Narcissus dubius, Polygala rupestris, Viola arborescens*. Despite differences among these species in particular ecological features of their niche, they all grow in habitats with a vegetation cover ranging from 35 to 50% and illustrate a shift from steep rocky habitat in central populations to more stony semi-open grassland with lower soil conductivity in peripheral populations. This shift is especially visible in the perennial species (*Convolvulus lanuginosus*, *Polygala rupestris, Viola arborescens*). The second group of species is composed of three species, *Dorycnopsis gerardi, Ophrys bombyliflora* and *Stipa capensis* that grow in a high cover of vegetation on soils with a lower mineral content in peripheral populations. However, no general trend in niche shift is observed in this group with *Stipa capensis* in annual grasslands, *Dorycnopsis gerardi* in dense fallow land with bushes and hemicryptophytes, and *Ophrys bombyliflora* in Mediterranean meadows with dense perennial grasses. Finally, in a group on its own, *Chiliadenus saxatilis*, the only « cliff plant » in our study, exhibits a different niche shift in northern peripheral populations, where it grows on steeper cliffs, with less vegetation, higher rock cover, and in soils with a higher water retention capacity. This species thus has the opposite trend to species in group 1.

We also detected a significant cross-taxa trend towards the occurrence of the studied species in more diverse communities (in particular the diversity of annual plants) in the peripheral part of their range. It is worth noting here that this trend is also observed in terms of the total species richness per quadrat assessed with the contact point method, and in terms of rare species richness (i.e. those present in the quadrat inventory but not detected in point quadrat analyses, G Papuga, unpublished data). It is possible that local climatic conditions, and the fact that peripheral populations occur in a less xeric Mediterranean-type climate than do most of the central populations (e.g. Papuga *et al.* 2015) may contribute to this higher community diversity in peripheral populations.

Despite overall broad habitat similarity, the study species show clear ecological originality in peripheral populations in terms of their precise ecological niche. These results clearly illustrate the importance of making explicit descriptions of the fine-scale habitat characteristics where plants grow, instead of simply identifying climatic conditions and broad vegetation types (see also Hall *et al.* 1997; Seddon, Armstrong & Maloney 2007). Similar results have been found elsewhere in terms of habitat differentiation between closely related species (Ojeda, Arroyo & Marañón 2000; Cavender-Bares & Pahlich 2009; Martinell *et al.* 2010) and ploidy levels (Rothera & Davy 1986; Lumaret *et al.* 1987; Johnson, Husband & Burton 2003). To better understand the role of the ecological niche in plant species distribution patterns thus clearly requires a fine-scaled appreciation of ecological variation that affects species presence.

Finally, we detected a trend towards a reduction of niche breadth in the periphery of the range of the 11 studied species. However, this reduction is not homogenous across species and traits. For the broad habitat niche, there was a clear trend for reduced variability in the altitudinal amplitude of species in the peripheral part of their range. For the micro-ecological niche, soil parameters showed the most notable change in variability, with a clear shift towards soils with lower and less variable conductivity in peripheral populations. It is difficult to conclude on the causes of this trend towards reduced niche variability in peripheral populations, as it may result from very different ecological processes. First, it may reflect ecological specialization of the organism in relation to stabilizing selective pressures in peripheral populations (Devictor *et al.* 2010). Second, it may reflect a lack of local availability of different niche conditions in the peripheral part of the species' ranges (Eriksson & Ehrlén 1992), especially regarding the regeneration niche that might influence recruitment (Grubb 1977). Third, in the peripheral part of their range species may not yet have colonized available sites where their habitat occurs, due to a limitation in their dispersal abilities (Eriksson & Ehrlén 1992; Baack, Emery & Stanton 2006). This has been shown to be the case in micro-endemic species in the Mediterranean flora for which dispersal limitation and past isolation events explain distribution patterns (Youssef *et al.* 2011). Yet in some species, micro-climatic conditions can also prevent dispersal at range margins due to reduced seed set (Hennenberg & Bruelheide 2003). Those mechanisms can limit dispersal despite the availability of suitable habitat, and could, in relation to local climatic constraints, contribute to the reduced altitudinal range of species in the peripheral part of their range.

Ecological differentiation and species divergence

The patterns of ecological differentiation between central and peripheral populations detected here for 11 Mediterranean plant species are of particular interest in terms of the divergence and speciation of Mediterranean endemic plants. For the Califonia Floristic Province, Anacker & Strauss (2014) provide evidence that species divergence may often be associated with a large ranged progenitor that gives rise to a restricted endemic derivative species. Such 'budding' speciation is enhanced by the occurrence of the progenitor in peripherally isolated populations and in ecological different conditions (Grossenbacher, Veloz & Sexton 2014). A consequence is a marked range asymmetry between progenitor and derivative species (Crawford 2010). Similar range asymmetry and probable cases of progenitor-derivative species that illustrate budding speciation are frequently observed in the Mediterranean flora where many narrow range endemic species have allopatric sister species that are more widespread (Favarger & Contadriopoulos 1961; Contandriopoulos & Cardona 1984; Debussche & Thompson 2002; Quézel & Médail 2003; Lavergne *et al.* 2004; Martinell *et al.* 2010; Hardion *et al.* 2014). In addition many endemic plant species in the Mediterranean flora show ecological differentiation from their proposed progenitor taxa (Lumaret *et al.* 1987; Petit & Thompson 1998; Debussche & Thompson 2003; Lavergne *et al.* 2004; Martinell *et al.* 2010), and several other studies have reported evidence of ecological specialization of endemic Mediterranean or Mediterranean-mountain species in relation to substrate type (Casazza, Barberis & Minuto 2005; Casazza *et al.* 2008).

The peripheral populations of ten of the 11 plant species in our study occur in a markedly isolated part of the range with major geographical (distance and geology) and ecological barriers that reinforce spatial isolation from the main part of the range. Seven of the eleven studied species have their northern peripheral populations exclusively located in a very small number (<3) of highly localized zones that have been evoked as potential refugia for Mediterranean taxa during the Last Glacial Maximum (near Narbonne, to the east and north of Marseille and in the southern tip of the Maritime Alps, see chapter IV). These zones host many endemic species, studies which illustrate a genetic footprint (population differentiation) in relation to range contraction and persistence in micro-refugia at the southern limits of last glacier expansion (Diadema *et al.* 2005; Minuto *et al.* 2006; Szövényi *et al.* 2009).

Our study thus provides support for the idea (Fréville *et al.* 1998; Thompson 1999; Crawford 2010) that widespread species with disjunct distributions and peripheral isolates such as our study species may be prone to diversification. As Crawford (2010) argued, already differentiated sister species offer limited promise for exploring the processes that produced them. In contrast, the examples of recent population divergence cited above and our 11 species with peripheral populations that show ecological differentiation represent particularly favorable examples for the study of the initial processes and thus of particular interest for exploration of the initial processes that drive plant species divergence via the budding model of speciation.

Conservation value of peripheral populations

The conservation value of peripheral populations remains controversial (Hunter & Hutchinson 1994). Using resources to protect widespread species in regions where they are rare may represent an inefficient use of resources if focus is lost for rare and vulnerable species, unless peripheral populations show some form of genetic (geographic) and ecological distinctiveness or have some form of cultural value (Lesica & Allendorf 1995; Leppig & White 2006). Peripheral populations may be of particular interest here due to an evolutionary potential related to the occurrence of unique gene combinations that results from isolation (Petit *et al.* 1998) and sometimes hybridization with closely related species (Thompson *et al.* 2010). However, the lack of knowledge regarding the ecology of plant species at their range periphery compared to elsewhere in their distribution strongly has limited our understanding of the evolutionary significance of peripheral populations (Woodward 1987; Crawford 2010).

Common elsewhere under different and more variable ecological conditions, 10 of the 11 study species, and many others with similar peripheral distributions, are rare in Mediterranean France. The ecological originality of these populations and their geographical isolation from the main area of their distribution argues for their conservation significance (following Lesica & Allendorf 1995; Leppig & White 2006). Indeed, an integral part of the evolutionary potential of species is their existence in variable environments, which exposes them to divergent selection (Givnish 2010). Our study illustrates that peripheral populations may have this ecological significance and thus be of significant conservation interest, particularly in view of the need to conserve populations that may contribute to species' adaptation to ongoing climate change. Due to their range limit position at the northern periphery of species in the Mediterranean climate region, our study species are of particular interest here. However they occur close to the Mediterranean coast and as a consequence of the rapidly growing human population (both permanent and seasonal) they occur in highly vulnerable habitats (Vimal, Mathevet & Thompson 2012, Gauthier et al. unpublished).

Our results also have direct application in conservation management programmes for vulnerable species at their range limits. Poor identification of the suitable habitat has been listed as a major cause of the failure of many endangered plant species reintroduction programmes (Godefroid *et al.* 2010). When peripheral populations of such species occur in distinct ecological conditions our results illustrate the importance of precisely describing the species' micro-niche in any project aimed at the reinforcement or reintroduction of species impacted by human development (see also Gómez-Aparicio *et al.* 2004).

CHAPTER 4: Climatic niche and distribution patterns of peripheral isolates in Mediterranean plants

To be cited as:

Papuga, G., Farris, E. & Thompson, J.D. (in prep) Climatic niche and distribution patterns of peripheral isolates in Mediterranean plants.

Introduction

The study of species distributions has a long tradition in ecology and biogeography (Gaston 2009a). In the last few decades, understanding range limits has become a crucial issue to anticipate the impact of global changes on wildlife, especially in range shifts in relation to biological invasions (Mack *et al.* 2000; Peterson 2003) and climate change (Thuiller *et al.* 2005; Parmesan 2006). Yet, this question still generates debates (Geber 2008), and understanding remains poor despite many empirical studies (see Hargreaves, Samis & Eckert 2014) and important theoretical background (Sexton *et al.* 2009). In this respect it remains necessary to disentangle the effects of the ecological niche, biotic interactions and organism characteristics (such as dispersal) on range limits (Hargreaves *et al.* 2014; Louthan *et al.* 2015). In addition, evolutionary processes that limit adaptation and imped species to spread further their range edge need to be clearly identified (Kirkpatrick & Barton 1997; Bridle & Vines 2007).

Climate is central to the understanding of spatial boundaries, and a fundamental driver of species occurrence (Gaston 2003; Holt 2003; Thuiller *et al.* 2004; Geber & Eckhart 2005). Indeed a decrease in climatic suitability toward the periphery of species distribution has received some support from the literature (Hennenberg & Bruelheide 2003; Boucher-Lalonde *et al.* 2012; Hargreaves *et al.* 2014). In a recent review, Pironon, Papuga *et al.* (in prep), showed that 80% of studies that tested for a decrease in species occurrence toward their periphery confirm this trend. However, these authors did not find any general trend regarding a decrease in abundance of individuals or demographic traits from range centre toward periphery, which pinpoints the lack of general mechanisms involved in the setting climatic distribution limits.

The correspondence between a species' fundamental climatic niche and its actual distribution is not however straightforward, as pointed out by a recent meta-analysis on plant transplant studies (Hargreaves *et al.* 2014). These authors showed that range limits often do not match the climatic niche limit, probably because of limits imposed by dispersal capacity. Roughly 26% of the species considered had their range limit that fell short of their climatic niche limit. In contrast, other species can occupy habitat beyond a species climatic range in what are population sinks maintained by immigration beyond the fundamental niche (Pulliam 2000). In addition, other ecological mechanisms can limit species distribution (Holt & Keitt 2004), *e.g.* micro-ecological characteristics (Woodward 1987; Kephart & Paladino 1997) and the availability of habitat in the landscape (Eriksson & Ehrlén 1992). Climate estimations based on large scale datasets may also be misleading (Hennenberg & Bruelheide 2003; Canu *et al.* 2015), due lack of precision regarding micro-climatic phenomena (Patsiou *et al.* 2014; Maclean *et al.* 2015). For example, evapotranspiration is as a key mechanism in plant physiology (Onoda & Anten 2011; Dilts *et al.* 2015), but it cannot be assessed by climatic data usually used in species distribution models (Fisher, Whittaker & Malhi 2011). Finally, current distribution may also be a legacy of historical range contraction and expansion during Pleistocene glaciations (Schönswetter *et al.* 2005; Casazza *et al.* 2008; Jadwiszczak *et al.* 2011).

Many widespread and common western-Mediterranean plant species reach their northern limit in continental France (Jahandiez 1937; Medail *et al.* 2002) with a distribution pattern that varies from continuously distributed (Papuga *et al.* 2015) to high isolation beyond the main range area (Medail *et al.* 2002; Lhotte, Affre & Saatkamp 2014, Papuga *et al.* chap. III). These peripheral isolates - rare in France and disconnected from their main range -

constitute a major conservation issue (Olivier *et al.* 1995). In a recent study, Papuga *et al*. (chap. III) have demonstrated multiple shifts in the micro ecological component of the ecological niche – despite marked similarity of the broad habitat types - for eleven such species.

Here we investigate the extent to which the climatic niche shapes the distribution of these eleven species. To do so, we analyzed three specific questions. First, is the climatic niche different at the northern periphery compared to the central part of the distribution? Second, are northern peripheral populations climatically marginal, with respect to the global climatic niche of each species? Third, which species share a similar localized position of their peripheral isolates in areas that correspond to potential refugia during the Last Glacial Maximum?

Material and methods

Data collection

In order to constitute a set of reliable data to sample climatic data, we collected precise distribution of the eleven Mediterranean plants selected for this study (table 1) from several databases. The 11 species are *Atractylis cancellata, Chiliadenus saxatilis, Convolvulus lanuginosus, Dorycnopsis gerardi, Hyoseris scabra, Merendera filifolia, Narcissus dubius, Ophrys bombyliflora, Polygala rupestris, Stipa capensis, Viola* arborescens. For France, we used the Silene database of the Conservatoire Botanique National Mediterranéen de Porquerolles (http://silene.eu). For the rest of the Mediterranean basin, we gathered information from Anthos (www.anthos.es), Valencian community database (http://bdb.cma.gva.es/) and GBIF database (http://www.gbif.org/). We completed those data with personal data (see acknowledgements). Only data with a resolution inferior of 1km² were retained. We restrained our dataset to the western part of the Mediterranean basin in Italy, France, Spain and Mediterranean islands (Corsica, Sardinia, Sicily, and the Baleraric Islands), as they were the only places where we managed to get accurate data.

For each population in our database, we extracted 19 Bioclim variables using Worldclim (www.worldclim.org) at a resolution of 30 seconds, and added the altitude extracted from a Gis layer downloaded from the Diva-gis website (http://www.diva-gis.org/Data). We checked the dataset and eliminated duplicates for each species.

