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ÉCOLOGIE ÉVOLUTIVE, FONCTIONNELLE ET DES COMMUNAUTÉS

Par **Adélaïde THERAROZ**

**Ressources génétiques du pin maritime : variabilité
géographique, pressions de sélection et adaptation future**

Sous la direction de Santiago C. GONZÁLEZ-MARTÍNEZ, directeur
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Soutenue le 05/11/2024

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Ressources génétiques du pin maritime : variabilité géographique, pressions de sélection et adaptation future

Résumé:

Le changement climatique affecte déjà les écosystèmes forestiers sur tous les continents, comme en témoignent la migration des espèces vers le nord et vers les plus hautes altitudes et l'augmentation du dépérissement des forêts en réponse, non seulement à des conditions climatiques plus rigoureuses, mais aussi à des épidémies de ravageurs et de maladies résultant d'événements climatiques sans précédent ainsi que de l'intensification des activités humaines. Ces phénomènes ont des conséquences négatives sur le fonctionnement des écosystèmes forestiers et la persistance des espèces et des populations, car ils menacent la disponibilité des ressources, perturbent la dynamique des populations et remettent en question les limites physiologiques et la résistance aux agents pathogènes. L'avenir des populations d'arbres de forêts naturelles face au changement climatique, compte tenu de leur nature sessile et de leur long temps de génération, est donc préoccupant, que ce soit en termes d'extinction, de capacité à migrer ou à s'adapter par le biais de changements génétiques. Du point de vue de la conservation, nous devons comprendre dans quelle mesure les arbres forestiers seront capables de survivre face au changement climatique actuel et futur. L'énorme quantité de données génomiques disponibles grâce aux outils de séquençage de nouvelle génération révolutionne notre compréhension de la base génétique de l'adaptation. À son tour, elle accélère le développement de nouvelles méthodes statistiques qui peuvent prédire la vulnérabilité génomique des arbres forestiers au changement climatique dans l'espace et dans le temps, et déterminer le potentiel de maladaptation génétique dans des conditions climatiques changeantes. Dans cette thèse de doctorat, j'ai utilisé le pin maritime (*Pinus pinaster* Ait.), un conifère à longue durée de vie originaire de la partie occidentale du bassin méditerranéen, comme étude de cas pour démêler les schémas spatiaux de la variation génétique à l'échelle de l'aire de répartition et à l'échelle régionale en fonction de différents gradients, anticiper les réponses des populations au changement climatique et donner un aperçu des tendances actuelles en matière de sélection naturelle. Le premier chapitre vise à comprendre comment, à l'échelle de l'aire de répartition de l'espèce, la variation génétique, l'adaptabilité et le potentiel d'inadaptation à court terme aux conditions climatiques futures sont distribués du cœur de l'aire de répartition vers les marges géographiques et climatiques. Le deuxième chapitre examine les

schémas spatiaux de la sélection naturelle contemporaine en analysant les changements phénotypiques en réponse aux pressions sélectives actuelles, et donne un aperçu des tendances actuelles de l'adaptation locale au changement climatique pour le pin maritime à l'état sauvage. Le troisième chapitre vise à identifier les schémas spatiaux de variation génétique du pin maritime dans l'île de Corse, caractérisée par des particularités spécifiques et constituant des ressources génétiques précieuses pour l'espèce, et à analyser leurs capacités d'adaptation actuelles et futures au changement climatique. Dans l'ensemble, cette thèse de doctorat étudie les facteurs sous-jacents et le potentiel des réponses adaptatives du pin maritime aux conditions environnementales changeantes à différentes échelles spatiales et temporelles, contribuant ainsi au développement d'un cadre intégratif essentiel pour anticiper les réponses des populations au changement climatique, sur la base duquel des prédictions solides pour les stratégies de conservation et de gestion peuvent être développées.

Mots-clés: Génétique des populations, Ressources génétiques forestières, Populations marginales, Régions Méditerranéenne et Atlantique, Sélection naturelle, Modélisation écologique, Génomique du paysage, Variation génétique adaptative, Potentiel adaptatif, Maladaptation, Arbres forestiers, Changement climatique

Maritime pine genetic resources: geographical variability, selection pressures and future adaptation

Abstract:

Climate change is already affecting forest ecosystems on all continents, as evidenced by the northward and upward migration of species and the increase of forest dieback in response to not only harsher climate conditions but also to pest and disease epidemics resulting from unprecedented climatic events as well as the intensification of human activities. These phenomena have negative consequences for the functioning of forest ecosystems and the persistence of species and populations, as they threaten the availability of resources, disrupt population dynamics and call into question physiological limits and resistance to pathogens. The future of natural forest tree populations in the face of climate change, given their sessile nature and long generation times, is therefore worrying, whether in terms of extinction, ability to migrate or adapt through genetic change. From a conservation point of view, we need to understand the extent to which forest trees will be able to survive in the face of current and future climate change. The huge amount of genomic data available from next-generation sequencing tools is revolutionising our understanding of the genetic basis of adaptation. In turn, it is accelerating the development of new statistical methods that can predict the genomic vulnerability of forest trees to climate change in space and time, and determine the potential for genetic maladaptation under changing climatic conditions. In this PhD thesis, I used maritime pine (*Pinus pinaster* Ait.), a long-lived conifer native to the western part of the Mediterranean basin, as a case study to unravel the spatial patterns of genetic variation at the range-wide and regional scales function of different gradients, anticipate population responses to climate change and provide insight into current trends in natural selection. The first chapter aims to understand how, at the scale of the species range, genetic variation, adaptability and the potential for short-term maladaptation to future climatic conditions are distributed from the range core towards the geographical and climatic margins. The second chapter examines the spatial patterns of contemporary natural selection by analysing phenotypic changes in response to current selective pressures, and provides an overview of current trends in local adaptation to climate change for maritime pine in the wild. The third chapter aims to identify the spatial patterns of genetic variation of maritime pine in the Corsica Island, characterized by specific features and constituting valuable genetic resources for the species, and to analyse their current

and future adaptive capacities to climate change. Overall, this PhD thesis studies the underlying drivers and potential of maritime pine adaptive responses to changing environmental conditions at different spatial and temporal scales, thus contributing to the development of an integrative framework essential for anticipating population responses to climate change, on the basis of which robust predictions for conservation and management strategies can be developed.

Keywords: Population genetics, Forest genetic resources, Marginal populations, Mediterranean and Atlantic regions, Natural selection, Ecological modeling, Landscape genomics, Adaptive genetic variation, Adaptive potential, Maladaptation, Forest trees, Climate change

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I. Introduction

1. General context

1.1. The benefits of forests for natural ecosystems and human societies

Over 30% of the Earth's surface is covered by forests (FAO, 2020). Forests constitute a vital component of almost every facet of life on our planet; they provide immense ecosystem services and their role in regulating the Earth's climate can hardly be overstated.

Healthy forests are powerful carbon sinks, the second largest carbon sink after the oceans. They absorb and store carbon dioxide, reducing the amount of greenhouse gases in the atmosphere. Estimates show that, at global level, between 2001 and 2019, forests absorbed twice as much carbon as they emitted, i.e., 7.6 billion metric tonnes of CO₂ per year (Narain & Goswami, 2022).

Forests regulate the water cycle by purifying and gradually redistributing water in the soil and in the atmosphere through evapotranspiration, generating precipitation and therefore reducing droughts. Another direct effect of evapotranspiration is the thermal regulation of the habitat close to the trees, reducing the impact of heat waves on their immediate surroundings, and creating a multitude of ecological niches for biodiversity (Brockerhoff et al., 2017; Lindenmayer et al., 2016). More generally, forests are home to around 80% of the world's terrestrial biodiversity (FAO & UNEP, 2020). Forests also maintain soil structure, thanks to the organisation of their root systems, preventing landslides and soil erosion, thereby reducing the risk of land-based climate disasters.

Forests also play a very important socio-economic role too, being the basis of the economic, ecological and socio-cultural well-being of many communities around the world. Globally, almost a billion people depend on forests for access to drinking water, food and medicines (Shackleton & de Vos, 2022)

Worldwide, around 1.15 billion hectares of forest are managed mainly for the production of wood (energy production, construction and manufacture of objects) and non-wood products (FAO, 2020). A further 186 million hectares of the world's forests are allocated to non-profit social services, such as recreation, tourism, education and spirituality, and provide a space for leisure and inspiration for the arts.

However, with the dramatic increase in man-made greenhouse gases, deforestation and forest degradation, forests can also become sources of carbon (Green & Keenan, 2022; Mitchard, 2018). Furthermore, as global temperatures continue to rise, forests are becoming increasingly sensitive to the increase and unpredictability of droughts, forest fires, and new pests and diseases; the persistence of forests is on a knife-edge, raising worrying prospects for their future sustainability.

1.2. Past and present climate change: different pace and evolutionary consequences for forest trees

Plants have been subject to climate change for thousands of years. During the Pleistocene (2.58 million to 11,700 years BP), long before human-induced climate change, a succession of glacial-interglacial periods occurred as a result of the variation in astronomical forces; a combination of changes such as Earth's orbital parameters, continental ice sheets (Batchelor et al., 2019), sea-surface temperature and ocean circulation, and atmospheric greenhouse gases concentration (carbon dioxide, methane and ozone), mainly due to changes in Milankovitch oscillations (Berger, 1988; Elderfield et al., 2012; Hays et al., 1976; Rohling et al., 2014).

The most recent of these glacial-interglacial episodes is known as the 'Last Glacial Maximum' (LGM; 26,000-20,000 years BP). During the LGM, the ice sheets covered large areas of the Northern Hemisphere and the sea level decreased globally for an average of 120 meters, modifying the shapes of the continents (Peltier, 2002). The repeated glaciations severely affected land biota, driving large-scale extinctions and migrations in plant and animal populations, which significantly shaped the limits of the distribution areas and induced large fluctuation in the census size (N_e) of many plant species (Normand et al., 2011; Petit et al., 2008; Tzedakis et al., 2013). Binney et al. (2009), Heikkilä et al. (2009) and Willis, (1994) (among others), demonstrated that, on the basis of pollen, stomata and plant macrofossils stratigraphy, tree species such as *Pinus*, *Betula* and *Larix* shifted their range towards northern latitudes during the LGM glacial episodes. In addition, Birks, (1986) showed that pollen and plant macrofossil diagrams depicted unique combinations of tundra and steppe plants colonising the northern Europe following the LGM.

The LGM is considered one of the main drivers of the current distribution of genetic diversity in plants, resulting in genetic divergence between populations in the south and

northern range (Binney et al., 2009; Cheddadi et al., 2006; Pearson, 2006; Petit et al., 2003). Indeed, the species ranges were restricted to certain geographical areas where the climatic conditions were favourable, generally representing a small fraction of their original range (Cheddadi et al., 2006; Stewart et al., 2010). These regions are usually described as refuge areas or “*refugia*”, which created a reservoir of isolated groups of individuals with a specific genetic composition and limited dispersal, resulting in a unique genetic make-up (Milesi et al., 2023a; Petit et al., 2003).

During interglacial periods, change in climatic conditions towards more favourable climate resulted in range expansions. These demographic expansions and contractions may have strong genetic implications, inducing either depletion or increase in genetic diversity depending on the species’ dispersion abilities and the speed of the demographic change (Arenas et al., 2012). For example, *Pinus sylvestris* and *Pinus pinaster*, two conifers widely distributed in the boreal and Mediterranean regions, respectively, have undergone spatiotemporal changes that have shaped their current genetic structure and phylogeographic profile (Tóth et al., 2019). In the case of *Pinus pinaster*, range expansion from glacial refugia (González-Martínez et al., 2007), influenced by natural physical barriers such as seas and mountains, has strongly shaped its current genetic structure (Burban & Petit, 2003), resulting in distinct gene pools along a fragmented distribution (Baradat & Marpeau-Bezard, 1988; Bucci et al., 2007; Jaramillo-Correa et al., 2015). Numerous studies have shown that past demographic history has had a strong impact on the current spatial patterns of *Pinus pinaster* genetic resources, notably shaping its genetic diversity (González-Martínez et al., 2002; Jaramillo-Correa et al., 2010; Naydenov et al., 2014).

The paleoclimate record combined with global models shows past ice ages as well as periods even warmer than today. But the paleoclimate record also reveals that the current climatic warming is occurring much more rapidly than past warming events (IPCC, 2007). As the Earth moved out of ice ages over the past million years, the global temperature rose a total of 4 to 7 °C over about 5,000 years (IPCC, 2007; Jouzel et al., 2007; Mann et al., 2008; Uprety et al., 2019). In the last century alone, the temperature has risen by 1.1 °C, around ten times faster than the average rate of warming during the ice ages (IPCC, 2021; Uprety et al., 2019).

Anthropogenic pressure of this magnitude is creating unprecedented habitat disturbances in forest ecosystems, with consequences affecting all levels of organisation (Mihoub et al., 2017; Young et al., 1996). At the beginning of the 21st century, a plethora of studies sounded the alarm

by demonstrating the direct impacts of anthropogenic greenhouse gases on climate change in the Earth's main taxonomic groups, on every continent and in every ocean. Parmesan & Yohe, (2003) in their meta-analysis estimated that 59% of 1,570 species comprising numerous taxa such as birds, amphibians, fish, butterflies, herbs, shrubs and trees, showed significant changes in their phenologies and/or distribution range over the past 20 to 140 years. More specifically, forest ecosystems will have to adapt not only to changes in average climate variables, but also to an increased risk of extreme meteorological events, such as prolonged droughts, storms and floods (Lindner et al., 2010). Increased atmospheric CO₂, ozone and nitrogen deposition will affect tree physiology, carbon allocation and plant interactions (Lindner et al., 2010; McLaughlin et al., 2007). Not only climatic events, but also biotic (pest and disease epidemics, Volney & Fleming, 2000) and abiotic (changes in fire intensity and occurrence) disturbances will have strong implications for forest ecosystems (Lindner et al., 2010). Human-induced climate change and its associated consequences will pose a major challenge to the persistence of forest tree populations in a changing world.

“There are three possible fates for forest tree populations in a rapidly changing environment: persistence through migration to track ecological niches spatially; persistence through adaptation to new conditions in current locations; and extirpation” (Aitken et al., 2008).

In the coming years, we will need to shed light on the extent to which forest trees will be able to persist in the face of current and future climate change, which will disrupt their habitat and the nature and intensity of interactions with it. This is necessary in order to find an acceptable balance between preserving the integrity and function of the forest ecosystem and ongoing human activities for a sustainable future (Bacles & Jump, 2011).

1.3. Role of genomics for adaptation

Global climate change is affecting all forms of life in all biomes, with adverse consequences for ecosystem functioning and species persistence (Merilä & Hendry, 2014), disrupting phenology, resource availability and competition dynamics, and challenging physiological limits and resistance to pathogens. The future of natural populations in the face of climate change, whether in terms of their extinction, their ability to migrate or to adapt through genetic change, is therefore of increasing concern. Understanding the genetic basis of organisms'

adaptation to changing environments is a fundamental subject of modern evolutionary ecology, but progress in this field has been (till recently) hampered by the lack of data at the genome level.

The 1970s saw the first revolutionary steps in DNA sequencing through Sanger methodology (Sanger et al., 1977), but these were marked by very long processing times and very high costs, making it impossible to obtain sufficient quantities of high-quality genomic data for most organisms. At the beginning of the 21st century, the development of ‘next-generation sequencing’ (NGS) approaches (Hudson, 2008) provided cheap genotyping of hundreds of thousands of common allelic markers or even whole genome sequencing for a growing number of individuals and species. With the growing amount of genomic data, the development of downstream analytical tools gave a new dimension to most areas of biology, enabling the screening of whole-genome variation within and between species across space and time (Stange et al., 2021). Notably, this has the potential to make possible the characterization of the genome-wide architecture that underlies adaptive traits and the genome-wide response to selection induced by natural or anthropogenic factors (Bernatchez et al., 2024).

How complex traits respond to new selection pressures at the genomic level has been the subject of a long debate. On the one hand, classical population geneticists considered that phenotypic adaptation occurred through mutations at a single or few linked loci (selective sweeps) (Smith & Haigh, 1974). On the other hand, quantitative geneticists considered adaptation to take place by simultaneous selection of a large number of loci with minor (additive) effects, as originally proposed by Fisher, (1918) and formalized as the infinitesimal model of polygenic adaptation (Barton et al., 2017; Bulmer, 1980).

The detection of polygenic responses at the genomic level by small allele-frequency changes at loci of minor effect only became feasible with the increasing amount of genetic sequence data (Götsch & Bürger, 2024). Genome-wide association studies (GWAS) aimed at finding associations between genome-wide markers and quantitative traits have led to groundbreaking discoveries in humans, with for example the first genetic markers firmly associated with schizophrenia (The International Schizophrenia Consortium, 2009), and in other species, such as cultivated (maize, rice and wheat, Alseikh et al., (2021); Coq--Etchegaray et al., (2023) and wild plants (*Arabidopsis thaliana*, Brachi et al., (2010); *Quercus petraea*, Coq--Etchegaray et al., (2023). This wealth of studies made it possible to discover genetic variants that confer, for example, biotic resistance to diseases (Kump et al., 2011; Liu et al.,

2024) and abiotic tolerance related to temperature and drought stresses (Ludwig et al., 2024). In addition, GWAS studies have unambiguously demonstrated the (mostly) polygenic architecture of complex quantitative traits, highlighting that, in most cases, a large number of genes underlie phenotypic variation (Tam et al., 2019; Visscher et al., 2017).

Plastic responses to new environmental conditions through changes in gene expression and epigenetic modifications are also main mechanisms that allow populations to cope with climate change (Merilä & Hendry, 2014). Plastic responses can increase phenotypic variation and evolutionary potential (Gianella et al., 2021), which can dampen the effects of climate change in genetically impoverished populations (O’Dea et al., 2016). Plastic responses can be investigated using molecular approaches, such as transcriptomics, epigenomics and proteomics, in both controlled conditions and natural environments (Götsch & Bürger, 2024; McCaw et al., 2020; McGaughan et al., 2021).

Finally, population genomics, including landscape genomics, a recent analytical method, can also predict genomic vulnerability to climate change through space and time and determine the potential for genetic maladaptation in future climates, enabling the development of appropriate management and conservation plans. Landscape genomics will be discussed further in section 3.4.

2. How do tree populations respond to global changes?

2.1. Migration and range shifts

Species ranges are dynamic and fluctuate in time and space (Brown et al., 1996; Davis & Shaw, 2001; Gaston, 2003), in response to complex positive and/or negative interactions of climatic, edaphic and biotic factors (Aitken et al., 2008).

Parmesan, (2006) and Thomas, (2010) in their meta-analysis reported that, already during the 20th century, a number of species have already shifted range in response to contemporary climate change. In England, Ford, (1945) described northward shifts of several Lepidoptera species, and linked it to an increase in temperature that occurred around 1915 in the country. Kaisila, (1962) described repeated demographic contraction and expansion of moth species populations in Finland in response to climate fluctuation. Similar range shift patterns were

found for European birds associated with the 1930s-1940s warming period (Gudmundsson, 1951; Harris, 1964; Kalela, 1949; Salomonsen, 1948), and for both birds and butterflies associated with the 1950-1960 cool and wet periods (Burton, 1975). These observations (among others) demonstrate a globally coherent signal of contemporary climate change impact on wild species, which plays a preponderant role in shaping species range boundaries (Chen et al., 2011).

In the case of forest trees, although there is evidence for upward elevational migration (Beckage et al., 2008; Holzinger et al., 2008; Kullman, 2002; Lenoir et al., 2010), few studies clearly document empirical evidence of populations shifting to higher latitudes (Figure I.1). Boisvert-Marsh et al. (2014) found significant distributional shifts consistent with northward migration for five deciduous tree species (*Acer rubrum*, *Acer saccharum*, *Betula papyrifera*, *Fagus grandifolia*, and *Populus tremuloides*) but other three species (*Abies balsamea*, *Picea glauca*, and *Picea mariana*) had southward shifting trends. In contrast, Mamet et al. (2019) found that *Larix* species in Siberia and North America appear to be shifting their distributions northward. These shifts are often strongly linked to recent (21st century) global temperature increase (Chen et al., 2011; Gottfried et al., 2012; Parmesan & Yohe, 2003), where lower latitudes and altitudes are characterized by warmer temperatures, whereas colder temperatures are found at higher latitudes or elevations. In addition, these results suggest that range shifts may be a species-specific response (Lawlor et al., 2024; Monleon & Lintz, 2015).

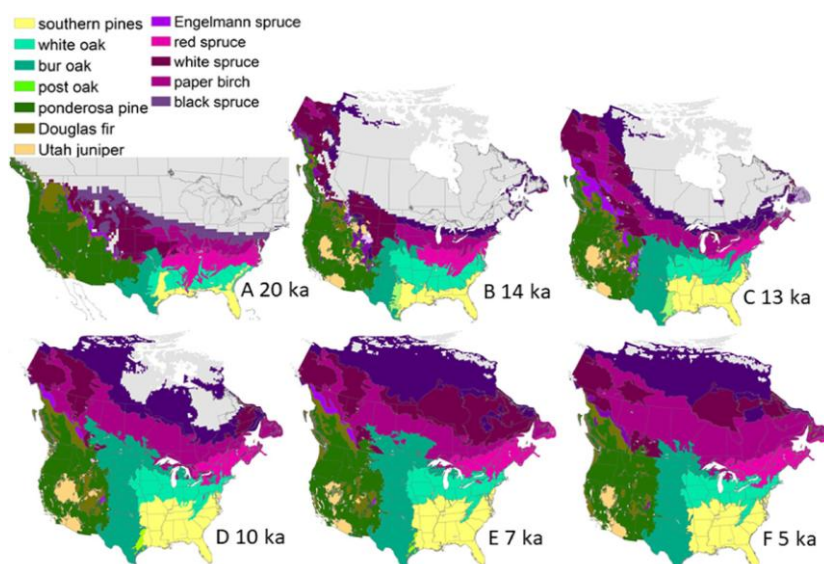


Figure I-1. Shifting potential tree species distributions from the Last Glacial Maximum to the Mid-Holocene in North America, with a correlation assessment. *Source: Figure modified from Hanberry (2023).*

Factors other than climate undoubtedly influence forest dynamics (Rubenstein et al., 2023). Dispersal and successful migration and establishment into newly suitable habitats are key mechanisms constraining range shifts. The latter will arise from the individual response to change in climatic conditions, short and long-distance dispersal events, habitat biotic (e.g., negative effect of competition) and abiotic (e.g., soil quality) conditions, and disturbances that provide opportunities for recruitment (Boisvert-Marsh et al., 2014).

Although palaeobotanical data indicate that trees have migrated in response to global climate cycles, these migrations were relatively slow and potentially did not exceed 100 m per year (Aitken et al., 2008). Studies of plant latitudinal range boundaries rely heavily on predictive models such as species distribution models (SDMs) (Elith & Leathwick, 2009; Guisan & Thuiller, 2005), because of the lack of empirical data coverage (Shoo et al., 2006) and difficulty to assess accurate spatial positions of adult trees and juveniles (Tingley & Beissinger, 2009). However, predictive models such as SDMs do not take into account non-climatic factors that may limit migration, such as ecological barriers to seed and pollen dispersal, as well as the probability of successful establishment. The latter is limited by biotic (Case & Taper, 2000) and abiotic ecological factors (Clark et al., 2013; Hampe & Jump, 2011) that can act differently on different tree species. In addition, the levels of genetic diversity across species ranges, the effective size of populations and the central-peripheral geographical structure are not well-known, despite all of them having a major impact on the species' potential for differential adaptation to new habitats (Aitken et al., 2008).

In the face of the current unprecedented rate of climate change, tree species, given their specific characteristics such as sessile form and long generation times, may not be able to migrate quickly enough (Savolainen et al., 2013) and thus may be subject to local extinction in their current ranges (Aitken et al., 2008; Dauphin et al., 2021). However, Bürger & Lynch, (1995), Koskela et al. (2007), Scotti et al. (2016, 2023) and Budde et al. (2024) (among others) have demonstrated that populations can persist in the face of climate change by remaining locally adapted, which above all requires a sufficient level of genetic diversity (Lefèvre et al., 2013; Scotti et al., 2016). Local adaptation depends on both the extent of genetic variation available and the turnover of allele frequencies to allow rapid evolutionary changes necessary to keep pace with unprecedented future climatic conditions (Blumstein et al., 2020).

2.2. Genetic diversity is the fuel of evolution

The genetic variation of a given population or an entire species is referred to as “genetic diversity” (Chung et al., 2023) and could be seen, through a theoretical perspective, as reflecting the balance between appearance and fixation of genetic variants. Global genetic diversity represents the amount and variation in neutral and adaptive allelic variants and can be estimated at different scales, from the individual to the population level. The genetic composition of populations is the raw material on which evolutionary processes operate (Frankel & Soulé, 1981; Jump et al., 2006) through the widely acknowledged process of pleiotropy (single genes that may be linked to a number of different phenotypes based on its function) and its effects on fitness (Orr, 2003; Otto, 2004; J. Zhang, 2023). The notion of individual fitness was conceptualised by Darwin, (1859) in his seminal work (Ariew & Lewontin, 2004), and is defined as an individual’s ability to survive and reproduce.

Insights about past demographic processes is key for understanding the relationships between population size and genetic diversity (López-Delgado & Meirmans, 2022; Willi et al., 2020). Population sizes are finite and fluctuate over time and often only a subset of individuals (relative to the census size of the population) contribute to efficient reproduction, making stochastic fluctuation of allele frequencies inevitable. The rate, amount and distribution of standing genetic diversity (within and between individuals and populations) is driven by the effective population size (N_e), through its interaction with evolutionary forces such as mutation, selection, migration and recombination (Figure I.2) (Barton & Charlesworth, 1984; Ellegren & Galtier, 2016; Wang et al., 2016). In populations with small effective sizes, there is more stochasticity and the rate of the change in allelic frequencies is faster than in those with larger effective sizes.

Standing genetic variation can be divided into two categories with contrasted evolutionary implications. Neutral molecular markers provide information on historical evolutionary divergence and demographic processes as well as evolutionary forces such as genetic drift (i.e., the random fluctuation in allele frequency), mutation and migration. Moreover, they are often used by population geneticists and landscape ecologists because they give unbiased estimates of genetic variation (e.g., heterozygosity), population structure, and gene flow (Schwartz et al., 2010). However, neutral genetic diversity is unsuitable for quantifying genetic changes in response to particular selection pressures (Ouborg et al., 2006) as it involves parts of the genome that are not targeted by natural selection (Sgrò et al., 2011).

The adaptive genetic diversity represents the part of the genome on which natural selection operates, thanks to the plurality of possible associations or interactions between alleles through pleiotropy and linkage disequilibrium. Adaptive allelic variants are expected to fluctuate according to the ecological gradients that constrain and drive natural selection and the persistence of species (Saccheri & Hanski, 2006), occurring at higher frequencies where they result in an increase of fitness (Savolainen et al., 2013). However, local adaptation may not involve necessarily substantial allele frequency changes, and could result mainly from small, potentially undetectable, covarying shifts in frequency at many loci (e.g., from highly polygenic traits) (S. Hoban et al., 2016). For example, Daniels et al. (2019) for *Pinus halepensis* and Scotti et al. (2023) for *P. pinaster* and *Cedrus atlantica*, found only few loci showed consistent patterns of allele frequency shifts along elevational gradients.

New allelic variants can arise via the process of spontaneous mutations due to DNA replication errors and/or the effect of mutagen agents. Their fate in a population is mediated by their effects on fitness and the population effective size (Ellegren & Galtier, 2016; Kimura & Ohta, 1969). Interactions between mutation rates and genetic diversity are not straightforward. Natural selection is considered to be more efficient in larger populations. A considerable proportion of newly arising mutations have moderate-to-severe deleterious effects and are expected to be purged by natural selection (Halligan & Keightley, 2009). However, in their heterozygous state, the expression of these mutations tends to be weak and thus not efficiently removed by purifying natural selection. Therefore, these mutations can still contribute to the mutational load of large populations (García-Dorado, 2012).

In addition, in a population subject to specific selective pressures, a mutation at a given site can confer a selective advantage for the individuals that bear it (Lewontin, 1974). Through the process of natural selection, this mutation will propagate in the population and eventually become 'fixed'. Allele fixation can arise through linkage disequilibrium when the selected allele is linked to nearby loci, reducing the overall neutral diversity and resulting in uneven amounts of neutral diversity across the genome. A similar but random process reducing diversity is the genetic drift, the random fluctuation of allele frequency for neutral variants across generations that can result in allele loss or fixation. However, beneficial mutations appear at a small rate and genetic drift alone could cause the extinction of newly arising beneficial mutations with high probability (Pénisson et al., 2017). For the sake of simplicity, we have considered in this paragraph the two types of fitness-effect mutations separately,

although in reality, these mutations can be present simultaneously and influence their reciprocal fate through linkage (Charlesworth, 2009; Charlesworth & Jensen, 2021) or a given mutation can even be neutral or beneficial depending on the environment (Cvijović et al., 2015). Thus, while genetic diversity is widely recognised as the fuel of evolution, its correlation with population fitness is not obvious (Pénisson et al., 2017).

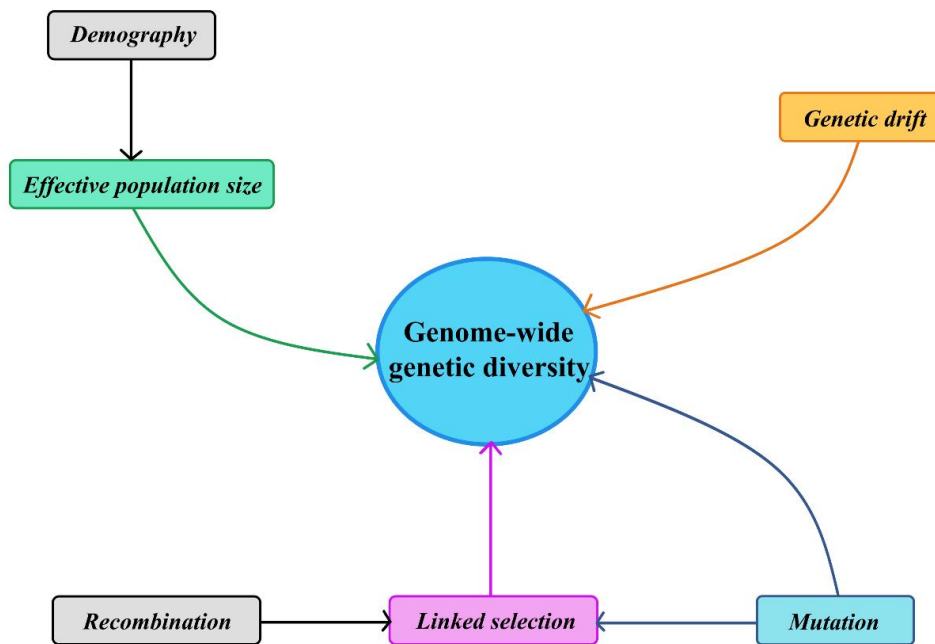


Figure I-2. Determinants of genetic diversity. Effective population size, selection, mutation and genetic drift are the main factors affecting diversity. *Source: Modified from Ellegren & Galtier (2016).*

2.3. The special case of small and isolated populations, and the Centre-Periphery Hypothesis (CPH)

The starting point for Frankel & Soulé, (1981) influential book *Conservation and Evolution* was the observation that endangered species are represented by a small number of individuals in small isolated populations. These populations are characterised by both low census size and low effective size. As mentioned in section 2.2, the effective size of a population is the key parameter governing species evolutionary dynamics such as the balance between natural

selection and genetic drift, which themselves condition the rates of population genetic diversity and evolutionary capacities (Lande, 1993).

Small and isolated populations are more vulnerable to demographic stochasticity than larger populations, the latter resulting either from environmental stochasticity or unpredictable catastrophes, which have a major impact on the effective population size (e.g., when a species undergoes a strong demographic reduction in population size also known as ‘bottleneck’) and on the population growth rate (Lande, 1988). When the effective population size decreases, genetic drift increases (the intensity of genetic drift being inversely proportional to the effective population size (Wang et al., 2016). With strong genetic drift in these populations, allele loss is almost inevitable, leading to an erosion of genetic diversity and an increased probability of random fixation of deleterious alleles (Lande, 1988; Ouborg et al., 2006; Sachdeva et al., 2022). Because of their small size, reproductive events occur mainly between relatives (Frankham et al., 2002), leading to an increase in inbreeding and homozygosity within the population (Hedrick & Garcia-Dorado, 2016). This can lead to inbreeding depression and an accumulation of genetic load (i.e., an accumulation of moderately or highly deleterious mutations due to reduced efficiency of natural selection), which has a negative impact on individual’s fitness (Charlesworth & Charlesworth, 1999). A negative impact on fitness can in turn lead to a further reduction in population size and create an ‘extinction vortex’ (Lande, 1988), which results, as described before, from a complex interaction between population size, the extent of genetic drift, existing genetic diversity and environmental fluctuations (Lande, 1988; Ouborg et al., 2006; Sachdeva et al., 2022). In addition, the loss of genetic diversity, associated with increased homozygosity and mutational load, may prevent these populations from adapting effectively to changing environments (Frankham, 1995; Nunney & Campbell, 1993) and may increase their probability of extinction (Bijlsma & Loeschcke, 2005).

A widely held assumption is that small isolated populations are often found on the periphery of the species’ range (Brown et al., 1996), as this area is considered to be characterized by sub-optimal environmental conditions compared to the core range (Birch, 1957; Gaston, 2003; Nicholson, 1958; Richards, 1961; Whittaker, 1971). This conception of species ranges is commonly referred to as the “Centre-Periphery Hypothesis” (CPH) (Brown, 1984; Gaston, 2003; Hengeveld & Haeck, 1982; Pironon et al., 2015) and has influenced much thinking on the evolution of species ranges (Sagarin & Gaines, 2002).

Locally adapted populations may have different climatic optima, resulting from contrasted climatic conditions that maximize fitness at their local origin (Aitken et al., 2008; Rehfeldt et al., 1999). Gene flow can have contrasted consequences in these marginal populations, due to asymmetrical dispersal (García-Ramos & Kirkpatrick, 1997; Lenormand, 2002; Rehfeldt et al., 1999; Savolainen et al., 2007). The CPH predicts that gene flow from core populations experiencing less extreme environments may bring allelic variants that are adaptive under the specific climatic conditions experienced by these core populations, promoting adaptation lags in the marginal populations experiencing a different environment (Rehfeldt et al., 1999). This process may prevent marginal populations from getting closer to their local optimum (Fréjaville et al., 2020; García-Ramos & Kirkpatrick, 1997; Lenormand, 2002). Levels of maladaptation would depend on migration rates, distance to the core populations and selection intensities (Slatkin, 1985). Adaptive lags due to asymmetrical gene flow have been reported in the literature (Fréjaville et al., 2020; Sáenz-Romero et al., 2019). Gene flow can reduce inbreeding and the resulting mutational load by introducing new alleles into marginal populations, but this process can also have a negative effect on the effectiveness of selection against deleterious alleles by diluting the homozygous mutational load through increased heterozygosity (Sachdeva et al., 2022). Overall, geographically peripheral populations should exhibit lower genetic diversity and higher genetic differentiation than central populations (Eckert et al., 2008a), which may limit their evolutionary potential, and inhibit local adaptation (Blows & Hoffmann, 2005; Eckert et al., 2008a; Gaston, 2003).

Such CPH predictions have not been supported in all studies in the literature. (Eckert et al., 2008b) in their review, found that around 60% and 70% of studies supported the CPH assumptions of declining genetic diversity and increasing genetic differentiation, respectively, towards the range margins. However, Gaston, (2003), Sagarin & Gaines, (2002), Samis & Eckert, (2007) and De Kort et al. (2021) (among others) have estimated demographic parameters from across entire species ranges and concluded that they provide only a weak support. Indeed, the CPH is based on the strong assumption that environmental conditions are necessarily harsher at the periphery, which is not necessarily the case. Furthermore, this paradigm does not take into account the level of fragmentation and the specific ecological conditions (topography, biotic factors) that characterize the core versus the periphery. Consequently, a quantitative analysis of population marginality should help to disentangle the different aspects of marginality itself, dissociating the roles of geography and ecology in

shaping range-wide patterns of genetic variation (Lira-Noriega & Manthey, 2014; Sexton et al., 2009).

Despite the expected lower diversity and potential maladaptation brought about by gene flow from core populations, there is empirical evidence that marginal populations may still be currently adapted to their local climate due to the existence of specific allelic variants (Castro et al., 2004; Petit et al., 2003). Thus, such marginal populations may constitute valuable genetic resources for strengthening local adaptation as the climate changes, if the climatic conditions experienced by these populations extend to the rest of the range (Etterson & Shaw, 2001; Fady et al., 2016; Parmesan, 2006). As Petit et al. (2003) pointed out, “*their genetic uniqueness should largely outweigh their low diversity for long-term conservation purposes*”.

Islands are by their very nature, isolated. This isolation influences the movement of individuals and therefore gene dispersal among the island and the mainland, which decreases with increasing distance and which are expected to result in significant population genetic structure (Franks, 2010). Additionally, island populations are expected to display lower census size than mainland populations, from which they are likely to be founded from (Franks, 2010). Such founder events should result in population bottlenecks (Barton & Charlesworth, 1984; Nei et al., 1975) leading to a loss of genetic diversity in the island populations. This pattern has been demonstrated in the literature, notably in the review by (Frankham, 1997), and in (J. D. Chung et al., 2004) for *Cunninghamia konishii* (Cupressaceae) and (Boessenkool et al., 2007) for a bird species (*Petroica australis australis*). In addition, island populations are expected to display higher levels of inbreeding depression and an accumulation of mildly deleterious mutations, which in turn, together with the reduced genetic diversity, results in a higher risk of extinction than mainland populations (Diamond, 1984). As a conclusion, island populations evolutionary dynamics may be comparable to those of marginal populations, because they are expected to have also limited ability to adapt genetically to change, whether that be newly introduced diseases, global climate change, introduced predators, or competitors.

Consequently, given that the persistence and resilience of forests are highly dependent on the adaptive response of populations to prevailing climatic conditions, the future of marginal and island populations in the face of climate change is uncertain (Kolzenburg, 2022). Studies are therefore urgently needed to shed light on the genetic characteristics related to the adaptation of marginal and island populations to climate, relative to the rest of their range.

3. Chasing a moving optimum: natural selection and adaptation

3.1. Understanding natural selection: the fitness landscape

“No natural phenomenon can be explained by appeal to goals, ends or purposes” (Buller, 1999).

A longstanding goal of evolutionary biology is to understand the relationship between genotype, phenotype, and fitness, and its consequences for adaptation and evolution (Fragata et al., 2019). In nature, individuals are capable of a multitude of adaptive responses and often present different forms within the same species (Alfá et al., 1996; Etersson, 2004). The prevalence of a specific trait in a given population reflects the way in which that trait has contributed to the ability of individuals to survive and reproduce, because whenever there are differences in these abilities between individuals, selection occurs (Walsh, 2000).

An organism’s ability to survive in a given environment is reflected by the space of all possible allelic combinations (and the resulting genotypes and phenotypes) against its fitness value (Wright, 1932). The “fitness landscape” was first introduced by Sewall Wright in 1932, and allows each genotype to be represented in a reduced multidimensional space as a function of its fitness value (Walsh, 2000). Indeed, as stated by Walsh (2000) *“There isn’t just one solution to the problems of surviving and reproducing, there are enormously many”*. Consequently, fitness landscapes should be ‘rugged’, that is, characterised by multiple peaks of fitness separated by ‘valleys’ of low-fitness genotypes, which may represent a fundamental challenge for evolution (Papkou et al., 2023) because natural selection only favours high-fitness genotypes (Kauffman & Levin, 1987). In a population, the accumulation of small genetic changes creates an individual’s phenotype with a greater adaptive value than its neighbour. This individual generally climbs the fitness landscape towards adaptive peaks, bringing its fitness closer to the optimum, resulting in a displacement of the population mean phenotype (Figure I.3) (Walsh, 2000). Therefore, the probability of a single step towards the adaptive optimum is given by the probability of fixation of the corresponding beneficial mutation and its selective effect on an individual’s phenotype (Walsh, 2000). Consequently, change in adaptive allele frequencies among and within evolving populations is mediated by those processes (i.e., selective agents) that determine the individual’s capacity to survive and reproduce; in other words, there is a covariance between those selective agents and fitness.

The characterization of fitness landscapes in nature is extremely difficult, because of the tremendous number of possible genotypes resulting from the complex and intertwined gene-by-gene and gene-by-environment interactions (Feng et al., 2012). Therefore, studies have focused on simplified situations looking to particular selection drivers or correlations between genotypes/traits and fitness in experimental sites (Kingsolver et al., 2001).