Climate comparison between central and peripheral populations

In order to depict changes in each climatic variable for central (C) and peripheral (P) populations of each species, we fitted one liner model per ecological factor, with the ecological factor as response variable, and position (C or P) as a fixed factor. For each species we plotted the mean value of each Bioclim variable in the northern periphery (France) against the mean value for central part of the range and ran a linear mixed effect model with climate variable as response variable, position as explanatory factor, and species as a random factor.

To provide a global vision of potential climatic niche differentiation in peripheral populations, we used a simplified version of the "PCA-environment" (*e.g.* Principal Component Analysis) procedure (Broennimann *et al.* 2012) to compare climatic niche volumes in French peripheral populations with central populations located in Italy, Spain or Mediterranean islands. We assumed that all populations in the database occurred in a Mediterranean climate with small numbers in the temperate oceanic submediterranean climate (nomenclature following Rivas-Martínez 1996). Thus, we defined our study area as the emerged land in the western Mediterranean basin (France, Spain, Italy and the Mediterranean islands) characterized by those climates using maps published by Rivas-Martínez (1996) and Rivas-Martínez, Sáenz & Penas (2011) available online (http://www.globalbioclimatics.org/form/bi_med.htm). Then, we extracted all climatic information contained in each cell of the study area, merged this dataset with climatic information for each population and ran a first PCA to select relevant ecological variables that limit correlation between them. Next we ran a second PCA with selected variables, retained the first two principal components and drew convex hulls to represent the global climatic envelope occupied by peripheral and central populations.

Distribution patterns

Papuga *et al*. (in prep) showed that 8 out of the 11 species occurred in the same broad habitat type (Mediterranean calcareous xeric grasslands) in both central and peripheral populations. We thus made a spatial analysis to identify if these eight species share similar distributions. To do so, we accessed to the Silene Database and extracted information on the presence/absence of 4676 taxa referenced in the French flora and present in southern France across 10*10km grid (https://inpn.mnhn.fr/telechargement/cartes-et-information-geographique/ref). We listed all cells containing recent data (>1990) for at least one of the eight species. We only considered recent data to limit erroneous localization. We created a list of species for which half of their distribution (evaluated as the number of cells containing at least one record) was included in cells with one of the eight target species. From this total list of species we deleted introduced species, and subspecies in sympatry with other subspecies, as they do not provide accurate information on global distribution across their range. We made maps for the number of species per cell for the eight target species as for the complete list. Finally, we gathered information on species biology, ecology and global distribution (figure 4), and discuss those parameters for each group of species presented.

Persistence of the Mediterranean climate at the LGM

In order to assess the potential persistence of a Mediterranean climate in southern France during the Last Glacial Maximum, we randomly chose 4000 geographical points in southern France, that were included in two climate layers encompassing the limit of the Mediterranean climate (Rivas-Martínez 1996), *i.e.* the Mediterranean pluviseasonal oceanic belt, and the Temperate oceanic submediterranean climate. The points, on either side of the limits were classified as “Mediterranean” (1) or non-Mediterranean (0) respectively. Then, we fitted a General Linear Model for binomial distribution with Mediterranean climate (1 or 0) as binomial response variable and the six Bioclim variables in the PCA as fixed factors. Then, in order to predict climate suitability, we applied the model for both current climatic prediction and two Last Glacial Maximum scenarii.

Results

Climatic niche

From the results of an initial first PCA which included 19 Bioclim variables and altitude, we retained six variables that made the most important contribution to the PCA (Table 1): mean annual temperature (bio_1), temperature seasonality (bio_4), maximum temperature of the warmest month (bio_5), minimum temperature of the coldest month (bio_6), annual precipitation (bio_12) and precipitation of the driest month (bio_14). These six variables represent the major elements that characterize a Mediterranean-type climate.

There was a cross taxa trend for peripheral populations to occur under climate with a lower mean annual temperature, which is significantly shared by 8 species out of 11 (figure 1, table 2-3). Similarly, a significant cross taxa trend toward lower maximum temperature of the warmest month and lower minimum temperature of the coldest month was found for peripheral populations. Nearly all species shared those trends, excepted *Chiliadenus saxatilis* that follow the exact opposite trend. Temperature seasonality exhibited no cross taxa trend, as species varied in different ways. A significant cross taxa trend was detected toward greater precipitation for peripheral populations, both in *mean* values (*i.e.* annual precipitation) and *extremum* values (*i.e.* precipitation of the driest month) (figure 1, table 2-3). Again *Chiliadenus saxatilis* followed the exact opposite trend.

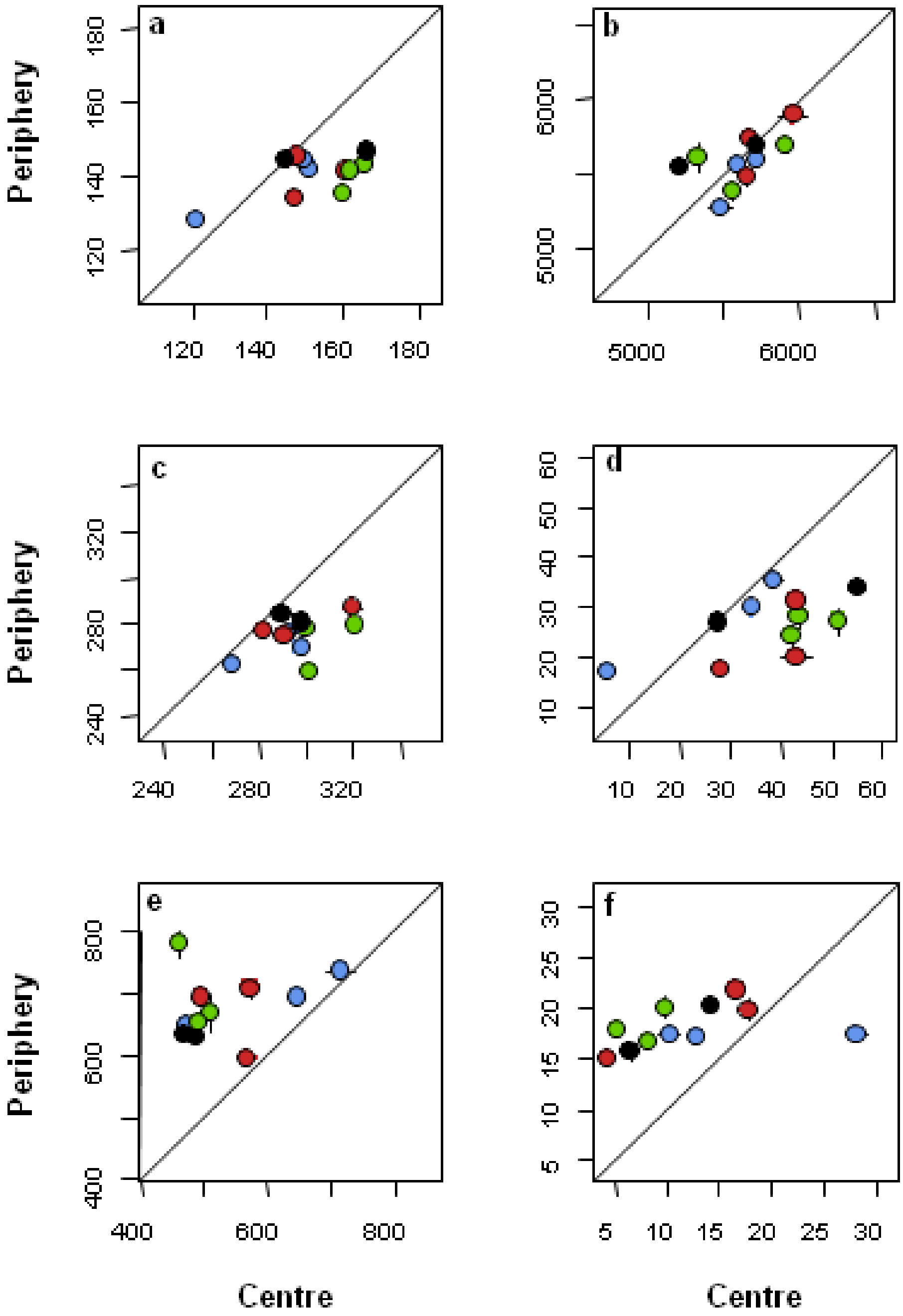


Figure 4-1. Altitude and *Bioclim* climatic characteristics for all central (X axis) and peripheral (Y axis) populations of 11 Mediterranean plants included in our database.
The bisector represents equal mean values for central and peripheral populations.Graphic (a) is for mean annual temperature, (b) is for temperature seasonality, (c) is for maximum temperature of the warmest month, (d) is for minimum temperature of the coldest month, (e) is for annual precipitation and (f) is for precipitation of the driest month.

Then, the two first axis of the PCA representing climatic niche synthesized 82% of cumulated inertia (table 1; figure 2). The Axis 1 of the PCA (x axis) represented an aridity gradient, and was driven by mean annual temperature, maximum temperature of the warmest month, and precipitation of the driest month. Axis 2 (y axis) was driven by temperature seasonality and in a lesser extent by the minimum temperature of the coldest month and annual precipitation (table 1, figure 2l).

When comparing the relative position of climatic niches for each species, we found that the climatic niche space of peripheral populations was almost entirely included in the climatic niche space of central populataions (figure 2). Only three species (*Hyoseris scabra, Narcissus dubius* and *Viola arborescens*) had a very small proportion of the central climatic niche space of peripheral populations outside of that for central populations. For most but these three species, the climatic niche of peripheral populations did not approach the limits of the climatic niche of central populations, hence, for these major climatic factors, peripheral populations are not climatically marginal.

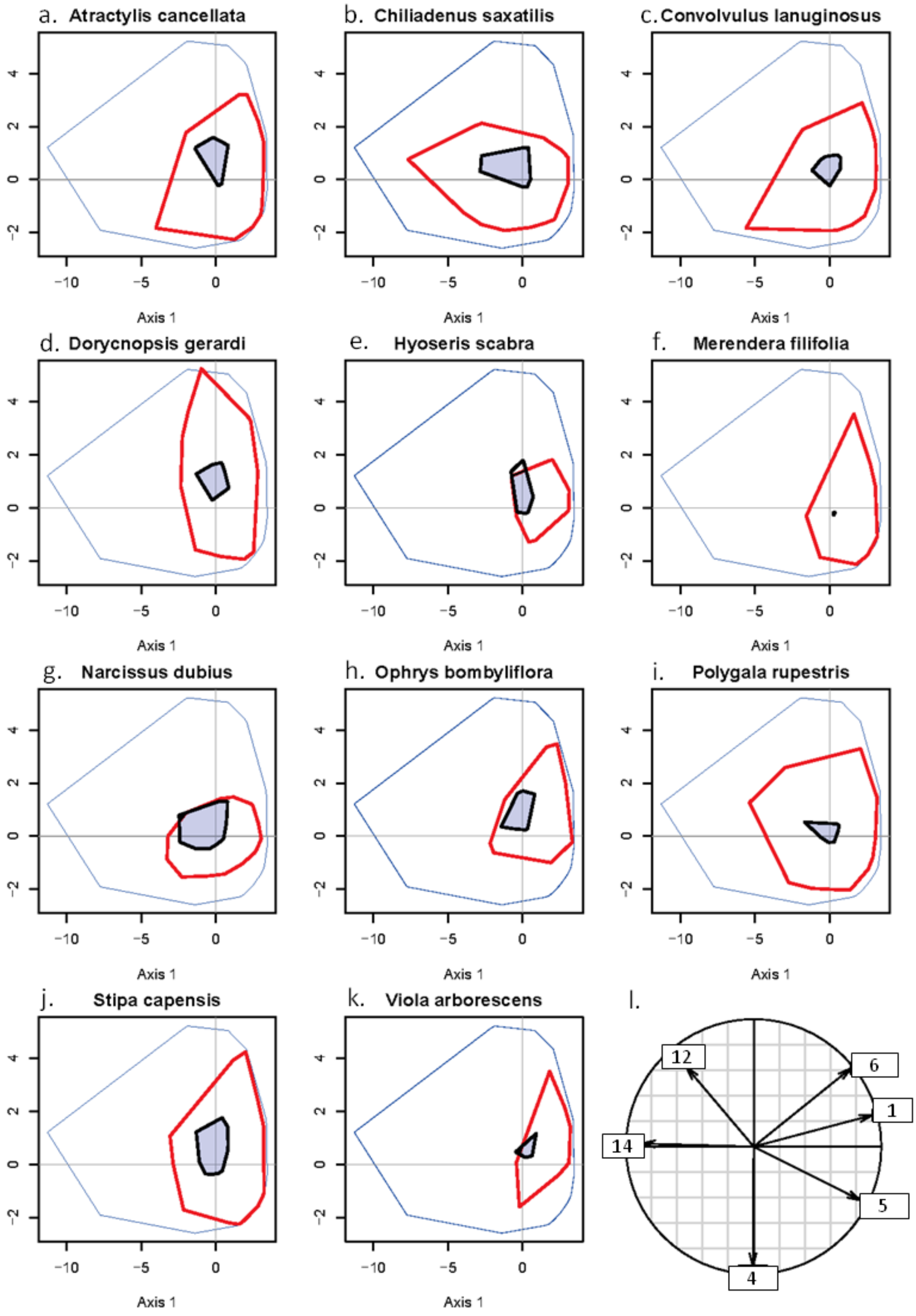


Figure 4-2. Climatic niche of 11 Mediterranean plants on the first two axes of a Principal Component Analysis of the Mediterranean climate in the Western Mediterranean basin.

The blue line represents the climatic limits of the western Mediterranean basin. The red polygon represents the climatic niche of central populations. The black polygon represents the climatic niche of peripheral populations. Blue are symbolize the intersection between the two polygons. Caption (l) represents the correlation circle of the six BIOCLIM variables: BIO1 - mean annual temperature, BIO4 - temperature seasonality, BIO5 - maximum temperature of the warmest month, BIO6 - minimum temperature of the coldest month, BIO12 - mean annual precipitation, BIO14 – mean precipitation of the driest month.

Table 4-1. Results of the Principal Component Analysis.
Variables are BIO1 - mean annual temperature, BIO4 - temperature seasonality, BIO5 - maximum temperature of the warmest month, BIO6 minimum temperature of the coldest month, BIO12- mean annual precipitation, BIO14 – mean precipitation of the driest month.

	Principal components		
	PC-1	PC-2	PC-3
Eigenvalues:	3.18	1.88	0.54
Projected inertia (%)	53.04	31.31	8.92
Cumulated inertia (%)	53.04	84.35	93.28
Pearson *r* with			
BIO1	0.93	0.25	-0.18
BIO4	-0.01	-0.94	-0.31
BIO5	0.84	-0.42	-0.29
BIO6	0.76	0.61	-0.06
BIO12	-0.53	0.62	-0.53
BIO14	-0.87	0.02	-0.2

Distribution patterns

Among the eleven species we studied, eight species shared a similar broad habitat, growing in Mediterranean xeric grasslands on neutral to basic soils. Despite the wide distribution of this habitat, those species have a restricted distribution in France localized in three distinct areas, separated by two important ecological barriers (figure 3a). The first area was located on the Mediterranean coast (west area), near the towns of Narbonne, Gruissan and Port-la-Nouvelle where the species' broad habitat occurs on low hills (la Clape Mountain and Leucate plateau). The second area is in low hills around Marseille (Middle area). The third area was located in the Riviera at the the southern tip of the Maritime Alps (East area). The west and the middle areas were separated by the Rhône valley, while the middle and the east areas by the silicicolous Maures plain.

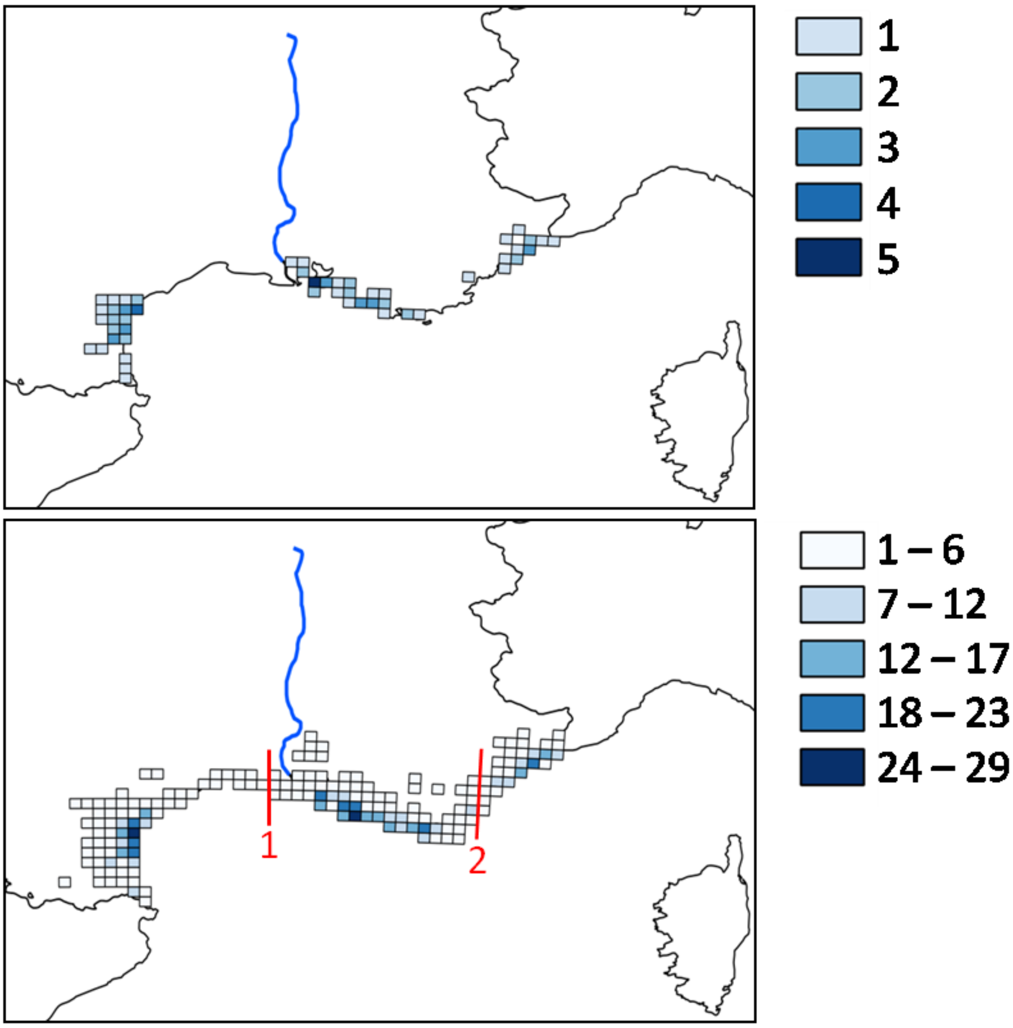


Figure 4-3. Distribution of Mediterranean plants represented in France in a 10*10km grid.
Pannel (*a*) represent the distribution of the eight target species and (*b)* the distribution of 86 species with a similar distribution pattern with northern peripheral populations in Mediterranean France Two major ecological barriers symbolized by red lines are the Rhône river valley and estuary (west) and the siliceaous Maures massif to the east.

86 species had at least half their distribution occurrences in cells occupied by the eight target species. While their distribution extended out of those cells, their distribution patterns are aggregated in the same three areas (Figure 3b). The western area contained 52 species, among which 21 (40%) were present in France only in this particular area (figure 4a). The middle area contained 64 species, among which 19 (30%) were exclusively found there, and the east area contained 38 species among which 8 (21%) were exclusively found there. Inside those three areas, the distribution of species was aggregated, with a few cells

including a high number of species: the maximum number of species observed in one single cell (10*10km) was 25, 29 and 19 representing 48%, 45% and 50% of the flora of the west, the middle and the east area respectively.

We analyzed the global distribution of the 94 species (the 8 targets species and the 86 associated), and found 4 and 2 species endemic to the west and the middle areas respectively (figure 4b). The remaining 88 taxa consisted of Mediterranean species that were present somewhere else in the Mediterranean basin in Italy, Spain or on the western Mediterranean islands. The number of species that occur in both Italy and Spain was similar in the three areas (27, 33 and 23 in the west, middle and east area, representing 52%, 52% and 61% of the total number). The proportion of species whose distribution is in Spain but not in Italy decreased from west to east representing 33%, 19% and 8% of the total flora of west, middle and east area (n = 17, n = 12, n = 3, respectively). Likewise, the proportion of plants found in Italy but not in Spain increased from west to east, representing 8%, 27% and 32 % of the total flora of west, middle and east area (n = 4, n = 17, n = 12, respectively). The proportions of biological growth forms were broadly similar across the three areas (figure 4d). Only one phanerophytes was found in middle and east area

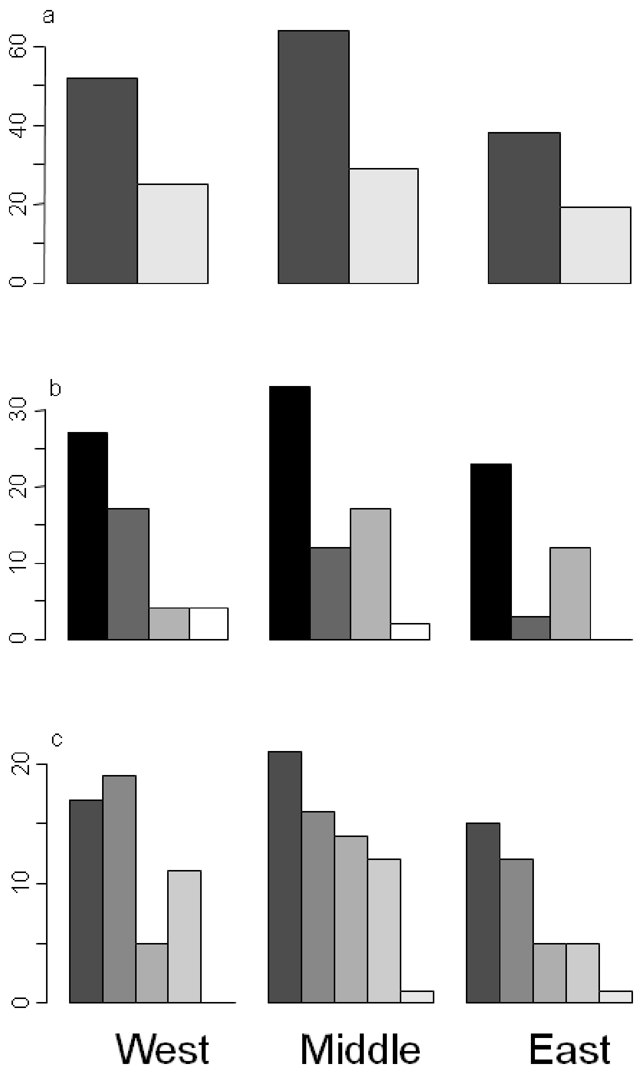


Figure 4-4. Distribution patterns of species in each of the three areas where an aggregation in their distribution is observed (west, middle and east groups).
(a) The total number of species in each area (black bar) and the maximum number of species in a single grid cell (grey bar). (b) The number of species present in Spain and Italy (black), present in Spain but not in Italy (dark grey), present in Italy but not Spain (light grey), or narrow endemics (white). (c) The number of nationally listed species (dark grey) and regionally listed species (light grey). (d) The number of therophytes, hemicryptophytes, geophytes, chamephytes and phanerophytes, from blak to white respectively.

Historical climate

The climatic model closely fitted the current distribution of Mediterranean climate (figure 5a). We used it to estimate climate suitability based on past climate simulations, and two contrasting scenarii were observed. With the MIROC prediction, our model predicted the persistence of Mediterranean climate in two large suitable areas (figure 5b). The first one west of the Rhône valley corresponded to a large area currently submerged by the Gulf of Lions. The closest area currently uncovered by the sea was the eastern tip of the Pyrenees (the Albere and Creus cap) and northern Catalonia (in Spain). East of the Rhone valley, a narrow strip of suitable climate close to the coast is predicted to have persisted. With the CCSM prediction, the model predicted two very small areas where Mediterranean climate could have potentially persisted, principally located at the eastern tip of the Pyrenees in the west, and in the east near the east region previously described (figure 5c).

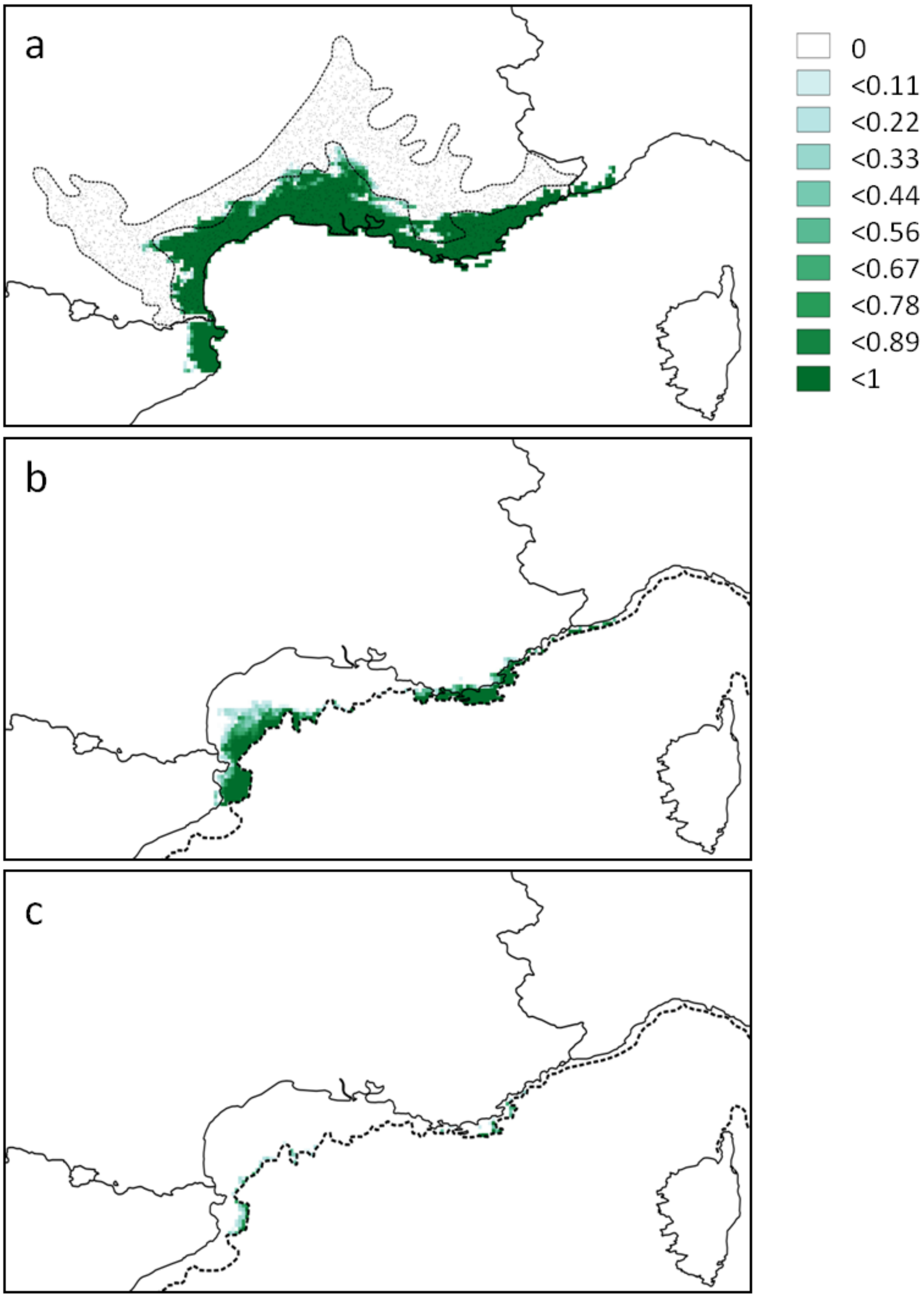


Figure 4-5. Distribution of the Mediterranean climate in southern France.
(a) Modeled probability of occurrence of Mediterranean climate under current conditions. The color scale represents the probability of climate suitability. Dots represent the 4000 random locations chosen to sample climatic conditions to characterize the Mediterranean climate. Maps b and c present the projection of the modeled probability of occurrence of Mediterranean climate at the Last Glacial Maximum, according to MIROC and CCSM models respectively. For the two historical projections, historical sea level is drawn as a dotted line, while the contemporary coastline is drawn by a solid line.