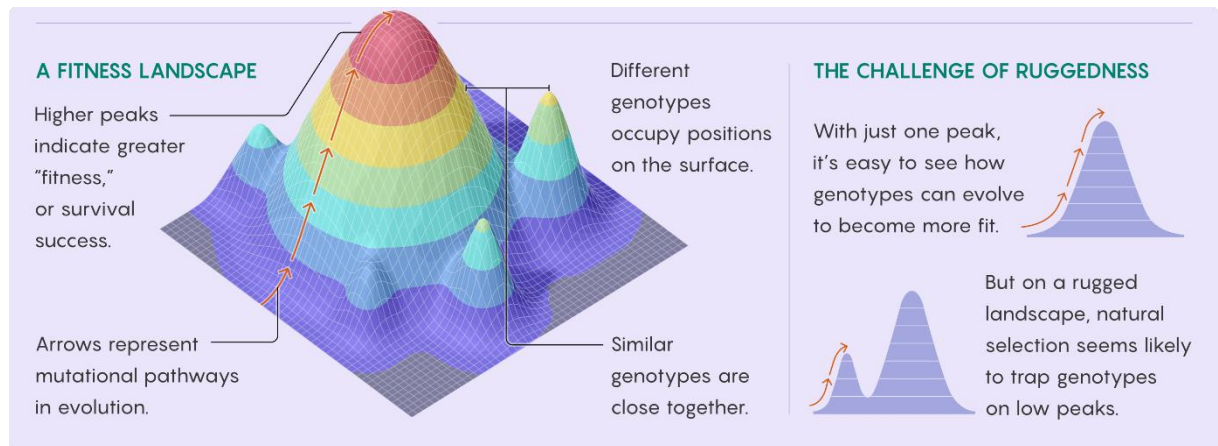


Figure I-3. The fitness landscape and the challenge of robustness for evolution. *Source: Figure modified from original produced by Merrill Sherman, Quanta Magazine.*

3.2. Measuring natural selection: the phenotypic selection gradients and their limits

“Natural selection acts on phenotypes, regardless of their genetic basis, and produces immediate phenotypic effects within a generation that can be measured without recourse to principles of heredity or evolution.” Lande & Arnold, (1983).

Natural selection can take many forms. While it may affect the average value of a trait (‘directional’ or ‘linear’ selection), it can also modify phenotypic variation with non-linear forms of selection; ‘stabilising’ selection will tend to reduce phenotypic variance, while ‘disruptive’ (or diversifying) selection will tend to increase it (Figure I.4) (Brodie et al., 1995). Natural selection is dynamic, and can vary in strength (Hereford et al., 2004; Kingsolver et al., 2001), direction (Alexandre et al., 2020; Brodie et al., 1995; Westergren et al., 2023), space and time (Siepielski et al., 2009, 2013).

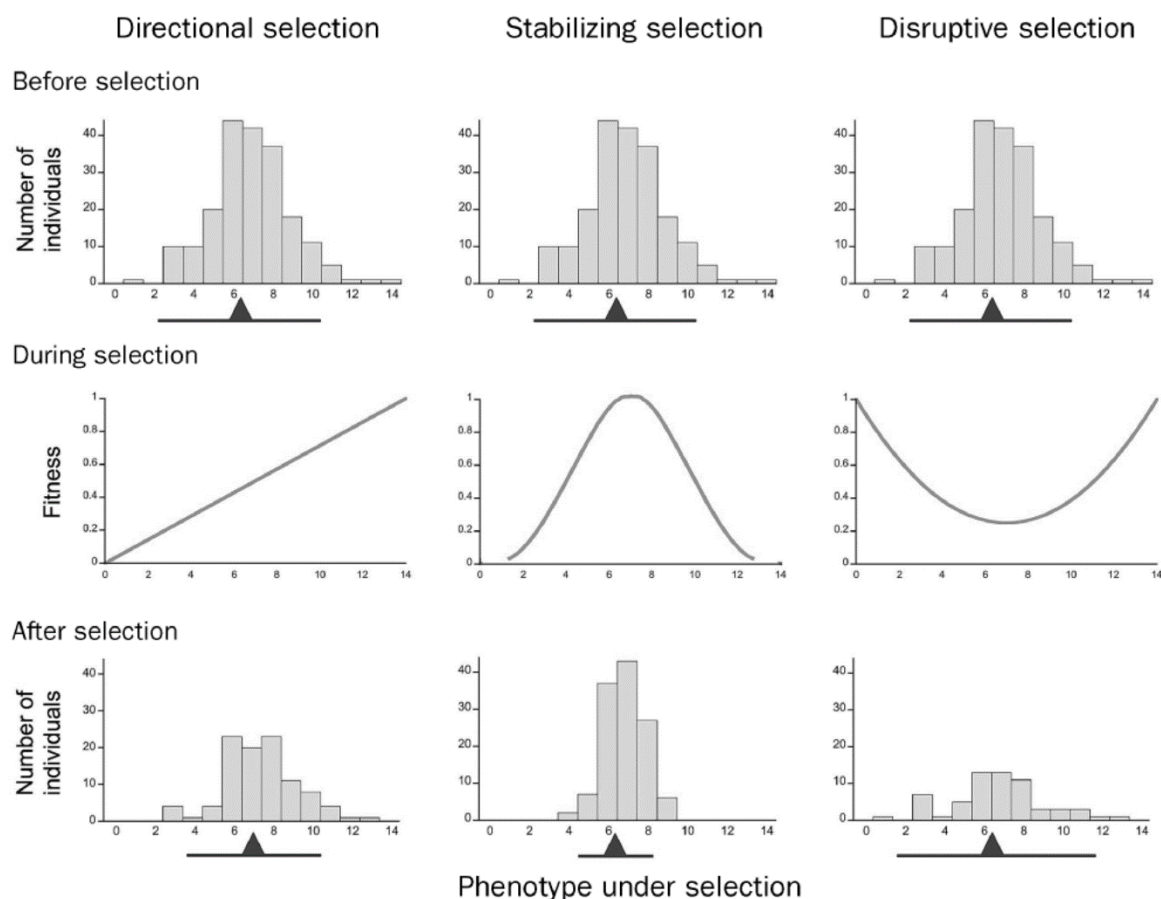


Figure I-4. Three different modes of selection (directional, stabilizing, and disruptive), showing the trait distribution of a hypothetical population before selection (top), the fitness function (centre), and the trait distribution after selection among the survivors (bottom) for each mode. The triangle under each histogram indicates the mean of each population; the bar under each histogram indicates the variation (± 2 standard deviations) of each population. *Source: Extracted from Kingsolver & Pfennig (2007).*

In 1983, Lande & Arnold developed a statistical framework for quantifying linear and nonlinear selection on multiple quantitative traits. This was particularly influential because it provided researchers with a simple tool to obtain standardized estimates of the strength, direction and form of selection (so-called ‘differentials’ and ‘gradients’) (Endler, 1986; Hereford et al., 2004; Hoekstra et al., 2001; Kingsolver et al., 2001; Siepielski et al., 2009). These estimates of selection make it possible to understand how selection acts simultaneously on several traits and how to detect the targets of selection (Siepielski et al., 2009); in other words, how selection shapes the phenotypes. In addition, estimates of selection from selection gradients are very useful because, combined with the traits’ heritabilities and genetic correlations, they can be used to predict micro-evolutionary changes (Alexandre et al., 2020; Kruuk et al., 2003; Westergren et al., 2023).

Phenotypic selection gradients allow the measurement of the association between a phenotypic trait and fitness (Falconer & Mackay, 2004), which is a requirement for an evolutionary change to occur. They are formally defined as the vector of partial regression coefficients of the relative fitness of individuals on traits (Lande & Arnold, 1983). The trait values are often standardized to unit of standard deviation, so that the selection gradient gives the proportional change of fitness for a change of one standard deviation in the trait, thus facilitating cross-study comparisons (Lande & Arnold, 1983; Kingsolver et al., 2001).

One of the main conditions for calculating selection gradients is the measurement of fitness. As mentioned previously, fitness is defined as an individual's ability to survive and reproduce (Darwin, 1859). However, there is little consensus on how to measure fitness. A robust estimate of an individual's fitness should be a measure of its survival and reproductive capacity throughout its life, also known as 'lifetime reproductive success', which is particularly challenging for long-lived species such as forest trees due to the difficulty of tracking progeny (random vs. non-random juvenile mortality; Martin et al., 2018) and accurately assigning parents (Van De Walle et al., 2022).

Facing the difficulties in measuring lifetime individual fitness, it has become common practice to calculate selection gradients using fitness proxies (or components) of various kinds. For example, seed set (i.e., the number of seeds) has often been used; however, it is not well correlated with lifetime individual reproductive success (Moran & Clark, 2012), as many seeds may abort (the well-known trade-off between seed quality and quantity) or produce seedlings that will not survive the strong selection pressures in the early years of establishment (Gerzabek et al., 2017). A more robust alternative is the use of the number of successfully established offspring that are likely to contribute to the next generation (known as the 'realized fecundity'; Moran & Clark, 2012; Oddou-Muratorio et al., 2018; Westergren et al., 2023). Realized fecundity as a proxy for fitness can be measured using mating models and parentage analyses, which have proven robust in many studies, including studies calculating selection gradients for forest trees under natural conditions (Alexandre et al., 2021; Westergren et al., 2023).

Natural selection acts simultaneously on multiple and correlated traits, which disproportionately contributed to fitness (or some components of the latter) in the past. Traits correlation can result from shared genetic (i.e., pleiotropy) or developmental basis and shared functional role to microenvironmental variation (Arntz & Delph, 2001; Denney et al., 2020; Schlichting, 1989). Correlated traits imply that selection on a particular trait produces an

indirect effect on the distribution of other correlated traits, which complicates its measurement (Lande & Arnold, 1983). Indeed, selection within a generation produces changes in the means, variances and covariances of traits that are indirectly selected, if they are correlated with the trait(s) under selection (Lande & Arnold, 1983). To avoid this bias, multivariate models (i.e., multiple regression of fitness) using only the first principal components of phenotypic variation as traits reduces dimensionality and creates sets of uncorrelated principal components, were proposed by Lande & Arnold (1983) and have been used in selection measures since then (see Alía et al., 2014; Costa E Silva et al., 2018; Gauzere et al., 2020; Morgan & Conner, 2001; Westergren et al., 2023).

In a study published in 2003, Kruuk and colleagues reviewed recent evidence that environmentally induced covariances between phenotypes and fitness can ‘short-circuit’ the measurement of natural selection, leading to an overestimation of its strength (although this concern has already been addressed in other studies, see Price et al., 1988; Rausher, 1992). The requirement behind natural selection analysis is that there is a causal relationship between the trait and fitness. However, this relationship may not be the consequence of the trait being the target of selection, but can be the artefact of some environmental variable which has an impact on the focal trait and independently, on fitness (Figure I.5). In that case, these artefactual correlations would create a phenotypic selection gradient of a given strength and direction, which may contrast with the expected evolutionary predictions (Kruuk et al., 2003). Stinchcombe et al. (2002) came to the worrying conclusion that around 25% of the estimates of selection gradients were biased by environmental covariances, suggesting that “[...] *our view of the magnitude of selection on phenotypic traits might be seriously distorted.*” (Kruuk et al., 2003).

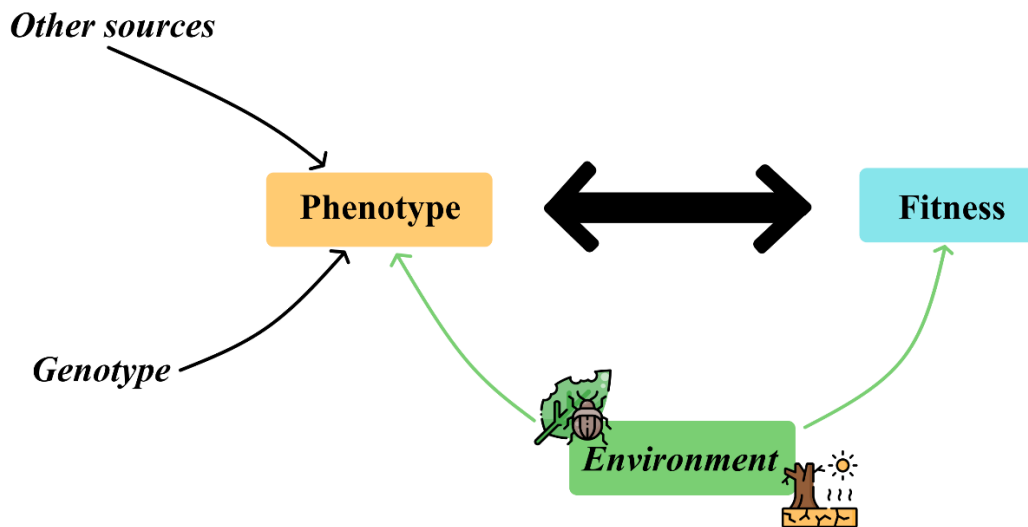


Figure I-5. How environmental covariance biases the measurement of selection on a phenotypic trait. The phenotype of an individual is determined by its genotype and by environmental conditions, and possibly by other factors. Environmental conditions are correlated both with the expression of the phenotypic trait and with fitness, giving the impression of selection on the trait. Single-headed arrows show causality, and the double-headed arrow shows the resulting statistical correlation between fitness and the trait. *Source: Figure modified from Kruuk et al. (2003).*

Stinchcombe et al. (2002) suggested that such environmentally induced covariances can be statistically controlled. Alexandre et al. (2020) and Westergren et al. (2023) took into account the ecological and environmental conditions close to each adult tree by adding covariates related to soil water content, competition index and spatial autocorrelation of fitness (which is known to be an important source of bias, as extensively discussed in Marrot et al., 2015). However, although these covariates can attenuate the covariance induced by the environment, which is already a step towards a more accurate picture of the targets, strength and direction of natural selection, it is very difficult to fully control the microenvironment in wild forest stands, notably because the source of microenvironmental variation may be unknown or the relevant spatial scale of variation could be too small to fully capture environmental covariances (Rausher, 1992).

3.3. Spatial variation of selection

Environments can be very heterogeneous within species' ranges, particularly for wide-ranging species such as forest trees that occupy multiple different environments. This pattern is accentuated for species with fragmented ranges, characterised by limited gene dispersal and increased isolation-by-distance. As a result, we observe adaptive geographic variation in traits (Alía et al., 2024; Benomar et al., 2015; Brousseau et al., 2021; Postolache et al., 2021; Scotti et al., 2023), and often strong population genetic structure, revealing local adaptation along climatic and ecological gradients as a consequence of spatial variation in selection (Figure I.6) (MacColl, 2011; Thompson, 2005; Wade & Kalisz, 1990).

Adaptive genetic differentiation has been shown for a wide range of taxa: from annual plants (Dubin et al., 2015 for *Arabidopsis thaliana*), broadleaf trees (Jump et al., 2006 for beech; Shen et al., 2022 for *Liriodendron species*) and conifers (Alía et al., 2024; Grivet et al., 2011 and Serra-Varela et al., 2015, for maritime pine), to animals such as toads (Luquet et al., 2015) and the well-known case of guppies (Endler, 1980), among many others (Charmantier et al., 2016; Keller et al., 2013; Kraemer & Boynton, 2017).

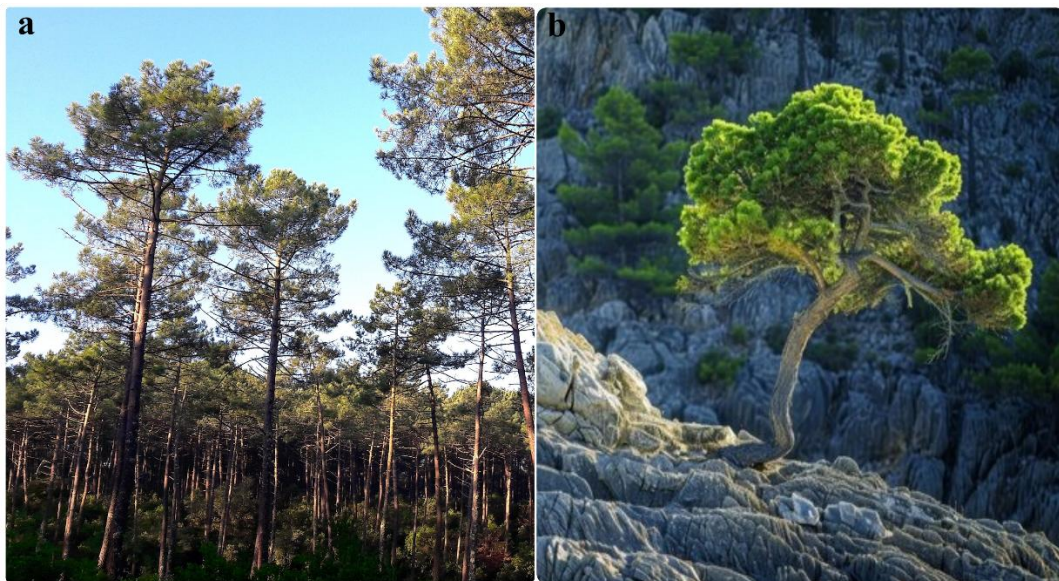


Figure I-6. Maritime pine phenotypic differences with a potential genetic basis in response to contrasted a) Atlantic and b) Mediterranean environments as a consequence of spatial variation in selection. *Source: (a) A. Theraroz, (b) stock.adobe.com*

Across spatially distant populations, natural selection tends to vary mainly in strength, which can accentuate their adaptive divergence (Siepielski et al., 2013). Local adaptation

should occur when a population carries alleles that maximise fitness in the local environment (Savolainen et al., 2013). Populations more strongly adapted to ecological, in particular climatic features, which are known to be important selective pressures for local adaptation (e.g., temperature; (Saxe et al., 2001), may experience weaker selection than populations experiencing some adaptive lags in response to similar selective pressures (Siepielski et al., 2013). In other words, adaptive lags, or ‘maladaptation’, occurs when fitness is reduced below the optimum for a particular environment, given the range of adaptive alleles present within the species (Rehfeldt et al., 2002). Consequently, the spatial variation of natural selection across a species range can be translated, from a population genetic perspective, into different levels of adaptation resulting from demographic fluctuations (Lande, 2007; Olazcuaga et al., 2023), heterogeneous selective pressures, genetic constraints such as genetic correlation among traits (Chevin, 2013), and different level and composition of adaptive genetic diversity.

From an ecological perspective, spatial variation of selection could also be the outcome of environmental heterogeneity, the intensity of species interactions (positive and/or negative) (Stephan et al., 2021; Vanhoenacker et al., 2013) and the competitive interactions for light, resources and space resulting from conspecific density (Magee et al., 2021; Yin et al., 2023). These factors can create differences in the functional basis of trait-fitness relationships between populations, resulting in contrasting targets, strength and direction of selection towards different fitness optima.

Gene flow, as explained in section 2.3, can have important consequences for spatial variation in the strength and direction of selection and hence for local adaptation. If gene flow originates from a source population subject to similar selective pressure and therefore similar selection trends, it can benefit the local adaptation of the recipient population by increasing adaptive genetic diversity (Garant et al., 2007; Lenormand, 2002; Slatkin, 1987). However, gene flow from a source population subject to contrasting selective pressures can bring genetic variants into the recipient population that would hinder local adaptation and lead to maladaptation. As a result, these maladapted populations may be characterised by an increase in the strength of selection relative to populations that benefit from gene flow for local adaptation (Siepielski et al., 2013).

Spatial variation in selection may result from processes other than those mentioned above. Populations that experience similar ecological conditions are expected to display similar trait-fitness relationships. Still, they may experience differences in the strength and direction of

selection if they differ in the mean and/or variance of the average phenotype, resulting in differences in the distance to the optimal phenotype (Steele et al., 2011; Siepielski et al., 2013). These patterns of variation in selection will have strikingly different consequences for the evolution of phenotypic diversity in natural populations (Caruso et al., 2003).

Although our understanding of the strength and form of selection has progressed, a general understanding of the spatial dynamics and causes of selection in nature is lacking (Richardson et al., 2014; Siepielski et al., 2009). Furthermore, the spatial analysis of natural selection can be biased if only few spatial replicates are available, thus restricting the diversity of environments in which the species occurs, as well as the selection pressures and potential covariances that may arise. In addition, because selection is often weak (Kingsolver et al., 2001), large sample sizes (several hundred individuals) are needed to have enough statistical power to detect significant selection (Hersch & Phillips, 2004; Siepielski et al., 2009).

Despite the usefulness of selection gradients for estimating the strength and direction of current selection and predicting phenotypic changes in the face of climate change, selection patterns have only revealed a snapshot of selection in time and space, as populations may exhibit some degree of temporal and spatial variation in selection (Alexandre et al., 2020; Siepielski et al., 2009, 2013; Westergren et al., 2023). Lack of a wider spatial or temporal scale may hamper our ability to predict how fitness landscapes will evolve in response to climate change or other anthropogenic perturbations, and the resulting (mal)adaptation (Capblancq et al., 2020) (Capblancq et al., 2020). The resulting (mal)adaptation can be counterbalanced by sufficient and adequate adaptive variation, which can allow rapid evolution towards the new phenotypic optimum (Brady et al., 2019).

Climate change will fundamentally alter many aspects of the natural world. To understand how species may adapt to these changes, we need to identify which aspects of climate change exert the most powerful selective forces and whether these patterns are consistent at the local and/or range wide scale. We also need to understand the extent to which natural populations will have sufficient adaptive genetic variation to enable them to adapt to climate change and the associated selective forces.

3.4. Landscape genomics

Landscape genomics is becoming a popular field of research notably since the availability of dense population-level genomic datasets, which create the possibility of investigating the genetic basis of local adaptation (Berg & Coop, 2014; Tiffin & Ross-Ibarra, 2014; Tigano & Friesen, 2016), as well as understanding the spatial distribution of adaptive alleles in natural systems and across species ranges (Hoban et al., 2016). Contrarily to ‘landscape genetics’ studies that focus on spatially neutral processes with the use of neutral genetic variants, ‘landscape genomics’ focuses on adaptive processes through the analysis of many loci potentially under selection (Manel et al., 2010). Indeed, it focuses on identifying the environmental factors that shape the geographical patterns of adaptive genetic diversity across the landscape (Manel et al., 2010, 2010; Rellstab et al., 2015) and has been applied across multiple taxonomic groups and ecological settings.

Landscape genomics most commonly used approaches are F_{ST} -outlier analysis and environmental association analysis (Rellstab et al., 2015), also called genetic environment association analysis (GEA). Methodologies for F_{ST} outlier detection assess locus-specific signals of local selection among populations as those with stronger allelic differentiation (as measured by F_{ST}) than expected under a neutral model (e.g., (Foll & Gaggiotti, 2008; Lotterhos & Whitlock, 2015). GEA is used to identify associations between population-level genomic data (genotype or allele frequencies) and environmental variables, measured at the sample location (Capblancq et al., 2020; Frichot et al., 2013; Günther & Coop, 2013; Rellstab et al., 2015). In forest trees, GEA is expected to be more informative than phenotype-based methodologies such as genome-wide association analyses (GWAS), because the difficulty to measure fitness traits in species with long life spans and complex life histories (Capblancq et al., 2020).

As we saw in section 3.3, the heterogeneity of the spatial distribution of adaptive genetic variation could have contrasting effects on the persistence of populations in the face of climate change in the decades to come. These contrasting effects depend above all on the extent and nature of the change in the local environment, as well as on the distribution of adaptive genetic composition across the species range (Aitken et al., 2008; Chhatre et al., 2019; Rehfeldt et al., 2002). If the change in the local environment is substantial, locally adapted populations will lag behind in some way from their fitness optimum on the adaptive landscape, therefore creating some level of disruption between the existing genotypes and the new fitness optimum. All

depend on the magnitude of “some level”. If the level of disruption is too high, the required amount of change in the adaptive genetic composition to approach the fitness optimum in the new fitness landscape, and minimize maladaptation, will be too high relative to the capacity and speed of adaptation (Bürger & Lynch, 1995; Chevin et al., 2010; Gomulkiewicz & Holt, 1995) (Bürger & Lynch, 1995; Chevin et al., 2010). Unfortunately, climate change is expected to strongly disrupt the gene-environment relationships in many natural systems. Spatially explicit predictions of patterns of climate (mal)adaptation can help highlighting the relative vulnerability and determine the possible fate of populations under scenarios of future climate change (Capblancq et al., 2020; Dauphin et al., 2021; Fitzpatrick & Keller, 2015; Gougherty et al., 2021), which may serve to guide conservation policies.

An increasing popular way to make such predictions is the genomic offset approach (Fitzpatrick & Keller, 2015), which attempts to represent the change in allele frequencies required to maintain the current gene-climate relationships under climate change (Figure 1.7) (Fitzpatrick & Keller, 2015). Various univariate and multivariate methods have been developed to date to estimate genomic offsets, such as the ‘risk of non-adaptiveness’ (Rellstab et al., 2016), redundancy analysis (Capblancq & Forester, 2021a), latent factor mixed models (Gain & François, 2021), gradient forest (Ellis et al., 2012) and generalized dissimilarity modelling (Ferrier et al., 2007), reflecting the growing interest in this approach. Genomic offset predictions are now often recommended to guide management strategies for many systems and organisms (Lachmuth et al., 2023; Rhoné et al., 2020).

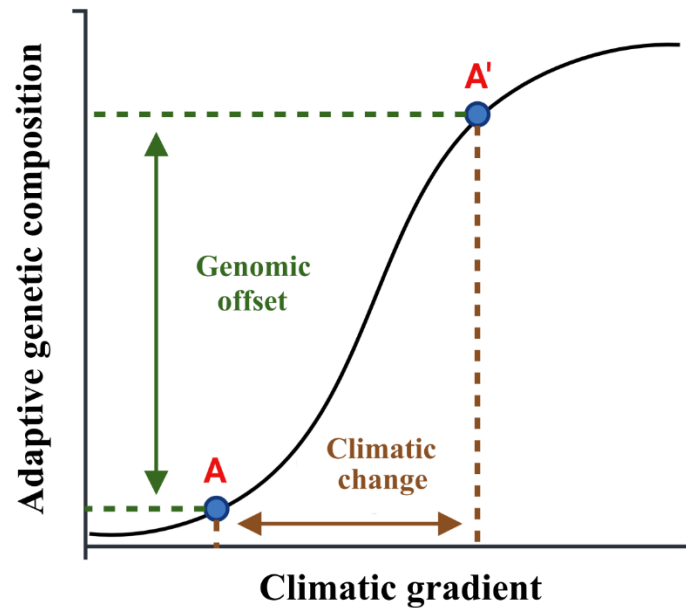


Figure 1-7. Schematic representation of the genomic offset concept based on the turnover of the adaptive genomic composition along one climatic gradient. A change from A to A' on the climatic gradient occurs in a region of high turnover in adaptive genomic composition, resulting in a large predicted genomic offset. *Figure adapted from Thomas Francisco, personal communication and Capblancq et al. (2020).*

However, the genomic offset computation relies on several strong assumptions that do not accurately reflect the eco-evolutionary processes of natural populations and therefore compromise the accuracy of its predictions (Ahrens et al., 2023; Archambeau et al., 2024a; Capblancq et al., 2020; Forester et al., 2013; Gougherty et al., 2021; Lotterhos, 2024; Rellstab et al., 2021). The first key requirement is that this approach assumes that populations are adapted to their local environment (Rellstab et al., 2021). Then, it assumes that adaptive alleles have been correctly identified, which therefore require the validation of GEA outliers (Ioannidis & Khoury, 2011; Oetting et al., 2017). One other key assumption is that populations are currently optimally adapted to their local environment, which is often violated. For example, (Rehfeldt et al., 2002, 2003, 2018) and (Fréjaville et al., 2020) demonstrated that forest trees populations from boreal and temperate forests at the northern limit of their range may not be locally adapted and may benefit from the increase in temperatures resulting from climate change, at least in the short term. Furthermore, another central assumption is that populations from different geographic locations but occupying similar environments have the same adaptive alleles, which is often violated too. (Rellstab et al., 2017) showed that, at a regional scale within

the same species, the genetic basis of climate adaptation can differ substantially. In addition, the current gene-environment relationships are expected to remain unchanged over space (spatial extrapolation) and time in a changing climate. This latter assumption strongly depends on the variation in genetic background across the landscape and processes such as gene dispersal and demographic fluctuations (Capblancq et al., 2020; Hoffmann et al., 2021; Rellstab et al., 2021).

Population genetic structure has been the subject of much debate as to whether it should be taken into account in the calculation of the genomic offset, and no real consensus has emerged on this point. Indeed, the climatic gradients that determine local adaptation can covary with neutral genetic variation (e.g., species migrating along climatic gradients during range-shifts). (Capblancq et al., 2023) have shown that the selection of outliers using methods that take account of neutral genetic structure results in the removal of most of the adaptive signal. Therefore, to obtain a set of candidate SNPs representative of climate adaptation, it is suggested to use a combination of GEA methods that correct and do not correct for population genetic structure, and to select as candidates for local adaptation the loci that have been identified by at least two of them (Archambeau et al., 2024a; Capblancq et al., 2023).

Nevertheless, a growing number of studies have demonstrated the (partial) validity of genomic offset predictions. Lind et al. (2024) have shown for Douglas fir and Jack pine that genomic offset methods perform as well or better than climate or geographic distance metrics when predicting fitness-related phenotypes in transplant experiments. Fitzpatrick et al. (2021) for balsam poplar and Archambeau et al. (2024) for maritime pine, have shown that populations with higher genomic offset exhibit a reduction in population growth performance and survival, respectively. These studies therefore concluded there is potential of genomic offset predictions to provide an estimate of the degree of expected maladaptation to future climate in natural populations.

4. Study species

Maritime pine (*Pinus pinaster* Ait., Pinaceae) is an outcrossing, monoecious, wind-pollinated conifer. Maritime pine is native to the Mediterranean region, where several potential glacial refuges have been identified on the Iberian Peninsula, Morocco and Italy (González-Martínez

et al., 2007; González-Martínez et al., 2004). Its area of distribution spreads as far north as French Brittany, and as far west as the Atlantic coast of the Iberian Peninsula and as far east as the island of Corsica. It was introduced to the Landes de Gascogne under Napoleon III, where it now forms the largest artificial forest in Europe, covering around 820,000 hectares, and where it is of major economic importance to the timber industry. Consequently, maritime pine covers a wide range of contrasting environments, from the coastal dunes of the Atlantic Ocean in France to the High Atlas Mountains in Morocco, and it is considered as a keystone species supporting forest biodiversity in large parts of its range. Its natural distribution is extensive but fragmented, resulting in a large number of small, isolated populations. More generally, given its long lifespan and the speed of climate change, the persistence and vulnerability of maritime pine to climate change is a major concern, particularly for isolated natural systems such as populations located at the edge of their range and island populations. Will the genetic resources present in natural populations of this species be sufficient to enable it to persist in the face of climate change? How will the current climate change affect the selective pressures and targets of natural selection, and hence the local adaptation of natural populations?



Figure I-8. Genetic Conservation Unit (GCU) of maritime pine located in Lacanau (southwestern French Atlantic coast). *Source: A. Theraroz.*

5. Objectives

The main objectives of this PhD thesis are to 1) determine the spatial distribution of maritime pine genetic resources at different scales, from the population level to the full distribution range, 2) to highlight its potential for future adaptation to climate change and 3) to disentangle the effects of the latter on natural selection dynamics. This work enabled us to provide relevant knowledge on the current state of genetic resources and the adaptive capacity of this species, which will help to improve its management and conservation plans towards the threats caused by climate change.

Chapter 1 aims at understanding how, at the scale of the species range, genetic variation, adaptability and the potential for short-term maladaptation to future climatic conditions are distributed from the range core towards the geographical and climatic margins. To this aim, I use quantitative indicators to demonstrate the distinct effects of geographical and ecological marginality on the distribution of maritime pine genetic resources and to test the predictions of the ‘Centre-Periphery Hypothesis’ (CPH) in this species. More globally, this chapter provides insights into which populations may be able to adapt more quickly to climate change since the adaptive potential of populations depends directly on their genetic variation.

Chapter 2 aims at identifying the spatial patterns of contemporary natural selection by estimating its strength and direction in two natural populations of maritime pine located in contrasting environments (Mediterranean *vs.* Atlantic), as well as to identify the targets of selection (i.e., relevant traits) for survival and reproductive success (i.e., fitness) in response to current selective pressures. We used different types of models, standard selection gradients (Lande & Arnold, 1989) and zero-inflated models (Brooks et al., 2017), allowing us to partially control for microenvironmental variation and spatial autocorrelation within populations. Therefore, this chapter provides some predictions of phenotypic change in response to current selective pressures, and insights into ongoing trends in local adaptation to climate change for maritime pine in the wild.

Finally, **Chapter 3** aims at the genetic characterisation of maritime pine populations in Corsica, a Mediterranean island with highly contrasting climatic regions and altitudinal range, in order to study the spatial patterns of genetic variation and analyse their current and future adaptive capacities to climate change across the island. More specifically, I study here the spatial patterns of genetic variation along latitudinal and altitudinal gradients, disentangling the

fine-scale population genetic structure, and modelling the projection of adaptive gradient(s) across space (i.e., the adaptive landscape). This chapter sheds lights into the genetic features and adaptive potential of maritime pine in Corsica, which has been little studied in recent decades. Consequently, this chapter will provide valuable perspectives for the conservation and development of management plans for this species on Corsica.

Chapters 1 and 3 present a first step towards prediction of the adaptive responses of maritime pine populations to future environmental conditions at two scales, that of the species' range (**Chapter 1**) and that of an island that harbours important genetic resources of the species (**Chapter 3**). I assess which populations will have sufficient genetic variation and adaptive potential to perhaps adapt in the short-term (**Chapter 3**), which populations will be the most genetically vulnerable across the range and those that will likely maintain current gene-environment relationships (**Chapter 1**). **Chapter 2** gives insights on current trends of phenotypic changes in response to contemporary selective pressures that may contribute to local adaptation and their variation across contrasting environment, providing valuable information to determine whether these populations can undergo rapid microevolution to adapt to changing climatic conditions.

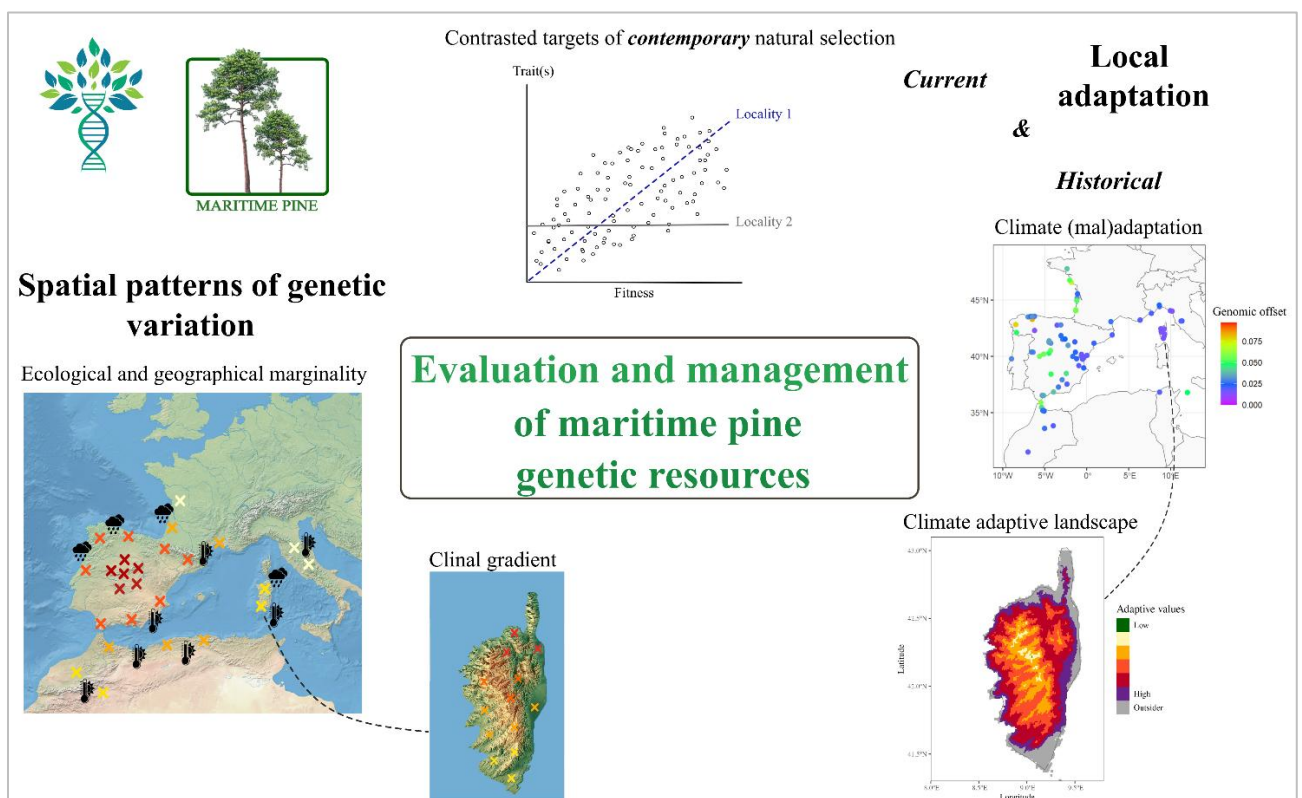


Figure I-9. Graphical abstract of the thesis.

II. CHAPTER 1

The genetic consequences of population marginality: a case study in maritime pine

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Abstract:

Aim: Marginal tree populations, either those located at the edges of the species' range or in suboptimal environments, are often a valuable genetic resource for biological conservation. However, there is a lack of knowledge about the genetic consequences of population's marginality, estimated across entire species' ranges. Our study addresses this gap by providing information about several genetic indicators and their variability in marginal and core populations identified using quantitative marginality indices.

Location: Southwestern Europe and North Africa.

Methods: Using 10,185 SNPs across 82 populations of maritime pine (*Pinus pinaster* Ait.), a widespread conifer characterised by a fragmented range, we modelled the relationship of seven genetic indicators potentially related to population evolutionary resilience, namely genetic diversity (based on both all SNPs and outlier SNPs), inbreeding, genetic differentiation, recessive genetic load and genomic offset, with population geographical, demo-historical and ecological marginality (as estimated by nine quantitative indices). Models were constructed for both regional (introducing gene pool as random factor) and range-wide spatial scales.

Results: We showed a trend towards decreasing overall genetic diversity and increasing differentiation with geographic marginality, supporting the centre-periphery hypothesis (CPH). However, we found no correlation between population inbreeding and marginality, while geographically marginal populations had a lower recessive genetic load (only models without the gene pool effect). Ecologically marginal populations had a higher genomic offset, suggesting higher maladaptation to future climate, albeit some of these populations also had high genetic diversity for climate outliers.

Main conclusions: Overall genetic diversity (but not outlier-based estimates) and differentiation patterns support the CPH. Ecologically marginal populations and those at the southern edge could be more vulnerable to climate change, due to higher climate maladaptation, as predicted by genomic offsets, and/or lower potentially adaptive genetic diversity. This risk is exacerbated by typically small effective population sizes and increasing human impact in marginal populations.

Keywords: Centre-periphery hypothesis, Ecological modelling, Forest genetic resources, Genetic indicators, Marginal populations, Mediterranean and Atlantic regions

1. Introduction

All species thrive and reproduce within an environmentally limited geographic area, which sets the boundaries of their range. Current global warming may restrict the climatic suitability of some parts of the species' ranges and, together with other factors (e.g., typically competitive biotic interactions, Loehle, (1998); but also positive, often unaccounted-for, interactions with other species, Stephan et al., 2021), modify their geographic and ecological margins. The 'centre-periphery hypothesis' (hereafter CPH), a major paradigm in biogeography that aims to disentangle the genetic, demographic, and ecological causes of species' range limits (Gaston, 2009; Sexton et al., 2009), defines marginality as the level of geographic isolation from the species' centre of distribution, which in turn is related to the species' suitability for its environment (Brown, 1984; Hengeveld & Haeck, 1982). According to the CPH, marginal populations are expected to be less abundant and more prone to extinction than those in the centre, due to harsher environmental conditions at the periphery (Birch, 1957; Gaston, 2003; Nicholson, 1958; Richards, 1961; Whittaker, 1971). However, as specific environmental conditions in the core of the species distribution may also induce harsher environmental conditions than in the periphery (e.g., temperature extremes, rugged topography, peculiar edaphic features), Soulé, (1973) distinguished between geographical and ecological marginality when describing centre-periphery gradients, defining ecological marginality as a population's exposure to extreme environmental variables irrespectively of their geographical location.