Discussion

In this study, we detected marked differences, but not marginality, of the climatic niche in peripheral and central populations of eleven Mediterranean plant species whose northern distribution limit is situated in southern France. The species tend show an aggregated distribution pattern in peripherally isolated populations. The identification of their possible historical distribution pattern at the LGM and the fact that many other species show similar patterns provides insights into the occurrence of potential floristic micro-refugia during the LGM.

Niche and dispersal limitation in peripheral populations

Among the eleven species we studied, all except *Narcissus dubius* were rare and had a very restricted distribution pattern in France. Most of them (with the exception of *Chiliadenus saxatilis*), occurred in France under a cooler and wetter climate, with less extreme maximum temperatures and drought, compared to the mean climatic conditions in the southern more central part of their distribution. However, most peripheral populations are not climatically marginal when their climatic niche is compared to central populations (figure 2). This contrasts with expectations of the centre-periphery hypothesis that assumes ecological conditions are less optimal or marginal at the periphery (Hengeveld & Haeck 1982; Brown 1984; Sagarin *et al.* 2006), especially at the northern edge (Louthan *et al.* 2015).

Among those ten species rare in France, eight exhibited a very restricted and similar distribution at their periphery, despite the fact that their broad habitat was widespread there, and that suitable Mediterranean climate was not restricted to those particular areas. Our analysis have shown that the realized climatic niche of most species even extended to cooler and wetter Mediterranean climate in the central part of their range compared to the northern periphery. Thus, why do those species exhibit a restricted distribution in France, and do not extend their distribution to nearby Mediterranean xeric grasslands? Here we discuss three hypotheses that can shed light on this question.

First, the availability of suitable micro-habitat may be such that the species are constrained to one or more of the three main areas of presence (Eriksson & Ehrlén 1992). Indeed, while the occupation of a common broad habitat type has been shown across the range of eight of the 11 study species (i.e. those in calcareous open grassland and shrubland), variation in micro-habitat characteristics may be fundamental to their persistence in peripheral populations (Papuga *et al*. 2015, chap. III), as proposed elsewhere (Woodward 1987; Kephart & Paladino 1997). However, micro-ecological niche appeared to be different among the 8 calcareous-related species in terms of soil characteristics and cover of abiotic and biotic component (Papuga *et al*, chap. III). Hence, it seems unlikely that micro-habitat characteristics alone could explain the restricted distribution of all species, because some Mediterranean xeric grassland includes at least some suitable micro-niche in southern France (G. Papuga, personal observation). Yet, we do not exclude that it can contribute in some extent to limit the distribution of several species, especially regarding the distribution of *Dorycnopsis gerardi*, which is restricted to acid soil that only occupy very small areas in southern France.

Second, our representation of the climatic niche of species could be misleading. A correlative approach using broad-scale climate data may exclude important factors that could be essential to species distribution patterns, especially at fine regional scales. For example, wind intensity and direction were not included in our analysis, although it can drastically increase evapotranspiration (Fisher *et al.* 2011), and totally modify plant physiology in relation to climate stress (Onoda & Anten 2011). This is especially valid for ecosystems with prolonged drought such as the Mediterranean basin, where water limitation in the hottest period of the year is of crucial importance for plant growth (Schwinning & Sala 2004). Additionally, the resolution of climate information might artificially smooth local variations on microclimate (Torregrosa *et al.* 2013; Canu *et al.* 2015), which are known to be of prime importance regarding the persistence of species (Hennenberg & Bruelheide 2003).

Third, dispersal potential may differentially influence distribution patterns of central and peripheral populations (Holt 2009). Range limits have been shown to frequently fall short of niche limits due to limited dispersal, especially at the leading edge of species distribution (Hargreaves *et al.* 2014). Due to their potentially higher occurrence in central areas, populations could be more prone to disperse toward habitats at the margin of their ecological niche, simply because of a greater numbers of seed produced (Holt 2009). As a result, this could enlarge the realized niche toward peripheral situations. However this question requires proper experimental investigation of the climatic niche.

Description of the geographical distribution of peripheral isolates in France

For those eight species, only three small areas contained most of their peripheral populations in southern France. Additionaly this pattern was shared by 86 other plant species, including 6 narrow endemic species (*i.e.* exclusive of southern France). The remaining 80 species were western Mediterranean taxa, also widely distributed in Iberian and/or Italian peninsulas and/or insular systems. They nearly all reach their northern limit in one, two or the three areas described. This aggregated distribution of species isolated from their main range suggests that the historical distribution of species could have also played a major role in shaping contemporary distribution patterns. It is worth noting that two of the zones of species aggregation (the west and middle areas) in southern France coincided with the two potential refugia evoked for *Narcissus dubius* during the Last Glacial Maximum (LGM) (Papuga *et al.* 2015). Thus, the distribution of Mediterranean plants during the LGM could have contributed to contemporary distribution patterns of Mediterranean peripheral isolates. Although broad patterns of refugia have been identified in the different Mediterranean peninsula for many temperate and oceanic (mostly tree) species (Hewitt 1999, 2004; Petit *et al.* 2003; Petit, Hampe & Cheddadi 2005), the identification of refugia for Mediterranean species is more complex and probably involves several micro-refugia (Cozzolino *et al.* 2003; Diadema *et al.* 2005; Minuto *et al.* 2006; Gómez & Lunt 2007; Feliner 2011) that remain largely unknown.

First, it is worth noting that the *east area* occured very closely to the refugia identified by Médail & Diadema (2009) as the “Maritime and Ligurian Alps” hotspot (Casazza *et al.* 2008). This area is known for its high richness in endemic species, and represents a crossroad between Mediterranean and Alpine biogeographic ensembles. However, little is known regarding the persistence of peripheral isolates of currently widespread Mediterranean taxa. Second, on the eastern side of the Rhône valley, the Mediterranean climate may have persisted in a narrow strip of land close to the actual shoreline, where calcareous mountains existed. Thus, this area could have act as a refugia for Mediterranean species, because suitable climate and broad habitat coexisted in a very restricted area close to (even including) currently emerged land. The proximity with the middle area (figure 3) may have enabled many species to persist locally and which could have contributed to the contemporary richness of this area in terms of peripherally isolated plant populations.

On the western side of the Rhône valley, potentially suitable climate could have persisted in a large area now submerged by the sea, and mostly constituted of sand and alluvia (known today as Gulf of Lions). The closest rocky habitat is the eastern tip of the Pyrenees, but it is mostly comprised of siliceous rocks, which makes it unsuitable for most of our study species and the other 86 species. The closest calcareous hills are located on either side of the Pyrenees: to the north, the area surrounding Narbonne (corresponding to the west area described herein), and to the south, in Catalonia. However, the model used here did not support the persistence of Mediterranean climate in the *west area* during the LGM. In consequence, this area might have been less suitable than the middle area for species persistence during the LGM. However, the Gulf of Lion could have provided suitable habitat and allowed the persistence of species living in coastal habitats (*e.g. Limonium* spp., see annex A). Thus, genetic analysis are required to assess whether calcareous species isolated at the northern part of their range subsisted under local microclimates not identified here, or recolonized those areas from Spain (or from the east) after the LGM.

Finally, the Rhône valley may have been an important biogeographical separation, due to unsuitable climate. This is exemplified by the decrease in Italian taxa west of the Rhône valley, and in Spanish taxa east of the Rhône valley. This is congruent with the hypothesis raised by Papuga *et al.* (2015) on the separated persistence of two hubs of Mediterranean climate on each side of the Rhône valley. It was also demonstrated by Lumaret *et al.* (2002) through a genetic study on *Quercus ilex*. This pinpoints the importance of large rivers as major geographic barriers to shape actual patterns plant distribution (Médail & Diadema 2009).

Conservation value

The majority of species in our study are locally rare but globally common, an issue that has raised debate in the scientific literature in regard to the conservation significance of such species where they are rare (Hunter & Hutchinson 1994; Bunnell, Campbell & Squires 2004). Such peripheral isolates represent key populations for the conservation of evolutionary potential in the wild, due to their ecological originality (Papuga *et al*. chap. III) and disjunct distribution that could promote speciation (Lesica & Allendorf 1995; Givnish 2010; Grossenbacher *et al.* 2014).

Those species live in xeric Mediterranean grasslands, coastal dunes and salt marshes, which are among the most threatened habitats in southern France, mainly because of urbanization and coastal development (Thompson & Gauthier 2011; Vimal *et al.* 2012b). This highlights a major conservation issues associated with peripheral isolates of Mediterranean plants in continental France, as they occur almost entirely in highly vulnerable habitats.

The restricted distribution of peripheral isolates is also an opportunity to integrate potential refugia into conservation planning. These areas contain many endemic and locally rare species, and are also prone to preserve ancient lineages of more widespread species (Ledig 1993; Petit *et al.* 2003; Médail & Diadema 2009). Their climatic stability through time, and their role in the processes of range contraction, persistence and recolonisation make them valuable areas to conserve processes that create and maintien regional biodiversity. Additionnaly, those areas can be of prime importance in a climate change context, especially as they occur at the northern periphery of their distribution and are thus susceptible to form a future colonization front with further climate warning and drought, predicted for the Mediterranean region (Giorgi & Lionello 2008; Valladares *et al.* 2014).

CHAPTER 5: Linking ecological factors and position across the range to explain local abundance of 11 Mediterranean plants

To be cited as:

Papuga, G., Gauthier, P., Pons, V., Pironon, S., Farris, E. & Thompson, J.D. (in prep.) Linking ecological factors and position across the range to explain local abundance of 11 Mediterranean plants.

Introduction

Analysis of population features across species range has driven intense research from the early days of modern ecology (Gaston 2003). In particular, how ecological factors shape population characteristics across the range remains a central question (Gerst, Angert & Venable 2011). In this context, the centre-periphery hypothesis represents a biogeographical paradigm which postulates that populations at the edge of species range are genetically depauperate (Eckert *et al.* 2008), ecologically marginal (Sagarin *et al.* 2006) and show reduced demographic performance as a result (Sexton *et al.* 2009; Abeli *et al.* 2014). In this context, the abundant-center model (Haeck & Hengeveld 1981; Brown 1984) predicts that abundance should peak in the centre of the range, and decrease toward margins. Abundance strongly impacts a series of mechanisms that shape population characteristics, such as pollinator attractiveness (Schmitt 1983), reproductive system (Vaupel & Matthies 2012; Berjano *et al.* 2015), recruitment (Eriksson & Ehrlén 1992), demographic performance (Buckley *et al.* 2001; Kéry, Matthies & Fischer 2001), herbivory (Maron & Crone 2006), genetic features (Vucetich & Waite 2003).

However, recent syntheses have brought little support to this hypothesis (Pironon et al., in prep). In particular, plants are highly dependent from local factors that are thought to blur large scale spatial patterns of abundance and population performance (Woodward 1987). Both climate (Good & others 1964; Hennenberg & Bruelheide 2003; Sunmonu & Kudo 2015), abiotic environmental characteristics (Kephart & Paladino 1997; Wiser, Peet & White 1998; Baack, Emery & Stanton 2006), biotic interactions (Bruelheide & Scheidel 1999) and population dynamics (Gerst *et al.* 2011) interact to shape population features, and precise investigation of the ecological niche are required to disentangle those mechanisms (Pulliam 2000).

Measuring abundance is itself a complicated issue due to the diversity of biological strategies involved and the difficulties of identifying individuals in the field (especially in high density patches and in clonal species). In a recent review, Pironon *et al.* (chap. I) examined 44 studies analyzing abundant-centre patterns in plants, among which 31 used local density as a proxy for it (e.g. Csergo, Molnar & Garcia 2011). Density may refer to individual count (Van Treuren *et al.* 1993), ramet counts (Ribeiro & Fernandes 2000; Dorken & Eckert 2001; Csergo *et al.* 2009) or even shoot counts (Barkham 1980; Meeus *et al.* 2012). However, plant abundance is better described by the cover of a species in a given area (Kent & Coker 1992; Krebs 1999; Damgaard 2009), provided a standardized method is used (Floyd & Anderson 1987). This measure is not biased by the size and the distribution of individuals, and gives precise insights on the place of a species in its community, which is crucial to infer processes described above. In the Pironon *et al.* review, only two studies used plant cover to estimate abundance (Hennenberg & Bruelheide 2003; Van Couwenberghe *et al.* 2013).

In a previous paper, we have documented variation in local ecological conditions between central and northern peripheral populations for 11 Mediterranean plants (Papuga *et al*, chap. III). We have also shown that northern peripheral populations occur in a climatic context with less severe summer drought and milder temperatures than central populations (Papuga *et al.*, chap. IV; Papuga *et al.* 2015). We did not however examine the relationship between local abundance and variation in ecological factors. Merging those two factors would bring insights to the abundant-centre theory (Brown 1984) and the importance of ecological factors and range structure to determine species abundance patterns. The purpose of the present study is to assess the impact of micro-ecological niche conditions detected in our previous work (Papuga *et al*, chap. III), climatic features and position across the range (central or peripheral) to drive within-population local abundance of 11 Mediterranean plant species.

Material and methods

Species selection

We focused on the eleven plants studied by Papuga et al. (in prep), which were selected by a step by step procedure to fill a series of criteria. Species had to be native in the western Mediterranean basin, listed for protection in continental France (with the exception of *Narcissus dubius* and *Polygala rupestris*) and not recently spread by human activities (i.e. horticultural or commercial use). Species had to be largely distributed in Spain and/or Italy in the south (central populations), and attain their northern range limits in Mediterranean France (peripheral populations). In addition, they had to be known from at least five distinct locations per geographical position (central and peripheral) to apply the initial sampling protocol. Following these five criteria, authors selected 11 herbaceous and small chamephyte species in order to apply a common method, and tried to maximize the number of families and genera represented. They also paid attention to balance biological growth forms. Species are detailed in table 1, and further information on species selection is provided in Papuga *et al.* (chap. III).

Table 5-1. Description of studied species.
Species are Mediterranean endemic plans (with the exception of *Stipa capensis*) extensively present in the western part of the Mediterranean basin. They have been studied in Papuga *et al.* (in prep).

Species	Familly	Biological type	Flowering	Quadrat size (m^2)
Atractylis cancellata L.	*Asteraceae*	Therophyte	Late spring	1
Chiliadenus glutinosus Fourr.	*Asteraceae*	Hemicryptophyte	Autumn	4
Convolvulus lanuginosus Desr.	*Convolvulaceae*	Hemicryptophyte	Late spring	4
Dorycnopsis gerardi (L.) Boiss.	*Fabaceae*	Hemicryptophyte	Late spring	4
Hyoseris scabra L.	*Asteraceae*	Therophyte	Mid-spring	1
Merendera filifolia Cambess.	*Colchicaceae*	Geophyte	Autumn	1
Narcissus dubius Gouan	*Amaryllidaceae*	Geophyte	Early Spring	4
Ophrys bombyliflora Link	*Orchidaceae*	Geophyte	Mid Spring	1
Polygala rupestris Pourr.	*Polygalaceae*	Chamephyte	Mid spring	1
Stipa capensis Thunb.	*Poaceae*	Therophyte	Late spring	4
Viola arborescens L.	*Violaceae*	Chamephyte	Autumn	1

Sampling

Field data of the micro ecological niche

For each species, five central and five peripheral populations were randomly chosen based on the information gathered from several databases. Once located, each population was sampled thanks to a simple standardized protocol that aimed to describe the micro-ecological niche. Three quadrats per population (each either 1m^2 or 4m^2 depending on the species, see Table 1) were randomly set in high-density patches, each patch at least 5m apart from the nearer. First, one soil sample per quadrat was collected and analyzed at the lab. Then, point contact method was used to measure the cover of each ecological parameter (Floyd & Anderson 1987) (Table 2). Each quadrat was divided into 100 contact points, for which contact with one or more of habitat element was compiled. Living plants were identified and classified in one of 5 categories of Raunkiaer biological type (Raunkiaer 1934), considering chamephytes and small phanerophytes together due to their low cover. If several components were touched at a given point, the value of each contact point was constrained to 1, so that the total cover per quadrat could not exceed 100%.

For each species, field investigations were carried at peak flowering during 2013 and 2014. Experimental laboratory analyses were conducted during spring 2015.

Table 5-2. Ecological variables used in the study to characterize the ecological niche.
Columns "biotic", "abiotic" and "soil" gather variables that describe the micro-ecological niche, and were extracted from Papuga et al. (in prep). Climate variables were extracted from the Worldclim database.

Biotic	Abiotic	Soil	Climate
Lichen	Bedrock	pH	Annual Mean Temperature
Moss	Blocks (>25cm)	Conductivity	Temperature Annual Range
Therophyte	Stones (2.5 – 25 cm)	Water retention potential	Annual Precipitation
Hemicryptophyte	Gravel (0.5 – 2.5 cm)		Precipitation of Driest Quarter
Geophyte	Bare soil		Altitude
Woody species	Litter		
	Herbaceous litter		
	Woody litter		

Estimation of the local abundance

The point contact method enabled us to extract an unbiased and standardized estimation of the cover of each target species in each quadrat (Floyd & Anderson 1987; Damgaard 2009). This proxy was used here as a single metric representing local-abundance of plants in their micro-habitat, no regard to the biological characteristic of each species (especially growth form and clonality). This allowed us to make cross taxa comparison without accounting for heterogeneity in measures used.

Climate data

For each studied population, we extracted the 19 bioclimatic variables available in the Worldclim website (http://www.worldclim.org/). In order to limit redundancy between variables, we ran a Principal Component Analysis on those values and retained four variables that are uncorrelated, and representative of the Mediterranean climate: annual mean temperature, temperature annual range, annual precipitation and precipitation of the driest quarter, to which we added the altitude of the site.

Statistical analyses

Three different analyses were conducted to investigate changes in small scale abundance. First, we compared density between central and peripheral populations for each taxon separately. We ran Fisher test to assess the homogeneity of variances, and then compared mean population density between central and peripheral populations using Welsh two-sample t-test, with the alternative “greater”.

Second, to investigate cross-taxa trend on mean plant density, we plotted the mean value of species cover (± standard error) for each species in central and peripheral populations. A bisector represented the line of equality between central and peripheral populations, and helped to depict any variation in terms of deviance from the bisector. To statistically test this relationship we fitted a general mixed effect model, with density as response variable and species, position (central or peripheral) and population as explanatory variables. Species and population were random factor with population nested into species, while position was a fixed effect.

Third, we tried to link the density of each species with all ecological niche variables investigated. Previous to analysis of each species, we deleted variables that had no value in more than 80% of the quadrat. We then fitted a linear model with density as a response variable, while position (a binary variable representing *central* or *peripheral* position) and all the other environmental characteristics were used as explanatory variables. We tested the homogeneity of the residuals with Harrison-McCabe test, otherwise we linearized the response variable following a Box-Cox method. We followed a stepwise procedure with both *backward* and *forward* method to identify the model that minimized the Akaike Information Criterion (AIC). The validity of the model was tested with a Fisher test.

All statistical analyses were performed using R:3.2.1 (R development Core Team 2010). We corrected *p*-values following the Benjamini-Hochberg false discovery rate method (Benjamini & Hochberg 1995). We present *p*-values that fall between 0.05 and the corrected value as weakly or marginally significant (*) and those that are less than the corrected threshold as highly significant (**).

Results

No species showed significant differences in the homogeneity of their variance (Table 3). When comparing mean local abundance, two species showed a weakly significant trend toward higher values in central populations: *Dorycnopsis gerardi* and *Stipa capensis*. It is worth noting that those species showed the highest local abundance value in our dataset, covering more than twenty-five percent of the quadrat in mean, while all the other species did not exceed fifteen percent of cover (and covered generally way less). As a result, no overall trend toward higher local abundance of target plant species in central populations could be seen (Figure 1, Analysis of Deviance: χ^2= 0.5, *df* = 1, p > 0.05).

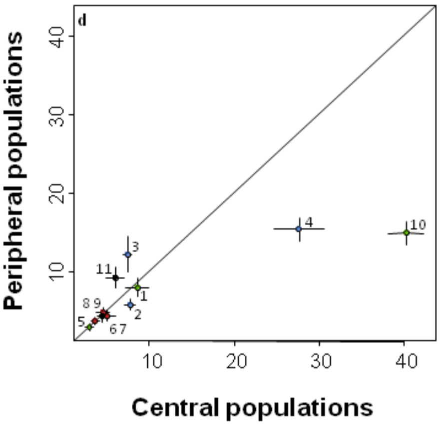


Figure 5-1. Mean local abundance of eleven plant species for five central (X axis) and five peripheral (Y axis) populations. The bisector represents equal values for each position. Biological types are colored differently: therophytes in green, geophytes in red, hemicryptophytes in blue, woody species in black. Numbers are 1. *Atractylis cancellata*, 2. *Chiliadenus glutinosus*, 3. *Convolvulus lanuginosus*, 4. *Dorycnopsis gerardi*, 5. *Hyoseris scabra*, 6. *Merendera filifolia*, 7. *Narcissus dubius*, 8. *Ophrys bombyliflora*, 9. *Polygala rupestris*, 10. *Stipa capensis*, 11. *Viola arborescens*.

Table 5-3. Comparison of mean abundance between central and peripheral populations for each species separately. Fisher variance test is used to detect the homogeneity of variance among central and peripheral populations. Welsh t test is used to compare mean abundance value between central and peripheral populations. Then, a summary of the each model is detailed to explicit the model statistics, and the variables retained after a stepwise model selection

Species	Fisher variance				Welsh t.test			
	F	df	p	P corrected	t	df	p	P corrected
Atractylis cancellata	0,32	11	0,07	0,206	-1,96	23	0,617	0,952
Chiliadenus glutinosus	1,11	14	0,84	0,844	1,51	28	0,928	0,952
Convolvulus lanuginosus	0,40	14	0,09	0,206	-0,94	24	0,179	0,328
Dorycnopsis gerardi	0,42	14	0,11	0,206	-2,36	24	0,013	0,140
Hyoseris scabra	0,28	14	0,02	0,123	-1,01	21	0,163	0,328
Merendera filifolia	0,24	14	0,01	0,123	0,62	20	0,730	0,952
Narcissus dubius	0,51	14	0,23	0,355	1,73	25	0,952	0,952
Ophrys bombyliflora	1,22	14	0,72	0,792	0,19	28	0,573	0,901
Polygala rupestris	1,62	14	0,38	0,521	1,26	27	0,891	0,952
Stipa capensis	0,70	14	0,51	0,620	-1,84	27	0,038	0,140
Viola arborescens	0,41	14	0,10	0,206	-1,40	24	0,087	0,240

When linking species cover to ecological niche variables, models failed to establish a significant relationship for *Hyoseris scabra,* and detected a weakly significant relationship for

Atractylis cancellata, despite the fact that no parameters taken individually were statistically significant (table 5). Therefore, the density of those two low cover therophytes could not be explained by neither their geographical position nor their ecological niche characteristics. The geographic position was a significant positive constant in selected best model for six species, but was not included in models for *Merendera filifolia*, *Ophrys bombyliflora* and *Polygala rupestris*. Each model was composed by both micro ecological niche and climate variables, which suggested that they both elements impacted local-abundance of studied plants. However, there was no converging trend toward some variables that would have impacted all taxa in a similar way.

Table 5-4. Correlation between variation in plant local abundance, ecological features of the plant micro-niche and regional climatic variables in central and peripheral populations of 11 Mediterranean plant species.

Estimated coefficients are presented with their significance level. NS : non-significant, * : 0.05 > *p* > corrected significance level, ** : *p* < Corrected significance level. Species are 1. *Atractylis cancellata*, 2. *Chiliadenus glutinosus*, 3. *Convolvulus lanuginosus*, 4. *Dorycnopsis gerardi*, 5. *Hyoseris scabra*, 6. *Merendera filifolia*, 7. *Narcissus dubius*, 8. *Ophrys bombyliflora*, 9. *Polygala rupestris*, 10. *Stipa capensis*, 11. *Viola arborescens.*

Species	1	2	3	4	5	6	7	8	9	10	11
lambda	0.3										-0.3
R adjusted	0.79	0.87	0.84	0.83	0.62	0.89	0.89	0.66	0.51	0.97	0.74
F stat	2.74	5.52	8.62	9.30	1.77	15.84	9.96	5.02	3.28	37.18	13.45
DF	15	16	11	10	14	10	13	8	7	13	5
DF	11	13	18	19	15	19	16	21	22	16	24
P	0.049	0.002	< 0.001	< 0.001	0.143	< 0.001	< 0.001	0.001	0.015	< 0.001	< 0.001
P corrected	0.054	0.002	< 0.001	< 0.001	0.143	< 0.001	< 0.001	0.002	0.019	< 0.001	< 0.001
(Intercept)	40.025 (ns)	-370.3 **	-106.93 (ns)	1055.803 **	523.12 **	-975.3 **	197.047 **	69.605 **	-7.636 (ns)	192.527 (ns)	5.979 **
Position		-103.7 **	44.97 **	150.163 **	309.171 **		106.102 **			82.478 **	1.643 **
S1.Water retention capacity	0.031 (ns)	-0.297 (ns)	0.505 (ns)		0.118 (ns)			0.124 (ns)			
S2. Conductivity	0.001 (ns)	0.013 (ns)	-0.016 (ns)			0.008 (ns)	0.012 **	-0.015 **			0 (ns)
S3. pH		-4.618 (ns)	23.021 **	-7.516 **	3.325 (ns)			2.733 (ns)			
A4. Rock	-0.037 (ns)	0.745 **	-0.243 (ns)	not tested	-0.33 **		0.152 **	not tested		-4.929 **	
A5. Stone	-0.054 (ns)	0.793 **			-0.168 (ns)	-0.18 (ns)				-5.043 **	
A7. Gravel	-0.041 (ns)	0.793 **			-0.252 **		0.151 (ns)	-0.231 **		-4.882 **	
A8. Bare soil	-0.029 (ns)	0.909 **			-0.088 (ns)	-0.04 (ns)			-0.246 (ns)	-5.122 **	
A9. Liter	-0.056 (ns)	0.918 **		0.382 (ns)			0.246 **			-4.845 **	
B11. Total biotic cover	-0.046 (ns)	0.972 **	0.376 **	0.688 **	-0.299 **		0.079 (ns)		-0.08 **	-4.937 **	
B12. Therophyte cover	not tested	not tested		-0.422 *	not tested		0.159 (ns)			not tested	
B13. Hemicryptophyte cover	0.018 (ns)	not tested	not tested	not tested	0.189 (ns)	0.054 (ns)	-0.071 (ns)	-0.07 **		-0.575 (ns)	
B14. Geophyte cover	0.037 (ns)	not tested		not tested	0.462 *	not tested	not tested	not tested	1.251 **	-0.747 **	
B15. Woody vegetation cover	-0.008 (ns)	-0.24 **	-0.518 **	-0.569 **		0.142 (ns)			not tested		not tested
Altitude	-0.002 (ns)	0.114 **	-0.096 **	-0.358 **	-0.322 **	0.541 **	-0.127 **		0.012 **		-0.003 **
Annual Mean Temperature	-0.093 (ns)	2.989 **	-1.2 **	-6.708 **	-4.338 **	8.226 **	-2.455 **	0.228 **	0.171 *	-1.046 **	-0.039 **
Temperature Annual Range	-0.058 (ns)	-0.22 (ns)	0.478 **	0.564 **		-1.435 **	0.194 **	-0.652 **	-0.077 *	1.264 **	
Annual Precipitation		-0.223 **		-0.205 **	-0.448 **	-0.537 **	0.311 **			0.332 **	
Precipitation of Driest Quarter	-0.087 (ns)	1.429 **	-0.1 (ns)		4.549 **	6.332 **	-1.23 **	0.522 **	0.085 **	-0.937 **	0.006 **
Number of variables	16	19	12	13	15	11	14	10	8	14	6

Discussion

The abundant-centre Model (Brown 1984) is a long standing hypothesis in the study of the centre-periphery hypothesis (Gaston 2003). While it has received some support from empirical studies on animals, evidences from plants remain sparse, probably due to blurring local ecological factors (Pironon et *al.*, in prep). In this context, understanding factors that drive local abundance of plants in their micro-habitat is the first step necessary to investigate plant abundance at a population scale (Csergo *et al.* 2011). Additionally, very few tests have considered species cover as a proxy for plant local abundance, preferring the use of density. Here we use a standardized method to bring some insights on plant abundance (*sensu* Floyd & Anderson 1987), based on a cross taxa study in a Mediterranean context.