While several studies have identified marginal populations based on different criteria (e.g., for maritime pine, Alía et al., 1996; Burbán & Petit, 2003), we often lack evidence on the extent to which population marginality is associated with particular genetic features. Classic studies at the range-wide scale suggested a general trend for lower genetic diversity and higher genetic differentiation in marginal populations, but they typically did not distinguish between geographical and ecological marginality (Eckert et al., 2008b; Johannesson & André, 2006; Pironon et al., 2015). More recent studies often called for decoupling the roles of geography and ecology in shaping range-wide patterns of genetic variation (Lira-Noriega & Manthey, 2014; Sexton et al., 2013). To that end, a clear distinction needs to be made between different kinds of population marginality. In a recent multispecies study, Picard et al. (2022) evaluated the ability of quantitative measures to distinguish between geographical, demo-historical (i.e., related to the demographic history of the target species) and ecological marginality.

Past global climate dynamics rather than demographic stochasticity seem to have played a crucial role in the establishment of current range limits (e.g., Hampe & Petit, 2005, for forest trees). Postglacial migrations after the Last Glacial Maximum (LGM) would have resulted in a mosaic of relatively small and isolated populations at the rear and, in a lesser extent, at the front edges of the expansion. In this context, the level of connectivity among marginal populations and between a given marginal population and the species distribution core is especially important (Sachdeva et al., 2022), as gene flow may increase genetic diversity and reduce differentiation (e.g., Lynch et al., 1995; Young et al., 1996). Gene flow can also bring adaptive alleles and contribute to the evolutionary rescue of small, isolated populations by buffering the effect of genetic drift, and reducing the fixation and accumulation of deleterious alleles within populations (Sachdeva et al., 2022). However, marginal populations may also carry specific alleles derived from local adaptation to atypical environments, constituting valuable genetic resources, and making the contribution of external gene flow harmful (i.e., the so-called ‘migration load’; Kimura et al., 1963).

Overall, marginal populations are considered to be more vulnerable to climate change than core populations (Kolzenburg, 2022; Soulé, 1973). Marginal populations are expected to accumulate deleterious variants (i.e., genetic load), a process governed by effective population size, N_e (Kimura & Ohta, 1969). However, genetic purging due to inbreeding tends to reduce genetic load over time, even in relatively small populations (Hedrick & Garcia-Dorado, 2016), and the overall outcome is context-dependant (Sachdeva et al., 2022). Current developments in population genomics have provided metrics to estimate maladaptation to future climates e.g., by estimating genomic ‘offsets’ or ‘gaps’ (a measure of the mismatch in genotype-climate association between current and potential future climates, Capblancq et al., 2020; Fitzpatrick & Keller, 2015; Gougherty et al., 2021; Rellstab et al., 2021). Studies aimed at validating genomic offset predictions with data from common garden experiments and natural populations have shown that populations with higher genomic offset exhibit a reduction in population growth performance (e.g., Fitzpatrick et al., 2021; for balsam poplar) and survival (Archambeau et al., 2024; for maritime pine), and concluded on the potential of this indicator to provide an estimate of the degree of expected maladaptation to future climate. Thus, despite several limitations (Ahrens et al., 2023; Láruson et al., 2022; Lotterhos, 2024; Rellstab et al., 2021), the calculation of genomic offsets may still enable for much needed systematic studies on the connection between population marginality and maladaptation in the face of climate change (Archambeau et al., 2024).

Maritime pine (*Pinus pinaster* Ait., Pinaceae) is an outcrossing, wind-pollinated conifer, with a widespread but fragmented natural distribution in southwestern Europe and North Africa, covering a wide range of contrasted environments from coastal dunes next to the Atlantic Ocean in France to the High Atlas Mountains in Morocco. Maritime pine population genetic structure is a consequence of historical and current dynamics of range expansion-contraction, resulting in distinct genetic clusters (Jaramillo-Correa et al., 2015). This species is also characterised by a fragmented distribution due to human-induced habitat loss and ecological disturbances such as forest fires (De-Lucas et al., 2009). Nowadays, some maritime pine populations are found in ecologically marginal environments (e.g., under very dry conditions in southern Spain and northern Morocco). In addition, the species' range margins are characterised by small, geographically isolated populations, in particular in the southern and eastern parts of the distribution (Alía et al., 1996; Wahid et al., 2004). Reduced dispersal with distant core populations, coupled with demographic and environmental stochasticity, may push such populations into an 'extinction vortex' (Lande, 1988). Few studies have focused on describing the particular genetic characteristics of marginal populations of maritime pine (Salvador et al., 2000; Wahid et al., 2004; González-Martínez et al., 2007), whose potentially valuable genetic resources could be lost in the near future.

In this study, we used 10,185 Single Nucleotide Polymorphisms (SNPs) genotyped in 82 maritime pine populations (1,510 individuals), including ecologically and geographically marginal ones, to compute seven genetic indicators potentially related to population evolutionary resilience (defined as the property of an ecosystem to undergo adaptive evolution in response to biotic or abiotic disturbances; Sgrò et al., 2011) and correlated them with quantitative measures of marginality. The main objective of this study is to assess the relationship between marginality and population genetic features at the scale of the whole species range, by testing predictions of the CPH and adding new elements to its general framework. More specifically, we i) assessed the losses of genetic diversity and increases of genetic differentiation in marginal populations, distinguishing overall genetic diversity from that estimated using different kind of outlier loci; ii) evaluated the levels of accumulation of recessive genetic load based on counts of deleterious alleles; and iii) tested whether marginal populations are maladapted to future climate conditions, applying genomic approaches that consider the contribution of pre-adapted variants to future climates (i.e., genomic offset models).

2. Materials and Methods

2.1. Plant materials and molecular markers

Needles were collected from 1,510 individuals in 82 maritime pine populations covering all previously identified gene pools throughout the species range (Jaramillo-Correa et al., 2015; Milesi et al., 2023). Populations were selected based on gene pool size, density of maritime pine in the area, and representativeness in terms of climatic conditions specific to their geographical position (e.g., orography), as to achieve a regular sampling across the full distribution range of the species. This sampling is, to date, the most complete in the species (see Figure III-1 and Table III-S1 in Supplementary Information), and includes several populations from the distribution margins, as well as isolated populations that have not been considered in genetic studies before. Population C6mpeta (COM), with only three samples, was removed from all data analyses but the gene-environment association (GEA) methods used to estimate the genomic offset. The accuracy of landscape genomic approaches, such as GEA, is highly improved by increasing the number of populations and environments, while being less sensitive to unbalanced sampling designs (Santos & Gaiotto, 2020). In addition, the two stands of Maures population (MAU) (see Table III-S1) were kept separate for these analyses as they were sampled at different altitudes.

DNA was extracted using the DNeasy 96 plant kit (QIAGEN, Germany), following the manufacturer's instructions. All the samples were genotyped for SNPs using the multispecies 4TREE Axiom array (Thermo Fisher Scientific, USA). For maritime pine, the 4TREE Axiom array combines SNPs identified in two previous studies: the 9K Illumina Infinium array generated by Plomion et al. (2016) and the exome capture experiment used in Milesi et al. (2023). The new array has a conversion rate of 79%, as well as 99% genotype reproducibility (based on genotyping of duplicated samples; see additional Excel file #1 available at <https://anonymous.4open.science/r/ddi-3790/>). Apart from potentially neutral genetic polymorphisms, this array comprises also SNPs from candidate genes that showed signatures of natural selection or significant environmental associations with climate at the range-wide spatial scale, orthologs for gene families with important adaptive functions in model species, and coding regions with differential expression under biotic and abiotic stress in maritime pine (see details in Plomion et al., 2016; Milesi et al., 2023). Only SNPs with high-quality scoring following the Best Practices Workflow implemented in the Axiom™ Analysis Suite v5.2 were

selected and filtered by missing data (<30%), yielding a total of 10,185 SNPs. To assess the impact of missing data in the calculation of genetic indicators, SNPs were also filtered for missing data using a 5% threshold, resulting in a subset of 6,390 SNPs. SNP annotation based on SnpEff v5.1 (Cingolani et al., 2012) was retrieved from Cahn (2023) for a set of 1,325 SNPs in common with our study.

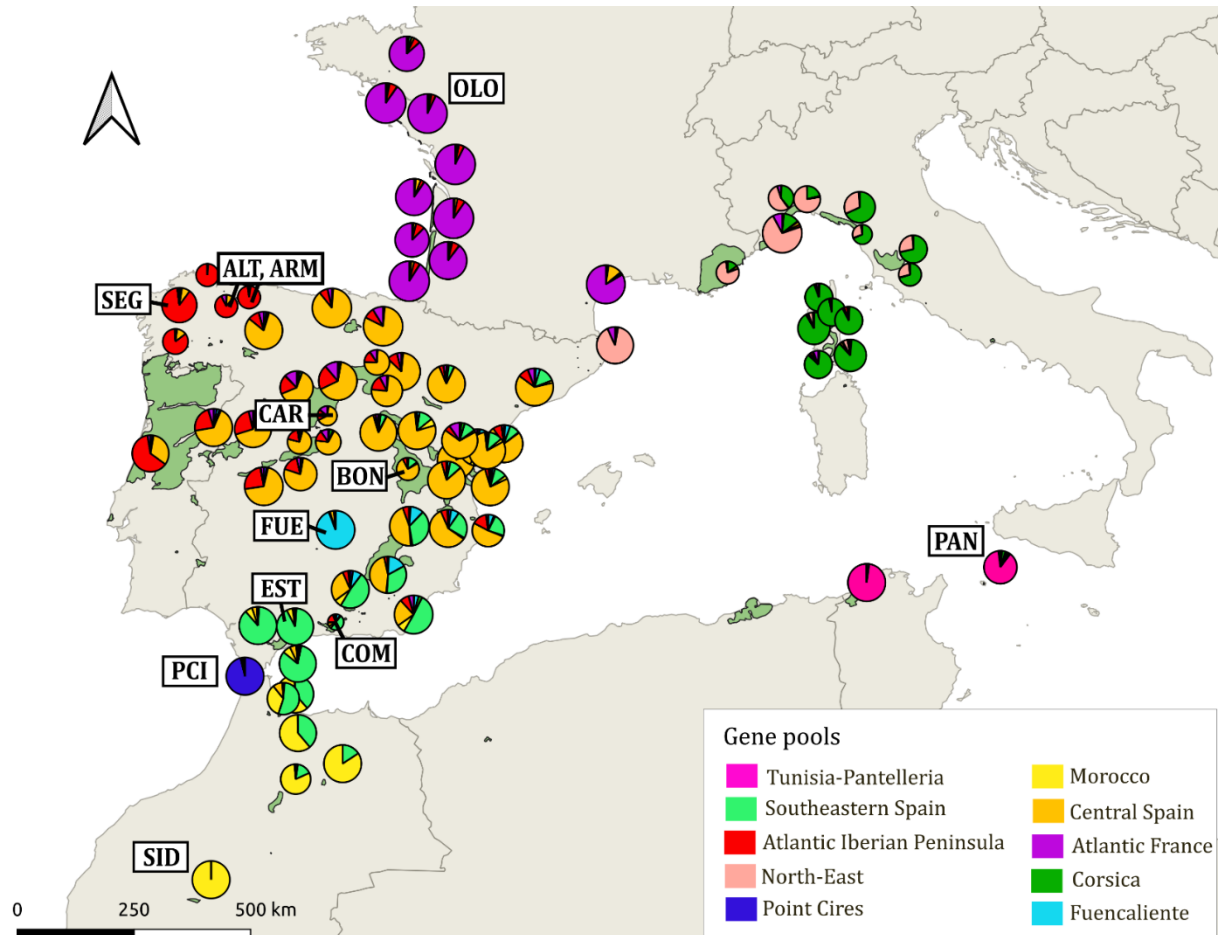


Figure II-1. Genetic pools in *P. pinaster*. Pie charts depict membership proportions of each genetic cluster ($K=10$) for each studied population, calculated by STRUCTURE v2.3.4. The natural distribution of the species is shadowed in light green (see details in Figure S1). Population codes are only provided for those populations specifically mentioned in the main text (see full population information, including population names and geographical coordinates, in Table II-S1).

2.2. Data analysis

2.2.1. Population marginality indices

To assess population marginality, we first produced a new distribution map for maritime pine that includes only natural populations (Figure III-S1), building on that of Caudullo et al. (2017) but adding information from National Forest Inventories and specific publications for less-known parts of the distribution range (Abad Viñas et al., 2016; Alía et al., 1996; Fkiri et al., 2019; Marques et al., 2012; Wahid et al., 2004, 2006).

Second, we computed eight quantitative marginality indices that consider both geographical distribution and demographic history, following Picard et al. (2022) (see Table II-1 and Table III-S2 in Supplementary Information). The demo-historical indices, which are related to the postglacial colonization history of the species (see, e.g., Bucci et al., 2007; Jaramillo-Correa et al., 2015), and the centroid index were computed from the distribution map. The centroid of the species' distribution corresponded to the location whose geographic coordinates were the average of the geographic coordinates of all locations where the species is present (in our case, eastern Spain, a known glacial refugia of maritime pine; Salvador et al., 2000; see Figure III-S2). Then, the centroid index was defined as the 'cost distance' between any population and the centroid location. Cost distances were computed using a conductance matrix (the inverse of a resistance matrix), reflecting the conductance of gene flow. In the conductance matrix, sea cells were assigned low conductance, land cells where the species was absent were assigned intermediate conductance, and land cells where the species was present were assigned high conductance (see Table II-1). This index reflects the level of long-distance gene flow between a given population and the geographical core of the species distribution. The other geographical indices relied on a morphological spatial pattern analysis (MSPA), which considers a binary image (1-presence/0-absence and NA for water) with emphasis on the connectivity within the image (Soille & Vogt, 2009). Presence/absence maps were structured in three categories (cores, edges, and other classes including loops, islets, bridges and branches) using BioManager package in R version 4.2.2.

Table II-1. Geographical (*geo*) and demo-historical (*histo*) marginality indices computed for maritime pine populations; ‘(-)’ and ‘(+)’ indicate that higher values of the index correspond to lower and higher population marginality, respectively; ‘(-)(+)’ indicates that both higher or lower values of the index correspond to higher population marginality. *Adapted after Picard et al. (2022).*

Marginality index	Category	Link with marginality	Description
Area	<i>geo</i>	(-)	Size in ha of the core (i.e., continuous patches of the species’ presence) that is the nearest to the location of the studied population.
Gravity	<i>geo</i>	(-)	Spatially continuous alternative to the area index, computed as the weighted mean of the core areas with weights inversely proportional to the distance squared from the location to the cores.
Centroid	<i>geo</i>	(+)	Eccentricity computed as the cost distance from the centroid of the species distribution to any location, taking into account the terrestrial and marine connectivity linked to pollen circulation capacity. Cost distances are based on a conductance matrix (the inverse of a resistance matrix) reflecting the permeability of land and water cells to gene flow. This index is expected to capture the level of long-distance gene flow.
Edge	<i>geo</i>	(-)	Distance to the nearest border of the species distribution.
Isolation	<i>geo</i>	(+)	Isolation with respect to the core species distribution, computed as the distance from the focal population to the nearest core greater than 100 ha and further than 50 km away.
Second nearest-core	<i>geo</i>	(+)	Spatially continuous alternative to the isolation index, computed as the distance from a location to the second nearest-core greater than 100 ha.
North-South	<i>histo</i>	(-)(+)	Proximity to the species rear-edge (southernmost limit of the species distribution) or leading-edge (northernmost limit of the species distribution) along a latitudinal gradient.
East-West	<i>histo</i>	(-)(+)	Proximity to the species leading-edge or rear-edge along a longitudinal gradient.

Third, we calculated an index of ecological marginality (henceforth ‘ecological index’) based on climatic data for the period 1901-1970, as follows. For each population, we extracted the climatic information provided by the Climate Downscaling Tool (ClimateDT, <https://www.ibbr.cnr.it/climate-dt/>) for the Summer Heat Moisture (SHM) aridity index, an indicator of exposure to drought (see, e.g., De La Torre et al., 2014; Marchi et al., 2020), and temperature (*bio4*) and precipitation seasonality (*bio15*). This set of climatic variables was selected because it best explained the climatic variation across the species range in previous studies (e.g., Archambeau et al., 2024). The ecological index was constructed by computing the standardized Euclidean distance for *SHM*, *bio4* and *bio15* between each population and the overall average. Thus, this index represents the climatic distance of the population from the average climate (Table III-S2). Finally, we reduced the set of marginality indices by removing those that were highly correlated based on Pearson’s correlation coefficients (Pearson’s correlation ≥ 0.6) and a principal component analysis (PCA) using FactoMineR package in R v4.2.2 (Figure III-S3).

2.2.2. Population genetic structure and genetic indicators

Population genetic structure was evaluated using the Bayesian clustering algorithm implemented in STRUCTURE v2.3.4 (Pritchard et al., 2000). To assess the optimal individual’s assignment probabilities ($Q_{ancestry}$) in K genetic clusters (or gene pools), we ran models from $K=1$ (no structure) to $K=10$ with a burn-in length of 100,000 and run lengths of 200,000 MCMC steps. The number of K that best describes the genetic structure was determined based on the delta K method (Evanno et al., 2005) and the visual observation of bar plots.

All genetic indicators were computed at the population level using the full dataset of 10,185 SNPs (Table III-S3). In a few cases where more than one stand was sampled for a population (see Table III-S1), genetic indicator values were averaged. The computation of genetic indicators was robust to the inclusion of missing data, as shown by the high correlations (Pearson’s correlation > 0.7) with genetic indicator estimates computed using the dataset (6,390 SNPs) with missing data lower than 5% (Figure III-S4a,b).

Genetic diversity was estimated as $1-Q_{inter}$, with Q_{inter} being the observed frequencies of identical pairs of alleles among individuals within populations, using GenePop v4.7.5 (Rousset, 2008), after standard correction for sample size (N), using $(N/N-1)$. Notice that this estimate

averages over monomorphic and polymorphic loci. In addition to overall genetic diversity, we also calculated two indicators of genetic diversity based on outlier loci. The first was calculated on the basis of climate-associated (GEA) outliers (i.e., 73 outlier SNPs selected for the genomic offset computation, described below). The second indicator was calculated on the basis of general outliers due to unknown factors (i.e., 151 outlier SNPs common to two environment-independent F_{ST} -outlier-detection methods, as implemented in the R package *pcadapt* and BayeScan v2.1; Foll & Gaggiotti, 2008). Population inbreeding (F_{IS}) was estimated following Weir & Cockerham, (1984). Population-specific divergence was estimated as the genetic differentiation (population-specific F_{ST}) of each population from a common ancestral gene pool using BayeScan v2.1 (Foll & Gaggiotti, 2008), as well as Jost's D (Jost, 2008) estimated with MMOD package in R v4.2.2.

Finally, we computed two additional genetic indicators more specifically related to potential maladaptation to climate change, i.e., the recessive genetic load and the genomic offset. The recessive genetic load represents the accumulation of predicted deleterious mutations in the population standardized by the population genetic diversity. This statistic was estimated by counting different kind of mutations (annotated by SnpEff v5.1; Cingolani et al., 2012) averaged over individuals, as the number of derived moderate- (i.e., non-synonymous) and high-impact (i.e., loss of function) mutations in homozygosity divided by the number of derived low-impact (i.e., synonymous) mutations in homozygosity, following González-Martínez et al. (2017). The genomic offset is estimated as the change in genetic composition required to maintain the current gene-climate relationships under future climates (see Fitzpatrick & Keller, 2015) and thus captures the degree of maladaptation a population will undergo when the environment to which it is currently adapted will change, either from a spatial or temporal perspective (Rellstab et al., 2021; Lotterhos, 2024). Briefly, we first identified outlier SNPs for climate adaptation with two univariate GEA methods, BAYPASS (Gautier, 2015) and Latent Factor Mixed Model (LFMM; Frichot et al., 2013), and three multivariate ones, Redundancy Analysis (RDA; Capblancq et al., 2020), partial RDA (Van Den Wollenberg, 1977) and Gradient Forest (GF; Ellis et al., 2012). For RDA-based methods, missing data were imputed based on the individual's main ancestry by using the corresponding gene-pool most common allele at each locus. Then, the genomic offset was estimated using the set of outlier SNPs identified by at least two methods (see the GitHub detailing this analysis and referenced below) and the GF approach, which showed the best empirical validation in a previous study based on a smaller sample of populations and SNPs (Archambeau et al., 2024), and six climatic variables

related to maritime pine expected exposure to climate change (Table III-S4; see also Archambeau et al., 2024). Future climates for 2070 were described using the predictions from the moderately alarming shared socio-economic pathway (SSP) SSP3-7.0 and five global circulation models (GCMs; IPCC, 2021). As genomic offset predictions across GCMs were highly correlated (Pearson's correlation coefficient >0.75 ; Figure S5), we used population averages for the five GCMs. Additional details and scripts are available at https://anonymous.4open.science/r/ReadyToGO_Pinpin-FA56/README.md. All analyses were undertaken under R v4.2.2 (R Core Team, 2022).

2.2.3. *Effects of population marginality on genetic indicators*

We estimated the relationship between genetic indicators and population marginality by fitting two series of seven linear mixed-models with pairwise interaction terms (one model for each genetic indicator), using the R packages LME4 and LMER, respectively. Models M1 to M7 included population marginality indices as fixed effects irrespectively of the gene pool of origin while models M8 to M14 also included the gene pool of origin as random effects. Random effects in linear mixed-models allow the inclusion of non-independent data from a nested structure (populations sampled within gene pools), allowing each level of the grouping factor (gene pool) to have its own random intercept. The gene pools with a single population (Fuencaliente, FUE; and Point Cires, PCI) were assigned to the geographically closest gene pool (Southeastern Spain and Morocco, respectively). Model goodness-of-fit was evaluated with R^2 and both the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC). A visual evaluation of model fit to data was also performed using diagnostic plots (QQ and residual plots; Figures III-S12 to III-S17). Then, the best models were selected by considering goodness-of-fit (higher R^2 and lower AIC/BIC) and parsimony criteria (i.e., including only significant effects at $\alpha = 0.01$). For models showing poor goodness-of-fit (M5, M7, M9 and M14; see Figures III-S12 to III-S17), log and square-root transformation of predictors, as well as the computation of generalized linear models parametrized with a Gamma distribution and a log-link, were assayed. However, no goodness-of-fit improvement was obtained and thus the original models, as described above, were retained.

2.3. Results

2.3.1. Marginality indices

Pairwise Pearson's correlations and PCA identified some strongly correlated marginality indices (Figure III-S3). For example, the second nearest-core was positively correlated with the isolation index (Pearson's correlation of 0.64) and negatively correlated with the edge index (Pearson's correlation of -0.67), and the ecological index was negatively correlated with the East-West index (Pearson's correlation of -0.51). Thus, only five indices with low correlation (<0.6) were retained for further analysis, namely three geographical indices (centroid, second nearest-core and gravity; see definitions in Table II-1), one demo-historical (North-South), and the ecological index based on climate distances (Figure III-S6). Interestingly, the centroid index was positively correlated with the longitude (Pearson's correlation of 0.70) and the North-South index was negatively correlated with the elevation (Pearson's correlation of -0.56), with southern populations being, generally, at higher elevation (Figure II-S3).

2.3.2. Population genetic structure

Population genetic structure analyses identified ten distinct gene pools, among which two included only a single population (FUE in southern Spain and PCI in northern Morocco; Figure II-1). Remarkably, these two single-population gene pools were not identified as marginal populations by the geographical or demo-historical marginality indices whereas one of them, PCI, was characterized by high values of the ecological index (standardized value of 5.013; Table III-S2), indicating persistence in a marginal climate. FUE and PCI had also low levels of admixture with nearby gene pools. In contrast, the eight main gene pools (with the exception of the highly isolated Tunisia-Pantelleria one, see below) were not genetically isolated from each other, with populations often showing admixture with nearby gene pools. This suggests either historical or recent gene flow across neighbouring gene pools along a latitudinal cline in the western range of the species, and substantial shared ancestry among French (including Corsica) and Italian populations in the eastern one.

2.3.3. *Effects of population marginality on genetic indicators*

Our models revealed a decline in overall genetic diversity (corrected $1-Q_{inter}$, Figure II-2a) and an increase in genetic differentiation (population-specific F_{ST} , Figure II-2b; and Jost's D statistic, Table III-S5) with population marginality based on the centroid, second-nearest core and North-South indices (Tables II-2a and III-S4). Indeed, models M1 and M5 predicted lower genetic diversity and higher genetic differentiation in marginal populations based on the centroid index (Tables II-2a and III-S4), in particular in isolated populations from the southern maritime pine range (as shown by significant coefficients for the second nearest-core and North-South indices and their interaction; see also Figures II-2 and III-S7). Model M2 revealed a decrease in genetic diversity based on GEA outliers for southern range populations (Table II-2a; Figure III-S8a). Interestingly, model M3 revealed an increase in genetic diversity based on general outliers in marginal northern range populations, especially for those with high values of the centroid index (as shown by significant coefficients for North-South and centroid indices and their interaction; Table II-2a, Figure III-S9). However, this unexpected pattern may just result from confounded effects due to high genetic diversity for general outlier loci in the two northernmost gene pools (Atlantic France and North-East; compare Figure II-1 with Figure III-S8b and see M10 below).

Models including the gene pool of origin as a random effect (M8 and M12; Tables II-2b) significantly improved the fitting by 10% for overall genetic diversity and by 20% for population-specific F_{ST} (29% for Jost's D statistic; Table S5), but retained only the centroid and North-South indices and their interaction as explanatory factors (with the interaction having a similar interpretation as that for models without gene pool as random effect; Figure III-S10). For genetic diversity based on GEA outliers, the model including the gene pool as a random effect (M9) also improved the fitting (by over 30%) and revealed the same relationship with the North-South index as M2 while no significant relationship was found between genetic diversity based on general outliers and population marginality at the gene pool level (M10). Interestingly, we found no relationship between inbreeding and the indices of population marginality (see Figure III-S8c) for any model (M4, M11; Table II-2a,b).

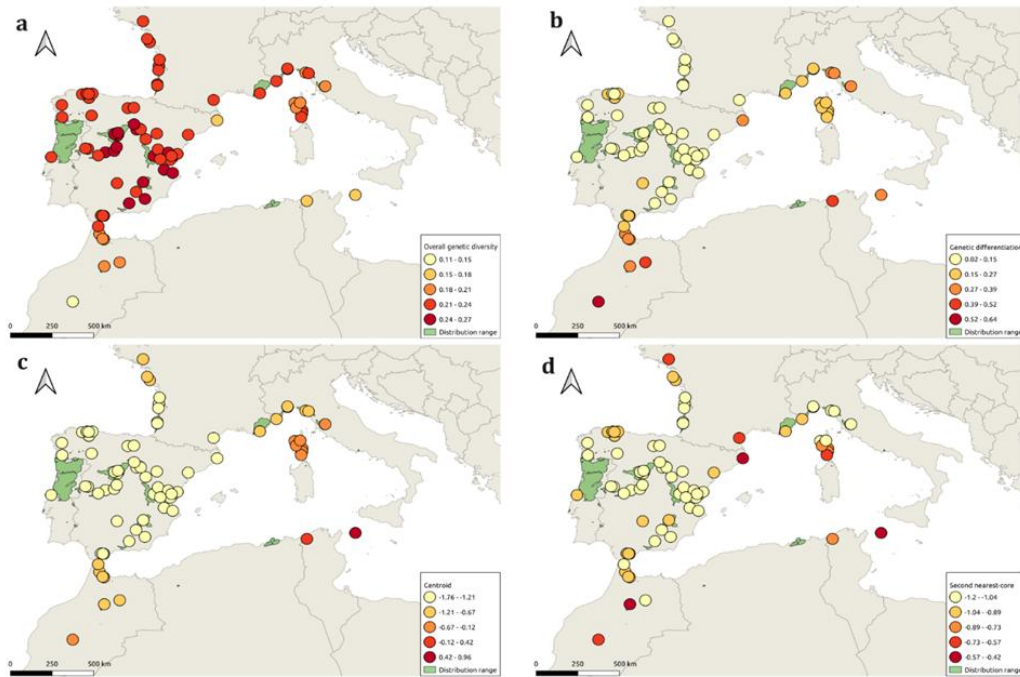


Figure II-2. Geographical distribution of a) overall genetic diversity ($1-Q_{inter}$) and b) genetic differentiation (population-specific F_{ST}), and two marginality indices involved in significant correlations with these genetic indicators, c) centroid index and d) second nearest-core index, for *P. pinaster* populations. See Table III-S1 for population information, including population names and geographical coordinates.

The model for recessive genetic load (M6) showed reduced genetic load for marginal populations based on the centroid index, this association probably stemming mainly from the high recessive genetic load found in some Iberian core populations (e.g., Carbonero el Mayor, CAR, and Boniches, BON; see Figure III-S8d). However, this model had a relatively low goodness-of-fit ($R^2 = 12\%$) and we found no relationship between recessive genetic load and any of the population marginality indices when we added the gene pool of origin as a random effect (M13, Table II-2b). Temperature seasonality (bio4) was the most important predictor contributing to the genetic turnover in genomic offset estimates (see Figure III-S11b and the GitHub detailing this analysis). Noticeably, this variable showed a steep slope between -2 and 0°C , which may indicate a rapid turnover in allele frequency in this range (see Figure S11a). Despite relatively poor goodness-of-fit (Table II-2a,b and Figures III-S16 and III-S17), both models including the genomic offset, without (M7) and with (M14) the gene pool of origin as a random effect, predicted an increased genomic offset for populations in marginal climatic conditions (Table II-2a,b and Figure II-3b). Accordingly, we observed a trend for higher genomic offset in the western gene pools along the Atlantic coast (average genomic offset of

0.047 ± 0.026 and 0.047 ± 0.016 for the Atlantic Iberian Peninsula and the French Atlantic gene pools, respectively), with remarkably high values for Segurde (SEG), Alto de la Llama (ALT), Armayán (ARM) and Olonne sur Mer (OLO) as well as for some southern Mediterranean populations (e.g., Point Cires, PCI; Fuencaliente, FUE; Estepona, EST; and Pantelleria, PAN; Figure II-3a).

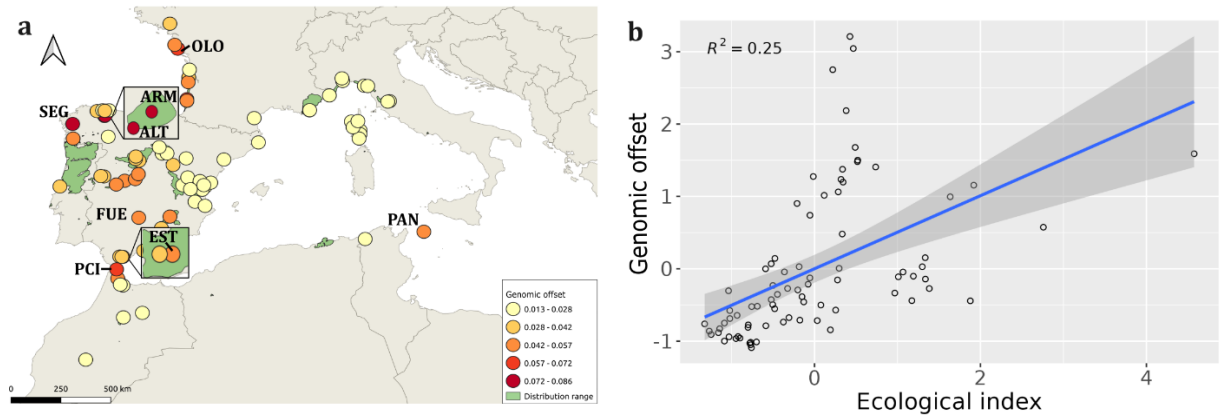


Figure II-3. a) Geographical distribution of genomic offset for *P. pinaster* populations and b) correlation between the genomic offset and the ecological index based on climate distances (standardised values), as shown by linear regression in the *ggplot2* R package. Population codes are only provided for populations specifically mentioned in the main text (see full population information, including population names and geographical coordinates, in Table III-S1).

Table II-2. Models evaluating the effect of population marginality on the estimated genetic indicators; a) Models without gene pool effect (M1-M7); b) Models including gene pool effect as a random factor (M8-M14). Significant fixed effect(s) are listed with their associated point estimates and 95% confidence intervals [in brackets]. R^2 : variance explained by fixed factors (M1-M7) or both fixed (marginal R^2) and random (conditional R^2) factors (M8-M14); ns: not significant.

a) Models without gene pool effect.

Model [R^2]	Genetic indicator	Fixed-effect #1	Estimate [95% CIs]	Fixed-effect #2	Estimate [95% CIs]	Fixed-effect #3	Estimate [95% CIs]	Interaction	Estimate [95% CIs]
M1 [0.59]	<i>Overall genetic diversity</i>	Centroid	-1.01 [-1.34, -0.67]	Second nearest-core	-1.47 [-2.43, -0.51]	North-South	1.61 [0.66, 2.55]	Second nearest-core × North-South	1.44 [0.50, 2.38]
M2 [0.26]	<i>Genetic diversity for GEA outliers</i>	North-South	0.62 [0.40, 0.85]	ns		ns		ns	
M3 [0.79]	<i>Genetic diversity for general outliers</i>	Centroid	1.26 [1.07, 1.45]	North-South	1.60 [1.32, 1.88]	ns		Centroid × North-South	1.16 [0.93, 1.40]
M4 [<0.01]	<i>Inbreeding</i>	ns		ns		ns		ns	
M5 [0.66]	<i>Population-specific F_{ST}</i>	Centroid	1.05 [0.74, 1.35]	Second nearest-core	1.43 [0.55, 2.31]	North-South	-1.90 [-2.76, -1.04]	Second nearest-core × North-South	-1.66 [-2.51, -0.80]
M6 [0.12]	<i>Recessive genetic load</i>	Centroid	-0.69 [-1.08, -0.30]	ns		ns		ns	
M7 [0.27]	<i>Genetic offset</i>	Ecological index	0.48 [0.28, 0.68]	ns		ns		ns	

b) Models with gene pool effect as random factor.

Model [R^2]	Genetic indicator	Fixed-effect #1	Estimate [95% CIs]	Fixed-effect #2	Estimate [95% CIs]	Interaction	Estimate [95% CIs]
M8 [0.41, 0.69]	<i>Overall genetic diversity</i>	Centroid	-1.04 [-1.58, -0.50]	North-South	1.04 [0.34, 1.75]	Centroid × North-South	0.75 [0.25, 1.24]
M9 [0.13, 0.5]	<i>Genetic diversity for GEA outliers</i>	North-South	0.44 [0.10, 0.77]	ns		ns	
M10 [<0.01]	<i>Genetic diversity for general outliers</i>	ns		ns		ns	
M11 [<0.01]	<i>Inbreeding</i>	ns		ns		ns	
M12 [0.31, 0.86]	<i>Population-specific F_{ST}</i>	Centroid	0.74 [0.21, 1.28]	North-South	-1.40 [-2.15, -0.65]	Centroid × North-South	-0.96 [-1.45, -0.46]
M13 [<0.01]	<i>Recessive genetic load</i>	ns		ns		ns	
M14 [0.22, 0.40]	<i>Genetic offset</i>	Ecological index	0.44 [0.24, 0.65]	ns		ns	

3. Discussion

In this study, we revealed a trend towards declining genetic diversity and increased genetic differentiation in geographically and demo-historically marginal populations of maritime pine; however, this genetic diversity trend would not necessarily apply to genes potentially involved in local adaptation, as shown by genetic diversity analyses based on different sets of outlier loci. We also found lower recessive genetic load in geographically marginal populations and higher genomic offset in ecologically marginal ones (although some of these populations have also high levels of climate-associated genetic diversity). Models including the gene pool of origin as a random effect were similar to those without (with the notable exception of the models for genetic diversity for general outliers and recessive genetic load), suggesting that the underlying processes operate at both the regional and range wide geographical scales in this species. These results, taken together, provide support for the CPH and suggest that climate change may endanger valuable and untapped genetic resources in maritime pine, in particular at its southern distribution edge.

3.1. Patterns of genetic diversity and differentiation support the CPH

The lower overall genetic diversity and higher genetic differentiation of geographical and demo-historical marginal populations support the main predictions of the CPH. Our results are consistent with those of Eckert et al. (2008) and Pironon et al. (2016), who found a decline in genetic diversity and an increase in differentiation towards the limits of the species ranges in 47% and 45% of studies in various taxa, respectively. As in our study, lower genetic variation in peripheral compared to central populations was found for some other conifers, i.e., in Sitka spruce (*Picea sitchensis*; Gapare et al., 2005), Swiss stone pine (*Pinus cembra*; Gugerli et al., 2009) and common yew (*Taxus baccata*; Hilfiker et al., 2004), but not in Norway spruce (*Picea abies*), for which only genetic differentiation conformed to the CPH (Westergren et al., 2018). This pattern is partially supported by patterns of genetic diversity for GEA outliers (only southern edge). Interestingly, unlike the distribution of overall and climate-associated (GEA outliers) genetic diversity with population marginality, genetic diversity based on general outliers (identified by the R package *pcadapt* and BayeScan v2.1; see Methods) increased with geographic marginality in terms of distance from the centroid, especially for populations in the

northern margins. There are several ways to interpret this result. Firstly, geographically marginal populations may show more variation in outlier SNPs linked to unknown biotic or abiotic factors (other than climate) than central populations. Secondly, this pattern could result from a confounding effect linked to the distinct level of genetic variation in outlier SNPs in the different gene pools, which could be corroborated by the fact that no significant relationship with population marginality remains when models included the gene pool of origin as a random factor. Finally, we could hypothesize that no robust biological explanation can be drawn from this result, due to the uncertainty of these outliers to be related or not to adaptation. Indeed, Lotterhos & Whitlock (2014, 2015) and Hoban et al. (2016) showed that most outliers detected with F_{ST} -outlier tests are likely to be false positives when calculated on species with peculiar demographic histories such as range expansion (e.g., Excoffier et al., 2009; Travis et al., 2007), as is the case in maritime pine.

In addition to geographical marginality, demo-historical marginality showed a significant association with overall genetic diversity (M1 in Table II-2a), as well as with genetic diversity based on outlier loci (M2 and M3). This significant association is consistent with the pattern observed in plants in the Mediterranean basin (Fady & Conord, 2010) but differs from a more global pattern in which the neutral genetic diversity of plants (including pines) does not change significantly with latitude (De Kort et al., 2021). Genetic differentiation, which decreases with latitude in plants across their ranges (Gamba & Muchhala, 2020), showed a significant association with demo-historical marginality in this direction too (see M5 in Table II-2a and M5bis in Table III-S5). However, despite a general trend of decreasing genetic diversity with latitude, southern populations from the Moroccan and Tunisia-Pantelleria gene pools and northern populations from the North-East and Corsican gene pools exhibited the lowest overall genetic diversity (also the lowest GEA-outlier diversity for the southern populations), and the highest genetic differentiation in maritime pine (see Figures II-2 and III-S8a). Maritime pine gene pools are probably the result of population expansion from multiple glacial refugia, both in Mediterranean and Atlantic regions of the species (Bucci et al., 2007; Jaramillo-Correa et al., 2015), with Naydenov et al. (2014) also suggesting that, for this species, the high level of overall genetic differentiation may have resulted from long historical isolation predating the Last Glacial Maximum (~18,000 years ago). This was confirmed by estimates of genetic divergence between North-African (Moroccan) and Iberian populations of maritime pine, which dated back to 1.90 Ma (95% credibility interval: 1.41-2.76), probably due to the Strait of Gibraltar's effect as a major biogeographic barrier to pollen and seed gene flow (Jaramillo-Correa et al., 2010).

Consequently, southernmost Moroccan populations are likely to have been pre-glacial relict populations that survived in North-African refugia (Baradat & Marpeau, 1988; Vendramin et al., 1998). After range expansion from glacial refugia, the persistence of maritime pine in several isolated groups characterized by contrasting climatic conditions may have resulted in populations that are locally adapted to the climate in some way. However, our models revealed that the southernmost populations of this species (Moroccan and Tunisia-Pantelleria gene pools) may be more at risk of not displaying enough diversity, neutral or adaptive, than the central populations. This pattern may have been exacerbated by a reduction of effective population size (N_e) due to human impact (Wahid et al., 2004), as well as the incidence of recurrent forest fires resulting in population bottlenecks and genetic drift in this region (Vendramin et al., 1998). The demographic history of maritime pine in the north-eastern part of the continental range and Corsica Island has not been clearly assessed (Naydenov et al., 2014), however, the presence of an endemic mitotype in this region suggests long-term isolation of North-East and Corsican gene pools (Burban & Petit, 2003). Nevertheless, both overall and GEA outlier genetic diversity for these populations seem to be larger than for those from the southernmost gene pools (see Figures II-2 and III-S8a).

3.2. Lower recessive genetic load in geographically marginal populations

Our models revealed a significant, albeit weak, reduction in recessive genetic load with increased geographical population marginality. However, these models were only significant when the gene pool effect was not accounted for, suggesting the existence of gene pools with reduced/increased recessive genetic load and an important role of demographic history (see below). This was a surprising finding, as we were expecting marginal populations to be characterised by an accumulation of recessive genetic load due to the reduced effectiveness of purifying selection in small and isolated populations with high demographic stochasticity (Caballero et al., 2017; Sachdeva et al., 2022). The level of accumulation of deleterious mutations and the extent to which it represents a risk to a given population depends primarily on its effective size (N_e). Previous empirical studies of animal and plant populations that underwent historical range expansions or declines have often shown an increase in genetic load (e.g., Günther & Schmid, 2010, in *Arabidopsis thaliana*; González-Martínez et al., 2017, in *Mercurialis annua*; Feng et al., 2019, in *Nipponia nippon*; or Peischl et al., 2013, in humans). However, as in maritime pine, recent empirical studies based on genomic data suggested that

recessive genetic load can also be purged in long-term isolated and inbred populations (see review in Dussex et al., 2023). As an example, Dussex et al. (2021) found that current island populations of *Strigops habroptilus*, a New-Zealand flightless parrot, had lower deleterious mutation load compared to mainland populations. A similar pattern was found for the Alpine ibex (*Capra ibex*), which suffered severe population bottlenecks and nearly became extinct (Grossen et al., 2020), and for the Channel Island fox (*Urocyon littoralis*) that has remained at small population sizes with low diversity for many generations (Robinson et al., 2018).

Present-day levels of inbreeding in maritime pine are low and not significantly higher in marginal than core populations. Therefore, we hypothesise maritime pine marginal populations to have effectively purged recessive genetic load during past inbreeding events, operating at the regional scale. These events may have occurred during the range contractions and/or expansions associated to Quaternary glacial and interglacial forest tree migrations (Bucci et al., 2007; Naydenov et al. 2014; Jaramillo-Correa et al., 2015). Polyembryony, which is ubiquitous in gymnosperms such as maritime pine (Willson & Burley, 1983), could have also played a role in purging recessive genetic load, as it tends to dampen self-fertilisation's deleterious effects by more effectively removing the mutational load through selection between viable embryos (see Latta, 1995).

3.3. Higher genomic offset in ecologically marginal populations

Our models also revealed a higher genomic offset for ecologically marginal populations, but not for geographically or demo-historically marginal ones suggesting that the gap between the current and required genetic composition in future climates (mainly associated with an increase in temperature seasonality, see Results) will be greater for populations in marginal climatic conditions. This is consistent with the findings of Fréjaville et al. (2020), who observed that adaptation lags in several forest trees, including maritime pine, are consistently higher in climatically (cold/warm, dry/wet) marginal populations than in populations growing under climatically optimal conditions. Although studies estimating genomic offset in marginal populations are still scarce, two recent studies in widespread Asian forest trees provided support to our findings, as they showed a relatively high genomic offset in the northern and southern distribution margins of the Chinese thuja tree (*Platycladus orientalis*; Jia et al., 2020) and the sawtooth oak (*Quercus acutissima*; Yuan et al., 2023); but whether these range margins

represented also ecologically extreme environments was not assessed and more detailed studies are thus needed. Estimation of the genomic offset is becoming a popular approach to assess population vulnerability in the face of climate change.

Genomic offset predictions have been validated using data from common garden experiments and natural populations (e.g., Fitzpatrick et al., 2021), including for maritime pine (Archambeau et al., 2024), but it is not free of pitfalls (see Ahrens et al., 2023; Rellstab et al., 2021; Lind et al., 2024; Archambeau et al., 2024). Moreover, genomic offsets can gauge (at some extent) for maladaptation to future climates but not for the adaptive capacity of populations (Fitzpatrick et al., 2021; Archambeau et al., 2024). In our study, some of the populations with high genomic offset had also high genetic diversity based on GEA outliers (e.g., Armayán - ARM, Alto de la Llama - ALT, Sergude - SEG and to a lesser extent, Olonne sur Mer - OLO, in the Atlantic Iberian Peninsula and French Atlantic gene pools, respectively; see Figure III-S18), which could indicate a high capacity for adaptive responses to future climates. Indeed, marginal populations of forest trees can retain notable adaptive capacity, as shown in common garden experiments for the handful of species with available data (e.g., for the Sierra Nevada Scots pine, *Pinus sylvestris*, population in southern Spain, an isolated marginal population at the species southern distribution limit; Alía et al., 2001; Castro et al., 2004). Thus, the potential for both genetic adaptation and plastic responses needs to be integrated in models predicting the responses of marginal populations to climate change. Furthermore, species' range limits are not determined solely by climate and demographic processes. Loehle (1998) showed that the range limits of many low-latitude tree species are set by competitive interactions with other tree species. Other biotic factors, such as the positive interactions between species (Stephan et al., 2021), are known to have a strong influence on the definition of tree range boundaries. To better disentangle the relationship between genetic indicators and population marginality within a species' range, future research should address the development of predictive models that include species-specific indicators related to biotic interactions.

4. Conclusion

In maritime pine, a trend of decreasing in overall genetic diversity and increasing differentiation with geographic marginality supported the well-established centre-periphery hypothesis, at both range-wide and regional (gene pool) spatial scales. However, geographically marginal populations displayed also lower recessive genetic load compared to core populations, which, together with expected novel adaptations in the species range margins, highlight their importance in the context of future adaptation to climate change. Higher genomic offset in ecologically marginal populations suggests higher potential maladaptation of these populations to future climates; however, some of them have also high levels of climate-associated (based on GEA) genetic diversity, which may foster adaptive responses to future climates. In addition, lower levels of genetic diversity, both neutral and potentially adaptive, in southern margin populations highlights the urgency to develop specific management actions in this region. Overall, our study shows the importance of combining quantitative marginality indices and diverse genetic indicators, gauging for multiple evolutionary processes, to have a sound basis for conservation decisions.

5. Data archiving statement

Data are openly available in a public repository (Data INRAE) and was provided for the anonymized review process as a file. Scripts for preparation of data, selection of climate variables and computation of genomic offset statistics can be found in a GitHub public repository, and were cloned and anonymised for the review process at https://anonymous.4open.science/r/ReadyToGO_Pinpin-FA56/README.md

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III. Supplementary information - Chapter 1

1. The data

1.1. The populations features

Table III-S1. Geographical location and sample size (N) of the 82 populations of *P. pinaster* included in the study; Abb.: Abbreviated population name.

Population	Abb.	Country	N	Latitude (°)	Longitude (°)	Elevation (m)
Aïn Babouch	ABA	Tunisia	22	36.815	8.715	201
Adeldal	ADE	Morocco	21	35.157	-5.079	830
Ahin	AHI	Spain	22	39.888	-0.332	733
Alto de la Llama	ALT	Spain	8	43.297	-6.463	526
Ania	ANI	France	12	41.968	9.284	578
Arenzano	ANO	Italy	11	44.418	8.671	403
Armayán	ARM	Spain	8	43.305	-6.458	559
Arenas de San Pedro	ARN	Spain	17	40.195	-5.116	663
Bavella	BAV	France	16	41.796	9.235	1042
Bayubas de Abajo	BAY	Spain	15	41.523	-2.877	925
Benicassim	BEN	Spain	22	40.079	0.025	520
Bonifatu	BOI	France	16	42.446	8.825	500
Boniches	BON	Spain	8	39.984	-1.662	1090
Cadavedo	CAD	Spain	8	43.540	-6.418	164
Cagna	CAG	France	12	41.597	9.142	995
Carbonero el Mayor	CAR	Spain	6	41.172	-4.277	844
Castropol	CAS	Spain	8	43.501	-6.983	158
Cazorla	CAZ	Spain	21	37.918	-2.927	1059
Cenicientos	CEN	Spain	9	40.278	-4.491	1079
Coca	COC	Spain	17	41.255	-4.498	784
Codos	COD	Spain	22	41.282	-1.418	1058

Cómpeta	COM	Spain	3	36.832	-3.925	904
Cortes de Pallás	CPA	Spain	22	39.178	-0.946	925
Cuéllar	CUE	Spain	23	41.335	-4.249	826
Estepona	EST	Spain	21	36.516	-5.121	458
Fuencaliente	FUE, stand 1	Spain	21	38.417	-4.254	913
	FUE, stand 2	Spain	25	38.417	-4.254	913
Gaucin	GAU	Spain	22	36.532	-5.301	630
Gea de Albarracín	GEA	Spain	22	40.365	-1.351	1367
La Bisbal	GIR	Spain	21	41.899	3.032	243
Guagno	GUA	France	12	42.173	8.879	572
Hourtin	HOU	France	25	45.183	-1.150	28
Jubrique	JUB	Spain	21	36.523	-5.185	958
Koudiat Erramla	KUD	Morocco	16	35.467	-5.383	480
F.D. de Lacanau	LAC	France	21	44.946	-1.187	36
Lamuño	LAM	Spain	9	43.559	-6.219	119
Les Corbières	LCO, stand 1	France	21	43.082	2.878	216
	LCO, stand 2	France	25	43.082	2.878	216
Leiria	LEI	Portugal	21	39.783	-8.958	79
F.D. de Lit et Mixe	LIM	France	25	44.052	-1.301	45
Madisouka	MAD, stand 1	Morocco	1	35.191	-5.166	1302
	MAD, stand 2	Morocco	21	35.191	-5.166	1302
Magra/Montemarcello	MAG	Italy	15	44.074	9.973	100
Maures	MAU, stand 1	France	7	43.233	6.365	361
	MAU, stand 2	France	8	43.233	6.365	606
Mazarete	MAZ	Spain	21	40.972	-2.222	1171
Mimizan	MIM	France	18	44.134	-1.303	18
Montignoso	MON	Italy	6	44.012	10.184	434
Pina de Montalgrao	MTG	Spain	21	40.030	-0.644	1148
Murlo	MUR	Italy	8	43.129	11.222	408

Olba	OLB	Spain	20	40.173	-0.623	989
Olonne sur Mer	OLO	France	24	46.566	-1.831	12
Oña	ONA	Spain	24	42.763	-3.535	753
Oria	ORI	Spain	23	37.513	-2.317	1221
Pantelleria	PAN	Italy	17	36.782	12.002	733
Point Cires	PCI	Morocco	22	35.904	-5.481	90
Pradell de la Teixeta	PDL	Spain	22	41.166	0.865	560
Petrocq	PET	France	22	44.064	-1.300	21
La Peza	PEZ	Spain	22	37.263	-3.403	1414
Pinofranqueado	PFQ	Spain	21	40.365	-6.385	724
Pineto	PIN	France	12	42.427	9.227	475
Pleucadec	PLE	France	19	47.781	-2.344	70
Puerto de Vega	PUE	Spain	7	43.548	-6.631	81
Quatretonda	QUA	Spain	16	38.990	-0.349	420
Quintana Redonda	QUI	Spain	22	41.533	-2.583	1046
Riopar	RIO	Spain	24	38.485	-2.425	1039
Rossiglione	ROS	Italy	10	44.451	8.675	955
San Cipriano de Ribarteme	SAC	Spain	10	42.116	-8.366	386
El Sahugo	SAH	Spain	22	40.381	-6.562	817
San Leonardo de Yagüe	SAL	Spain	10	41.833	-3.064	1070
Sierra Calderona	SCD	Spain	22	39.749	-0.495	746
Seborga	SEB	Italy	24	43.820	7.710	544
Sergude	SEG	Spain	19	42.817	-8.450	309
Sidi-Meskour	SID	Morocco	22	31.506	-6.995	1975
Sierra de Barcia	SIE	Spain	8	43.528	-6.493	264
Sinarcas	SIN	Spain	22	39.791	-1.203	888
Sobron	SOB	Spain	24	42.789	-3.086	895
St-Jean des Monts	STJ	France	25	46.764	-2.029	6
Tamjout	TAJ	Morocco	22	33.842	-4.007	1500
Talayuela	TAL, stand 1	Spain	21	40.000	-5.623	272

	TAL, stand 2	Spain	25	40.000	-5.623	272
Tamrabta	TAM	Morocco	14	33.600	-5.017	1729
Tabuyo del Monte	TBY	Spain	22	42.294	-6.212	988
Tocchi	TOC	Italy	12	43.132	11.243	441
Le Verdon	VER	France	25	45.552	-1.091	10
Villamalur	VMA	Spain	21	39.965	-0.401	639
Valdemaqueda	VMQ	Spain	10	40.514	-4.313	947

1.2. Population-specific marginality indices

Table III-S2. Standardized marginality indices for each of the 81 *P. pinaster* populations included in the analysis (population COM was removed due to low sample size), calculated according to Picard et al. (2022) but based on the native range of the species only (i.e., excluding plantations; see Figure S1), and ecological index based on climate distance.

Population	Area	Centroid	Edge	Gravity	Isolation	Second near-est-core	North-South	East-West	Ecological index
ABA	-0.287	0.339	1.301	-0.428	-0.920	-0.858	-0.927	0.501	-0.507
ADE	-0.265	-1.028	0.888	-0.252	-0.899	-0.919	-0.979	-1.396	1.757
AHI	-0.311	-1.625	1.310	-0.472	-1.335	-1.085	-0.519	0.053	-1.172
ALT	-0.313	-1.382	0.970	0.785	-0.942	-1.001	0.983	-1.544	0.516
ANI	-0.315	-0.152	1.307	-0.482	-1.353	-0.810	0.830	0.626	-0.718
ANO	-0.034	-0.780	1.331	0.052	-1.205	-1.166	1.216	0.498	-0.350
ARM	-0.313	-1.382	0.970	0.785	-0.942	-1.001	0.983	-1.544	0.589
ARN	0.004	-1.630	1.312	0.124	-1.299	-1.193	-0.315	-1.408	0.364
BAV	-0.315	-0.143	1.294	-0.472	-1.355	-0.767	0.738	0.621	-0.530
BAY	0.348	-1.730	1.313	0.779	-1.230	-1.194	0.515	-0.773	-0.305
BEN	-0.311	-1.593	1.217	-0.324	-1.272	-1.182	-0.393	0.065	-1.198
BOI	-0.102	-0.167	1.301	-0.079	-1.207	-1.169	0.902	0.515	-0.721
BON	1.057	-1.698	1.322	2.125	-1.271	-1.110	-0.448	-0.268	-0.227
CAD	-0.313	-1.363	0.897	0.661	-0.869	-0.928	1.040	-1.535	1.500
CAG	-0.317	-0.128	1.263	-0.441	-1.291	-0.702	0.585	0.599	-1.000
CAR	1.339	-1.687	1.326	2.659	-1.206	-1.167	0.225	-1.095	-0.350
CAS	-0.313	-1.333	0.871	0.775	-0.903	-0.899	1.030	-1.603	1.400
CAZ	0.246	-1.527	1.316	0.584	-1.171	-1.130	-0.875	-0.787	0.113
CEN	0.004	-1.652	1.301	0.125	-1.235	-1.199	-0.249	-1.185	0.289
COC	1.339	-1.675	1.380	2.659	-1.169	-1.128	0.289	-1.185	-0.266
COD	-0.328	-1.681	1.301	-0.502	-1.210	-1.172	0.325	-0.218	-0.415
CPA	-0.210	-1.629	1.316	-0.281	-1.327	-1.135	-0.746	-0.046	-0.893
CUE	1.339	-1.685	1.371	2.659	-1.160	-1.118	0.359	-1.083	-0.237

EST	-0.265	-1.275	1.316	-0.385	-1.060	-1.010	-0.971	-1.408	1.526
FUE	0.246	-1.438	0.966	0.001	-0.978	-0.994	-0.810	-1.083	0.468
GAU	-0.265	-1.266	1.291	-0.381	-1.019	-0.965	-0.971	-1.447	0.465
GEA	-0.296	-1.678	1.309	-0.446	-1.271	-1.149	-0.172	-0.206	-0.343
GIR	0.881	-1.268	0.516	-0.037	-0.459	-0.540	0.796	0.068	-0.823
GUA	-0.102	-0.164	1.301	-0.086	-1.276	-0.786	0.870	0.533	-0.591
HOU	-0.319	-1.325	1.192	-0.440	-1.255	-1.169	1.242	-0.117	-0.422
JUB	-0.265	-1.271	1.312	-0.385	-1.044	-0.992	-0.971	-1.426	0.515
KUD	-0.265	-1.076	0.986	-0.224	-0.819	-1.018	-0.976	-1.458	2.912
LAC	-0.319	-1.343	1.269	-0.470	-1.279	-1.143	1.241	-0.135	-0.277
LAM	-0.313	-1.372	0.894	0.618	-0.853	-0.925	1.044	-1.515	1.612
LCO	0.881	-1.232	0.594	-0.013	-0.422	-0.619	0.925	0.068	-0.855
LEI	5.369	-1.393	1.307	10.308	-1.080	-1.032	-0.585	-2.920	1.708
LIM	-0.234	-1.419	1.301	-0.327	-1.206	-1.168	1.172	-0.180	0.125
MAD	-0.265	-1.033	0.901	-0.246	-0.886	-0.932	-0.977	-1.426	0.156
MAG	-0.243	-0.695	1.316	-0.344	-1.329	-1.197	1.175	0.657	-0.771
MAU	0.881	-0.912	1.326	1.789	-1.035	-0.983	0.965	0.206	-0.579
MAZ	-0.199	-1.756	1.311	-0.260	-1.258	-1.157	0.111	-0.531	-0.032
MIM	-0.234	-1.414	1.309	-0.326	-1.229	-1.193	1.183	-0.180	0.082
MON	-0.328	-0.685	1.301	-0.487	-1.360	-1.144	1.167	0.664	-0.668
MTG	-0.269	-1.642	1.307	-0.394	-1.307	-1.176	-0.420	0.014	-0.918
MUR	-0.123	-0.592	1.316	-0.116	-1.132	-1.088	0.935	0.741	0.052
OLB	-0.269	-1.633	1.307	-0.394	-1.327	-1.190	-0.330	0.018	-1.052
OLO	-0.328	-1.113	0.936	-0.244	-0.835	-0.980	1.247	-0.319	0.205
ONA	-0.270	-1.600	1.309	-0.396	-1.130	-1.086	0.912	-0.903	-0.540
ORI	0.246	-1.472	1.123	-0.022	-1.180	-1.153	-0.880	-0.561	-0.017
PAN	-0.287	0.964	0.517	-0.244	-0.125	-0.539	-0.937	0.750	1.522
PCI	-0.265	-1.133	1.117	-0.245	-0.896	-1.149	-0.976	-1.464	5.013
PDL	-0.317	-1.488	0.895	-0.123	-0.921	-0.922	0.225	0.066	-0.876
PET	-0.234	-1.417	1.307	-0.326	-1.212	-1.174	1.175	-0.180	0.122
PEZ	-0.322	-1.434	1.307	-0.494	-1.242	-1.122	-0.882	-0.881	0.065
PFQ	-0.181	-1.533	1.318	-0.225	-1.266	-1.171	-0.172	-1.531	-0.334

PIN	-0.102	-0.186	1.307	-0.075	-1.238	-1.197	0.899	0.621	-0.495
PLE	-0.328	-0.957	0.537	-0.115	-0.457	-0.575	1.248	-0.576	-0.107
PUE	-0.313	-1.349	0.882	0.689	-0.871	-0.911	1.044	-1.559	1.588
QUA	-0.210	-1.582	1.202	0.024	-1.200	-1.161	-0.761	0.048	-1.325
QUI	0.348	-1.724	1.313	0.779	-1.239	-1.127	0.515	-0.676	-0.314
RIO	0.246	-1.573	1.328	0.584	-1.269	-1.004	-0.803	-0.605	0.313
ROS	-0.034	-0.778	1.320	0.052	-1.202	-1.164	1.222	0.498	-0.255
SAC	5.369	-1.410	1.288	9.639	-1.286	-1.120	0.863	-2.581	0.068
SAH	-0.181	-1.525	1.307	-0.225	-1.302	-1.193	-0.159	-1.551	-0.509
SAL	0.348	-1.707	1.326	0.779	-1.274	-1.075	0.762	-0.828	-0.175
SCD	-0.327	-1.631	1.301	-0.481	-1.349	-1.140	-0.608	0.026	-1.308
SEB	-0.034	-0.836	1.309	0.052	-1.251	-0.910	1.118	0.434	-0.745
SEG	5.369	-1.326	1.065	2.527	-1.096	-1.099	0.917	-2.646	0.633
SID	-0.323	-0.513	0.565	-0.255	-0.644	-0.586	-0.996	-1.603	-0.630
SIE	-0.313	-0.513	0.565	-0.255	-0.644	-0.586	-0.996	-1.603	1.363
SIN	1.057	-1.674	1.343	2.125	-1.248	-1.190	-0.585	-0.135	-0.539
SOB	-0.270	-1.599	1.258	-0.267	-1.125	-1.080	0.916	-0.834	-0.345
STJ	-0.328	-1.089	0.861	-0.208	-0.768	-0.904	1.247	-0.402	0.024
TAJ	-0.322	-0.816	1.022	-0.386	-1.080	-1.051	-0.982	-1.008	-0.161
TAL	-0.306	-1.599	1.307	-0.464	-1.360	-1.157	-0.448	-1.478	0.705
TAM	-0.322	-0.840	1.301	-0.492	-1.330	-0.416	-0.984	-1.372	-0.680
TBY	-0.313	-1.510	1.290	-0.352	-1.176	-1.136	0.886	-1.515	-0.776
TOC	-0.123	-0.590	1.313	-0.116	-1.127	-1.083	0.935	0.745	0.014
VER	-0.328	-1.297	1.301	-0.505	-1.153	-1.110	1.245	-0.094	-0.652
VMA	-0.311	-1.630	1.301	-0.442	-1.361	-1.112	-0.461	0.042	-1.114
VMQ	0.004	-1.671	1.318	0.124	-1.315	-1.048	-0.089	-1.109	0.334

1.3. Population-specific genetic indicators

Table III-S3. Genetic indicators for each of the 81 populations of *P. pinaster* included in the study (population COM was removed due to low sample size). Values for stands within populations were averaged (see Table S1). Overall genetic diversity: genetic diversity estimated as $I-Q_{inter}$ using all SNPs and corrected for sample size (see main text for details); Genetic diversity for GEA outliers: genetic diversity estimate based on 73 outlier SNPs selected from the GEA performed for the genomic offset computation; Genetic diversity for general outliers: genetic diversity estimate based on 151 outlier SNPs common to two environment-independent outlier-detection methods (see main text for details); F_{IS} : population inbreeding; Population-specific F_{ST} : genetic differentiation of each population from the common ancestral gene pool; Recessive genetic load: number of predicted deleterious mutations in homozygosity standardized by synonymous mutations; Genomic offset: change in genetic composition required to maintain the current gene-environment relationships under future climates.

Population	Overall genetic diversity	Genetic diversity for GEA outliers	Genetic diversity for general outliers	F_{IS}	Population-specific F_{ST}	Recessive genetic load	Genomic offset
ABA	0.147	0.276	0.220	0.045	0.440	0.444	0.020
ADE	0.200	0.149	0.125	-0.060	0.332	0.469	0.024
AHI	0.241	0.274	0.145	0.057	0.048	0.481	0.016
ALT	0.247	0.358	0.120	-0.010	0.098	0.480	0.087
ANI	0.209	0.359	0.400	-0.080	0.207	0.453	0.015
ANO	0.196	0.205	0.299	-0.040	0.259	0.436	0.018
ARM	0.230	0.351	0.119	-0.030	0.153	0.496	0.084
ARN	0.241	0.329	0.121	0.006	0.032	0.492	0.056
BAV	0.212	0.339	0.382	0.024	0.192	0.447	0.014
BAY	0.240	0.285	0.115	-0.040	0.030	0.465	0.027
BEN	0.230	0.318	0.147	-0.010	0.087	0.480	0.018
BOI	0.198	0.283	0.353	0.038	0.249	0.449	0.015
BON	0.271	0.242	0.115	-0.010	0.032	0.508	0.026
CAD	0.233	0.309	0.110	0.087	0.137	0.443	0.030
CAG	0.217	0.345	0.379	-0.020	0.176	0.430	0.016
CAR	0.264	0.409	0.161	-0.050	0.078	0.544	0.032
CAS	0.227	0.303	0.101	0.029	0.162	0.478	0.030
CAZ	0.215	0.216	0.133	-0.230	0.120	0.468	0.030
CEN	0.266	0.319	0.126	-0.010	0.028	0.480	0.049
COC	0.246	0.372	0.158	-0.010	0.023	0.484	0.033
COD	0.227	0.229	0.102	-0.010	0.077	0.442	0.022
CPA	0.249	0.315	0.167	-0.020	0.039	0.472	0.019
CUE	0.240	0.341	0.144	-0.010	0.029	0.462	0.034
EST	0.233	0.206	0.143	-0.010	0.167	0.492	0.052
FUE	0.211	0.264	0.132	-0.020	0.177	0.471	0.050
GAU	0.231	0.194	0.135	0.035	0.183	0.499	0.032

GEA	0.239	0.211	0.119	-0.070	0.069	0.476	0.023
GIR	0.171	0.285	0.294	-0.070	0.294	0.432	0.020
GUA	0.204	0.312	0.348	-0.070	0.227	0.437	0.014
HOU	0.227	0.310	0.141	-0.010	0.107	0.463	0.032
JUB	0.216	0.173	0.119	-0.120	0.217	0.487	0.035
KUD	0.185	0.134	0.108	-0.220	0.353	0.422	0.042
LAC	0.235	0.298	0.137	-0.020	0.109	0.473	0.053
LAM	0.226	0.304	0.099	-0.010	0.157	0.452	0.027
LCO	0.226	0.248	0.122	-0.020	0.116	0.478	0.027
LEI	0.227	0.256	0.082	-0.020	0.077	0.460	0.029
LIM	0.232	0.292	0.136	-0.020	0.114	0.474	0.058
MAD	0.202	0.157	0.132	-0.040	0.310	0.495	0.026
MAG	0.189	0.259	0.322	0.007	0.306	0.449	0.016
MAU	0.221	0.210	0.336	-0.020	0.219	0.446	0.019
MAZ	0.236	0.191	0.077	-0.010	0.039	0.460	0.032
MIM	0.233	0.322	0.153	0.024	0.102	0.457	0.061
MON	0.219	0.278	0.376	0.033	0.286	0.469	0.014
MTG	0.258	0.267	0.186	0.011	0.063	0.452	0.015
MUR	0.203	0.272	0.349	-0.050	0.288	0.474	0.023
OLB	0.245	0.268	0.144	0.008	0.034	0.453	0.017
OLO	0.224	0.296	0.150	0.013	0.112	0.459	0.070
ONA	0.231	0.275	0.117	-0.030	0.075	0.474	0.017
ORI	0.245	0.267	0.190	-0.010	0.089	0.483	0.020
PAN	0.164	0.281	0.242	-0.040	0.376	0.445	0.049
PCI	0.209	0.291	0.145	0.135	0.202	0.493	0.059
PDL	0.233	0.267	0.150	0.036	0.089	0.469	0.022
PET	0.234	0.334	0.161	-0.010	0.098	0.465	0.058
PEZ	0.254	0.266	0.184	-0.040	0.081	0.482	0.028
PFQ	0.224	0.328	0.132	-0.020	0.100	0.447	0.031
PIN	0.204	0.354	0.383	0.041	0.235	0.451	0.015
PLE	0.231	0.338	0.153	-0.040	0.098	0.467	0.040
PUE	0.231	0.390	0.147	-0.060	0.145	0.463	0.024
QUA	0.242	0.275	0.147	-0.010	0.058	0.466	0.023
QUI	0.226	0.266	0.104	-0.090	0.051	0.441	0.024
RIO	0.256	0.277	0.175	-0.020	0.053	0.507	0.045
ROS	0.223	0.294	0.383	-0.020	0.183	0.464	0.025
SAC	0.228	0.365	0.134	-0.030	0.105	0.421	0.048
SAH	0.238	0.329	0.130	-0.030	0.032	0.475	0.028
SAL	0.245	0.292	0.112	-0.010	0.038	0.454	0.025
SCD	0.225	0.246	0.135	-0.060	0.080	0.463	0.019
SEB	0.208	0.250	0.318	-0.030	0.176	0.428	0.021
SEG	0.216	0.317	0.116	-0.060	0.110	0.469	0.079
SID	0.114	0.094	0.065	-0.160	0.640	0.487	0.018
SIE	0.225	0.373	0.132	0.004	0.130	0.422	0.031
SIN	0.230	0.248	0.118	-0.070	0.086	0.490	0.023
SOB	0.236	0.278	0.116	0.050	0.060	0.496	0.029
STJ	0.225	0.318	0.153	0.000	0.112	0.466	0.053
TAJ	0.177	0.132	0.098	0.034	0.442	0.461	0.019

TAL	0.230	0.320	0.133	-0.040	0.068	0.474	0.056
TAM	0.185	0.132	0.134	-0.130	0.389	0.451	0.027
TBY	0.225	0.257	0.089	0.012	0.082	0.485	0.013
TOC	0.197	0.289	0.336	-0.050	0.287	0.458	0.020
VER	0.223	0.313	0.146	0.034	0.110	0.480	0.022
VMA	0.229	0.230	0.115	-0.060	0.087	0.471	0.017
VMQ	0.257	0.341	0.161	-0.070	0.029	0.447	0.054

1.4. Climatic variables

Table III-S4. Climatic variables used in the genomics offset analyses, as provided by the Climate Downscaling Tool (ClimateDT, <https://www.ibbr.cnr.it/climate-dt/>).

Label	Description	Unit
bio1	Mean annual temperature	Celsius degrees (°C)
bio3	Isothermality (bio2/bio7) (×100)	Index
bio4	Temperature seasonality (standard deviation ×100)	Celsius degrees (°C)
bio12	Annual precipitation	Millimeters (mm)
bio15	Precipitation seasonality (coefficient of variation)	Index
SHM	Summer Heat Moisture index	°C/mm

2. The results

2.1. The models, the natural distribution of maritime pine and its centroid

2.1.1. The models with and without gene pool effect

Table III-S5. Models a) without and b) with gene pool effect as a random factor, evaluating the effect of population marginality on population-specific Jost's D (average pairwise values), a measure of genetic differentiation that is independent of levels of genetic diversity. Significant fixed effects are given with their associated point estimates and 95% confidence intervals [in brackets]. R^2 : variance explained by fixed factors or both fixed (marginal R^2) and random (conditional R^2) factors; ns: not significant.

a) Models without gene pool effect.

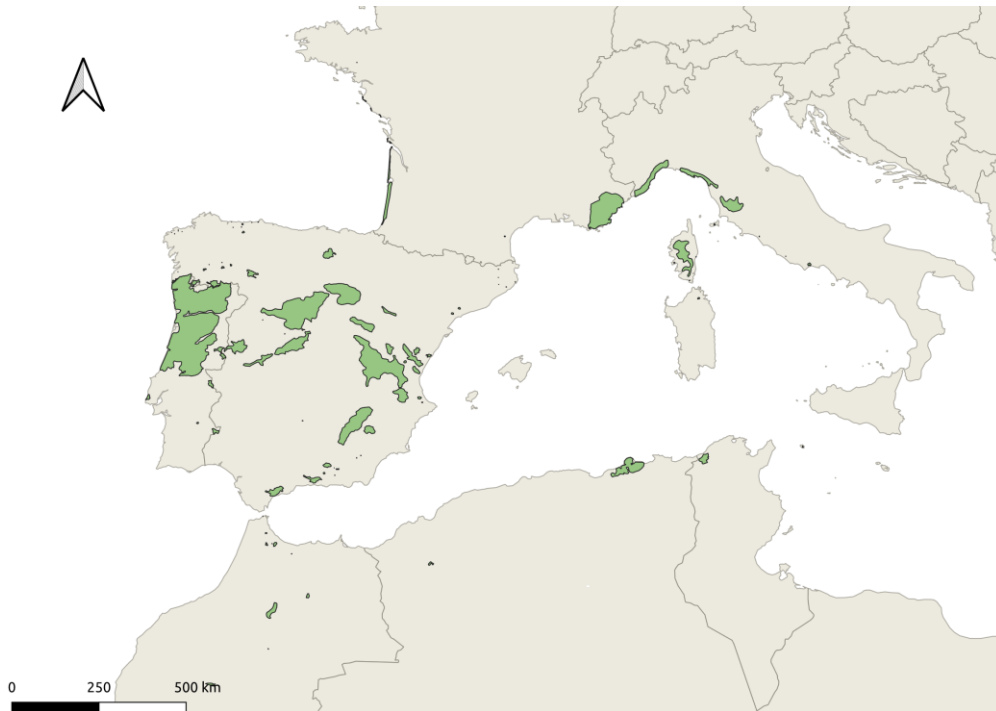
Model [R^2]	Genetic indicator	Fixed-effect #1	Estimate [95% CIs]	Fixed-effect #2	Estimate [95% CIs]	Fixed-effect #3	Estimate [95% CIs]	Interaction	Estimate [95% CIs]
M5bis [0.61]	<i>Population-specific Jost's D</i>	Centroid	0.76 [0.44, 1.09]	Second nearest-core	1.88 [0.94, 2.82]	North-South	-2.37 [-3.29, -1.44]	Second nearest-core × North-South	-2.03 [-2.95, -1.12]

b) Models with gene pool effect as random factor

Model [R^2]	Genetic indicator	Fixed-effect #1	Estimate [95% CIs]	Fixed-effect #2	Estimate [95% CIs]	Interaction	Estimate [95% CIs]
M12bis [0.31, 0.90]	<i>Population-specific Jost's D</i>	Centroid	0.88 [0.32, 1.44]	North-South	-1.76 [-2.57, -0.94]	Centroid × North-South	-1.19 [-1.73, -0.66]

2.1.2. The natural distribution of maritime pine

Figure III-S1. Distribution range of *P. pinaster* considering only natural populations (i.e., excluding plantations). This map was produced based on the distribution map of *P. pinaster* by Caudullo et al. (2017), which contains both natural populations and plantations. The boundaries of *P. pinaster* natural distribution were delimited with QGIS v3.22 based on information available in Alía et al., 1996; Marques et al., 2012; Abad-Viñas et al., 2016; Fkiri et al., 2019 and Wahid et al., 2004, 2006 and taking into account the National Forest Inventories of Spain, Italy and France.



2.1.3. *The centroid of the distribution range*

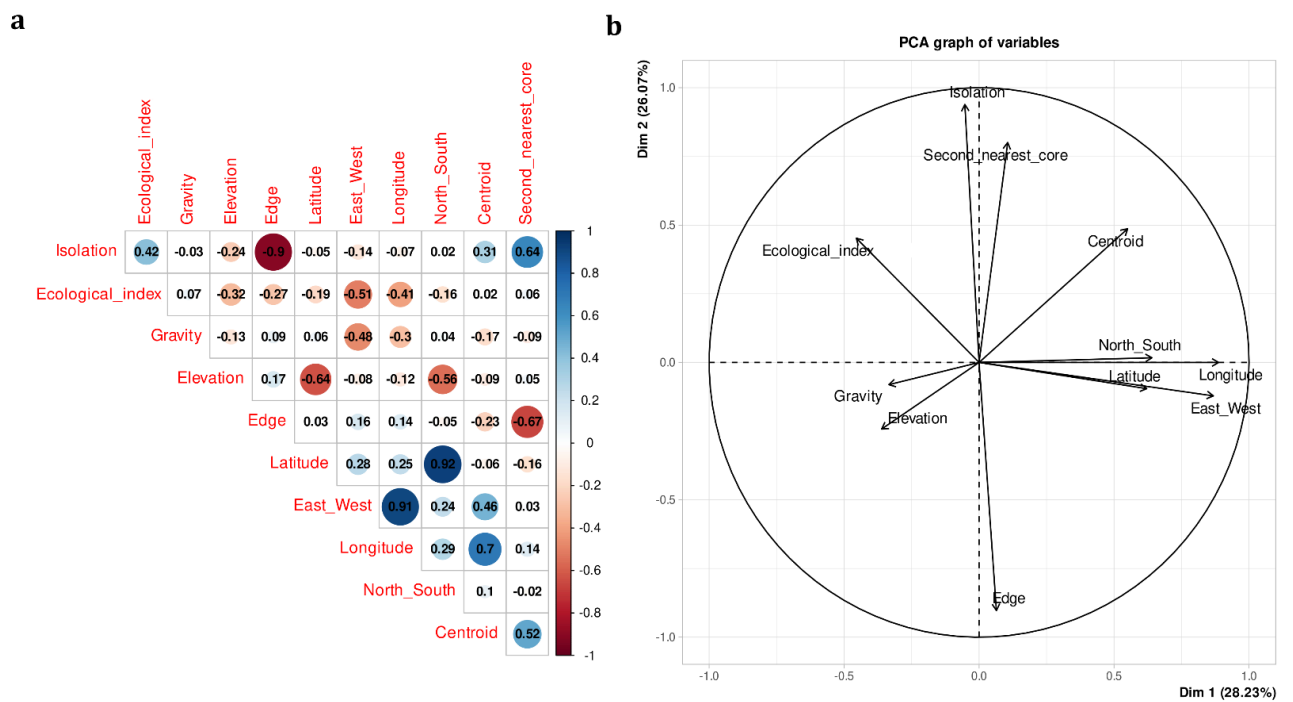
Figure III-S2. Map showing the position of the centroid of the maritime pine natural distribution (in blue), which corresponds to the location whose geographic coordinates are the average of all locations where the species is naturally present (see Figure II-S1).



2.2. The correlations: marginality indices, genetic indicators and General Circulation Models (GCMs)

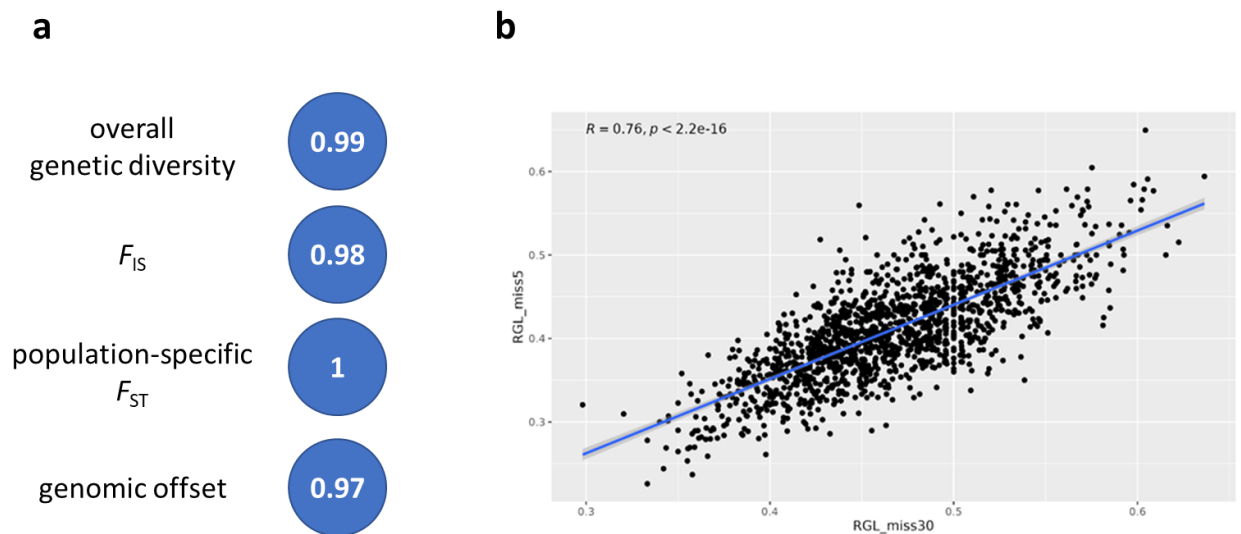
2.2.1. Correlation of marginality indices

Figure III-S3. Correlation of standardized marginality indices; a) Pairwise correlogram based on Pearson's correlation coefficients; b) Plot of the two first axes (explaining 54.3% of the variance) of the Principal Component Analysis (PCA).