Methodological issue

Abundance in plant population is a polymorphic concept, and it might require a dynamic analysis rather than a fixed picture to get a proper view of this feature. It is driven by three factors: 1. the extent of suitable habitat (Eriksson & Ehrlén 1992), 2. metapopulation dynamics that drive species occupancy of the available habitat (Gilpin & Hanski 1991; Eriksson & Ehrlén 1992; Eriksson & Kiviniemi 1999; Pulliam 2000), and 3. local abundance of the species in its habitat (Floyd & Anderson 1987). While local abundance gives restricted insights on the global abundance of a population, it is a key-step toward a better understanding of habitat requirement to shape larger patterns. The use of global plant cover per quadrat allows including species such as *Convolvulus lanuginosus* or *Dorycnopsis gerardi*, whose growth form avoid any count of individuals, ramet or shoots (Krebs 1999). Also, this proxy encompasses individual growth and density, which gives accurate perspectives on the importance of the species in the community. However, the use of a standardized method (such as point-contact) is strongly required to estimate cover in a normalized way, especially regarding low level of variations depicted in the dataset, which wouldn't have been detected by visual estimation.

Global differences between centre and periphery in plant cover

In accordance with previous literature, we found no evidence of a cross taxa trend toward higher abundance for central populations, at least for local abundance (Sagarin & Gaines 2002; Abeli *et al.* 2014, Pironon *et al.*, chap. I). This suggests that "pocket of suitable habitat" (Gerst *et al.* 2011) can be found all across the range of those species (Dinsdale, Dale & Kent 2000).

Nevertheless, two species (*Dorycnopsis gerardi & Stipa capensis*) exhibit weakly significant differences toward higher local abundance in central populations. Those two species grow in high cover vegetation, where they both can be considered as dominant species representing over one third of the total vegetation cover, despite different biological types and different habitat. Regarding the nine remaining species, the mean local abundance was similar between central and peripheral populations. This suggests that the status of a species in its habitat (i.e. dominant core species or rare satellites species, *sensu* Hanski 1982) can affect variations of its abundance across its range, with dominant species showing greater decrease than satellites species toward their periphery. This was already observed by Samis & Eckert (2007) who found no difference in the mean density of two dunes plants, that occur in very sparse populations across their whole range.

Annual plants abundance variability in space and time

No significant relationship was established between ecological conditions, geographic position and local plant cover for *Hyoseris scabra* and *Atractylis cancellata*. Those two species are low cover annual plants, whose abundance might be linked with variables not evaluated in this study. Notably, the density of annual plants is highly dependent on their seed bank dynamic (Kluth & Bruelheide 2005a; b) and their metapopulation dynamic (Gilpin & Hanski 1991). In addition, annual climatic conditions might strongly impact individual growth (Hobbs & Mooney 1991) and recruitment (Walck *et al.* 2011), which are important drivers of local abundance. Water is a limiting factor in semi-arid climat such as Mediterranean (Blondel *et al.* 2010), and the yearly pulse of precipitation might have a strong impact on vegetations (Schwinning & Sala 2004). Therefore, it is likely that we did not measure accurate variables to investigate processes driving local abundance of those annual species. However, while this phenomenon might be amplified in therophytes it is important to remind that it also impacts perennial growth forms (Schwinning & Sala 2004). Thus, we suggest that yearly surveys of abundance are important to understand the role of interannual processes driving plant populations.

Impact of range position on local-abundance

The significant positive constant representing the position (central or peripheral) indicates that, for six species, central populations tend to be significantly more locally abundant than peripheral when controlling for ecological conditions. It is worth noting that among the three species that did not include this positive constant, two at least (*Merendera filifolia, Polygala rupestris*) have their peripheral population that encounter climatic conditions relatively central regarding the global climatic niche of each species (Papuga *et al*., chap. IV), comparing to species that include this positive constant in their best model.

Two hypotheses can support this pattern: first, individuals are larger in the centre of the distribution, which can be due either to better climatic conditions fostering greater individual growth (plastic variability), or direct/indirect selection toward larger individuals (selection process). However, no evidence of general reduction in size toward periphery has been highlighted by Pironon *et al.* (chap. I), as exemplified by contrasted results from common garden studies (Stewart Jr & Nilsen 1995; Doudová-Kochánková *et al.* 2012; Vergeer & Kunin 2013; Kilkenny & Galloway 2013). Second, within quadrat plant density might be higher due to a higher recruitment in central population. This can result from a greater production of seeds due to larger population size and/or higher occurrence (Hanski, Kouki & Halkka 1993; Eriksson & Kiviniemi 1999), that produce higher seedling able to settle in the habitat. This can result also from a greater availability in regeneration niche at a very small scale, where seeds germinate and root (Grubb 1977; Eriksson & Ehrlén 1992; Baack *et al.* 2006). However, metapopulation dynamics is of great complexity and require detailed surveys to be assessed.

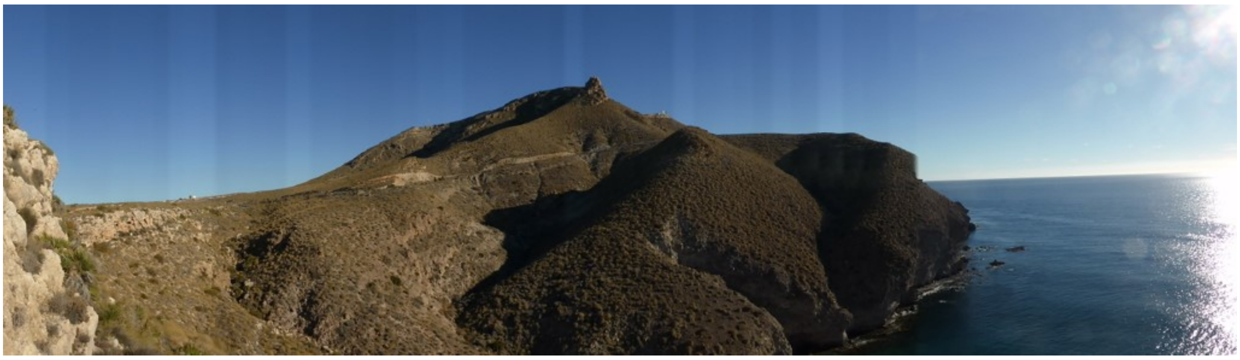
Interactions between local and climatic ecological factors

While climate is supposed to strongly drive large scale occupancy patterns (Boucher-Lalonde *et al.* 2012), local scale processes have been proposed to blur cross-range abundance patterns and therefore explain the low support for the abundant-centre model find in plant literature (Pironon et al., in prep). In our study, no converging pattern is observed across taxa for climatic and micro ecological niche variables. This suggests that both variables shape species local abundance. Hennenberg & Bruelheide (2003) have shown that temperature had an impact on seed setting, while the interaction between micro-climate (water availability) and soil characteristics had a strong impact on vegetative growth, which together condition local abundance. Therefore, we argue that ecological niche study must include all those local variables to infer fine scale processes shaping population features, especially those related with demographic performance.

Conclusion

Abundance of a species at the population scale is the result of the distribution of (more or less) suitable habitat, metapopulation dynamics and local abundance of species inside the different habitats colonized. This last part is tightly linked with both macro and micro ecological factors, which limit the observation of large scale spatial patterns suggested by the abundant centre model. Yet, a trend toward higher local-abundance in central populations is detected for several species when controlling for local and climatic ecological variables. Therefore, the next step will be to enlarge the study of micro-ecological niche to the whole populations, in order to include a broader range of habitat and understand local source-sink dynamics. Thus, spatio-temporal surveys are required to assess the role of meta-population dynamics on population structure, and get proper insights on processes driving abundance in plants species.

DISCUSSION



Through this work, we have revisited several aspects of the central-peripheral hypothesis (CPH), with a special emphasis on identifying fine-scaled ecological variability among central and peripheral populations, and disentangling ecological marginality and geographical periphery. We have tried to bring some insights to five main questions:

In chapter one, we asked what can we learn from the empirical literature dealing with the CPH, and what does it tell us regarding the importance of ecological niche in large-scale processes?

In chapter two, we asked how history, ecology and the dynamics of range structure interact to shape contemporary patterns of genetic variation, in particular spatial variation in a sexual polymorphism.

In chapter three we asked how the ecological niche varies across the range. Regarding micro ecological features, are there patterns of repeatable variations at the distribution limit that are shared by a group of species?

In chapter four we asked how the climatic niche varies across the range. How many Mediterranean species do share a common distribution pattern at their northern limit? What are the ecological drivers that may influence it?

In chapter five, we asked how the different ecological factors (both micro-ecological and climatic) interact across species range to influence the local abundance of species in their micro-habitat.

Each chapter produced interesting results that we have already discussed fairly independently. In order to replace these results in a more global perspective, we present a discussion based on three axes that these results have stimulated us to use as a basis for the concluding discussion. The first part will be dedicated to the ecological niche theory, regarding the variability of the niche and its implication on population processes. Then we will focus on the Mediterranean basin as a model region to illustrate the role of disjunct distribution and ecological differentiation on the evolution of diversity and endemism in its flora. Finally we discuss the potential importance of peripheral isolates, ecological marginality and ecological originality as issues that allow adopting an approach based on eco-evolutionary processes for plant biodiversity conservation.

The ecological niche

The theory

Differences that exist between organisms in terms of ecological optimum and amplitude have stimulated intense debates to understand their underlying causes and consequences (Cowles 1901; Transeau 1903; Grinnell 1928; Brown 1984). Indeed, the fact that species are able to live in limited ecological conditions gave birth to the concept of ecological niche, at the beginning of the 20th century. Grinnell (1928) proposed to focus species requirements and emphasized the role of abiotic components to determine suitable ecological condition for an organism. In parallel, Elton (1927) highlighted the need to integrate biotic interactions in the concept of the niche, especially competition. From then on, the concept of ecological niche was unified by Hutchinson (1957) who introduced the so-called “Hutchinson’s duality” (Colwell & Rangel 2009) to differentiate the ***biotope space*** from the ***niche space***. The first corresponds to the physical world and is represented by a map in which each cell is characterized by one value for each n-environmental factor. The second is an abstract space defined by the same n-environmental factors, in which two volumes are defined:

environmental space in which a population can grow autonomously (considered as inside the niche) and environmental space where a population fails to persist in the long term without regular immigration (Hutchinson 1978). Environmental space thus includes both biotic and abiotic factors.

The reciprocity between the two spaces is total: each localization of the biotope space corresponds to points in the niche space (Colwell & Rangel 2009). However, the effective occupation of the niche by the species (*i.e.* realized niche) differs from the fundamental niche due to several mechanisms. Some niche axis (named *bionomic*) involved interactions with species (*e.g*. competition, facilitation, symbiosis) that have their own population dynamic (Colwell & Rangel 2009), and impact the realized niche. Abiotic axes (named *scenopoetic,* representing environmental conditions s.l.), despite an apparent stability might change in space, leading to a discrepancy between the suitability of a place and its occupation by species. For example, the time for a species to become completely extirpated from a place after a modification in environmental conditions, or the time required by a species to colonize newly suitable environment, induce a lag directly related to life history traits of the species, and especially dispersal.

The concept of the niche and spatial limitation

The realized niche is modified by **species dispersal abilities**, which can lead species to colonize **sink** sites outside of the fundamental niche (Pulliam 2000), and thus enlarge the realized niche. Oppositely dispersal limitation can **impede species to reach sites** that are ecologicaly suitable (ask any field plant ecologist). In this thesis, we considered the realized niche as the spatial projection of species requirements (*i.e*. fundamental niche), under its interaction with other organisms, constrained or enhanced by its dispersal abilities (Eriksson & Ehrlén 1992; Colwell & Rangel 2009) (figure 1).

This functional perspective has ecological implications, especially regarding the centre-periphery hypothesis. The fact that some populations of a given species face harsh conditions more or less regularly on the basis of its dispersal abilities can influence population characteristics across the range. For example, the strong difference that exists between plants and animals regarding abundant-centre pattern (chapter I) might be due to their dispersal abilities. Contrary to plants, animals are able to disperse as adults, which give them the opportunity to avoid competition for resources, and to establish new populations at the periphery of their range. This increases the probability to encounter unsuitable environment in the long term, and diminish population performance which might as a result limit individual abundance (chapter I). It also increases the probability for the population to become extinct (in the case no migrant colonize the patch during several years), which results in a higher temporal variability (Curnutt *et al.* 1996).

But dispersal limitation might also affect differently populations located in different part of a species' range. We have shown in chapter IV that populations at the centre of the range tended to colonize sites under cooler and wetter climates in a greater extent that populations at the northern periphery (despite this climate is widespread there). One hypothesis is that northern peripheral isolates could not escape from small areas where they persist due to a limited colonization rate (see chapter IV). In a metapopulation perspective, the low number of populations limit dispersal events, and thus can impede colonization of new sites because immigrants do not reach a sufficient density to establish a viable population (see Holt 2009 for details on the establishment niche).