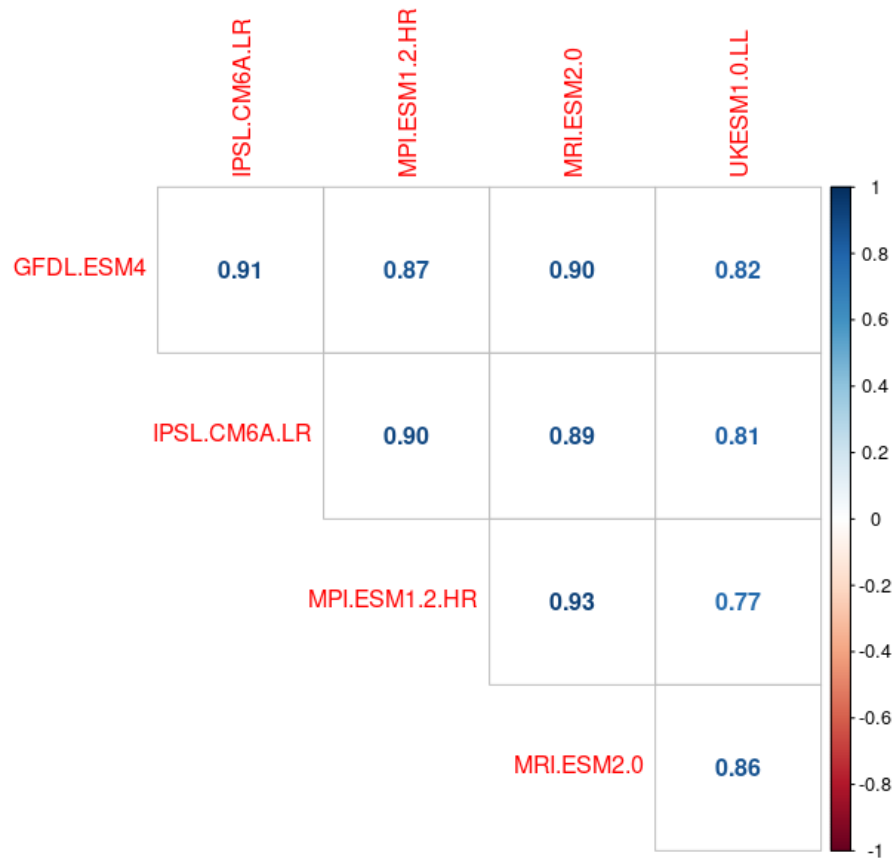
2.2.2. Correlation of genetic indicators

Figure III-S4. Correlation of genetic indicator estimates using the full dataset (10,185 SNPs) with missing data lower than 30% and a dataset (6,390 SNPs) with missing data lower than 5%, for a) overall genetic diversity, F_{IS} , population-specific F_{ST} , and genomic offset; and b) linear regression between recessive genetic load (RGL) calculated at the individual level from the full dataset with missing data lower than 30% (RGL_miss30) and a dataset with missing data lower than 5% (RGL_miss5). Numbers in a) correspond to pairwise Pearson's correlation coefficients. See full description of statistics in Table S3 and/or in the main text.



2.2.3. Correlation of GCMs

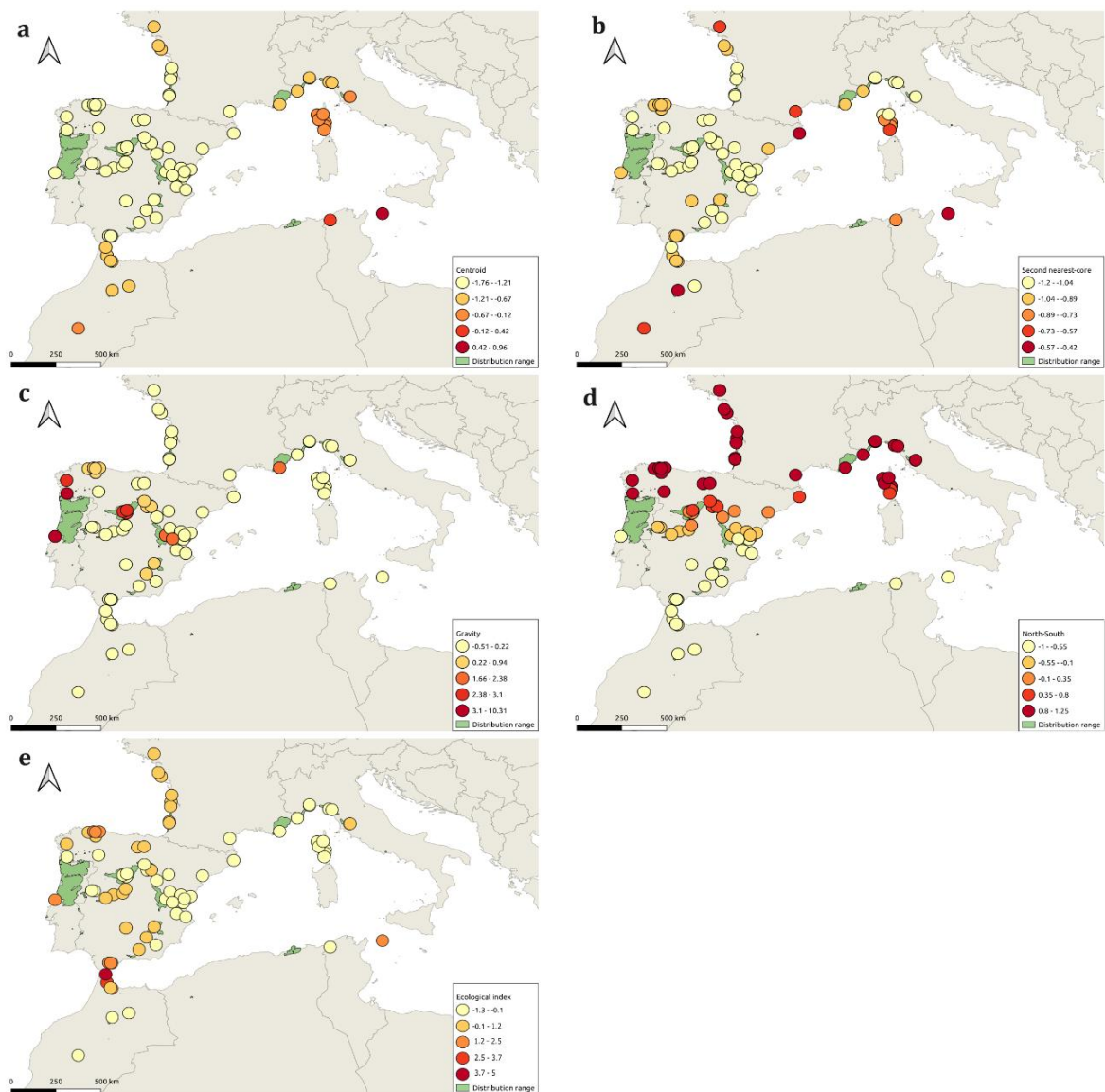
Figure III-S5. Pairwise correlogram based on Pearson's correlation coefficients of genomic offset predictions for the five GCMs used in this study.



2.3. Geographical distribution of marginality indices and genetic indicators and breakdown of model's interactions effects

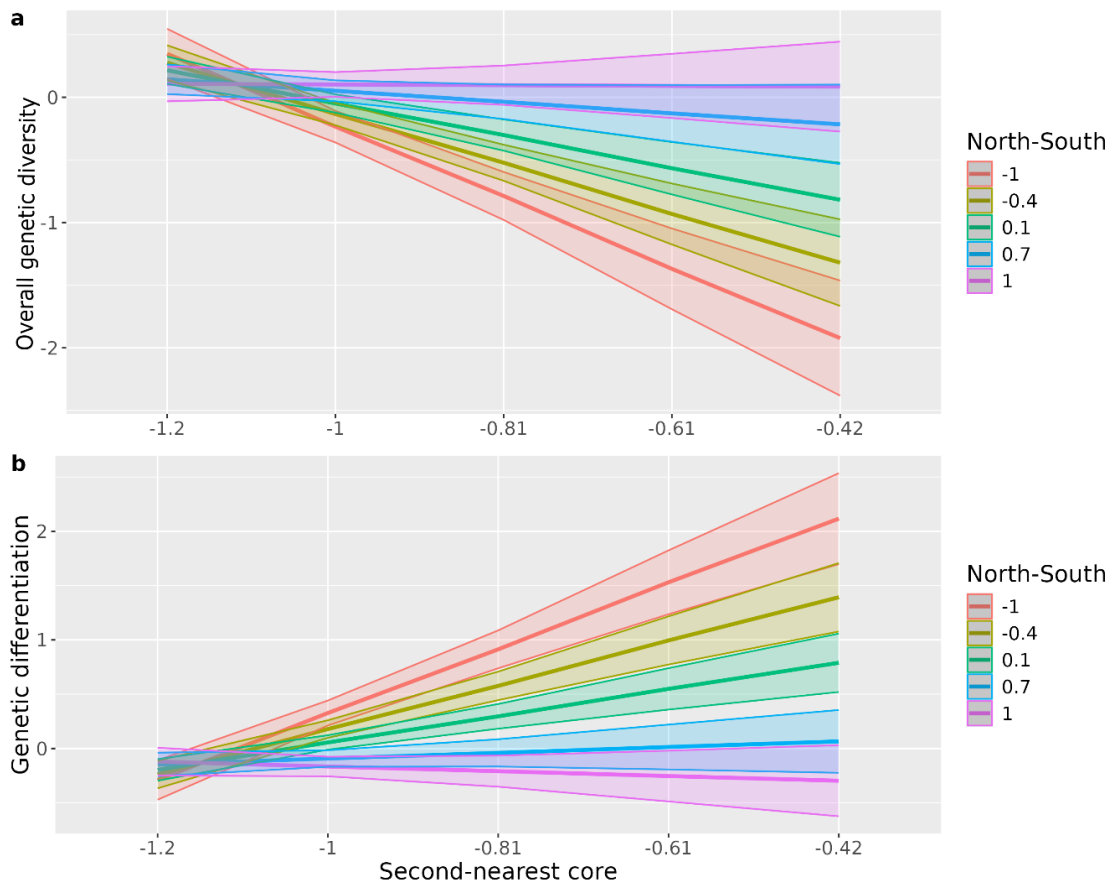
2.3.1. Geographical distribution of marginality indices used in this study

Figure III-S6. Maps depicting the geographic distribution of the marginality indices selected in our study for *P. pinaster* populations. a) Centroid; b) Second nearest-core; c) Gravity; d) North-South; and e) Ecological index.



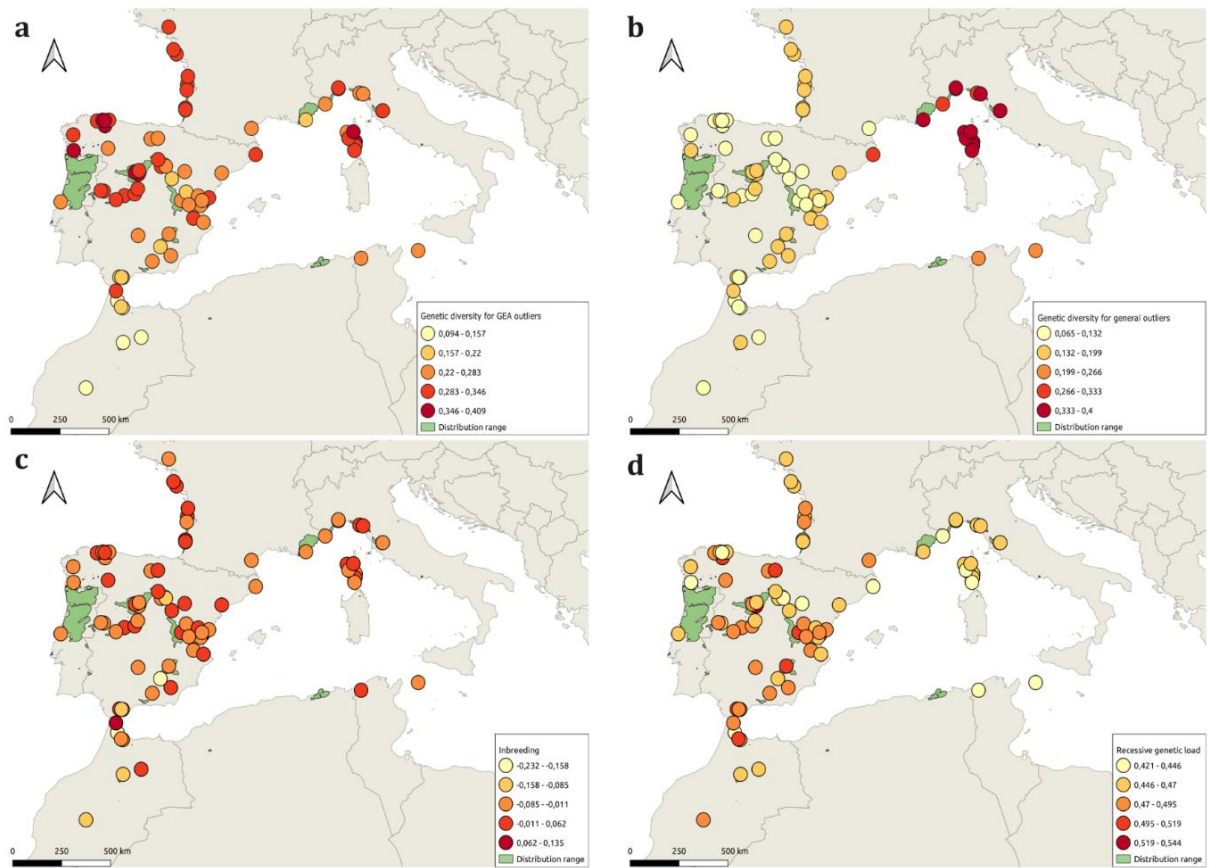
2.3.2. Breakdown of interaction effects: Model 1 & Model 5

Figure III-S7. Breakdown of interaction effects between the Second nearest-core and the North-South indices in M1 (Overall genetic diversity; $1-Q_{inter}$ corrected for sample size) and M5 (Genetic differentiation; population-specific F_{ST}). The fitted interaction values were calculated using the *effects* R package and the visual representation was produced with *ggplot2* R package. These figures show the decomposition of the interaction between distance to the second-nearest core (distance increases from left to right) and the latitudinal position of the populations (North-South index; where -1 represent southern latitudes and 1 represents northern latitudes), for a) overall genetic diversity and b) genetic differentiation.



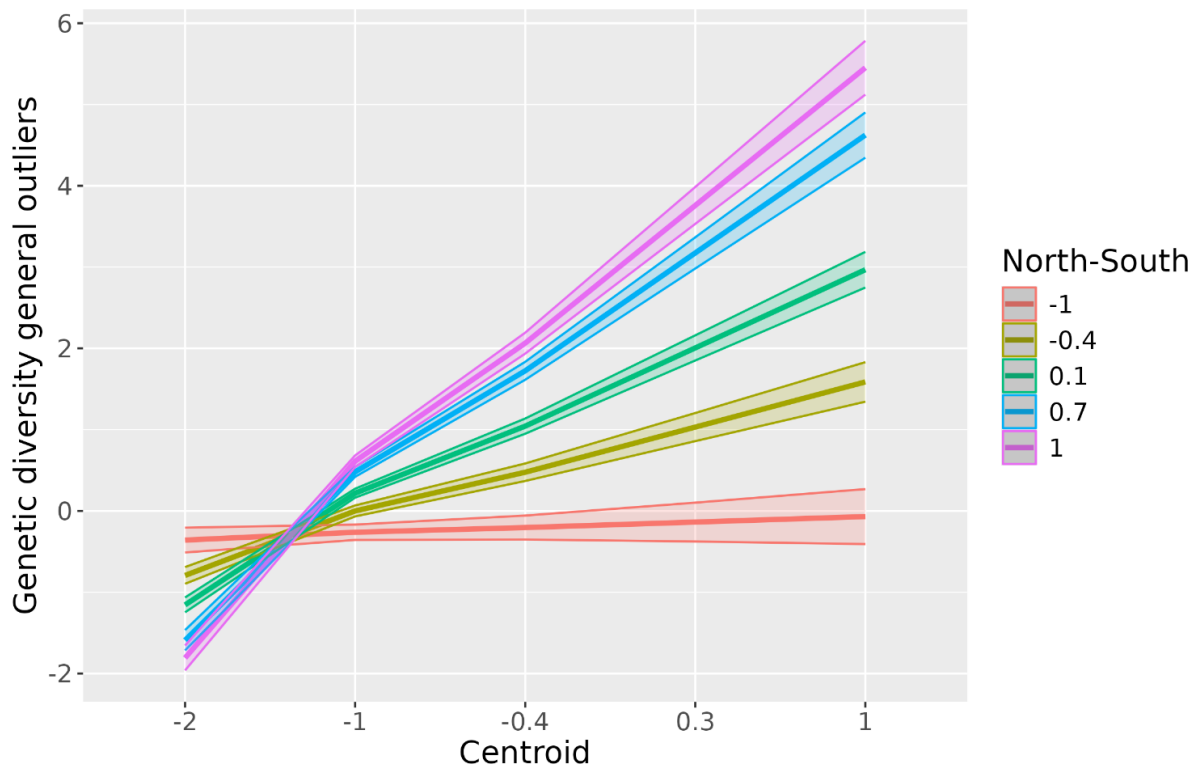
2.3.3. Geographical distribution of genetic indicators: genetic diversity (GEA & general outliers), inbreeding & recessive genetic load

Figure III-S8. Map representing the geographical distribution of a) Genetic diversity for GEA outliers, b) Genetic diversity for general outliers, c) Population inbreeding (F_{IS}) and d) Recessive genetic load, for *P. pinaster* populations across its distribution range.



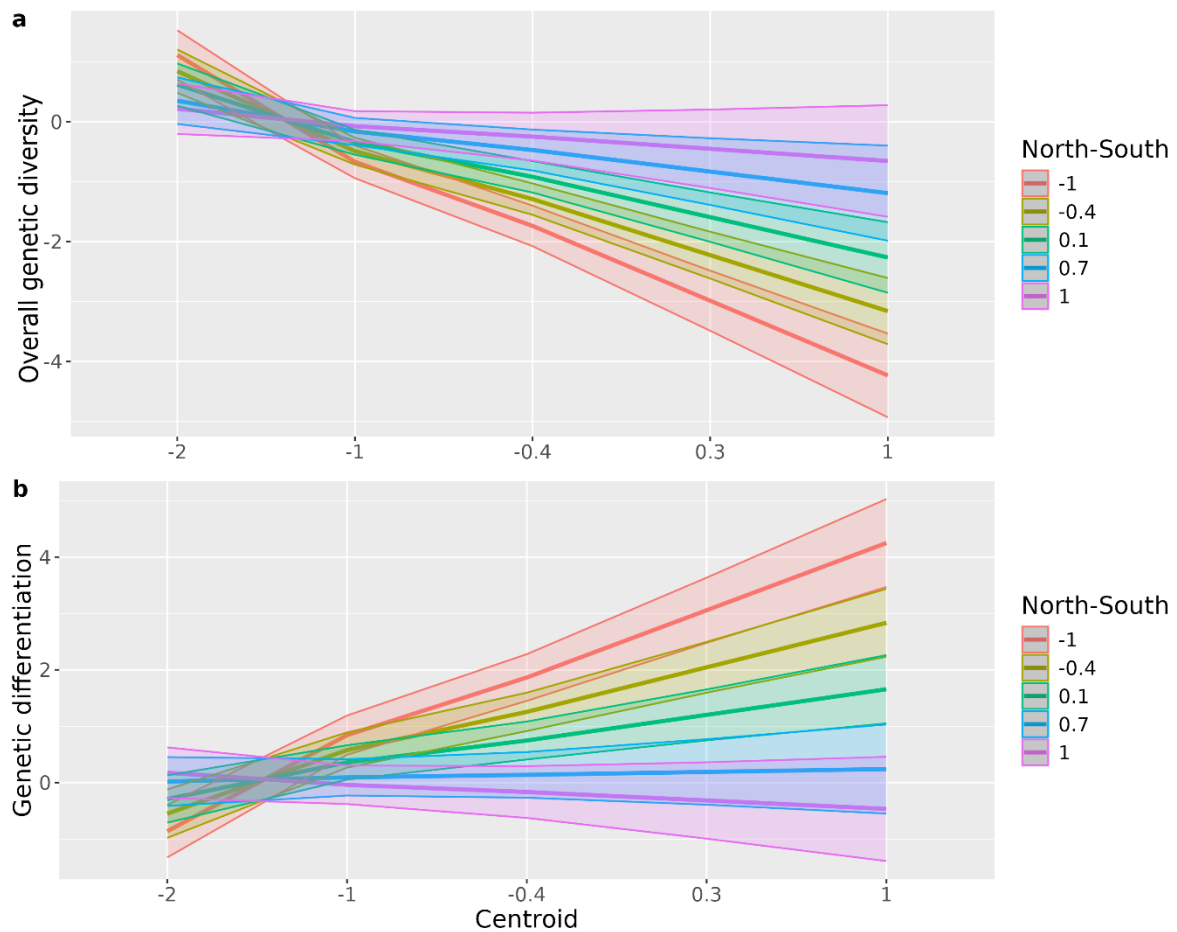
2.3.4. Breakdown of interaction effects: Model 1 & Model 5

Figure III-S9. Breakdown of interaction effects between the Centroid and the North-South indices in M3 (Genetic diversity based on general outliers). The fitted interaction values were calculated using the *effects* R package and the visual representation was produced with *ggplot2* R package. This figure shows the decomposition of the interaction between distance to the centroid (distance increases from left to right) and the latitudinal position of the populations (North-South index; where -1 represent southern latitudes and 1 represents northern latitudes).



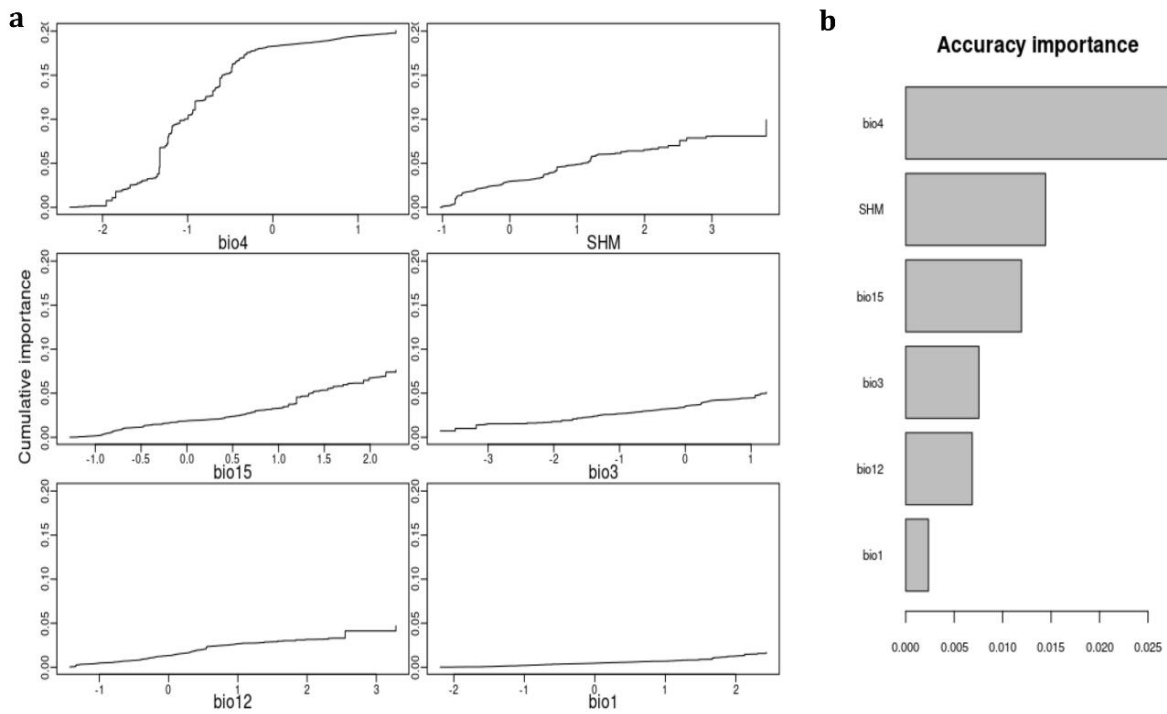
2.3.5. Breakdown of interaction effects: Model 8 & Model 12

Figure III-S10. Breakdown of interaction effects between the Centroid and the North-South indices in M8 (Overall genetic diversity; $1-Q_{inter}$ corrected for sample size) and M12 (Genetic differentiation; population-specific F_{ST}). The fitted interaction values were calculated using the *effects* R package and the visual representation was produced with *ggplot2* R package. These figures show the decomposition of the interaction between distance to the second-nearest core (distance increases from left to right) and the latitudinal position of the populations (North-South index; where -1 represent southern latitudes and 1 represents northern latitudes), for a) overall genetic diversity and b) genetic differentiation.



2.4. Genomic offset Gradient Forest: climate covariate's turnover functions & mean accuracy

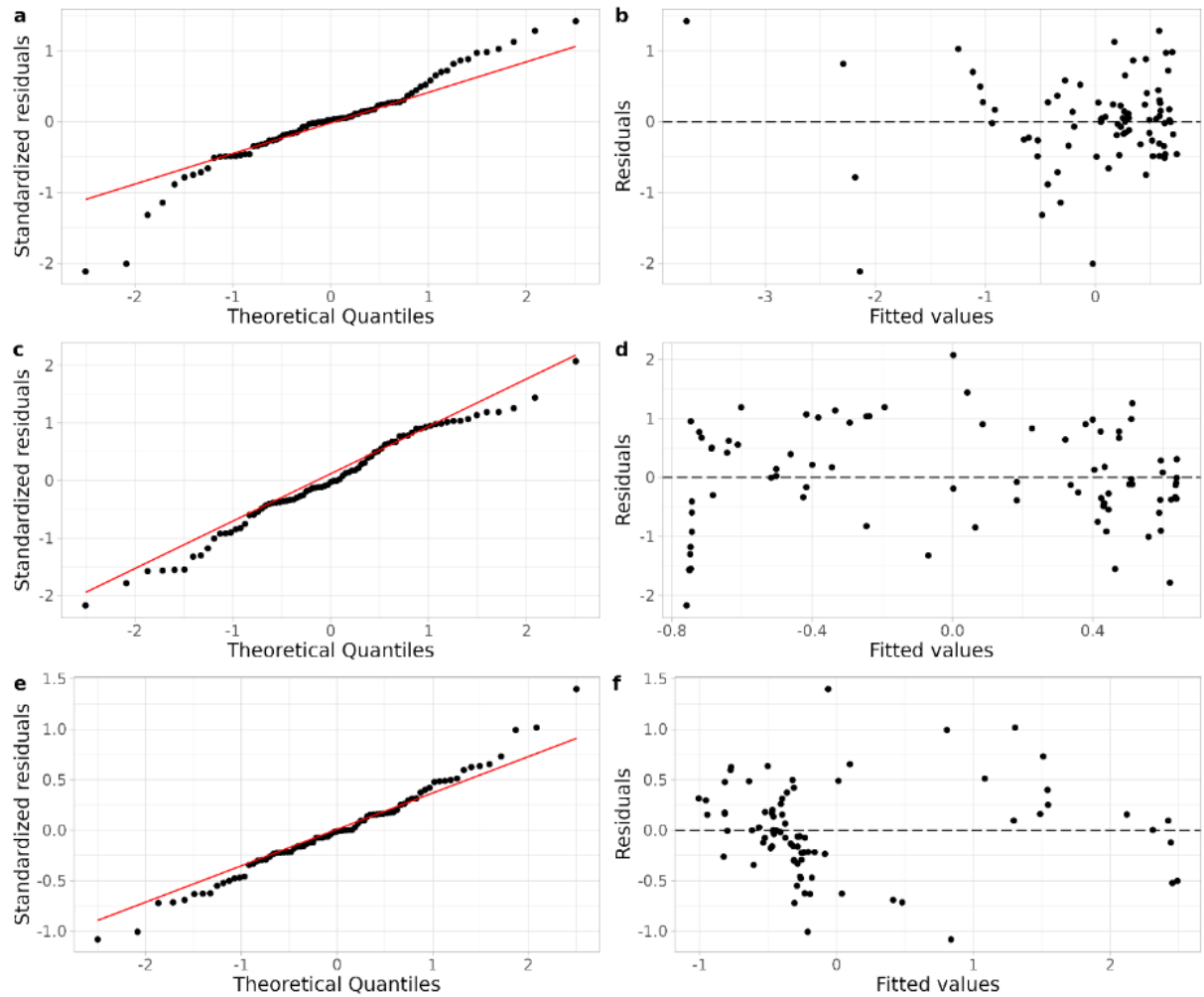
Figure III-S11. Gradient Forest (GF) analyses: a) Turnover functions and b) Mean accuracy importance, for each climate covariate (similar results were obtained for the mean importance weighted by SNP R^2). The full names and units of the climate covariates are given in Table III-S4. Find also additional details at https://anonymous.4open.science/r/ReadyToGO_Pinpin-FA56/README.md.



2.5. Diagnostic plots to check model fit to data

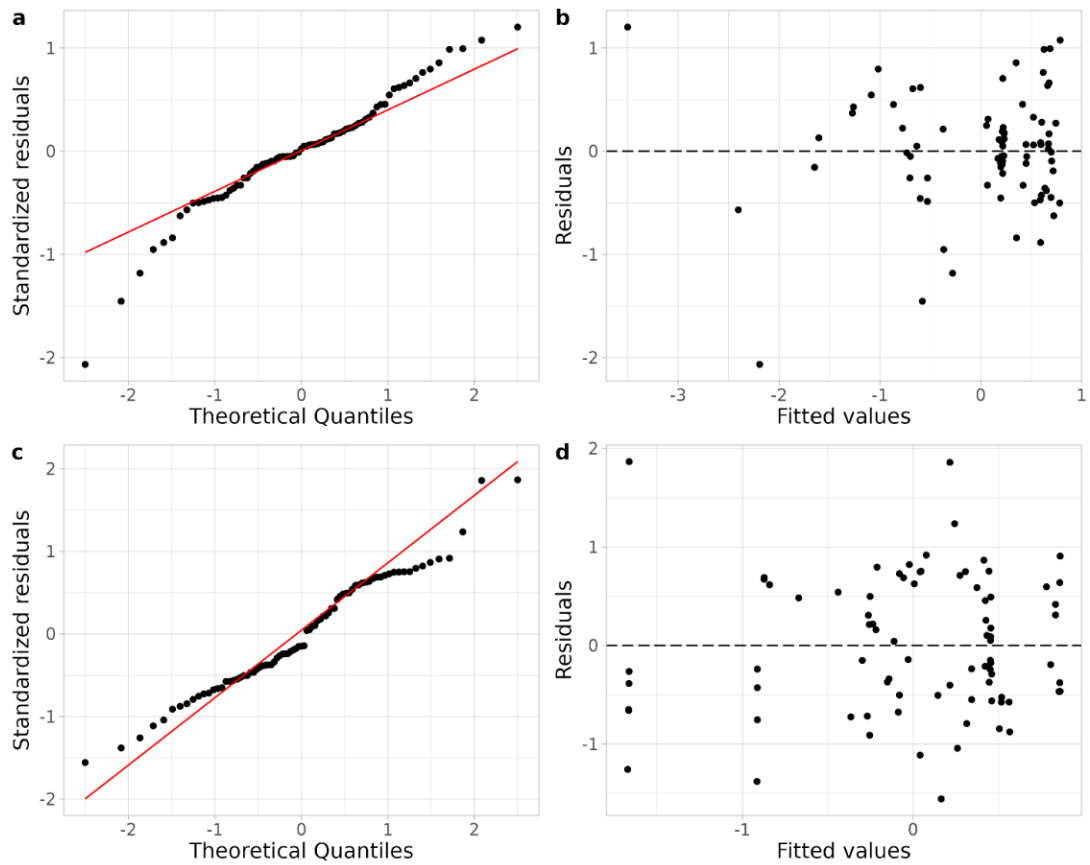
2.5.1. Diagnostic plots: Model 1, Model 2 & Model 3

Figure III-S12. Diagnostic plots to check model fit to data. QQ-plots a, c, e) and residual plots b, d, f) were computed for M1, M2 and M3, respectively.



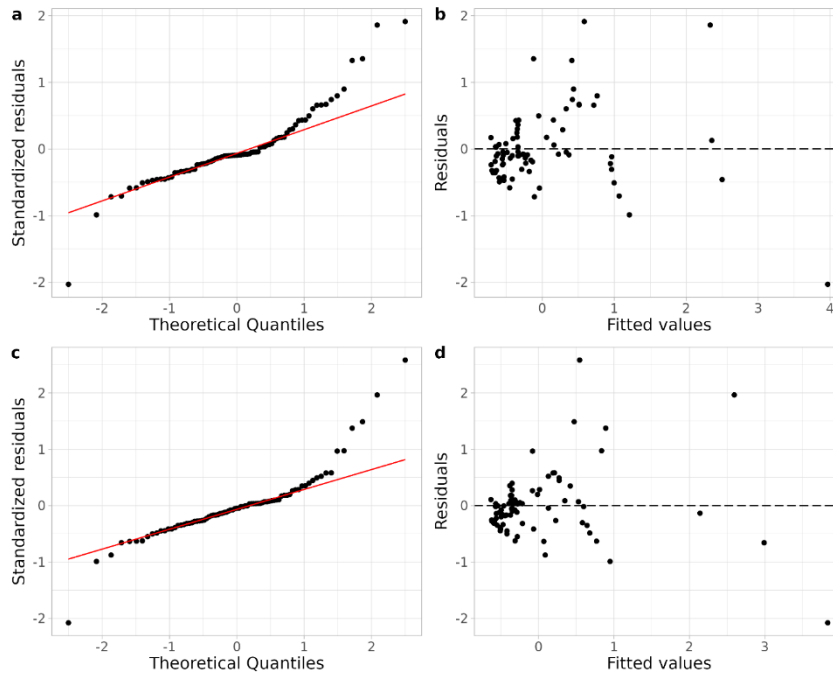
2.5.2. Diagnostic plots: Model 8 & Model 9

Figure III-S13. Diagnostic plots to check model fit to data. QQ-plots a, c) and residual plots b, d) were computed for M8 and M9, respectively.



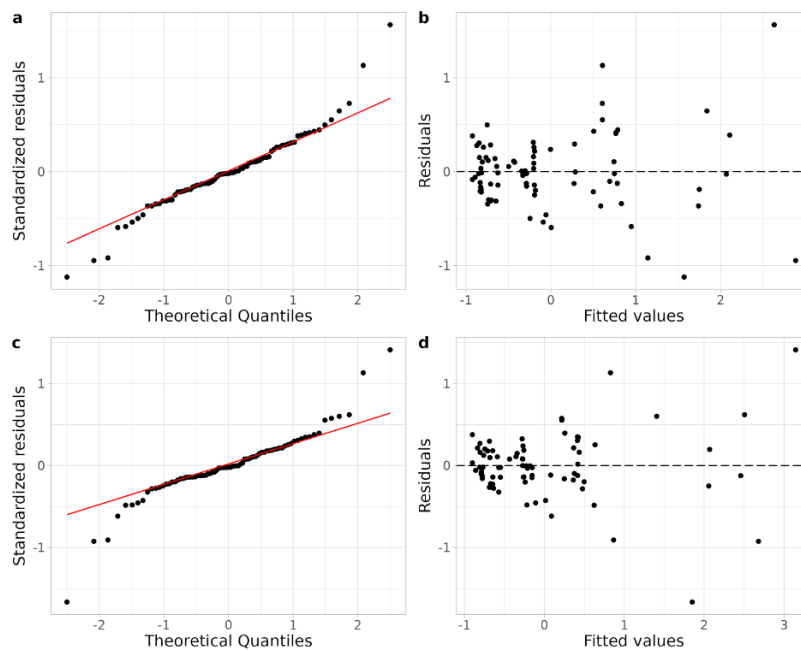
2.5.3. Diagnostic plots: Model 5 & Model 5bis

Figure III-S14. Diagnostic plots to check model fit to data. QQ-plots a, c) and residual plots b, d) were computed for M5 and M5bis, respectively.



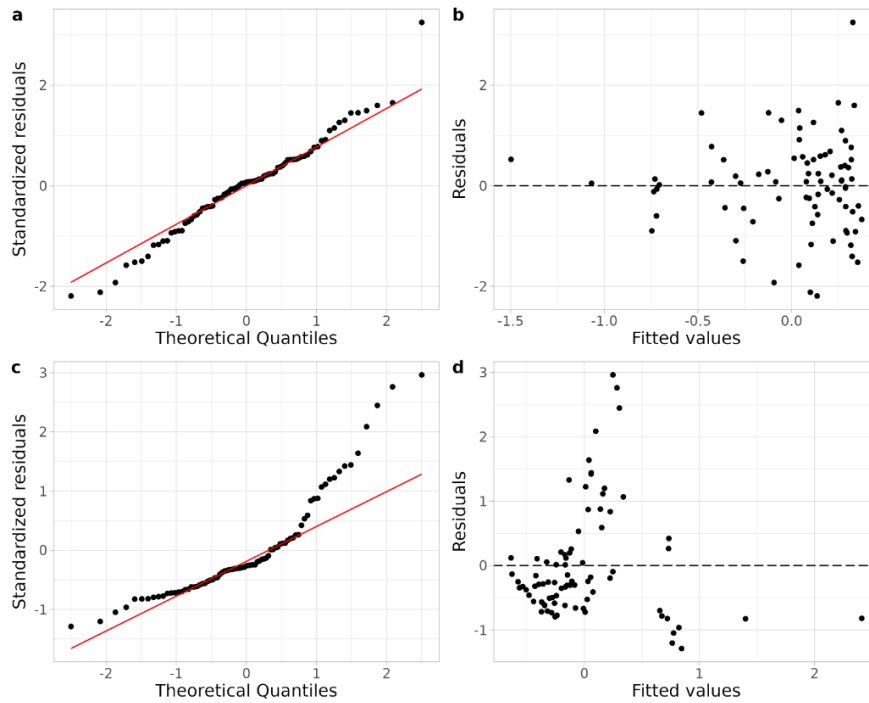
2.5.4. Diagnostic plots: Model 12 & Model 12bis

Figure III-S15. Diagnostic plots to check model fit to data. QQ-plots a, c) and residual plots b, d) were computed for M12 and M12bis, respectively.



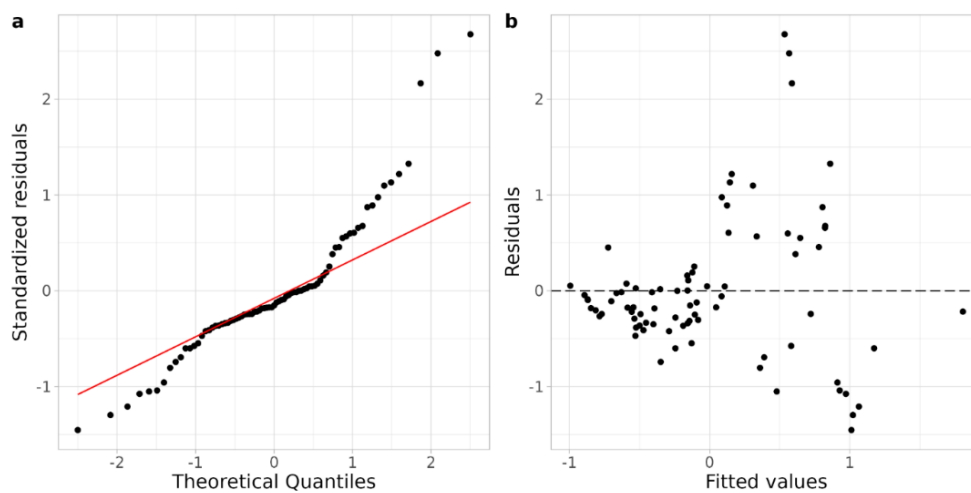
2.5.5. Diagnostic plots: Model 6 & Model 7

Figure III-S16. Diagnostic plots to check model fit to data. QQ-plots a, c) and residual plots b, d) were computed for M6 and M7, respectively.