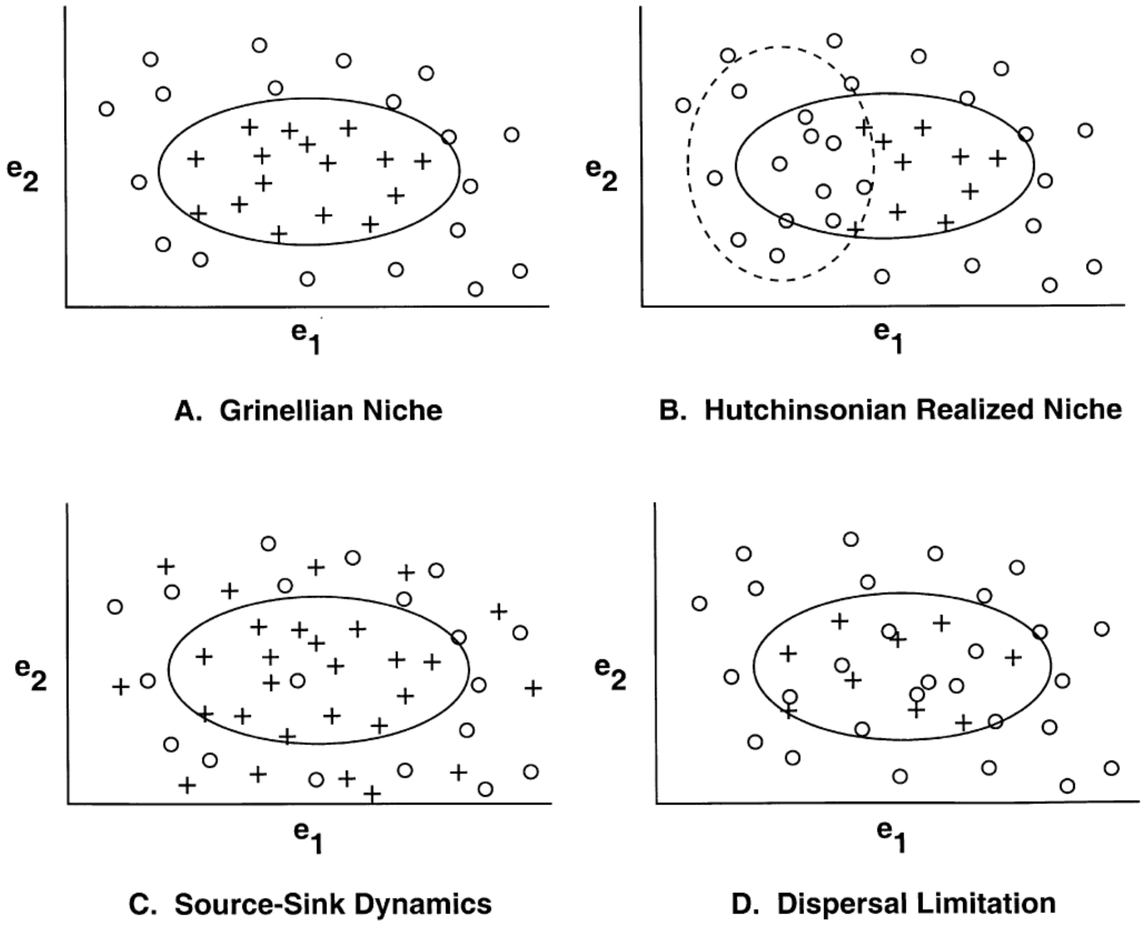


Figure 6-1. Different perspectives on the link between realized and fundamental ecological niche of a species.
In each diagram, the oval refers to the fundamental niche of a species in a niche space composed of two ecological gradients (e1 and e2). The "pluses" indicate the presence of the species in a patch of habitat characterized by particular value of e1 and e2, and the "circles" indicate the absence of the species in a patch. The panel A represents the Grinellian niche concept, in which a species occupy every site presenting suitable ecological conditions. The panel B represents Hutchinson's realized niche concept, in which a competitor (whose fundamental niche is represented with dashed line) excludes the species from suitable sites. The panel C represents the source-sink theory, in which the species disperse toward habitat outside its fundamental niche. The panel D represent a situation where the species is absent from suitable habitat patches due metapopulation dynamic and dispersal limitation, that induce a time lag between extinction and colonization of those patches. Figure and legend reproduced from Pulliam (2000).

Spatial patterns in the realized niche of plant

Due to their low dispersal abilities and their difficulties to escape perturbations, many plants are highly constrained by local factors (Woodward 1987). This increases the complexity of evaluating their ecological niche, as ecological factors impact life history processes in different extent (Davy & Smith 1988). For example, while climate has been invoked to explain many distribution patterns (chapter I), local ecological processes may drive fitness trait variation (Stanton-Geddes *et al.* 2012a; Granado-Yela *et al.* 2013). We have shown that the local abundance of individuals might be driven by climate, geographical position in the range and micro ecological features (chapter V), and that the relationship between each species, its ecological niche and its life history trait appear to be highly variable among taxa (chapter I & V).

In addition, our study (chapter III) suggests that local ecological factors are different between central and peripheral populations, as shown by many other studies (Carter & Prince 1985; Hennenberg & Bruelheide 2003; Leuschner *et al.* 2009; Moore & Stanton 2014). This has several implication regarding plant populations, as selective pressure will be different across the range (Givnish 2010), thus promoting evolutionary diversification at some points of the range (Lesica & Allendorf 1995). This can influence the way populations can settle in different habitats. However, it is not possible with our data to assess whether those shifts correspond to adaptive mechanisms or plastic responses due to the local availability of habitat (figure 2).

As a result, large scale patterns of suitable habitat appear difficult (if not impossible) to spatialize, because of the diffuse distribution of those variables in a given landscape.

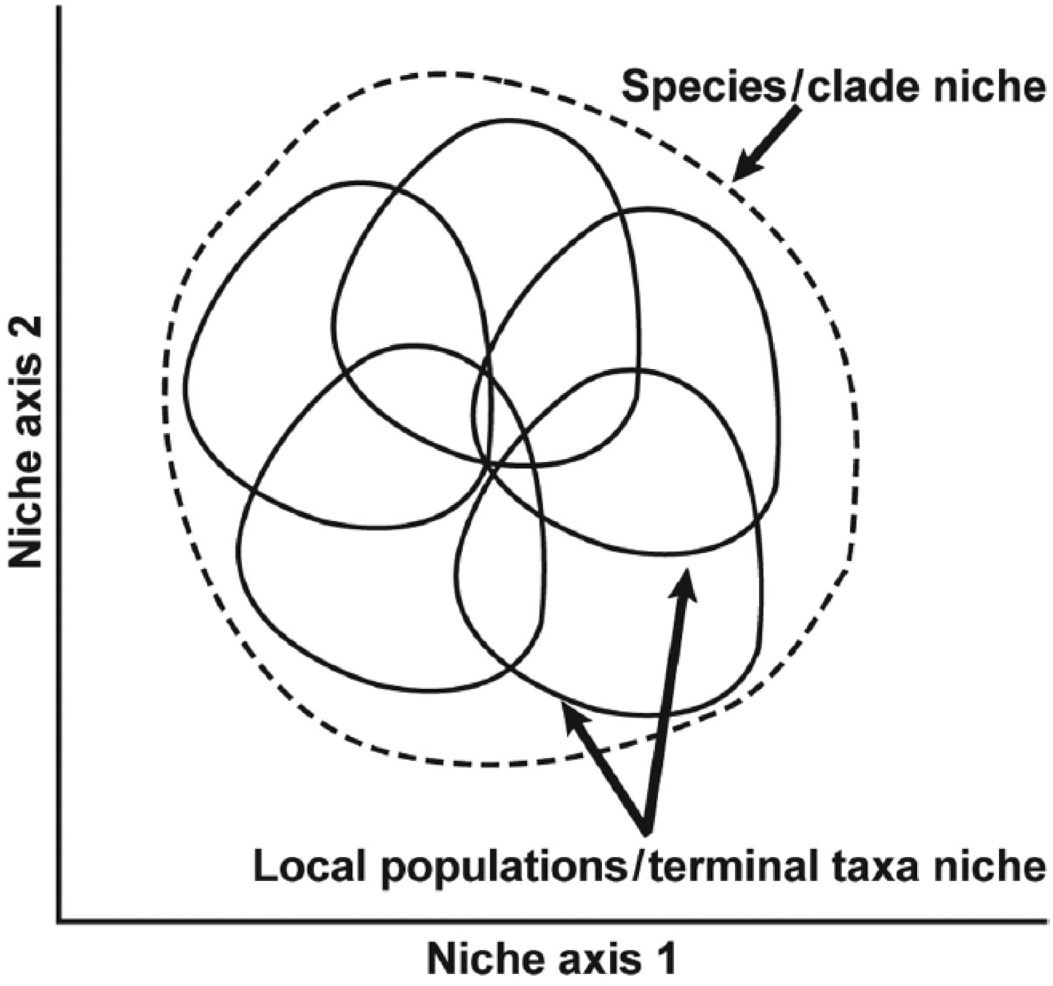


Figure 6-2. Relationship between population niche and species niche.
Several populations of a single species might have niches that overlap in different extent. Reproduced from Holt (2009).

Toward a roadmap for studying rangewide patterns of plant performance

The CPH postulates that population performance is dependant of ecological marginality (Sagarin *et al.* 2006). The low support found for this hypothesis might be due to the complexity to spatialize ecological marginality for plants, and optimum and marginal habitats might occur all across species range. Thus, to study range-wide patterns of plant population performance, we propose a framework based on three key points:

1. The precise assessment of **habitat suitability** at high resolution, to investigate how ecological gradient impact vegetative and reproductive traits. This requires a detailed analysis of both macro- and micro- ecological niche, including bionomic axes (*e.g.* competition, predation, facilitation).
2. The **spatial structure** of this habitat, in order to assess in which extent a given population exploits its surrounding environment.
3. The analysis of life history traits of the population and especially the **dispersal potential** of the population.

Those measures could bring clues to understand whether population performance is limited by habitat quality, habitat availability, biotic interactions or intrinsic drivers such as life history traits. Sexton *et al.* (2009) suggested that range limit might be characterized by an increase of sink populations, and this framework could be used to investigate such question.

The ecological niche and processes underlying contemporary patterns of plant diversity in the Mediterranean region

<u>The origin of floral biodiversity in the Mediterranean basin</u>

The Mediterranean basin is a biogeographical crossroad, a tension zone between Africa, Asia and Europe (Comes 2004).The development of the contemporary Mediterranean flora has a relatively recent origin. In the Tertiary period, most of the flora was broadly composed by tropical forests, including evergreen rainforests and laurel forests (Thompson 2005). Then, a drying processes begun in the middle Miocene, and continued through the Pliocene along with an amplified seasonality (Suc 1984). At the time of the Messinian salinity crisis, many places around the Mediterranean basin (especially in the north) already exhibited sclerophyllous forest with evergreen Oaks, along with Pines. This process has continued until the late Pliocene / early Pleistocene, when elements closer to the contemporary flora extended through the region. From then on, the Pleistocene was marked by alternately spreading of steppe like and forest vegetation, punctuated by glaciations. This period ended with the Last Glacial Maximum that took place 20 000 years ago. Through the Holocen, the basin was marked by the continuous presence of human civilizations that strongly influenced biodiversity (Blondel *et al.* 2010).

Recent speciation processes in the Mediterranean basin

Over the past million years, the relative climatic stability has favored the persistence of Mediterranean flora in a fairly restricted area, and has provided refugia for continental and mountain taxa during ice age periods. This characteristic is one of the key drivers of hotspot biodiversity across the world (Safriel *et al.* 1994; Araújo 2002; Médail & Diadema 2009). The Mediterranean basin is characterized the dynamism of contemporary speciation processes, as many endemic species are neo-endemic (Thompson 2005).

The contemporary distribution of species is often used to investigate the particular history of its range spread and contraction (Alba-Sánchez *et al.* 2010; Poncet *et al.* 2013; Besnard *et al.* 2013). The distribution of species in the Mediterranean basin ranges from large continuous to highly disjunct distributions, and micro endemic species. Their historical spatial and temporal dynamics are complicated to infer due to the lack of fossil records, but it is likely that refugia were spread all around the basin (Feliner 2011), and played a key role regarding those issues. The complex geology and topography are prone to create island-like populations in matrices of unsuitable habitat (Thompson *et al.* 2005). Isolation of peripheral populations is a key driver of genetic differentiation (chapter I), and several works showed that spatial isolation is a driver of plant speciation in the Mediterranean, source of vicariant taxa.

While allopatric isolatation is a major driver of plant speciation, it should not mask the importance of ecological divergence to drive selection processes. Indeed, peripheral populations might occur in unique ecological conditions, especially regarding their micro ecological niche (chapter III). Variations of fine scale-scale ecological parameters have been proven several time to be key differences between endemic species compared to their more widespread congeners (Lavergne *et al.* 2004; Youssef *et al.* 2011; Anacker & Strauss 2014).

Thus, we suggest that budding speciation (Anacker & Strauss 2014) can be a key mechanism in the Mediterranean basin. In this model, a small group of population differentiates from their widespread progenitor thanks to different isolation mechanisms (both sympatric and allopatric) and is favored by ecological differentiation (Givnish 2010; Grossenbacher *et al.* 2014). This creates a strong range asymmetry (Crawford 2010), which can be observed in pairs of endemic-widespread sister species (Lavergne *et al.* 2004; Anacker & Strauss 2014). The degree of divergence between relatives depends on the duration and the intensity of isolation, thus the rhythm of range contraction/expantion and the persistence of species in refugia condition those processes.

Historical range contraction / expansion Mediterranean flora

In this context the Last Glacial Maximum (LGM) strongly impacted plant distribution in the Mediterranean basin (Hewitt 1996, 1999; Cozzolino *et al.* 2003; Hampe *et al.* 2003). In chapter 2, we stressed the importance of this event on the current patterns of floral polymorphism of the style-dimorphic *Narcissus dubius*. Despite having a currently wide and broadly continuous range across Southern France and Northern Spain, the abrupt geographical discontinuities in its reproduction system may find its roots in an important range contraction during the LGM. In France, the limit was marked by the Rhône valley, which may constitute an admixture zone where populations formerly isolated on each side of this barrier are meeting. This hypothesis was supported by molecular evidences on *Quercus ilex* (Lumaret *et al.* 2002), and will be tested soon on *Narcissus dubius* and *Convolvulus lanuginosus* (see Box 2). However, the loss of floral polymorphism might result from very different processes (i.e. population reduction leading to bottlenecks *versus* founder effect during recolonization) which can have different genetic implication despite comparable effect on reproduction biology of the species.

Hypothesis on the recent biogeographical history of peripheral isolates

Isolation between peripheral and central populations is dependant on their persistence at range limit during glaciations. Despite a clear geographic isolation, sometimes up to 1 000 Km of their current distribution, those population appear to be (at least morphologically) similar to those in the centre part of their distribution, as no geographical subspecies have yet been described. Thus, isolation might have been quite recent, in regards to other groups that show distinct subspecies or disjunct sister species (Debussche, Garnier & Thompson 2004; Thompson 2005; Youssef *et al.* 2011; Santos-Gally *et al.* 2012). In chapter II and IV we discussed the potential role of micro-refugia that could have allowed Mediterranean species to persist in France during the LGM. Those patterns rely on biogeographical and ecological evidences, and require genetic investigations to be validated.

Hence, peripheral populations studied here could constitutes primers for future species, as they fit criteria supposedly involved in the budding model of speciation (Crawford 2010).

Climatic transitions as evolutionary hotspots for plant conservation

The importance of protecting peripheral isolates

Conservation policies are built by countries, which evaluate species conservation status through an administrative prism delimited by country's borders that usually does not correspond to biogeographical entities. As a result, this has led to what Hunter & Hutchinson (1994) named "parochialism" conservation: protecting species that are locally rare, but globally common across their range. Conservation values of those species have generated debates about the accurateness of such measures, regarding the limited resources devoted to biodiversity conservation (Araújo 2002; Channell 2004 p. 200). Indeed, the conservation of peripheral isolates raises a double dilemma.

First, due to their potentially reduced size and peripheral isolation, they are supposed to be less genetically diverse (Eckert *et al.* 2008). Despite this pattern has received mixed global support from the literature, we showed that a greater peripheral isolation increased the probabilities of a decline in genetic diversity (Chapter I). As a result, this poverty is suspected to impede adaptive response to local and global changes (Alleaume-Benharira, Pen & Ronce 2006; Bridle & Vines 2007). But on the other hand, due to their isolation these populations are prone to differentiate by drift, and are frequently exposed to different ecological conditions (Lesica & Allendorf 1995, chapter III). Peripheral populations might therefore be locally adapted, and contain unique genetic variations which makes them of significance for conservation (Leppig & White 2006). For some authors, the loss of genetic diversity would be as important as the extinction of a species (Ledig 1993).