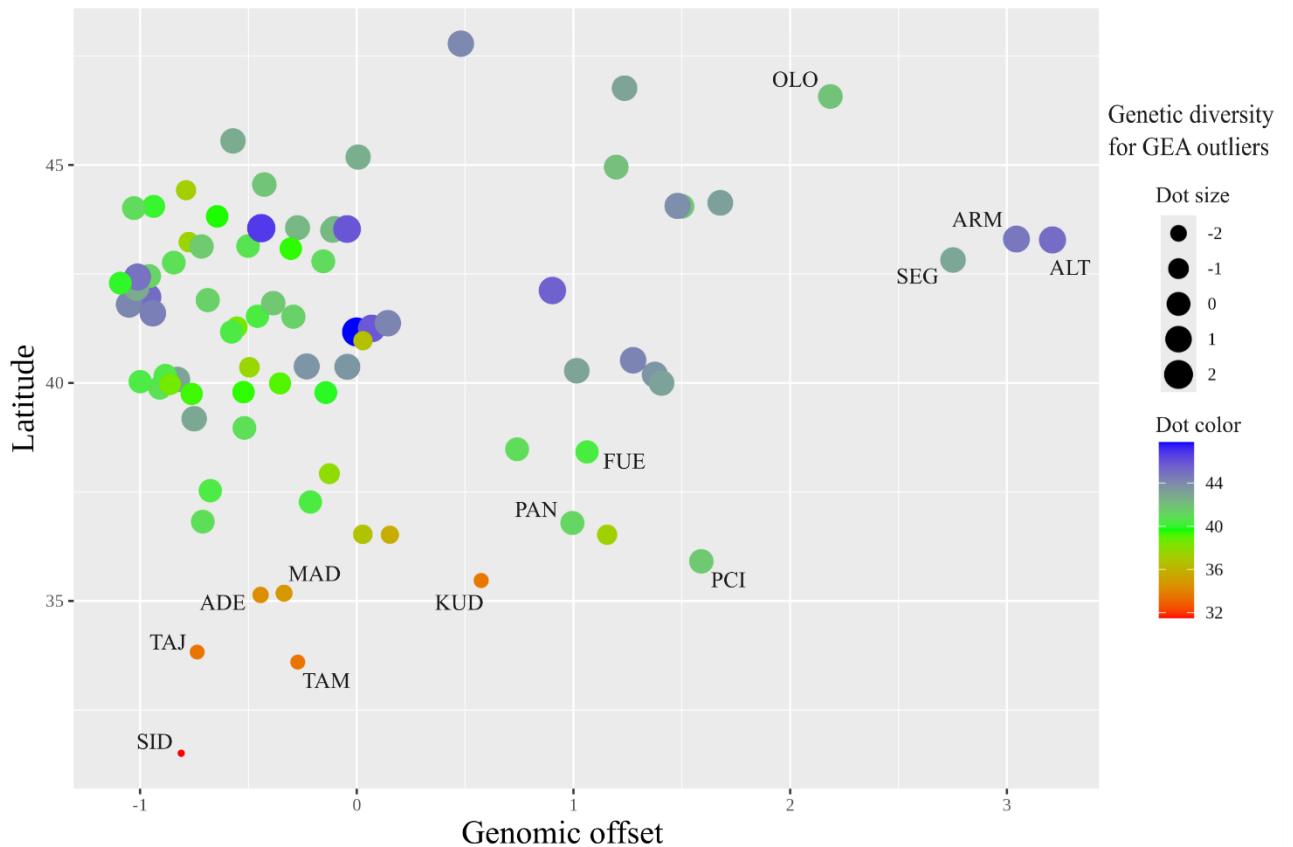
2.5.6. Diagnostic plots: Model 14

Figure III-S17. Diagnostic plots to check model fit to data. QQ-plots a) and residual plots b) were computed for M14, respectively.



2.6. Disentangling the relationships between the population's latitudinal position & genomic offset

Figure III-S18. Scatter plot disentangling the relationships between the latitudinal position of the populations used in this study (y-axis) and standardized genomic offset (x-axis) as a function of standardized genetic diversity calculated with climate-associated outliers (He_{GEA}). Size (dot size) and color (dot color) represent the range of values for the latter variable, with small dots and red color representing populations with the lowest values of putative climate-adaptive genetic diversity.



IV. CHAPTER 2

Contemporary natural selection on growth and functional traits in maritime pine, a keystone forest tree

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Abstract:

Natural forests are subject to natural and human selection pressures, which have increased as a result of climate change. How these pressures influence the adaptive potential of forest trees remains largely unknown. In a context of climate change, there is therefore an urgent need to identify the traits that are relevant for survival in new environments and to estimate the strength and direction of current selection. In this study, we sought to explore the spatial patterns of contemporary selection for natural populations of maritime pine, a key forest tree, in contrasting environments (Atlantic *vs.* Mediterranean). We measured growth and functional traits using field measurements, near-infrared spectroscopy (NIRS) and unmanned aerial vehicles (UAVs). Then, we regressed these traits on estimates of realised fecundity (i.e. a proxy for relative fitness) obtained from parentage analyses (CERVUS) and Bayesian mating models (MEMMseedlings). Both standard selection gradients and next-generation zero-inflated models were computed for single and multiple traits, while accounting for microenvironmental variation and spatial autocorrelation within populations. Altogether, our models revealed a general pattern of contemporary selection for growth and towards trait values that can, to some extent, prevent physiological stresses due to increasing drought and temperature. Surprisingly, we found maritime pines in the Mediterranean population to be under stabilising selection for cavitation resistance (P_{50}), raising concerns about their vulnerability to drought. Overall, our study highlights some population-specific contemporary selective trends and the need for long-term studies with a detailed assessment of microclimatic variations. It also opens up encouraging prospects for the implementation of this approach in natural forest tree populations.

Keywords: Natural selection, Maritime pine, Selection gradient, Fitness, Growth and functional traits, Zero-inflated models, Mediterranean *vs.* Atlantic environments.

1. Introduction

In nature, the distribution ranges of long-lived plant species, and in particular forest trees, are usually large. Organisms of the same species often occur in a multitude of environments subject to different abiotic (temperature, precipitation, access to light) and biotic (density of competitors, parasites, predators) stresses. The ability of organisms to successfully colonize, survive and reproduce in such diverse environments is the result of adaptive evolution, a process driven by natural selection (Darwin, 1859). Natural selection is a dynamic force that can vary in strength, direction, form, as well as in space and time (Siepielski et al., 2009). In nature, an optimal phenotype fluctuates moderately within an adaptive zone, depending on the intensity of contemporary selection pressures, the new mutations and standing genetic diversity, and the effective population size (Kimura & Ohta, 1969).

For adaptive evolutionary change to occur, two conditions must be met. Firstly, there must be sufficient heritable phenotypic variation in a population, and secondly, this phenotypic variation must be linked to fitness (i.e., it must affect an individual's ability to survive and reproduce), leading to differential reproductive success between individuals due to the selective advantages bestowed, in different orders of magnitude, by their traits (Endler, 1986; Gregory, 2009; and others). The association between a phenotypic trait and fitness can be measured using phenotypic selection gradients, which are defined as the vector of partial regression of individuals' relative fitness on the trait under consideration (Lande & Arnold, 1983). Selection gradients are a straightforward and simple tool to understand how selection works in nature, as they provide standardized estimates of the strength, direction, intensity and form (e.g., stabilizing, disruptive) of current selection acting on one or multiple quantitative traits (Kingsolver et al., 2012; Lande & Arnold, 1983).

Estimating selection gradients requires the computation of individual fitness values and access to traits for the same individuals. Under natural conditions, it is challenging to measure cumulative fitness of an individual over its entire lifespan (Barringer et al., 2013). For long-lived forest tree species, which produce a variable number of seeds, and take decades to reach maturity, an exhaustive count of the number of established offspring per mature individual is almost impossible. Moran & Clark (2012) reported that 75% of studies examining reproductive success in woody plants defined reproductive success in terms of seed production. However, given the high mortality rates at early stages of establishment (Gerzabek et al., 2017) and known

trade-offs between seed quality and seed quantity (Primack & Kang, 1989), seed production is not considered as a good proxy of tree fitness (Moran & Clark, 2012). A more robust proxy for fitness is then the ‘realized fecundity’, which can be estimated from mating models and parentage analysis of established offspring (i.e., offspring that have survived initial phases of strong selection and have a high probability of forming the next generation; Moran & Clark, 2012; Oddou-Muratorio et al., 2018; Primack & Kang, 1989; Westergren et al., 2023).

The traits commonly used in selection gradient analysis of forest trees, such as growth, phenology and leaf morphology, are relatively easy to assess, while functional traits, such as wood density or hydraulic traits, which are known to be important metrics for assessing tree vulnerability (Anderegg et al., 2015; McDowell et al., 2020; Serra-Maluquer et al., 2022), are overlooked, often because major efforts are required for their estimation on a large number of individuals. Wood density is a key functional trait linked to variation in mortality rates, timing of reproduction, and the relative mechanical strength of a plant as well as its resistance to wood-boring insects (Bultman & Southwell, 1976; Ulyshen et al., 2014). It also underlies the hydraulic capacities of the tree stem (see Swenson & Enquist, 2007). Moreover, hydraulic traits, such as resistance to cavitation (P_{12} , P_{50}), minimum leaf conductance (G_{min}) or branch capacitance, which measures water released from wood tissue during transpiration, have been shown to be important components of the whole-plant water balance and its vulnerability to drought (Delzon & Cochard, 2014; Urli et al., 2023).

The strength of natural selection, as estimated by selection gradients, has been quantified in numerous studies of short-lived species over the last years (e.g., Carlson & Fulkerson, 2022; Carvalho et al., 2022; Emel et al., 2017; Scopece et al., 2017), with an increasing number of recent studies in forest trees (Alía et al., 2014, 2024; Ramírez-Valiente et al., 2021; Warwell & Shaw, 2018; Westergren et al., 2023). For example, Warwell & Shaw (2018) found directional selection for greater shoot elongation (growth) in *Pinus albicaulis* seedlings associated with an increasingly warm and drier climate. Similarly, Ramírez-Valiente et al. (2021) highlighted that seed mass, emergence time and early growth rate play an adaptive role in the early stages of *Pinus sylvestris* development and that climate strongly influences selection patterns for these traits. However, these studies investigated selection under controlled conditions, while our understanding of the strength and speed of natural selection in wild forest tree populations remains limited.

Selection gradients are commonly estimated using Lande & Arnold's multiple regression approach (Lande & Arnold, 1983), which rely on several assumptions (see Mitchell-Olds & Shaw, 1987). In addition, environmentally induced covariances between fitness and traits act as confounding factors and can cause spurious correlations (Pemberton, 2010; Rausher, 1992; Stinchcombe et al., 2002). Spatial autocorrelation of fitness is another important source of bias (Marrot et al., 2015). It violates the assumption of the residual independence of regression models, which can lead to an increase in type I error (Legendre, 1993; Lennon, 2000), and it also affects the absolute value of the regression coefficients (Le Rest et al., 2013; Thayn & Simanis, 2013). Thus, model corrections based on the addition of covariates for spatial autocorrelation of fitness, intraspecific competition and micro-environmental variability has been suggested (see Alexandre et al., 2020), although their use is not widespread (see, e.g., Kingsolver et al., 2012; Westergren et al., 2023; Alía et al., 2024).

Forests cover c. 32% of European territory, providing essential ecosystem services, such as carbon sequestration, timber, improvement and maintenance of soil structure, and high biodiversity. Maritime pine (*Pinus pinaster* Aiton., Pinaceae) is a wind-pollinated conifer widespread in southwestern Europe and North Africa and has a high ecological and economic value, being considered a keystone forest tree (Jaramillo-Correa et al., 2015; Ramírez-Valiente & Robledo-Arnuncio, 2014). The species is characterized by a fragmented distribution range with a strong population genetic structure resulting in a mosaic of genetic groups or 'gene pools' (Jaramillo-Correa et al., 2015; Theraroz et al., 2024). Throughout its range, maritime pine inhabits environments characterized by steep ecological gradients (e.g., in precipitation) and by contrasting soil features and elevations (from the High Atlas Mountains in Morocco to the coastal dunes of the French Atlantic coast). Recent studies have shown that for some maritime pine populations adaptive lags are to be expected under modelled future climate conditions (Theraroz et al., 2024; see also Fréjaville et al., 2019), especially for populations belonging to the Atlantic gene pools (Theraroz et al., 2024; Archambeau et al., 2024). Thus, identifying relevant traits for survival in the new environments, as well as estimating the strength and direction of current selection, is urgently needed. Indeed, potential for adaptation of keystone species, such as maritime pine, affect the survival of whole ecosystems (Alía et al., 2014; Hamrick, 2004), being also key to predicting phenotypic changes in the face of disrupted climate.

In this study, we aimed to answer the following questions: i) Are growth and functional traits currently under selection in maritime pine? And what is the strength and direction of natural selection in the wild for this species? and ii) Does contemporary selection differ in populations growing under contrasted climatic conditions? And, if so, to what extent? We addressed these questions by measuring growth and functional traits (including wood density and hydraulic traits) in c. 500 adult trees per population in each of two contrasted (Atlantic vs. Mediterranean) maritime pine populations. Individual tree data was obtained from field sampling, near-infrared spectroscopy (NIRS) and Unmanned Aerial Vehicles (UAV), and regressed on estimates of realized fecundity (i.e., a proxy of relative fitness) obtained from parentage analyses (CERVUS; Marshall et al., 1998) and Bayesian mating models (MEMMseedlings; Klein et al., 2008) using both standard selection gradients (Lande & Arnold, 1989) and new-generation zero-inflated models (Brooks et al., 2017) for single and multiple traits, while controlling for the microenvironmental variation and spatial autocorrelation within the populations.

2. Materials and Methods

2.1. Study populations

The study was carried out in two study plots located in French and Italian maritime pine Genetic Conservation Units (GCUs). GCUs harbour populations of trees that have adapted to specific environmental conditions or display distinct phenotypes. They are designated at the national level to conserve forest genetic resources following common European minimum requirements developed by the European Forest Genetic Resources Programme (EUFORGEN).

The first study plot covered an area of 3.6 ha within the entire GCU (285.5 ha) in the Lacanau State Forest (Aquitaine, France; 44°57'48.6''N, 1°09'53.9''W; GCU code: FRA00051). The second study plot covered an area of 1.35 ha within the entire GCU (575 ha) in the Tocchi Biogenetic State Natural Reserve (Tuscany, Italy; 43°7'34.2''N, 11°15'14.2''E; GCU code: ITA00019). Located on the French Atlantic coast, the Lacanau GCU is characterized by sandy soils and flat topography, as well as an Atlantic climate with low temperature seasonality (mild winters), high annual rainfall and humid summers. The Tocchi GCU is a relatively isolated Mediterranean population at medium elevation (250-500 m a.s.l.) characterized by seasonal fluctuations in temperature and precipitation, as well as the predominance of sandstone, clay and limestone rocks in the soil.



Figure IV-1. a) Lacanau Genetic Conservation Unit (GCU) and b) maritime pine labelling during fieldwork. *Source: A. Theraroz.*

2.2. Field sampling and genotyping

In each study plot, 500 dominant or codominant adult trees, covering the entire study area, and 250 saplings from the natural regeneration were individually georeferenced (Figures V-S1 and V-S2 in Supplementary Information). Leaves were collected from both adults and offspring for DNA extraction and genetic analyses. DNA was extracted using the DNeasy 96 plant kit (QIAGEN, Germany), following the manufacturer's instructions. All samples were genotyped

for Single Nucleotide Polymorphisms (SNPs) using the multispecies 4TREE Axiom 50K microarray (Thermo Fisher Scientific, USA). Genotyping was successful for 500 adults and 249 saplings in Lacanau, and for 484 adults and 248 saplings in Tocchi. Only SNPs with high-quality scoring following the Best Practices Workflow implemented in the Axiom™ Analysis Suite v5.2 were selected and filtered by missing data (maximum missing data threshold of 30%), yielding a total of 10,652 SNPs for both datasets. For parentage/mating model analyses (see below), we retained only those SNPs successfully genotyped in Theraroz et al. (2024), resulting in 8,761 SNPs. SNPs were pruned for linkage disequilibrium (LD) (window size 50, maximum correlation 2) and minor allele frequency (MAF>0.4, to use only common high-resolution SNPs) using PLINK v.1.9 (Purcell et al., 2007), giving a final count of 599 SNPs for the Lacanau dataset and 578 SNPs for the Tocchi dataset.

2.3. Assessment of phenotypic traits

In both plots, a total of nine growth and functional traits were measured in the field or obtained from NIRS or UAV data (see Table IV-1, Tables V-S1 and V-S2).

For growth traits, we directly measured total height (HT) in Lacanau, as well as stem diameter at breast height (DBH) and height at the start of the crown (HSC) in both study plots. In addition to these direct measurements, we used unmanned aerial vehicles (UAVs) (i.e., drone flights) with integrated image acquisition, to obtain total height (HT) in Tocchi, and the sun-exposed crown area (CA) in both study plots. The complete, original and reproducible workflow for UAV-based estimates is available on a Gitlab repository (<https://gitlab.uni-marburg.de/reudenba/forgenius-pp>).

For functional traits, we first assessed relative wood density (WD) using a SC-650 resistograph (Rinntech, Heidelberg, Germany) equipped with a 500 mm long needle that goes bark-to-bark through the pith of the tree. Following Krajnc et al. (2023), we calculated median values of wood density for each tree from individual density profiles using the R package *densitR* (<https://github.com/krajnc/densitR>; Krajnc, 2020). Second, we estimated resistance to cavitation (P_{12} , P_{50}), minimum leaf conductance (the amount of water loss through the cuticle after stomatal closure; G_{min}) and specific leaf area (SLA) using a Near Infra-Red Spectroscopy (NIRS)-based procedure designed to measure complex traits indirectly on a large number of trees. Briefly, complex traits from leaves, branches and wood samples were measured *in situ*

on a subset of trees and were used as references for developing robust and highly-predictive NIRS calibration models.



Figure IV-2. Slovenian collaborator Luka Krajnc measuring wood density with a resistograph on maritime pines in the Lacanau Genetic Conservation Unit. *Source: A. Theraroz.*

Finally, pairwise Pearson's correlation coefficients (hereafter referred as ' r ') were calculated to assess correlation between traits. Traits were considered strongly correlated when $r > 0.7$, moderately correlated when $0.4 < r < 0.7$ and weakly correlated when $r < 0.4$ (Figure V-S7). These analyses enabled us to gain a better understanding of integrated phenotypes, as well as helping to select uncorrelated traits for the standard selection gradients and to assess the usefulness of using multivariate selection gradients.

Table IV-1. Description of the phenotypic traits used in this study.

Trait class	Trait acronym	Definition	Units	Origin of measurements
Growth	HT	Total height of the tree	m	Direct/UAV
	DBH	Diameter at breast height (1.30 m)	m	Direct
	HSC	Height at the start of the crown	m	Direct
	CA	Sun-exposed tree crown area	m ²	UAV
Functional	WD	Wood density	kg/m ³	Direct
	SLA	Specific leaf area	m ² /kg	NIRS
	G_{min}	Leaf minimum conductance	mmol m ⁻² s ⁻¹	NIRS
	P_{12}	Xylem pressure inducing 12% loss of hydraulic conductivity due to embolism	MPa	NIRS
	P_{50}	Xylem pressure inducing 50% loss of hydraulic conductivity due to embolism	MPa	NIRS

2.4. Fitness assessment using parentage/mating models

Adult tree fitness was estimated by determining the relative effective fecundity of each adult tree based on successfully established offspring at the time of sampling. Effective fecundity provides a more adequate proxy of individual's realized fitness than simpler estimates (e.g., fruit set), as it accounts for both fecundity and early survival (Oddou-Muratorio et al., 2018; Schaffer, 1974; Westergren et al., 2023).

First, we used MEMMseedlings software, an extension of the Bayesian spatially-explicit Mixed Effects Mating Model (MEMM) (Burczyk et al., 2006; Oddou-Muratorio et al., 2018; Oddou-Muratorio & Klein, 2008), to infer jointly individual male and female effective fecundities as well as pollen and seed dispersal kernels, accounting also for genotyping errors (Klein et al., 2008; Oddou-Muratorio et al., 2018; Tonnabel et al., 2021; Westergren et al., 2023). As a full mating model, MEMMseedlings does not use parentage assignment and instead focuses on the fractional contribution of all potential parents to each sapling. The models were run for 50,000 iterations of the Markov Chain Monte Carlo (MCMC) with a thinning step of 20

and a burn-in of 500. Genotyping error was set to typical values for SNPs, i.e., 0.05 error probability (*Perr*2), and allowing a maximum of five mismatches between parent and offspring genotypes. Our models showed that the majority of pollen came from outside the study plot (average pollen immigration rate of 94% for Lacanau and 78% for Tocchi; Figure V-S3b,d), while seed dispersal was more restricted (average seed immigration rate of 55% and 16%, respectively; Figure V-S3a,c). Thus, we restrained our analyses to only female effective fecundity, as a proxy of mother fitness (Tables V-S1 and V-S2).

Second, we calculated female effective fecundity using categorical maternity analysis as implemented in CERVUS 3.0.7 (Kalinowski et al., 2007; Marshall et al., 1998). CERVUS assigns offspring directly to parents. It is common to have many individuals without any offspring assigned to them, which may lead to datasets with a high number of zeros (see Kalinowski et al., 2007; Moran & Clark., 2012; Figure V-S5). To identify the most-likely mothers, CERVUS calculates the natural logarithm of the likelihood-odds ratio (LOD score) and assigns the offspring to the mothers with the highest LOD score. Maternity analyses were conducted considering 1% error rate and two confidence levels (relaxed, > 85% probability of assignment; and strict, > 95%). Total fecundity estimates were translated to relative fecundity following Lande & Arnold (1983) (Tables V-S1 and V-S2).

2.5. Selection gradients

2.5.1. Single-trait (univariate) selection gradients

We used two kinds of models to compute single-trait (univariate) selection gradients (or analogous, see below). First, we computed selection gradients using the standard linear model following Lande & Arnold (1983) based on relative fitness as estimated by MEMMseedlings, hereafter referred to as ‘standard models’. Second, because of the high number of zeros, we used zero-inflated generalized linear mixed models (zero-inflated GLMMs) with relative fitness estimates obtained from categorical parentage assignment in CERVUS to estimate analogous quantities to selection gradients. Zero-inflated models are statistically better suited than standard linear models for handling data with a large number of zeros (see Brooks et al., 2017).

Standard selection gradients were computed as follows:

$$w = \mu + C + P + S + \beta_x X + \left(\frac{\gamma_x}{2}\right) X^2 + \varepsilon \quad (1)$$

where w is the relative fitness as estimated from MEMMseedlings, μ is the population mean for the phenotypic trait, X is the trait value standardized by the standard deviation, β is the linear selection gradient and γ is the quadratic selection gradient. The latter estimates the curvature of the fitness function; stabilizing selection implies negative curvature ($\gamma < 0$), whereas disruptive selection implies positive curvature ($\gamma > 0$) (Kingsolver et al., 2001). Finally, C , P and S are standardized covariates accounting for the ecological and environmental conditions close to each adult tree (see below). Models with non-significant quadratic components were re-examined with linear selection gradients only. Models were constructed on log-transformed fitness (see Oddou-Muratorio et al., 2018; Westergren et al., 2023) but untransformed models were also computed to provide unscaled selection gradients for comparative purposes (see Lande & Arnold, 1983).

Following Alexandre et al. (2020), we accounted for bias due to spatial autocorrelation and environmental covariances between traits and fitness in the models by adding covariates (Tables V-S1 and V-S2). First, for each study plot, we calculated C , a competition index that considers both the size of competitors and their distance to the target tree (Martin & Ek, 1984; Oddou-Muratorio et al., 2018) (see Equation V-S1 in Supplementary Information). We calculated the competition index at two distances (radius of 10 and 20 m around the tree), but as estimates were highly correlated (> 0.95), we retained only the former. C was corrected for edge effects following Equation V-S2. Second, we calculated P , an index that accounts for spatial autocorrelation of fitness using the principal coordinates of neighbour matrices (PCNM, Borcard & Legendre, 2002; see also Alexandre et al., 2020). Eigenvectors were extracted from a distance matrix describing the spatial structure of the data. Following the authors recommendation, we included only one eigenvector as covariate to prevent overparameterization when computing the models. Third, we used S , a fine-scale soil moisture index. This index was extracted from a soil moisture map produced using a high-resolution digital elevation model, obtained from drone data and microtopography analysis. Covariates were standardized by the standard deviation before they were included in the models.

After testing for zero-inflation of the fitness estimates obtained from parentage categorical analyses in CERVUS (*DHARMA* R package), we used zero-inflated GLMMs to compute univariate linear (β) models analogous to selection gradients using *glmmTMB* R package (Brooks et al., 2017). Briefly, zero-inflated GLMMs have two main components, aimed at separating the two processes generating the zeros: 1) a conditional model formula (hereafter

referred to as ‘conditional component’) that describes the probability of observing sampling zeros (i.e., zeros due to limited sampling effort) and 2) a zero-inflation formula (hereafter referred to as ‘zero-inflation component’) that models the probability of observing ‘true’ (i.e., structural) zeros (i.e., not reproducing trees) that are not generated by the conditional formula (i.e., a tree not having an established offspring as a consequence of not reproducing rather than not sampling the offspring of this tree) (Brooks et al., 2017). In these models, we used the trait values standardized by the standard deviation, the log-transformed relative fitness as estimated with CERVUS, and the three covariates described above (i.e., C , P and S), using default parameters.

2.5.2. Multi-trait (multivariate) selection gradients

In nature, fitness is affected by numerous (life-history) traits simultaneously, which are also often correlated with each other and with environmental factors (Ghalambor et al., 2003; Lande & Arnold, 1983). To understand how natural selection acts on multiple traits, we first performed a Principal Component Analysis using *psych* v.2.4.3 R package (Revelle, 2023) (see Figure V-S4.1 & V-S4.2). Second, we computed linear (β) and quadratic (γ) multivariate selection gradients based on the Principal Components (PCs) which explained most variance (four PCs for each plot, explaining about 66% and 67% of variance in each plot for Lacanau and Tocchi, respectively). Models were constructed similarly to the standard selection gradients described above, as follows:

$$w = \mu + C + P + S + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \left(\frac{\gamma_1}{2}\right) X_1^2 + \left(\frac{\gamma_2}{2}\right) X_2^2 + \left(\frac{\gamma_3}{2}\right) X_3^2 + \left(\frac{\gamma_4}{2}\right) X_4^2 + \varepsilon \quad (2)$$

where w is the relative fitness as estimated from MEMMseedlings, subscripts (1 to 4) refer to each of the four first PCs and C , P and S are the three covariates described above. Models with non-significant quadratic components were re-examined with linear models only. All analyses were undertaken in R v4.3.1 (R Core Team, 2023).

3. Results

3.1. Effective fecundity as fitness proxy

Effective fecundity obtained from MEMMseedlings full mating model showed an asymmetrical distribution in both study plots, with higher densities for lower values (Figure V-S5a). Maximum effective female fecundity at Lacanau (8.5) was twice as high as at Tocchi (4.8). Overall, female fecundity was greater than one for 50 trees (10%) at Lacanau and for 72 trees (15%) at Tocchi. A similar asymmetrical distribution was observed for categorical offspring assignments using CERVUS (Figure V-S5b). Female fecundity was greater than one for 90 trees (18%) at Lacanau and for 134 trees (28%) at Tocchi. However, compared to MEMMseedlings results, with CERVUS maximum female fecundity was higher at Tocchi (11) than at Lacanau (9). The relative fitness estimates computed with MEMMseedlings and CERVUS were highly correlated in both study plots ($r = 0.79$ and $r = 0.85$ for Lacanau and Tocchi, respectively). They were also highly correlated ($r > 0.77$) with estimates provided by Adam & Birkes' (1991) neighbourhood model for Lacanau study plot, as implemented in NM π software (Chybicki, 2018) (see Figure V-S6).

3.2. Correlation across traits

Generally, the studied traits were not correlated with the notable exception of a high positive correlation between P_{12} and P_{50} ($r > 0.8$ in both plots; Figure V-S7). Nevertheless, both estimates were retained for further analysis, because these two values characterize different degrees of hydraulic failure and thus may provide different insights on patterns of natural selection. In addition, DBH was moderately positively correlated with HT at Lacanau ($r = 0.4$) indicating that in this plot, taller trees tend to have larger trunk diameters. HT was also moderately but positively correlated with HSC at Tocchi ($r = 0.61$), but not at Lacanau. A plot of the distribution of crown length as a function of tree height (Figure V-S8) showed that this correlation did not always translate into taller trees having a shorter crown length or shorter trees having a longer crown length.

3.3. Microenvironmental effects

The spatial autocorrelation of fitness (P) was significant in the standard models for both study plots, except for DBH and CA at Lacanau (Table IV-2). This result was also supported by the conditional component of the zero-inflated models at Lacanau (all traits except DBH and HSC; Table IV-3) and, partially, at Tocchi (only for HT and CA; Table IV-4). The other covariates were not significant in these models, with the exception of the soil moisture index, S , for HT with the standard models (Table IV-2) and the competition index, C , with the conditional component of the zero-inflated models, both at Tocchi. The latter predicted a decrease in fitness for all traits as competition increased (Table IV-4). Interestingly, the zero-inflation component of the zero-inflated models predicted a significant impact of soil moisture (S) on the probability that a tree will reproduce at Lacanau (except for DBH and CA; Table IV-3) and, partially, at Tocchi (significant for DBH, CA, SLA and P_{12} ; Table IV-4).

Finally, no covariate, with the exception of the spatial autocorrelation of fitness (P) at Tocchi, was significant in the multivariate selection gradients (Table IV-5).

3.4. Single-trait (univariate) selection gradients

3.4.1. Growth traits

Standard models with both linear and quadratic components showed directional and weak disruptive (Figure V-S9) selection in for larger DBH at both study plots while selection for HSC was going in opposite directions (Table IV-2), suggesting that natural selection may be environmentally dependent for this trait. It should be noted that the models computed with the linear component alone (Tables V-S3 and V-S4) gave similar results, with the exception of HT at Tocchi, which showed weak positive directional selection when the quadratic component was not taken into account (Table V-S4). Growth trait quadratic selection gradients were positive and significant for DBH and CA at Lacanau while none were significant at Tocchi (Table IV-2). This confirms cotemporary selection for bigger trees in Lacanau, as well as suggests that both trees with high or low crown exposure seem to be favoured by natural selection (i.e., disruptive selection) (Table IV-2).

These results were supported by the zero-inflated models, which also provided additional insights. For DBH, the estimates of the conditional component matched those of the standard models in both plots, as expected (Tables IV-3 and IV-4). However, at Lacanau and at Tocchi (although being marginally significant), the zero-inflation component predicted also a negative relationship between DBH and relative fitness (Tables IV-3 and IV-4), indicating that bigger trees may also have a higher probability of effective reproduction once sampling zeros have been taken into account (Brooks et al., 2017). For HSC, the conditional component predicted a negative relationship between the trait and relative fitness at Lacanau (Table IV-3), similar to that of the standard models above (Table IV-2), but did not predict any significant relationship for this trait at Tocchi (Table IV-4). However, the zero-inflation component predicted a strong negative relationship between HT and HSC with relative fitness at Tocchi (Table IV-4), indicating that tall trees and trees with crowns starting at higher heights may have a higher probability of effective reproduction in this plot.

3.4.2. *Functional traits*

Linear (directional) selection gradients were not identified for any trait by the standard models (Table IV-2). However, at Tocchi, a negative quadratic selection gradient was found for P_{50} , suggesting that stabilizing selection towards a P_{50} optimum may operate in this plot (Table IV-2). In addition, at Lacanau, the zero-inflation component of the zero-inflated model predicted a positive relationship between WD and G_{min} and relative fitness (Table IV-3), indicating that trees with denser wood and higher water loss after stomatal closure may have a lower probability of effective reproduction in this plot.

3.5. Multi-trait (multivariate) selection gradients

On both study plots, the linear selection gradient for PC2 (related to tree size, i.e., HT and DBH at Lacanau, Table V-S5a; HT and HSC at Tocchi, Table V-S5b) was significant and positively related to relative fitness, while we did not find any significant quadratic selection gradients (Table IV-5). At Lacanau, the linear selection gradient for PC4 (related to tree leaf hydraulics, i.e., SLA and G_{min} , Table V-S5a) was significant and negatively related to relative fitness, while at Tocchi, the linear selection gradient for PC1 (related to cavitation, i.e., P_{12} and P_{50} , Table V-

S5b) was significant and positively related to relative fitness (Table IV-5). It should be noted that the multivariate model calculated with the linear component alone at Lacanau (Table V-S6) gave similar results as the model computed taking into account both component (Table IV-5) with the exception of PC3 (related to HSC) which was significant and negatively related to relative fitness. At Tocchi, the multivariate model calculated with the linear component alone showed no significant principal component (Table V-S7).

Table IV-2. Standard selection gradients for Lacanau and Tocchi. β is the linear and γ is the quadratic selection gradient of the trait considered (obtained from models without log-transformation of relative fitness, see text), and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively. Significant univariate selection gradients are in bold. * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$; ns, not significant.

Trait	Lacanau					Tocchi				
	β	γ	C	S	P	β	γ	C	S	P
HT	0.042	-0.015	-0.049	-0.223	-0.085***	0.099	0.012	-0.038	-0.052*	-0.095***
DBH	0.177***	0.170***	-3.95e-03	-0.041	-0.048	0.108***	0.026	0.009	-0.039	-0.094***
HSC	-0.122*	0.055	-0.019	-0.014	-0.078*	0.095**	0.03	-0.035	-0.035	-0.104***
CA	8.72e-03	0.102***	-0.033	2.92e-03	-0.059	4.21e-03	-5.80e-03	-0.038	-0.037	-0.103***
WD	-0.044	0.012	-0.044	-0.013	-0.084*	-9.50e-04	-4.84e-03	-0.035	-0.02	-0.109***
SLA	-0.053	0.021	-0.042	-0.025	-0.088**	-0.022	-8.49e-03	-0.019	-0.032	-0.111***
P_{12}	9.37e-03	0.023	-0.034	-0.012	-0.099**	2.06e-03	-0.03	-0.019	-0.021	-0.107***
P_{50}	-0.035	-1.93e-03	-0.04	-0.02	-0.090**	7.05e-03	-0.034***	-0.016	-0.025	-0.109***
G_{min}	-0.05	-3.64e-04	-0.044	-0.021	-0.089**	-7.24e-03	-3.51e-03	-0.021	-0.029	-0.109***

Table IV-3. Zero-inflated models for Lacanau. β is the linear coefficient of the trait considered, analogous to Lande & Arnold's selection gradients, and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively. Significant univariate selection gradients are in bold. $0.05 < \alpha^m < 0.1$, marginally significant; $*\alpha < 0.05$; $**\alpha < 0.01$; $***\alpha < 0.001$; ns, not significant.

Trait	Conditional component				Zero-inflation component			
	β	C	S	P	β	C	S	P
HT	0.038 ^{ns}	-0.151 ^{ns}	-0.077 ^{ns}	-0.185*	-0.092 ^{ns}	0.151 ^{ns}	-0.305*	0.348*
DBH	0.288***	0.043 ^{ns}	-0.086 ^{ns}	-0.102 ^{ns}	-0.576***	0.106 ^{ns}	-0.192 ^{ns}	0.325*
HSC	-0.177*	-0.066 ^{ns}	-0.038 ^{ns}	-0.132 ^{ns}	0.199 ^{ns}	0.109 ^{ns}	-0.291*	0.346*
CA	0.029 ^{ns}	-0.104 ^{ns}	-0.049 ^{ns}	-0.180*	0.030 ^{ns}	0.155 ^{ns}	-0.277 ^{ns}	0.363*
WD	0.089 ^{ns}	-0.132 ^{ns}	-0.076 ^{ns}	-0.160*	0.269*	0.157 ^{ns}	-0.336*	0.363**
SLA	-0.038 ^{ns}	-0.146 ^{ns}	-0.081 ^{ns}	-0.191*	0.196 ^{ns}	0.151 ^{ns}	-0.310*	0.322*
P_{12}	0.072 ^{ns}	-0.123 ^{ns}	-0.075 ^{ns}	-0.186*	0.094 ^{ns}	0.142 ^{ns}	-0.349*	0.350*
P_{50}	-0.036 ^{ns}	-0.145 ^{ns}	-0.077 ^{ns}	-0.196*	-0.015 ^{ns}	0.146 ^{ns}	-0.325*	0.324*
G_{min}	-0.062 ^{ns}	-0.151 ^{ns}	-0.070 ^{ns}	-0.201*	0.256*	0.161 ^{ns}	-0.329*	0.353*

Table IV-4. Zero-inflated models for Tocchi. β is the linear coefficient of the trait considered, analogous to Lande & Arnold's selection gradients and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively. Significant univariate selection gradients are in bold. $0.05 < \alpha^m < 0.1$, marginally significant; * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$; ns, not significant.

Trait	Conditional component				Zero-inflation component			
	β	C	S	P	β	C	S	P
HT	0.153*	-0.259***	-0.063	-0.123*	-0.582**	0.267	-0.280	0.277
DBH	0.160*	-0.177*	-0.04	-0.072	-0.297^m	0.042	-0.315*	0.213
HSC	0.128	-0.302***	0.015	-0.086	-0.755***	0.272	-0.04	0.198
CA	-0.023	-0.266**	-0.014	-0.131*	0.25	0.298	-0.363*	0.309
WD	-0.068	-0.289***	-0.028	-0.1	-0.167	0.218	-0.249	0.174
SLA	-0.095	-0.232***	-9.53e-03	-0.092	-0.044	0.145	-0.336*	0.249
P_{12}	0.017	-0.234***	-0.027	-0.098	0.239	0.199	-0.371*	0.267
P_{50}	0.077	-0.221***	0.013	-0.091	0.329	0.163	-0.289	0.258
G_{min}	7.62e-03	-0.235***	-0.012	-0.097	-0.185	0.120	-0.305	0.267

Table IV-5. Multivariate linear models for Lacanau. β is the linear and γ is the quadratic selection gradient of the trait considered (obtained from models without log-transformation of relative fitness, see text). PC1, PC2, PC3 and PC4 are the principal components and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively.

Lacanau: PC1 main loading factors: P_{50} (0.92) and P_{12} (0.90); PC2 main loading factors: HT (0.88) and DBH (0.64); PC3 main loading factors: HSC (-0.74), and PC4 main loading factors: SLA (0.54) and G_{min} (0.54).

Tocchi: PC1 main loading factors: P_{50} (0.70) and P_{12} (0.73); PC2 main loading factors HT (0.66) and HSC (0.65); PC3 main loading factors: CA (0.67); and PC4 main loading factors: CA (0.65) and WD (0.62).

Significant univariate selection gradients are in bold. * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$; ns, not significant.

Plot	PC1		PC2		PC3		PC4		C	S	P
	β	γ	β	γ	β	γ	β	γ			
Lacanau	-2.65e ^{-03ns}	-0.013 ^{ns}	0.079*	-0.018 ^{ns}	0.093 ^{ns}	0.034 ^{ns}	-0.087**	0.012 ^{ns}	-7.27e-03 ^{ns}	-0.026 ^{ns}	-0.065 ^{ns}
Tocchi	0.070*	-0.013 ^{ns}	0.141***	0.311 ^{ns}	-1.50e ^{-03ns}	0.031 ^{ns}	0.025 ^{ns}	0.002 ^{ns}	-0.066 ^{ns}	-0.011 ^{ns}	-0.105**

4. Discussion

We investigated the relationships between several important life history traits (measured *in situ*) and realized fitness controlling for microenvironmental variation, competition and spatial fitness autocorrelation, in order to explore variation in the direction and intensity of natural selection in two maritime pine populations growing in contrasting climates and topographies. In both populations, we observed contemporary directional selection for growth traits, although its direction was not entirely consistent in the two populations. Compared to growth traits, selection patterns were less consistent for functional traits, both between populations and across the models used. In addition, the zero-inflated models revealed a potential trade-off between increased wood density and cuticular conductance with probability of reproduction at Lacanau.

4.1. Growth traits under contemporary selection

All investigated growth traits (HT, DBH, HSC, CA) were potentially under selection as revealed by different models. We found strong positive directional selection for radial growth (DBH) in both plots (supplemented by a weak trend towards disruptive selection for this trait in Lacanau). However, directional selection for HSC operated in opposite ways depending on the plots, indicating that larger crowns were more favoured in the humid Atlantic climate at Lacanau than in the dry Mediterranean climate at Tocchi.

At Tocchi, the multivariate selection gradient revealed a significant PC2, whose main loading factors were related to tree height and crown architecture (HSC and HT), highlighting their correlative relationship (as shown by the correlogram), and showing a contemporary selective trend towards taller trees with higher crown start. In this population, the zero-inflation component of the zero-inflated models revealed that above-than-average trait values for HSC and HT at Tocchi can positively impact a tree's probability of reproduction too.

In the literature, Yang & Huang (2018) found a positive relationship between HSC and HT for conifers such as lodgepole pine (*Pinus contorta var. latifolia* Engelm.) and white spruce (*Picea glauca* (Moench) Voss), as well as for a deciduous species, the trembling aspen (*Populus tremuloides* Michx.). Competition has also been shown to have a significant impact on HSC (Fu et al., 2017; Gill et al., 2000; Hasenauer & Monserud, 1996; Paulo et al., 2002) in a closed

canopy where competitive interactions are numerous, trees tend to limit the development of their crowns, both horizontally and vertically, whereas the opposite pattern is observed in stands of open-grown trees. Tocchi is characterised by a dense, continuous forest cover with a thick understory. Indeed, for the same number of trees sampled, the stand at Lacanau is 2.5 times larger than that of Tocchi. At Tocchi (but not at Lacanau), the conditional component of the zero-inflated models identified competition to be an important covariate modulating the relationship between traits and relative fitness because of its predicted negative impact on the number of established offspring. Consequently, the competitive interactions in this population may constitute a significant selective pressure, where trees with shorter crowns may have a selective advantage over trees with larger crowns, as well as a higher probability of effective reproduction.

At Lacanau, in addition to directional selection for DBH (favouring increased trait values) and HSC (favouring decreased trait values and therefore bigger crowns), maritime pines were subject to disruptive selection for sun-exposed tree crown area (CA). In addition, the multivariate model predicted simultaneous directional selection for tree size (PC2, loaded by correlated HT and DBH, illustrating the well-known allometric height-diameter relationship in trees; Vizcaíno-Palomar et al., 2017). Furthermore, the zero-inflation component of the zero-inflated model in Lacanau revealed a positive relationship between DBH and the probability of a tree reproducing, while it revealed a negative relationship for WD, indicating that trees with higher-than-average trunk diameter and lower wood density may have more chance to experience effective reproduction.

For both populations, our results are somehow in contrast with the literature. Indeed, theory for life-history traits has shown that, in response to biotic (e.g., competition) or abiotic (e.g., nutrients) limitations, trade-offs between fitness-related traits, expressed in terms of survival, growth and reproductive costs, are commonly used by plants to maximise their fitness (Roff, 2000). Climent et al. (2008) and Santos-del-Blanco & Climent (2014) showed that for *Pinus halepensis* in a common garden experiment, the cost of reproduction was too high for trees that invested a lot of resources in growth.

However, this pattern is not universal in nature. Bravo et al. (2017) found that for maritime pine, larger trees (with higher growth efficiency) also produced a greater number of cones on average, than smaller trees. This result has already been documented by Krannitz & Duralia (2004) for *Pinus ponderosa* and *Pseudotsuga menziesii* (El-Kassaby & Barclay, 1992), as well

as with the use of spatially explicit mating models and parentage analysis, where female fecundity increased with maximum stem diameter for *Fagus sylvatica* (see Oddou-Muratorio et al., 2018). Furthermore, tree diameter is generally positively related to relative tree fitness, indicating that trees with larger trunk diameters may have more established offspring (Alexandre et al., 2020, for *Quercus robur* and *Quercus petraea*; Westergren et al., 2023, for *Fagus sylvatica*).

This lack of compromise between growth and reproduction in our populations can probably be explained in part by the generally greater vigour of large trees in even-aged stands, where it has been shown that greater tree vigour is linked to a greater number of recruits in subsequent generations (González-Martínez et al., 2006). The ‘weather hypothesis’ (Knops et al., 2007) could be another possible explanation. This hypothesis states that the relationship between growth and reproductive output could be purely correlative, caused by unknown environmental variables (see Oddou-Muratorio et al., 2018; Vincent & Ibáñez, 2024; Żywiec & Zielonka, 2013).

4.2. Functional traits under contemporary selection

Atmospheric evaporative demand is the driving force behind the circulation of water in a tree, creating vapour loss through the leaves (i.e., evapotranspiration). Water always moves from a point of high water potential (the soil) to a point of lower water potential (the atmosphere), through capillary channels that run up the trunk through various physical resistances. In the event of a severe drought, the water transport capacity of the channels is reduced and may be interrupted, leading to very negative water potentials in the canopy (see Delzon et al., 2010, for conifers). Under such stress, channels can fill with water vapour and air, causing hydraulic failure (i.e., cavitation) which, in turn, is often considered the cause of tree mortality (Dietrich et al., 2018). In conifers, P_{50} (a 50% loss of hydraulic conductance) is tightly linked to survival under severe drought and is a major lethal hydraulic safety margin (Brodribb et al., 2010). In the literature, no differences in P_{50} values were found between maritime pine populations growing in contrasted climates (Lamy et al., 2014) although this may not be the case when a larger sampling was performed, M. Mencuccini personal communication based on FORGENIUS project new results). This trait has also been considered genetically canalized, suggesting that it is not targeted by current natural selection (Lamy et al., 2011), although, to

our knowledge, no previous direct assessment of selection gradients has ever been carried out on this trait. Our results suggest, however, that resistance to cavitation is correlated with fitness in Mediterranean environments.

In the multivariate model, P_{12} and P_{50} were the main drivers of PC1 loadings in Tocchi, highlighting their correlative relationship. In this population, we found a selective trend toward stabilising selection for P_{50} , however, no significant selective trend was observed for P_{12} in any of the models. These results may indicate the greater weight of P_{50} relative to P_{12} in driving PC1 loadings. Therefore, for maritime pine in a Mediterranean environment, our results suggest that a water potential inducing a 12% loss of water conductance may have less impact on drought resistance and fitness than a water potential inducing a 50% loss of water conductance. Moreover, the stabilizing selection found for P_{50} at Tocchi indicates a selective trend towards trees stabilizing around average values for this trait. This trend should be a cause for concern, as it could reduce the variance of the selected trait (Brodie et al., 1995), thus limiting the available variation on which natural selection can act in response to expected changing optima due to climate change.

The multivariate model also revealed a negative selection coefficient (albeit of low magnitude) for PC4 at Lacanau, which is linked to functional leaf traits, SLA and G_{min} . These traits are known to be related to plant water use efficiency (WUE; the ratio of net CO₂ uptake to water loss through transpiration), as they influence the transpiration rate per unit area (Pallardy, 2008), the photosynthetic capacity (leaves with lower SLA generally contain more photosynthetic material per unit area; see Reich et al., 1998; Ramírez-Valiente et al., 2011) and stomatal control (Bacon, 2009). Indeed, a negative relationship between WUE and SLA has been found in the literature (Hoffmann et al., 2005 for tree evergreen savanna species; Zhang et al., 2015 for maize), including for maritime pine (de Miguel et al., 2012), suggesting an adaptive role of SLA in reducing water loss (Lamont et al., 2002; Warren et al., 2005). Moreover, Fernández et al. (1999) showed that young maritime pine provenances subjected to more intense summer drought had lower SLA, which has also been reported in other Mediterranean species, such as *Quercus suber* (Ramírez-Valiente et al., 2011). Our findings confirm these correlations and reveal contemporary selection for trees with lower SLA, indicating thicker and/or denser leaves and increased photosynthetic exchange potentially leading to faster growth, as well as a potentially selective advantage towards reduced water loss. Such a selective trend for SLA was also found for *Quercus petraea* in Alexandre et al.

(2020), indicating that deciduous species may also be under contemporary selection for thicker leaves and reduced water loss.

The importance of cuticular conductance in drought survival is increasingly recognised (Cochard, 2021; De Kauwe et al., 2020; Martin-StPaul et al., 2017). Drake et al. (2018) reported that cuticular conductance is reduced in *Eucalyptus parramattensis* leaves subjected to conditions that increase evaporative demand. Pine species are known to be isohydric, as they maintain a constant leaf water potential regardless of drought conditions by reducing stomatal conductance to limit transpiration (Tardieu & Simonneau, 1998). Duursma et al. (2019) found that the G_{min} of Pinales species tended to be lower than for species of other orders, such as grasses (Poales), although the authors could not clearly explain the underlying causes of variation of this trait between species. Predictions from our multivariate model revealed a weak selective tendency for trees with lower G_{min} , which would have reduced water loss through the cuticle after stomatal closure, avoiding desiccation and eventual death (Duursma et al., 2018).

As additional insights at Lacanau, the zero-inflation component of the zero-inflated model revealed that trees with higher G_{min} have also a higher chance of not reproducing. This pattern confirms the selective trends of the multivariate model described above and provides additional information, showing that a tree with higher rates of passive evaporation through the cuticle after stomatal closure compared to its neighbours may be at a significant disadvantage during drought events with respect to several components of its fitness (i.e., survival, number of established offspring and probability of reproduction).

4.3. Advantages and limitations of different kind of models

Standard and multivariate models have enabled us to gain a better understanding of contemporary selection, and to take into account the traits correlative relationship, which is a fundamental requirement since natural selection does not act on a single trait, but on several correlated traits in nature. However, compared to zero-inflated models, they failed to identify any selective trend for WD and G_{min} . Zero-inflated models provided also additional insights on microenvironment effects on fitness, suggesting better overall performance of this type of models. Most relevant, zero-inflated models provided additional insight into selection patterns allowing us to split selection gradients into the zero-inflated (i.e., probability of reproduction)

and the conditional (i.e., amount of reproduction) components, which cannot be achieved with standard models.

It is important to bear in mind that zero-inflated models are not strictly speaking selection gradients, as defined by Lande & Arnold (1983), and thus are not directly comparable with current literature. However, they can help us to better understand the relationship between phenotypes and potential selective pressures on some fitness components that cannot be provided by standard (including multivariate) models. Consequently, we suggest that zero-inflated models can be used as a complementary approach to that of standard selection gradients to enrich our understanding of the selective processes affecting different components of fitness.

4.4. Contrasting patterns of natural selection across environments

Multiple abiotic and biotic factors can act as selective agents in natural populations. These selective agents do not exert selection pressure individually, but often interact with each other, creating synergistic or antagonistic selection patterns on the phenotypes (Wadgymar et al., 2022). For example, in response to contrasted climatic factors, two spatially distant populations in contrasted environments may exhibit divergent mean phenotypes, whose distance to the optimum phenotype will vary, resulting in contrasting selection strength and/or direction towards this optimum (Siepielski et al., 2013; Steele et al., 2011). Siepielski et al. (2013) questioned the extent to which spatially distant populations were experiencing differences in the strength and direction of selection. The authors concluded that spatially distant populations could experience variation in the direction of selection when selection is weak, however, mostly, they tended to experience variation in the strength of selection.

Despite a common selection gradient for overall tree size, our models revealed opposing direction of selection for HSC in the two populations, as well as population-specific selection gradients, probably indicating local adaptation due to contrasted selective pressures. Alternatively, even if mean phenotypes from two spatially distant populations converge towards a similar optimum, selection pressure can be different depending on whether the current mean phenotype of each stand is lower (favouring higher trait values) or higher (favouring lower trait values) than the optimum, or if it has already reached the optimum (no selection) (Siepielski et al., 2013).

Westergren et al. (2023) found weaker directional selection for DBH in natural populations of beech, while Alexandre et al. (2020) found significantly stronger linear selection for radial growth traits in *Quercus petraea* and *Quercus robur* (calculated with female-only and male and female functions, respectively, using MEMMseedlings estimates of effective fecundity) than those found for maritime pine in Atlantic and Mediterranean climates. Furthermore, Alexandre et al. (2020) found a negative predicted genetic response for SLA for *Quercus petraea* only (despite the absence of significant selection gradients for this trait), indicating a shift towards trees with denser leaves and higher photosynthetic capacity, but did not find a significant selection gradient for WD for either species. These results demonstrate that growth- and leaf morphology-related traits are a common target of natural selection in natural tree populations (Vitasse et al., 2014) because they are fundamental elements of survival and productivity in natural and planted forests (Grattapaglia et al., 2009). Overall, these results demonstrate that selection targets and strengths can vary between years (Westergren and colleagues did not find consistent selective trends for trees sampled in different years, see also Siepielski et al, 2009) and site-specific environmental selective pressures which, together with gene-by-environment (GxE) interactions (Li et al., 2017; Westergren et al., 2023), will result in contrasting distance of the mean phenotype relative to the optimum.

The zero-inflated models clearly showed that the microenvironment, competition and fitness spatial autocorrelation had a significant impact on some component of an individuals' relative fitness, but populations and traits were not impacted consistently, indicating that contrasted selective pressures are probably driving the mean phenotype of each population towards a different selective optimum. Our results could also be explained by different biases due to correlated microenvironmental variation not measured in the study. Lande and Arnold's original selection gradients did not take into account the possible bias in predicted selection trends that may be caused by microenvironment being correlated with fitness (or its components) or the traits of interest. In our study, we corrected our models using covariates. Nevertheless, we must bear in mind the difficulty to fully control for the microenvironment in wild forest stands, not least because the source of microenvironmental variation may be unknown or the relevant spatial scale of variation too small to capture and eliminate microenvironmental covariances (Rausher, 1992). Consequently, the use of covariates can attenuate, but not eliminate, environmentally induced covariance at the individual scale, which is already an important step towards obtaining a more accurate picture of the targets, strength and direction of natural selection. To our knowledge, the studies of Alexandre et al. (2020) and

Westergren et al. (2023) are the only ones in the literature that used microenvironmental and ecological covariates in the computation of selection gradients, but the authors did not further discuss about the relationship of these covariates with fitness.

Trait evolution is governed by a balance between conflicting fitness advantages and life history trade-offs (Schluter et al., 1991), which are the result of the contrasting ecological features occurring in spatially distant populations. Our results demonstrate that contemporary selection favours different traits in spatially distant populations, despite belonging to similar functional classes, and support the idea that natural selection is uneven, varying along ecological gradients or randomly in space (Siepielski et al., 2013). It should also be noted that the selection patterns observed in the two populations represent only a temporal snapshot, with populations being expected to undergo some degree of temporal variation in strength and direction of natural selection (e.g., Morrissey et al., 2012; Siepielski et al., 2009; Westergren et al., 2023). We believe that a better understanding of the key features that determine the causes of spatial patterns of selection in multi-year studies will enable us to improve our appreciation of how, in a context of global change, patterns of phenotypic diversity are shaped at the range scale of species, and the resulting adaptive evolutionary processes.

5. Conclusion

This study is one of the first to explore the spatial patterns of contemporary selection for maritime pine *in natura* while taking account of microenvironmental variation using different types of models.

Under contemporary selective pressures in Mediterranean and Atlantic climates, maritime pines appear to be subject to directional selection for growth. Selection gradients for functional traits were found to be population-specific; however, they revealed a general pattern of contemporary selection towards trait values that can, to some extent, prevent physiological stresses due to increasing drought and temperature. Our models also suggested stabilising selection for P_{50} in the Mediterranean environment that could lead to higher vulnerability to drought, which is of particular concern given the predicted increase in severity of drought events in this region. The use of zero-inflated models allowed decoupling standard selection

gradients, giving insights on both growth (e.g., HT and HSC in Tocchi) and functional (e.g., WD and G_{min} in Lacanau) traits conferring higher probability of effective reproduction.

Both standard and zero-inflated models identified strong microenvironment effects on fitness. Therefore, although we collected evidence of ongoing contemporary selection for maritime pine in contrasting environments for some relevant growth and functional traits, the potential bias resulting from unmeasured environmental covariance between traits and fitness cannot be entirely excluded; yet it is mitigated by the use of microenvironmental variables in our models.

Overall, our study has highlighted some relevant contemporary population-specific selective trends, as well as the need for long-term studies with fine-grained assessment of microenvironmental variation. Despite potential limitations, our work opens up encouraging prospects for the implementation of this approach in natural forest tree populations subject to natural and anthropogenic selection.

6. Data availability

The data underlying this study will be made public and accessible to all on Data INRAE and scripts will be available on GitHub.

7. Acknowledgements

We thank Carmen García-Barriga and the PGTB (Plateforme Génome Transcriptome de Bordeaux, INRAE, France) for their contribution to genetic data production. We are grateful to the Mediterranean Forest Ecology Research Unit (URFM, INRAE, Avignon, France), Marie-Gabrielle Harribey and Thomas Francisco (INRAE, Bordeaux, France) for their contribution to data sampling.

V. Supplementary information - Chapter 2

1. The populations

Figure V-S1. Map illustrating the distribution of adult trees and offspring in the Lacanau stand.

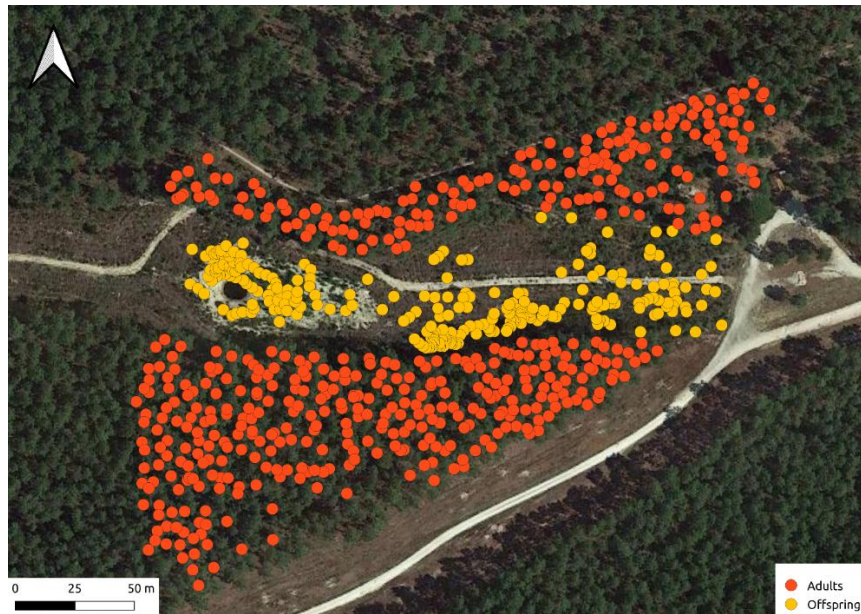
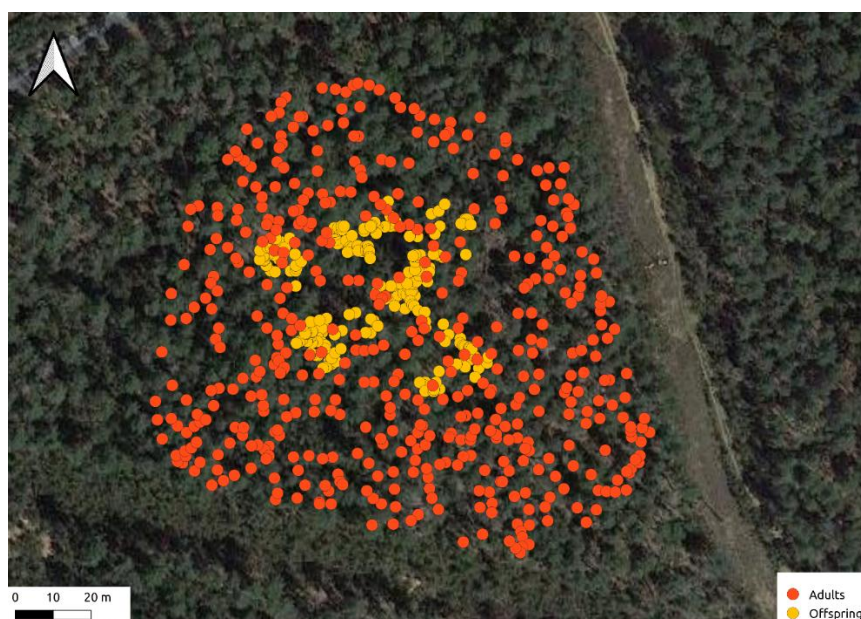


Figure V-S2. Map illustrating the distribution of adult trees and offspring in the Tocchi stand.



2. The data

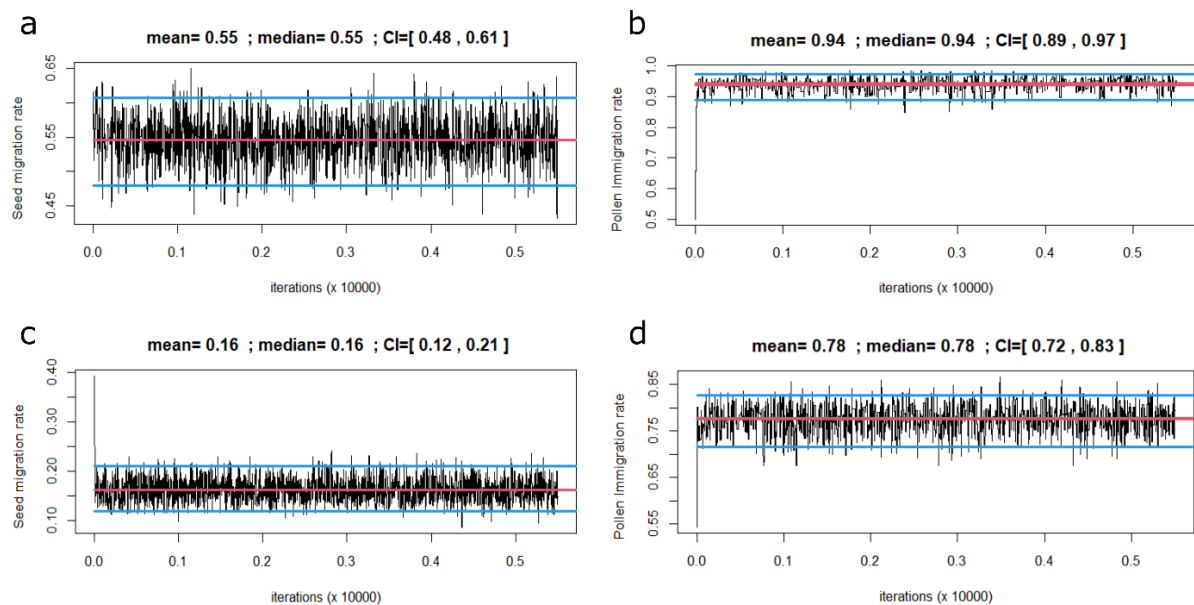
2.1. List of samples, standardized fitness proxies, phenotypic traits and covariates

Table V-S1. List of samples from Lacanau stand, standardized relative fitness proxies computed from MEMM and CERVUS softwares, and list of standardized phenotypic traits and covariates used in this study. Abbreviations: for the traits cf. Table V-1 and for the covariates cf. main text. NA; Non-Applicable. Table available on demand.

Table V-S2. List of samples from Tocchi study plot, standardized relative fitness proxies computed from MEMMseedlings and CERVUS softwares and list of standardized phenotypic traits and covariates used in this study. Abbreviations: for the traits cf. Table V-1 and for the covariates cf. main text. NA; Non-Applicable. Table available on demand.

2.2. Seed and pollen immigration rates from MEMMseedlings software

Figure V-S3. Mean, median and confidence intervals (CI 95%) of the seed immigration rate in Lacanau and Tocchi (a, c), respectively, and of the pollen immigration rate in Lacanau and Tocchi (b, d), respectively, computed from MEMMseedlings software.



2.3. The phenotypes

Figure V-S4.1 Projection of all the available phenotypes at Lacanau along the pairs of different combinations of the first four axes (explaining 66% of the variance) of the Principal Component Analysis (PCA). PC1 & PC2 a), PC1 & PC3 b), PC1 & PC4 c), PC2 & PC3 d), PC2 & PC4 e), PC3 & PC4 f).

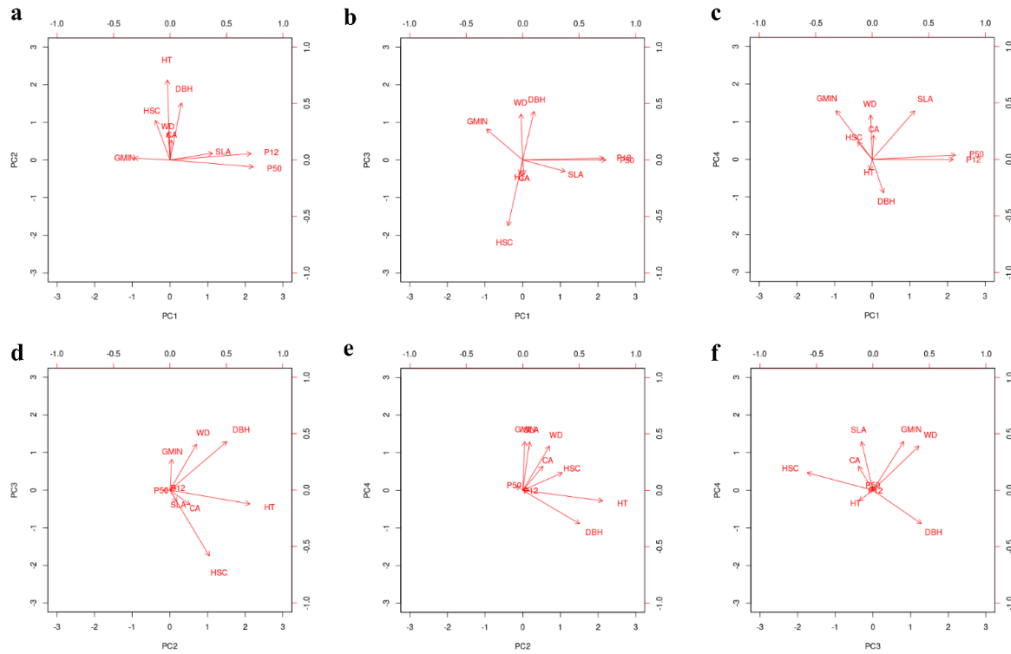
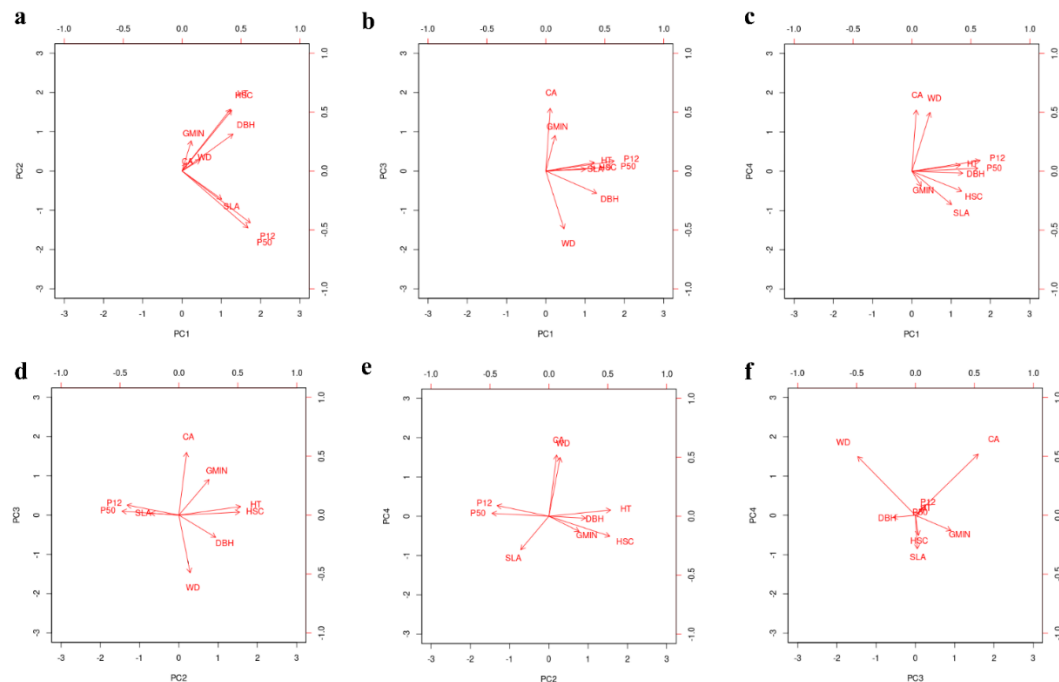


Figure V-S4.2 Projection of all the available phenotypes at Tocchi along the pairs of different combinations of the first four axes (explaining 67% of the variance) of the Principal Component Analysis (PCA). PC1 & PC2 a), PC1 & PC3 b), PC1 & PC4 c), PC2 & PC3 d), PC2 & PC4 e), PC3 & PC4 f).



3. The results

3.1. Fitness proxies from CERVUS and MEMMseedlings software's

Figure V-S5. Density plots showing the distribution of MEMMseedlings a) and CERVUS b) fitness proxies for each stand.

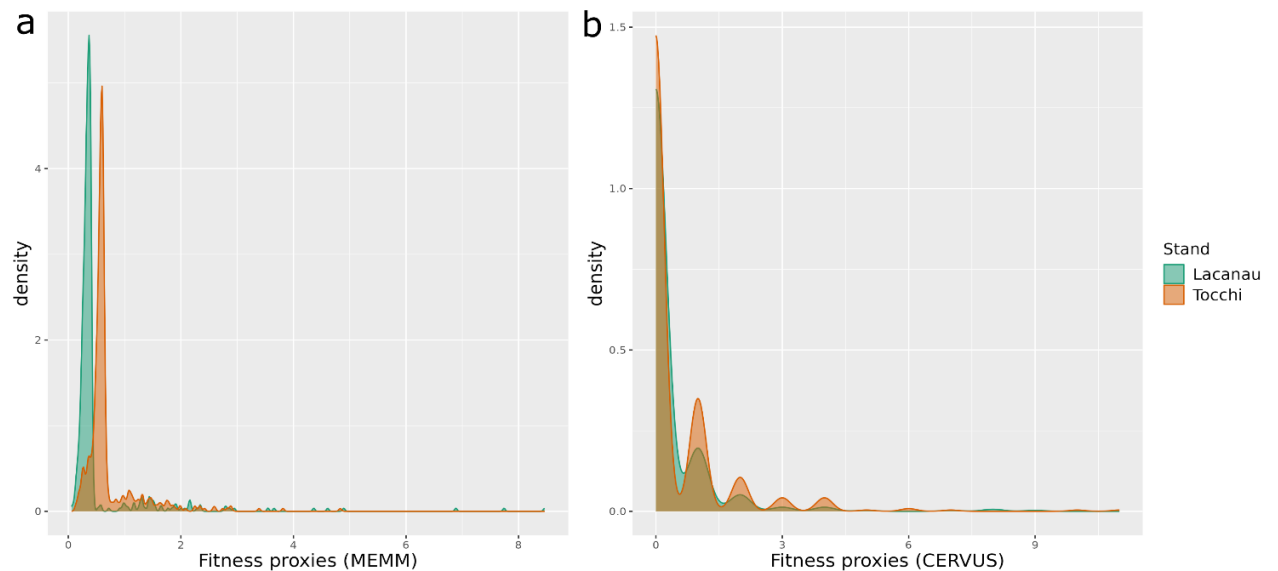
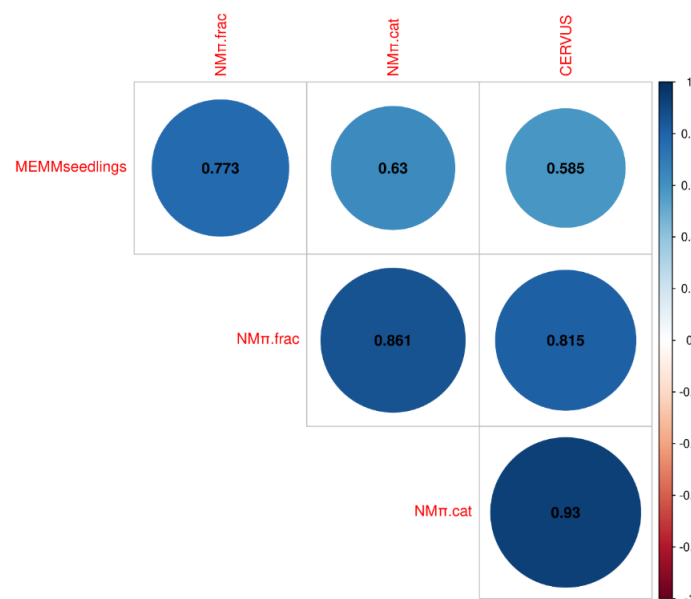


Figure V-S6. Pairwise correlogram based on Pearson's correlation coefficients of raw (i.e., no transformation applied to obtain estimates relative to each adult tree) female fecundity estimated by MEMMseedlings, CERVUS, $NM\pi$.frac (fractional estimates from $NM\pi$ neighbourhood model), and $NM\pi$.cat (categorical estimates from $NM\pi$ categorical parentage assignment) for the Lacanau study plot.



3.2. The phenotypes: correlogram and distribution of crown length (HT-HSC) in Tocchi

Figure V-S7. Pairwise correlograms based on Pearson's correlation coefficients between all phenotypes from the Lacanau a) and Tocchi b) plots. Blank cells represent non-significant coefficients using *p-values* at 5% significance level.

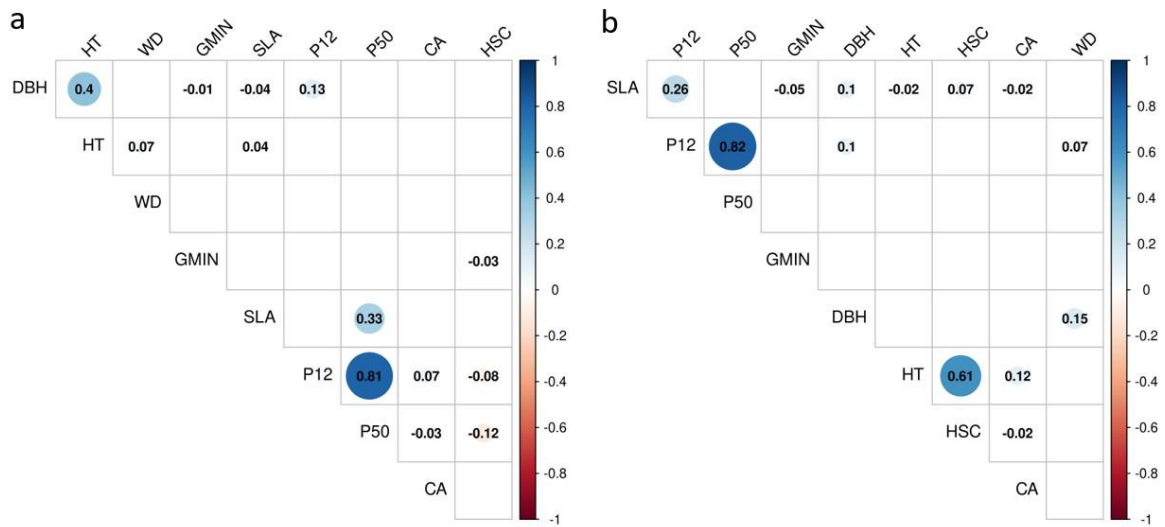
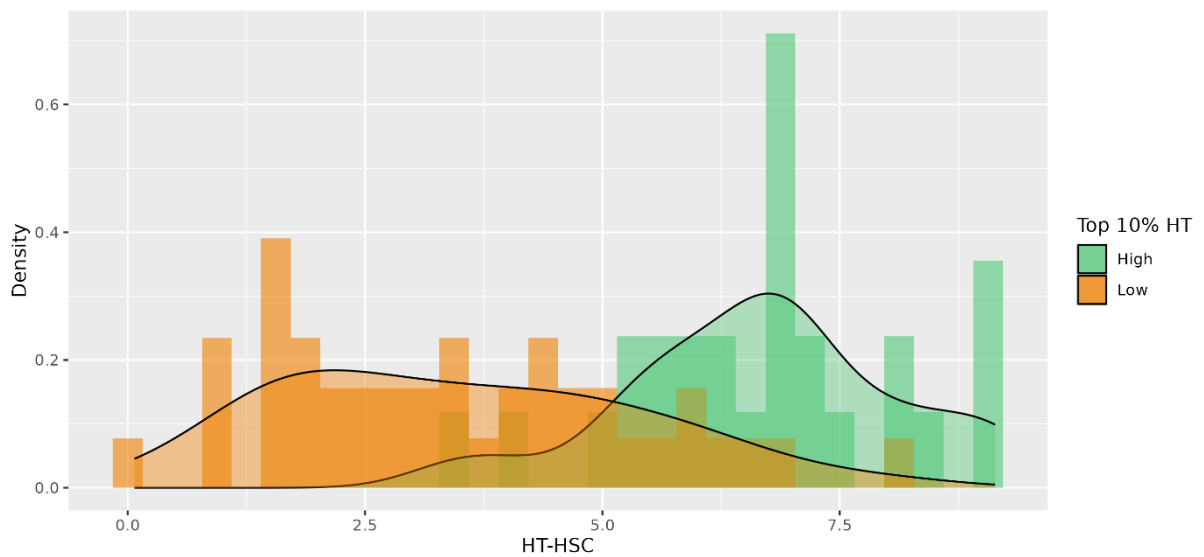


Figure V-S8. Density plots representing the distribution of crown length (HT-HSC) (x-axis) for the 10% tallest (in green; Top 10% HT High) and 10% smallest (in orange; Top 10% HT Low) trees in Tocchi.



4. The equations

4.1. Martin-Ek competition index

Equation V-S1. Martin-Ek equation index (Martin & Ek, 1984) to quantify the intensity of competition on a focal individual i . In the equation, dbh_i and dbh_j are the diameters at breast height (in cm) of the competed individual i and of the competitor j , i.e., any adult tree with $dbh_i > dbh_j$, n_{dmax} is the total number of competitors in a given radius d_{max} (in m) around each competed individual tree i , and d_{ij} is the distance between individuals i and j .

$$Compet_{dmax} = \frac{1}{dbh_i} \sum_{j=1}^{n_{dmax}} dbh_j \exp \left[\frac{-16d_{ij}}{dbh_i + dbh_j} \right] \quad (2)$$

4.2. Correction of edge effects

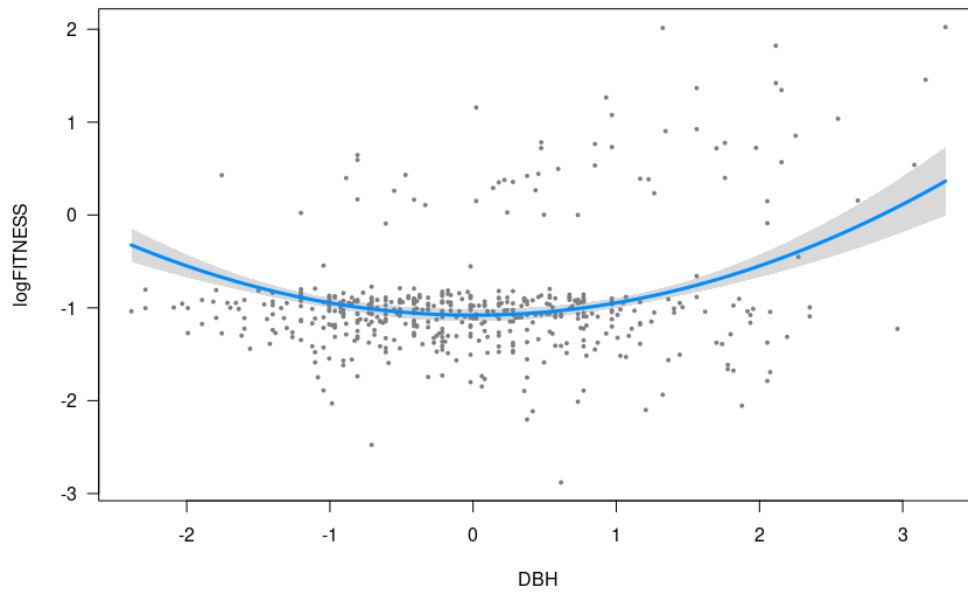
Equation V-S2. Equation used to correct the competition index for edges effects, where $dist_{max}$ is the maximum distance (in m) between the tree i and the border of the plot.

$$CorCompet = TotMartin_{dmax} + \left(TotMartin_{dmax} \times \left(1 - \frac{dist_{max}}{10} \right) \right) \quad (3)$$

5. The selection gradients

5.1. Graphic representation of standard model quadratic component for DBH at Lacanau

Figure V-S9. Quadratic component of the standard selection gradient for DBH at Lacanau. logFITNESS (x-axis) represents the log-transformed relative fitness as estimated from MEMMseedlings.



5.2. Standard linear selection gradients for Lacanau

Table V-S3. Standard linear selection gradients calculated for models whose quadratic component is not significant for Lacanau study plot. β is the linear selection gradient for the trait under consideration (obtained from models without log transformation of relative fitness, see text), and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively. Significant univariate selection gradients are in bold. * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$; ns, not significant.

Traits	β	C	S	P
HT	0.079 ^{ns}	-0.038 ^{ns}	-0.051 ^{ns}	-0.095***
HSC	-0.138**	-0.024 ^{ns}	-0.014 ^{ns}	-0.079*
WD	-0.030 ^{ns}	-0.045 ^{ns}	-0.012 ^{ns}	-0.085**
SLA	-0.058 ^{ns}	-0.042 ^{ns}	-0.025 ^{ns}	-0.088**
P_{12}	9.01e ^{-03ns}	-0.034 ^{ns}	-0.012 ^{ns}	-0.097**
P_{50}	-0.035 ^{ns}	-0.042 ^{ns}	-0.020 ^{ns}	-0.091**
G_{min}	-0.050 ^{ns}	-0.044 ^{ns}	-0.021 ^{ns}	-0.089**

Table V-S4. Standard linear selection gradients calculated for models whose quadratic component is not significant for Tocchi study plot. β is the linear selection gradient for the trait under consideration (obtained from models without log transformation of relative fitness, see text), and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively. Significant univariate selection gradients are in bold. * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$; ns, not significant.

Traits	β	C	S	P
HT	0.048*	-0.038 ^{ns}	-0.051*	-0.095***
DBH	0.111***	0.011 ^{ns}	-0.038 ^{ns}	-0.095***
HSC	0.091**	-0.031 ^{ns}	-0.033 ^{ns}	-0.104***
CA	3.56e ^{-04ns}	-0.039 ^{ns}	-0.037 ^{ns}	-0.104***
WD	-0.013 ^{ns}	-0.037 ^{ns}	-0.020 ^{ns}	-0.110***
SLA	-0.026 ^{ns}	-0.019 ^{ns}	-0.031 ^{ns}	-0.110***
P_{12}	1.13e ^{-04ns}	-0.018 ^{ns}	-0.024 ^{ns}	-0.107***
G_{min}	6.02e ^{-04ns}	-0.020 ^{ns}	-0.029 ^{ns}	-0.109***

5.3. Principal component scores of phenotypic traits

Table V-S5. Principal component scores of phenotypic traits measured in Lacanau a) and Tocchi b) with *psych* R package. SS loadings are eigenvalues, the sum of the squared loadings.