Second, peripheral populations are said to be less viable due to their ecological marginality (Lawton 1993). This statement is highly case specific, as the relationship between population performance, ecological marginality and geographic periphery is not straightforward (Soulé 1973; Pironon *et al.* 2015). For example, Mediterranean plants studied in this thesis were not always marginal regarding their climatic niche (Chapter IV), and high local abundances were found in both central and peripheral populations (Chapter V), suggesting that suitable habitats existed all across species range. Then, isolation from their main range can turn them into crucial stepping stone populations in case climate change would induce species migration (Provan & Bennett 2008; Médail & Diadema 2009; Tzedakis, Emerson & Hewitt 2013).

While several criteria are required to prioritize conservation issues (such as habitat threats, or human intrinsic value) new conservation stakes should integrate species evolutionary potential to preserve mechanisms that generate biodiversity (see box 2 for a case study).

Integration of peripheral isolates in conservation processes

Parochialism conservation might require to step down from a species perspective to a population perspective, and we propose to adapt Lesica & Allendorf (1995) theoretical model to assess populations evolutionary potential. This method ranks populations of a given species according to their isolation and ecological differentiation (figure 3). Isolation is supposed to drive stochastic genetic differentiation based on genetic drift, while different ecological conditions are thought to induce different selective pressures and local adaptation. While this dichotomy might seem simplistic it constitutes a comprehensive framework to integrate peripheral population into conservation strategies. Then, the main issue is to identify metrics that allow a normalized assessment of ecological marginality and range structure (especially regarding isolation) that could be applied to the whole flora of a given region in a homogenous way.

Nevertheless, other criteria are important to account for when evaluating populations' evolutionary potential. In particular, the need to evaluate the probability of persistence of a population is crucial. Indeed, protecting sink populations would be useless if they are doomed to disappear (Channell & Lomolino 2000).

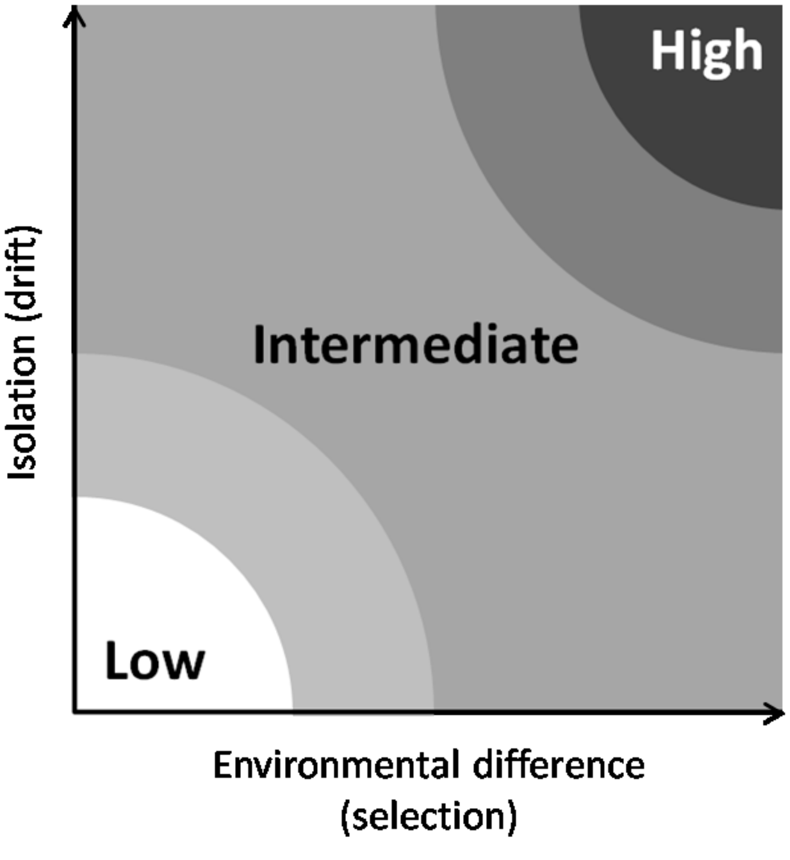


Figure 6-3. Relative conservation value of peripheral populations from an evolutionary perspective.
Redrawn after Lesica and Allendorf (1994)

France, a crossroad for plant conservation in the Mediterranean

In this context, areas of ecological transition are of prime importance for conserving biodiversity (Smith *et al.* 2001; Araújo 2002). As stated by Spector (2002), "protecting biogeographic crossroad provide long term biodiversity benefit by conserving evolutionary processes such as speciation and coevolution".

Southern part of continental France constitutes the northern border of Mediterranean climate in the Mediterranean basin. However, this limit is a narrow strip known as mesomediterrean stage (Rivas-Martínez 1996). The flora of this special area is original and consists in an association of taxa that have very different range. Therefore, several groups of species are present in a marginal situation, despite their "opposite" situation (Lavergne *et al.* 2005). Those groups of species are under different threats (Thuiller *et al.* 2005), and identifying causes of decline is the first step to prevent species loss (Lavergne *et al.* 2005). In this paper, authors pointed out the fact that euro-Siberian plants have shown the greatest decrease during the last century, mainly because of changes in land use and human impact on ecosystems (especially through agricultural change). While Mediterranean species were globally stable during the period considered (Lavergne, Molina & Debussche 2006), pressures might have moved to those species, as recent urbanization threat their habitat (Vimal *et al.* 2012b).

This is especially true for coastal areas that have been shown to contain most species included in this thesis (chapter IV). Human pressures through urbanization has induced population destruction and fragmentation during the last 50 years (Blondel *et al.* 2010; Thompson & Gauthier 2011), which is a threat to biodiversity in general and a legal issue for protected species (which cannot legally be destroyed). While different legal procedures exist to limit the impact of such pressures on biodiversity (Struillou 2004; Prieur 2005), the use of reinforcement or translocation have increased recently (see box 1 for examples). The fine scale evaluation of the micro-ecological niche might be crucial to assure their success.

Finally, the identification of micro refugia and their potential importance to conserve peripheral isolates can provide clues design protected areas. In our case, we have shown that much localized areas host many species (chapter IV), and were concordant with areas of high endemism and potential refugia for Mediterranean plants (chapter II). Those potential micro-refugia could also constitute genetic hotspots that concentrate ancient lineages of species that persisted there, but are more widespread now (Petit *et al.* 2003). Thus, they represent places of high interest to conserve biodiversity in the long term, especially regarding species adaptative potential (Erwin 1991; Klein *et al.* 2009).

Box 6-1. The ecological niche and the reintroduction of listed species

The destruction of plant population has become a major threat on biodiversity during the last few decades, primarily because of development projects and urbanization. Legal obligations related to the destruction of protected species have led state agencies in charge of biodiversity issues to create mechanisms to avoid, reduce and compensate the impact of such projects on protected plants. Population displacement has become a key tool during past decades to achieve these objectives. Yet, the success of this kind of operation is generally low (Godefroid *et al.* 2010) and strongly dependant on the protocol used, especially concerning the choice of the micro-habitat where practitioners choose to plant individuals (Godefroid *et al.* 2010). Hence, the use of a precise and standardized protocol is to capture the fine-scaled variation in ecological characteristics, which may condition the success of the operation.
The species studied in this thesis are nearly all listed for protection in France, therefore their destruction is legally regulated and translocation processes are currently undertaken to limit the impact of several development programs. Here I present four examples of such impact on populations.

Convolvulus lanuginosus is a Mediterranean hemicryptophyte, impacted in 2016 by a development project which will destruct one population. Further details are provided in box 2.

Dorycnopsis gerardi is a Mediterranean hemicryptophyte present alongside the highway between Perpignan and Spain, in the department of Pyrénées Orientales. Several populations will be destroyed due to the enlargement of the highway. Thus, the Conservatoire Botanique Mediterranéen de Porquerolles is integrating data gathered in this thesis into the transplantation protocol and the choice of micro-habitat locations to plant seeds and create new populations.

Stipa capensis is a Mediterranean annual grass that has been impacted by the settlement of industrial storehouses near the Marseille industrial harbor (Bouches-du-Rhône, France). Several populations are now monitored by John Thompson's team at the CEFE. Data collected in this thesis have been used to propose a reinforcement protocol for this species in a report to the DREAL-PACA in 2014.

Ophrys bombyliflora is a Mediterranean orchid for which several populations will be impacted by the settlement of industrial storehouses. The populations are located around Narbonne (Aude, France), near two important highways, which make them highly vulnerable to human pressure on land use. A program managed by an engineering office in ecology in collaboration with the CEFE has been discussed as a possibility for a future reintroduction program for this species.

Other species not included in this thesis (*Iris xiphium, Gagea granatelli s.l.*, Allium *chamaemoly*) have suffered population destruction and have been translocated to protected areas thanks to collaboration between our research team, conservation management staff, private companies and government staff. The data and experimental protocols have been freely provided to collaborators to help set up (hopefully successfully) conservation operations.

Box 6-2. A reintroduction program for peripheral isolates of *Convolvulus lanuginosus*

Convolvulus lanuginosus is a Mediterranean endemic species whose distribution is centered on southern Spain, from Andalusia to Catalonia, along the Mediterranean coast. The species reaches its southern limit in Andalusia and northern Morocco, while its northern limit occurs in the south of France in two distinct and isolated zones. This species is rare in southern France and is listed for regional protection in the Provence region (PACA).

In 2016, a development project by RTE (Electricity Transport Network) will impact a population of *C. lanuginosus* near the town of Castellet (Var, France). In accordance with the French law on Nature protection, development measures have been adapted to avoid and reduce the impact of the project on this population. Nevertheless, part of the population will be destroyed and to complement the measures adopted to reduce the impact of the development project, a detailed study of the genetic structure of this species has been requested by the state agents that instruct the dossier for this species in order to prepare a reintroduction plan for the population.

Based on the results of my study of the ecological niche of this species, we have set up collaboration with population geneticists, state agents and conservation agency staff to include knowledge on the ecology of the species in the preparation of the reintroduction protocol. In addition, we provided leaf samples from ten individuals per populations studied in my thesis. This material has constituted a most useful first set of samples to develop microsatellites markers and to begin to analyze genetic variation across the range of this species.

This project constitutes an applied use of my data on a specie's ecology for conservation action that involves scientists, conservation management staff and government agents. The application of the protocol developed in my thesis could help to ensure the technical success of the project. In addition, the extension of the genetic study to the whole distribution of the study species, in relation to our data on the ecology of the species in its central and peripheral populations will provide elements concerning the phylogeographic history of the species. Thus, the future project will help test hypothesis of the persistence of Mediterranean species such as *C. lanuginosis* in peripheral refugia during the LGM (see chapters 2 and 4, a corner stone of this thesis).

Conclusion and perspectives

"Hutchinson's niche concept is a powerfull tool, greatly underutilized by ecologist"

Pulliam, 2000

In this thesis, we have tried to tackle a broad range of ecological questions related to population biology, biogeography and conservation. The common denominator of all this work is the concept of ***ecological niche***. Through those five chapters, we have brought new perspectives on the use of the ecological niche to get insights on mechanisms that shape population features, and might lead to species diversification.

The **chapter 1** is a literature review dealing with the Centre-Periphery Hypothesis (CPH). While this hypothesis relied on an assumed concordance between geographic periphery and ecological marginality, we show that this assumption is misleading, and has led to confuse understanding of the CPH. Thus, we propose a new framework that requires explicit characterization of range structure, ecological niche and species history to assess range-wide variations in population performance and genetic variation.

This framework is used in **chapter 2**, as we investigate the ecological niche of *Narcissus dubius* to infer its potential past distribution during the Last Glacial Maximum, and bring insights on factors that have shaped its reproduction system.

Chapter 3 is dedicated to a comparative study of spatial variation in the ecological niche of 11 Mediterranean plants between their central distribution (in Spain and Italy) and their northern periphery in southern France. While their broad habitat remains similar across their range, micro-ecological component of the niche vary greatly between central and peripheral populations. This highlights the ecological originality of peripheral population which, associated with their spatial isolation, confer them a high evolutionary potential.

In chapter 4, we analyze the climatic niche of those 11 species, and show that while growing under globally cooler and wetter climate in France, peripheral populations are not climatically marginal compared to their central relatives. Thus, we discuss how ecological factors impact the realized climatic niche. Additionally, most of them exhibit a common distribution pattern that could result from their past distribution in cryptic refugia during Pleistocene glaciations. This pattern was shared by more than 80 other Mediterranean species.

Finally, **chapter 5** is conceived as a short synthesis that merges ecological niche and position across the range to explain patterns of local abundance. Both climatic and micro-ecological factors impact plant local abundance, but no converging pattern across taxa is observed.

This thesis has also generated many questions and research perspectives in different fields of biology. Here we conclude this work by detailing some of them that seem relevant.

First, regarding **evolutionary biology**, it is of prime importance to investigate whether variations observed in the realized ecological niche of peripheral populations are due to phenotypic plasticity, or result from adaptative mechanisms driven by selection. Then, consequences on plant life-history traits should be a matter of close interest, as it can shed light on the role of habitat differentiation in plant speciation.

Regarding **population biology**, a striking element is the heterogeneity of analyses testing the abundant-centre model of Brown (1984). This model includes “abundance” in its name, but was conceptualized on spatial patterns of plant frequency (Haeck & Hengeveld 1981; Brown

1984), and has been mostly tested using plant density. Those 3 features of plant population are not analogous, and could respond differently to ecological gradients. We propose a framework in chapter 5 that rely on a precise description of the ecological niche to assess global habitat quality and local availability, and relate it to life history traits of the population to get insights on mechanisms driving population performance and abundance.

A crucial point of this thesis remains in the ecological evidences suggesting a persistence of Mediterranean taxa in southern France during the Last Glacial Maximum. This hypothesis requires genetic investigations in order to shed light on mechanisms that have driven **biogeographical patterns** of plant diversity in the Mediterranean basin.

Finally, we have emphasized on the need to integrate species evolutionary potential in **conservation** programs. While the theoretical model proposed by Lesica & Allendorf (1995) is interesting, it still requires a complete methodology to quantitatively assess the degree of spatial isolation and ecological differentiation essential to rank populations.

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