(a)

Lacanau	HT	DBH	HSC	CA	WD	P_{50}	P_{12}	SLA	G_{min}	SS loadings	Cumulative (%)
PC1	-0.03	0.13	-0.16	0.02	-0.02	0.92	0.9	0.47	-0.4	2.08	0.23
PC2	0.88	0.64	0.41	0.22	0.3	-0.08	0.07	0.07	0.03	1.52	0.4
PC3	-0.17	0.52	-0.74	-0.17	0.5	0	0.02	-0.13	0.34	1.26	0.54
PC4	-0.12	-0.37	0.2	0.27	0.49	0.05	0	0.54	0.54	1.08	0.66

(b)

Tocchi	HT	DBH	HSC	CA	WD	P_{50}	P_{12}	SLA	G_{min}	SS loadings	Cumulative (%)
PC1	0.51	0.54	0.53	0.05	0.19	0.7	0.73	0.42	0.1	2.08	0.23
PC2	0.66	0.39	0.65	0.08	0.12	-0.6	-0.55	-0.3	0.32	1.88	0.44
PC3	0.09	-0.24	0.03	0.67	-0.61	0.04	0.11	0.02	0.38	1.04	0.55
PC4	0.07	-0.02	-0.21	0.65	0.62	0.03	0.11	-0.35	-0.16	1.02	0.67

5.4. Multivariate linear selection gradients

Table V-S6. Multivariate linear model calculated for those variables whose quadratic component is not significant for Lacanau study plot. β is the linear selection gradient of the trait considered (obtained from models without log-transformation of relative fitness, see text). PC1, PC2, PC3 & PC4 are the principal components and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively. Significant univariate selection gradients are in bold. * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$; ns, not significant.

PC1	PC2	PC3	PC4	C	S	P
β	β	β	β			
$-4.3e^{-03ns}$	0.087*	0.114*	-0.097**	-0.011^{ns}	-0.028^{ns}	-0.068*

Table V-S7. Multivariate linear model calculated for those variables whose quadratic component is not significant for Tocchi study plot. β is the linear selection gradient of the trait considered (obtained from models without log-transformation of relative fitness, see text). PC1, PC2, PC3 & PC4 are the principal components and C , S and P are the coefficients of the covariates: the competition index, the soil moisture index and the PCNM, respectively. Significant univariate selection gradients are in bold. * $\alpha < 0.05$; ** $\alpha < 0.01$; *** $\alpha < 0.001$; ns, not significant.

PC1	PC2	PC3	PC4	C	S	P
β	β	β	β			
0.072^{ns}	0.136^{ns}	$7.66e^{-03ns}$	$3.01e^{-03ns}$	-0.067^{ns}	$-5.42e^{-03ns}$	-0.108**

VI. CHAPTER 3

Genetic characterisation of maritime pine on the island of Corsica: a landscape genomics approach

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Abstract:

Over the last few decades, very few molecular studies have been carried out on maritime pine on the island of Corsica, which is characterised by a specific orography and represents precious genetic resources for the species. At a time when the climate is changing at an unprecedented rate in the Mediterranean basin, the persistence of maritime pine on the island of Corsica is potentially under threat. There is an urgent need to gain a better understanding of the spatial distribution of maritime pine genetic resources on the island, and to assess its adaptive potential in current and predicted future climates. In this study, we genotyped with a large set of SNP markers used 355 individuals from 25 maritime populations from the CORSAPIN common garden to (i) unravel the spatial patterns of genetic variation across the island along clinal gradients; (ii) describe the fine-scale genetic structure; (iii) evaluate the potential of climatic variables to explain its genetic structure; and (iv) identify the adaptive variation of maritime pine to climate and use it to model future adaptive gradient(s). We found that demographic history and past climates were potentially important factors shaping maritime pine genetic resources on the island. Projection of current and future adaptive composition revealed that this species is currently genetically well adapted to coastal and middle-altitude localities compared to high altitude localities. In the future, we highlighted the potential for maritime pine to expand to higher altitudes, but we were unable to obtain information on its future adaptive potential on the coast. Our results confirm the existence of local adaptation of maritime pine to the climate in Corsica and highlight, to a certain extent, its potential for adaptation in the short term.

Keywords: Mediterranean basin, Corsica Island, Maritime pine, Spatial distribution of genetic resources, Short-term adaptive potential, Adaptive landscape

1. Introduction

The western Mediterranean basin is home to around 25,000 plant species, including over 13,000 endemic plants representing half of all flora, making it the second richest area of endemic flowering plants in the world (Valavanidis & Vlachogianni, 2011). This richness results from a complex topography and strong climatic variability, including during the Last Glacial Maximum (LGM, around 20,000 years ago) when the Mediterranean region represented a refuge for biodiversity (Fady & Conord, 2010; Médail, 2017; Médail & Diadema, 2009). Historical human activities such as long-term deforestation at lower elevations for wood, pastures and orchards (Barbet-Massin & Jiguet, 2011) as well as man-made forest fires, have long shaped the Mediterranean basin's landscape (Blondel, 2010; Pausas et al., 2008). Concerning current and future anthropogenic climate change, the Mediterranean basin appears to be particularly sensitive (Giorgi, 2006; Giorgi & Lionello, 2008; IPCC, 2021). Over the last few decades, temperatures in this region have risen faster than the global average, and model projections point to future warming and low precipitations, with a likely increase in heat waves and periods of drought (Lionello et al., 2014).

The islands of the Mediterranean basin have been defined as a “*kaleidoscope of abiotic and biotic conditions*” (Médail, 2017) resulting from highly heterogeneous historical biogeographic and ecological processes (Médail, 2013), and leading to an impressive diversity of landscape and vegetation types, which constitute biodiversity “hot spots” (Médail & Myers, 2004) (Médail & Myers, 2004). The Corsica Island is the fourth largest Mediterranean Island, covering ca. 8,680 km². The island is 90 km away from Italy (Tuscany) and 170 km away from France (Côte d’Azur). Corsica is the northernmost, wettest and most mountainous of the Mediterranean islands, with many peaks over 2,000 m a.s.l. The climate is typically Mediterranean with dry summers and wet winters (annual precipitations ranging from 600 to 2,000 mm), up to alpine regions with continuous snow cover in winter and several frost days (Mouillot et al., 2008). The strong variation in topography within the island creates many different microclimates and habitats, with specific and unique vegetation communities (Heywood, 1995) from typical Mediterranean on the coast to alpine flora (Vogiatzakis et al., 2008), and with a rich composition of endemic species (Médail & Quézel, 1997).

Corsica is considered the most wooded island in the Mediterranean (Garbolino et al., 2016). Significant trends towards decreasing winter precipitation, increasing summer temperatures and

intensifying drought stress have already been observed on the island (Garbolino et al., 2016). These increasing physiological stresses raise serious concerns about the persistence of keystone species such as forest trees (Lindner et al., 2010), which have a major impact on climate and ecosystem regulation processes, providing resources, structuring ecosystems and sheltering an enormous amount of biodiversity. Indeed, Mouillot et al. (2012) showed that these shifts in climate have led to modifications in species composition, such as an increase in the dominance of shrubs over trees, which may result in an increase in vegetation flammability and more intense fire regimes (Mouillot et al., 2002; Vogiatzakis et al., 2016).

Past historical events (e.g., founder effects) resulting from the climatic fluctuations during the last glaciation have left a large and long-lasting evolutionary imprint on the Mediterranean basin biota (Conord et al., 2012; Fady & Conord, 2010), resulting in latitudinal and longitudinal gradients of genetic diversity. Island populations are expected to originate from one or more founding events from continental populations, resulting in a smaller population size linked to a lower carrying capacity than that of continental lands (Franks, 2010; Nei et al., 1975). Significant consequences are expected on their genetic composition, such as loss of genetic diversity (Chung et al., 2004; Frankham, 1997), a high level of inbreeding depression (resulting from mating between relatives) and an accumulation of moderately deleterious mutations (Diamond, 1984). Consequently, in conjunction with the impact of human activities (e.g., overexploitation, habitat destruction), the growing risk of biological invasion in response to increased disturbance (Pausas et al., 2006; Pretto et al., 2012), and past demographic events in the Mediterranean basin, Mediterranean island populations may face a higher risk of extinction (Caujapé-Castells et al., 2010; Diamond, 1984; Frankham, 1998; Médail, 2017; Veron et al., 2019).

Contemporary climate change is expected to have a major impact on island biota because it will condition the availability of suitable habitats at different altitudes or latitudes. Depending on island size, the land ruggedness and altitude, climate change can shift the climatic conditions suitable for many plant species up to hundreds of kilometres beyond the island's boundaries (Courchamp, 2014). Species unable to keep up with the movement of suitable habitats via migration may potentially survive through rapid adaptation processes, while others may become extinct (Aitken et al., 2008).

Maritime pine (*Pinus pinaster* Ait., Pinaceae) is a thermophilous conifer, with a fragmented natural range which spans the western Mediterranean basin and southern Atlantic areas, from

Northern Africa to French Brittany. This species is characterized by a strong population genetic structure resulting in different gene pools (Jaramillo-Correa et al., 2015; Theraroz et al., 2024), which potentially reflect its survival within several isolated *glacial refugia* with limited gene flow (Bucci et al., 2007; Naydenov et al., 2014).

In Corsica, maritime pine expanded across the island between 1,000 and 2,000 BC, probably due to the high frequency of fires (Carcaillet et al., 1997). Maritime pines are fire-tolerant species, due to the development of thick bark and serotinous cones whose opening is prevented up to a temperature of 70-90°C (Fernandes & Rigolot, 2007). Nowadays, it constitutes forests covering ca. 45,000 hectares (<https://corse.cnpf.fr/les-essences-forestieres>) and grows on meso-mediterranean and mountainous vegetation belts (Figure VI-1) (Médail, 2017). Maritime pine is considered a keystone species in the island, essential to the structure and functioning of the Corsican ecosystems.



Figure VI-1. Maritime pines in Corsica. *Source: S.C González-Martínez.*

However, maritime pines in Corsica are threaten by the bast scale, *Matsucoccus feytaudi* Duc., (Burban et al., 1999). This pest also weakens the tree, making it more susceptible to attack by other pests such as the trunk moth, *Dioryctria sylvestrella* (Normand, 2005). After

proliferating in south-east France, the pest was discovered in Corsica in 1994 (Jactel et al., 1996) where it is spreading and producing extensive damage (Burban et al., 1999; Jactel et al., 1996, 1998, 2006; Normand, 2005), eliminating 30% of maritime pine forests on Corsica since 2000 (UICN France 2018).

The impacts of climate change on the Corsican's Island ecosystems could represent a serious impediment to the persistence of maritime pine. Mariette et al. (2001) found this species to be characterized by low genetic diversity in the island (see also Theraroz et al., 2024), whose current changing environment may lead to further genetic depletion notably to its adaptive potential. Despite these concerns, there have been surprisingly few molecular studies in the last decade aimed at evaluating the genetic resources of maritime pine in Corsica (Derory et al., 2002; Durel & Bahrman, 1995; Hurel et al., 2021; Mariette et al., 2001; Piñeiro et al., in prep). Consequently, there is an urgent need to obtain information on the spatial patterns of genetic variation in maritime pines across the island, as well as to analyse their current and future adaptive capacities to climate change.

In this study, we sought to: 1) disentangle the spatial patterns of genetic variation across the island along clinal (i.e., altitudinal, latitudinal and longitudinal) gradients; 2) describe the fine-scale genetic structure and evaluate the patterns of genetic isolation by distance, if any; 3) gain insight about how climatic variables of biological relevance for maritime pine may explain its genetic structure; and 4) identify the adaptive variation of maritime pine to climate and model the projection of the adaptive gradient(s) across space and time in the island.

2. Materials & Methods

2.1. Plant material

Plant material was collected in the CORSAPIN common garden. The CORSAPIN common garden is a provenance-progeny test structured into 30 populations and 30 half-sib families (with around 50 half-sibs in each family, see Durel & Bahrman, 1995) and located in the Landes region. These resources were collected in Corsica by the French National Research Institute for Agriculture, Food and Environment (INRAE) during two campaigns; in 1994 by CE Durel, N

Bahrman, JM Louvet, E Bertocchi and J Brach and in 2000 by C Plomion and J Brach. The selected populations covered the entire natural range of maritime pine on the island (including the central and marginal populations), with altitudes ranging from 0 to over 1,200 m and rainfall ranging from 400 mm to almost 2,000 mm.

Needles were collected for genotyping from 355 individuals from 25 maritime populations in the CORSAPIN common garden (Table VII-S1). Sampling covered the species' range and different ecological regions in the island, specifically the three sylvoecoregions (forest ecoregions) (hereafter, SER regions: K11 Western Corsica; K12 Corsican Mountains and K13 Eastern Corsica) defined based on Corsica's relief and geology (National Forest Property Centre in Corsica, <https://corse.cnpf.fr/>) (Figure VI-2). The SER K11, in the west, is a coastal region extending up to an altitude of 1,500 m away from the coast. It is characterized by marked seasonal rainfall and a significant summer drought. It comprises vegetation from the thermo-Mediterranean, meso-Mediterranean and supra-Mediterranean levels. The SER K12 in central Corsica lies almost entirely within the "Parc Naturel Régional de Corse" (Corsican Regional Natural Park), a region made up of a mountain range peaking at over 2,000 m. The region is characterized by highly seasonal rainfall, which on average is the highest on the island on an annual basis. As a result, this region displays all the vegetation of the subalpine and alpine levels and most of the montane level, dominated by conifers and beech trees. The SER K13, to the west, extends from the coast to the foothills of the central Corsican mountains (up to an altitude of over 1,500 m). This region has a typically Mediterranean climate, marked by severe summer droughts, and hosts vegetation from the thermo-Mediterranean, meso-Mediterranean and supra-Mediterranean stages. The quality of the bedrock, composed of shale, compensates to some extent for the severe summer drought that is typical of the region (Institut National de l'information géographique et forestière; IGN, <https://inventaire-forestier.ign.fr/>).

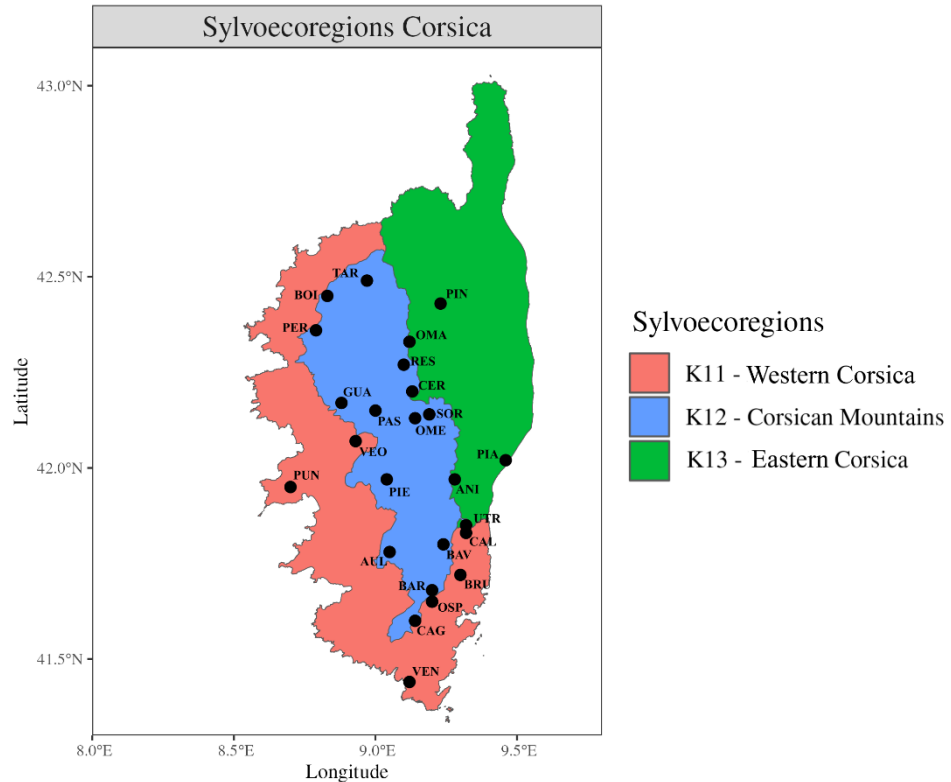


Figure VI-2. Sylvoecoregions (SERs) in Corsica.

2.2. Genotyping

DNA was extracted using the DNeasy 96 plant kit (QIAGEN, Germany), following the manufacturer's instructions. All the samples were genotyped for SNPs using the multispecies 4TREE Axiom array (Thermo Fisher Scientific, USA). For maritime pine, the 4TREE Axiom array combines SNPs identified in two previous studies: the 9 K Illumina Infinium array generated by Plomion et al. (2016) and the exome capture experiment used in Milesi et al. (2023). The new array has a conversion rate of 79% as well as 99% genotype reproducibility (based on genotyping of duplicated samples).

Apart from potentially neutral genetic polymorphisms, this array also comprises SNPs from candidate genes that showed signatures of natural selection or significant environmental associations with climate at the range-wide spatial scale, orthologs for gene families with important adaptive functions in model species, and coding regions with differential expression under biotic and abiotic stress in maritime pine (see details in Milesi et al., 2023; Plomion et al., 2016).

Only SNPs with high-quality scoring following the Best Practices Workflow implemented in the Axiom™ Analysis Suite v5.2 were selected and filtered by missing data (<30%), duplicates and monomorphic SNPs, yielding a final set of 7,313 SNPs.

2.3. Data analysis

All analyses were performed under R software, version 4.4.1.

2.3.1. Population genetic structure

Population genetic structure was assessed using R package *LEA* (see Frichot & François, 2015). This package includes the R function *snmf* that estimates individual admixture coefficients from the genotypic matrix (Frichot et al., 2014) and computes an entropy criterion that evaluates the quality of fit of the statistical model to the genotypic data by using a cross-validation technique (Frichot et al., 2014). Missing data were handled by the package. Hurel, (2019) found no population structure for 15 populations of Corsican maritime pine when tested with FastStructure from $K=1$ to $K=15$, and suggested the existence of a single gene pool on the island. In our study, we then limited the number of potential gene pools from $K=2$ to $K=5$, with ten repetitions for each K value. Nevertheless, Hurel, (2019) was also able to clearly differentiate one of the populations using a Principal Component Analysis (PCA). Therefore, we used *pcadapt* R package to detect population genetic structure based on two PCs, following Luu et al. (2017) and the associated tutorial available at (<https://bcm-uga.github.io/pcadapt/articles/pcadapt.html>). For visual representation, individual PC scores were averaged over populations and projected over PC1 and PC2.

2.3.2. Isolation by distance (IBD)

Genetic isolation by distance (IBD; Wright, 1943) was explored following Rousset, (1997), as implemented in GenePop v4.7.5 (Rousset, 2008). We used a linear regression between $F_{ST}/(1-F_{ST})$ against the logarithm of the geographic distance for all pairs of groups (i.e., populations). Minimal geographic distance was set to default value, and maximal geographic

distance was kept unrestricted. To assess significance, 10,000 permutations were performed in a Mantel test.

2.3.3. *Climatic envelope*

To better understand how climatic gradients may explain the genetic structure of maritime pine populations, we computed a climatic envelope for the Corsica Island.

Climatic data were selected because of their biological relevance to maritime pine and their contribution to explaining genetic variance across the species' range in Archambeau et al. (2024), and were extracted at the location of the populations from the Climate Downscaling Tool (Marchi et al., 2024). We extracted six climatic variables under the reference period 1901-1950, i.e., the mean annual temperature (*bio1*), the isothermality (*bio3*, the ratio of the mean diurnal temperature range to the annual temperature range), the temperature seasonality (*bio4*), the annual precipitation (*bio12*), the precipitation seasonality (*bio15*) and the summer heat moisture (*SHM*) index. To avoid multicollinearity, we removed *bio4* and *SHM* because of their high correlation (Pearson's correlation > 0.7) with *bio1*, *bio12* and *bio3*. Then, we kept *bio1*, *bio3*, *bio12* and *bio15* averaged by population as the final climatic dataset (Figure VII-S1; Table VII-S2).

Finally, to gain insight into the relative position of maritime pine populations within the island's climatic envelope, we performed a Principal Component Analysis (PCA) with the FactoMineR package, using all the climate variables extracted at island and population levels. We selected only two principal components (PCs) as they explained most of the variance (85.32%) (Figure VII-S2).

2.3.4. *Spatial patterns of genetic variation along altitudinal and latitudinal gradients*

Following Theraroz et al. (2024), we calculated four population-level genetic indicators (genetic differentiation, genetic diversity, recessive genetic load and inbreeding) that are likely to be representative of adaptive and evolutionary processes in island systems in a context of climate change (see Introduction). In a few cases where more than one stand was sampled for

a population (see Table VII-S1), genetic indicator values were averaged (Table VII-S3).

Population genetic diversity was estimated as $I-Q_{inter}$ with Q_{inter} being the observed frequencies of identical pairs of alleles among individuals within populations and then corrected for sampled size (N) using standard corrections ($N/N-1$). Population genetic differentiation (F_{ST}) was estimated for each pair of populations (pairwise- F_{ST}) and averaged over populations, from variances in allele frequencies using the unbiased estimator θ (Weir & Cockerham, 1984). Population inbreeding (F_{IS}) was estimated following Weir & Cockerham, (1984) too. All three indicators were computed using GenePop v4.7.5 (Rousset, 2008). The recessive genetic load was computed by counting different kind of mutations (annotated by SnpEff v5.1; Cingolani et al., 2012) averaged over individuals, as the number of derived moderate- (i.e., non-synonymous) and high-impact (i.e., loss of function) mutations in homozygosity divided by the number of derived low-impact (i.e., synonymous) mutations in homozygosity, following González-Martínez et al. (2017) and Piñeiro et al. (in prep.). This statistic represents the accumulation of predicted deleterious mutations in the population, normalized by the population genetic diversity, and could be linked to potential maladaptation to climate change (Table VII-S3).

To elucidate the patterns of spatial variation of these indicators along clinal gradients, we used Pearson's correlation coefficients (denoted as “ r ”).

2.3.5. *Current and future landscape of genetic adaptation to climate*

In order to predict the adaptive composition of maritime pine populations to future climatic conditions in the Corsican Island, we first identified the main climatic drivers of maritime pine adaptive variation. For that, we used the same set of climatic data as those selected for the climatic envelope (i.e., *bio1*, *bio3*, *bio12* and *bio15*; Table VII-S2). Then, we modelled the projection of the current and future adaptive gradient(s) across the landscape, following (Capblancq & Forester, 2021) influential review and associated tutorial (available at <https://github.com/Capblancq/RDA-landscape-genomics>). For further analysis, we filtered out SNPs with a minor allele frequency <5%, and estimated population allele frequencies at each of the remaining 4,394 SNPs.

2.3.6. *Partitioning of the genetic variance*

We estimated the proportion of genetic variation that can be uniquely attributed to climate (the four selected climatic variables) and geography (using population geographical coordinates, longitude and latitude) or both using RDA-based variance partitioning models implemented in the *vegan* R package and the filtered SNP dataset (Legendre & Legendre, 2012; Oksanen et al., 2001). We chose not to correct by the neutral population structure, given the absence of significant genetic structure for maritime pine in Corsica (see Figure VI-2a in Results and Figure VII-S5). As somehow expected, the pure effect of the geography was not significant (see Table VI-1 in Results); therefore, we discarded this variable for further analysis.

2.3.7. *Identifying SNPs potentially involved in climate adaptation*

We identified the main climatic drivers of maritime pine adaptive variation using the Redundancy Analysis (RDA) method, a gene-environment association (GEA) approach based on multivariate linear regressions (Fitzpatrick et al., 2021; Forester et al., 2018). The RDA-based GEA method is a constrained ordination method that models linear relationships among climatic predictors and genotypic information (i.e., SNPs), effectively identifying covarying loci associated with the multivariate climatic predictors (Capblancq et al., 2018; Capblancq & Forester, 2021).

We used population allele frequencies for the 4,394 filtered loci with $MAF > 5\%$ as response variables and the four selected climatic variables as predictors. Prior to GEA analysis, missing values were imputed using the most common genotype in the dataset. GEAs were estimated based on the average climate over the period 1901-1950 to capture the climatic conditions under which the populations may have evolved.

We identified outlier SNPs by estimating the Mahalanobis distances between each locus and the centre of the RDA space along the significant axes (K) (Capblancq et al., 2018). We used the first and the third axes ($K = 2$) which explained most of the genetic variance associated with the predictors (Figure VII-S3). We further selected outlier SNPs with extreme Mahalanobis distances based on a False Discovery Rate (FDR) threshold of 5% (François et al., 2016).

2.3.8. *Landscape of adaptive genetic variation to climate*

We performed a second RDA using the candidate adaptive markers (outlier loci) identified above and the same set of selected climate variables as explanatory variables to calculate an “adaptively enriched genetic space” (Capblancq & Forester, 2021). This adaptively enriched space will allow us to identify the climatic variables that are the most correlated with putatively climate adaptive genetic variation (Capblancq & Forester, 2021).

We then computed a genetic-based adaptive index, which allow us to extrapolate and predict the turnover of adaptive genetic variation across the species’ climatic landscape, following Steane et al. (2014):

$$\text{Adaptive index} = \sum_{i=1}^n a_i b_i$$

where a is the loading (climatic variable score) along the selected first axis of the adaptively enriched RDA, b is the standardized value of this variable at the focal pixel and i refers to one of the n different climatic variables used to build the RDA model. Other axis of the enriched RDA explained very low proportions of the variance and were not included in this analysis (see Figure VI-5a).

These loadings represent how each predictor (climatic variables) affect the adaptive genetic variation along the RDA axis, either in terms of magnitude or direction (Capblancq & Forester, 2021; Steane et al., 2014). Adaptive indices were estimated for each raster cell of the island and represent the adaptive genetic similarity or difference of all pixels on the landscape as a function of the values of the climatic predictors at that location. When projected on a map it allows visualizing the turnover of different adaptive genetic gradients across a species range (Capblancq & Forester, 2021).

2.3.9. *Future adaptive composition*

The predictions for maritime pine adaptive composition computed above were used to investigate the potential mismatch between their current distribution and that expected in future decades under projected climate conditions.

For future climates, we extracted climate predictions at the scale of the whole island, for the period 2041-2070 under the shared socio-economic pathway (SSP) 3.7-0 and from five GCMs, namely GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0 and UKESM1-0-LL, following Archambeau et al. (2024). To allow comparison between current and future climates, the values of future climate variables were normalized using the same standardization parameters (i.e., mean and standard deviation) used previously for current climate variables (see Breed et al., 2019; Capblancq & Forester, 2021; Hoste et al., 2024).

The computation of the future adaptive genetic index was similar to that of the current adaptive index, described above; we used the first-axis scores of the enriched RDA and the standardized future climate values at the focal pixel level to gain insight into the distribution of maritime pine adaptive composition under projected climate.

2.3.10. Characterization of climate adaptive outsiders

Finally, we extrapolated and plotted the distribution of adaptive genetic composition (first axis RDA scores) calculated for each cell in the study area (i.e., along the island's climatic range) for current and future climates. The range of values representing 99% of the current adaptive composition was considered to be the current climatic range of the adaptive gradient. We then identified all future values outside this range as “outsiders” (Hoste et al., 2024) (Figure S4). Outsiders represent predicted climatic conditions for those locations that have not been encountered by maritime pine in its current range on the island. We therefore decided not to infer the impact of climate on the adaptive genetic composition of maritime pine for these specific climatic conditions, as they were outside the training space of our model (Hoste et al., 2023).

3. Results

3.1. Population genetic structure and IBD

As expected, we did not find any significant population structure in the Corsican maritime pine populations (Figure VII-S5). However, the PCA calculated with *pcadapt*, although explaining

very little of the variance (2.7%), enabled us to identify three genetic clusters as well as a few isolated populations (Figure VI-3a). The first cluster was composed of Tartajine (TAR), Bonifatu (BON) and Peticato (PER). A second cluster was composed of Utriolu (UTR), Bruscaju (BRU) and Calzatoju (CAL). Finally, we observed a third cluster composed of Cagna (CAG), Barocaggio (BAR) and Ospedale (OSP). Ventilegne (VEN) and Pinia (PIA) were the most differentiated populations.

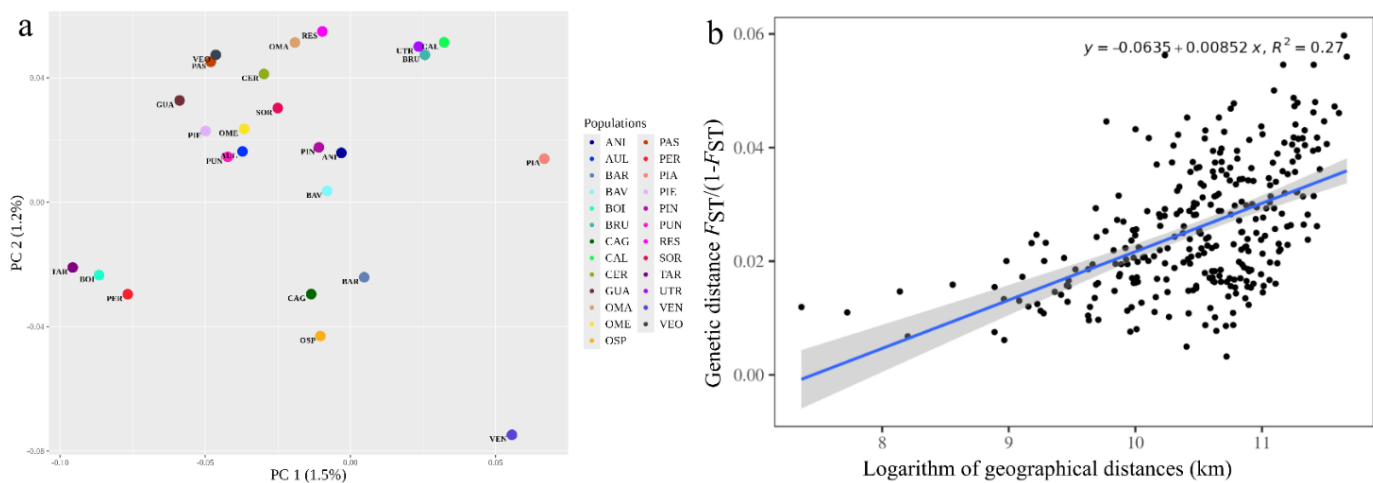


Figure VI-3. a) PCA depicting PC1 (1.5 % of explained variance) vs. PC2 (1.2 %) in the genetic structure analysis of Corsican maritime pine populations. b) Isolation by distance (IBD) pattern in maritime pine from Corsica. Regression of genetic differentiation estimated by $F_{ST}/(1 - F_{ST})$ against logarithm of geographical distances (km) for all pairs of sampled populations.

Finally, genetic differentiation between pairs of populations increased significantly with geographical distance ($r^2 = 0.27$), indicating a significant IBD pattern (see Figure VI-3b).

3.2. Climatic envelope

The PCA conducted on climatic variables showed that PC1 was driven by *bio1* (mean annual temperature) and *bio3* (isothermality). PC2 was driven by *bio12* (annual precipitation) and *bio15* (precipitation seasonality) (Figure VII-S2). The PCA distinguishes three climate groups (coloured circles in the figure) containing 84% of our populations, and four populations characterized by marginal climates (Ventilegne - VEN, Pinia - PIA, Pineto - PIN and Punta - PUN) (Figure VI-4). The “purple” climate group was characterized by high isothermality (i.e.,

lower variation in temperature throughout the year) as well as low precipitation seasonality (i.e., regular precipitation level throughout the year) (Figure VI-4). The blue climate group was characterized by a colder, wetter climate, with Guagno (GUA) and Vero (VEO) being the populations experiencing the island's wettest climate and with Cagna (CAG) characterized by high precipitation seasonality (Table VII-S2). The yellow climate group was characterized by a drier and hotter climate (Figure VI-4).

PIN was the population with the lowest precipitation seasonality on the island. VEN was characterized by the warmest and driest climate on the island, followed to a lesser extent by PIA. Finally, PUN was located in a climate with the most irregular distribution of rainfall along the year (Table VII-S2, Figure VI-4).

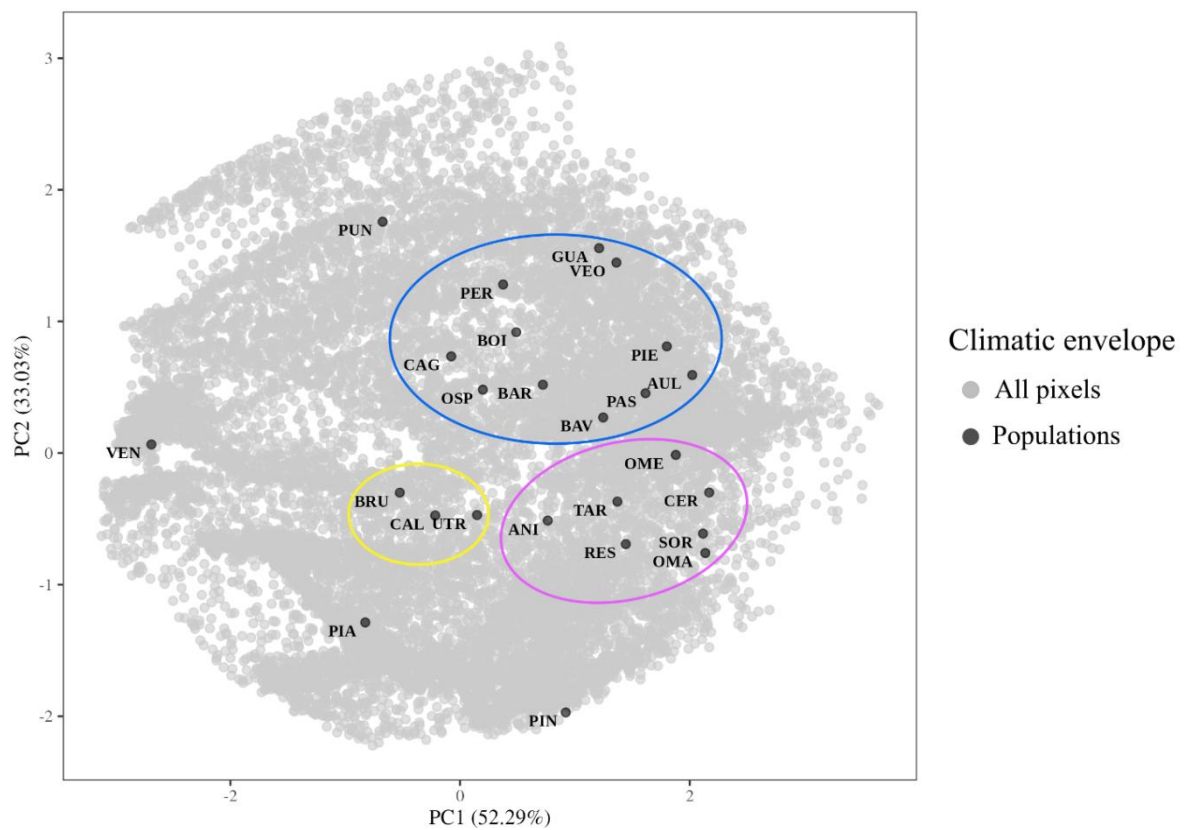


Figure VI-4. Climatic envelope of maritime pine in Corsica. Projection of climatic values extracted for the whole island (grey dots) and location in the climatic space of each of the populations (black dots).

3.3. Genetic indicators and geographical gradients

Overall, we observed little variation in the population genetic indicators (genetic diversity, pairwise- F_{ST} , F_{IS} and recessive genetic load) across the island (Figure VI-5). For genetic diversity, minimum and maximum values were found for Bruscaju (BRU) (0.194) and Tartagine (TAR) (0.227), respectively (Figure VI-5a). Pairwise- F_{ST} (averaged over populations) gave similar results for most populations (Figure VI-5b). The most genetically differentiated populations on the island were Ventilegne (VEN) (average pairwise- F_{ST} = 0.04) and Bonifatu (BOI) (average pairwise- F_{ST} = 0.038), followed to a lesser extent by Pinia (PIA) (average pairwise- F_{ST} = 0.034) and Tartagine (TAR) (average pairwise- F_{ST} = 0.035). The least differentiated populations were Sorba (SOR) (average pairwise- F_{ST} = 0.015), followed by Punta (PUN) (average pairwise- F_{ST} = 0.017) (Figure VI-5b). Corsican maritime pines were characterized by low inbreeding, with values ranging from F_{IS} = 0.11 to F_{IS} = 0.10, for Perticato (PER) and SOR, respectively (Figure VI-5c). Finally, we found a low level of variation for the recessive genetic load across the island as well, with minimum and maximum values in Pineta (PIE) (0.419) and Omenino (OME) (0.478), respectively (Figure VI-5d). Moreover, PIA (0.469) and VEN (0.468) exhibited some of the highest recessive genetic load values of the island (Figure VI-5d).

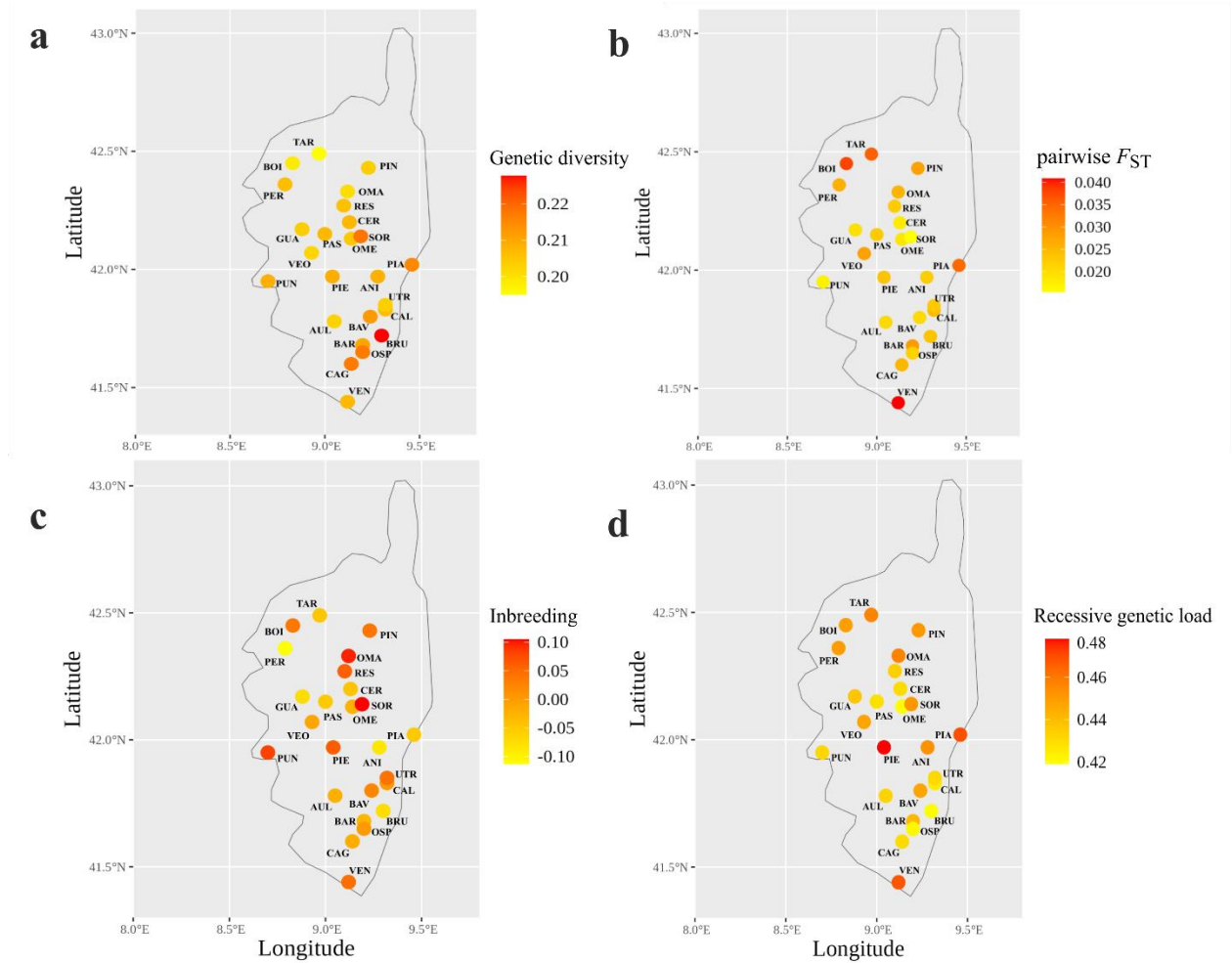


Figure VI-5. Spatial distribution of genetic indicators across the island. a) Genetic diversity, b) genetic differentiation, c) inbreeding and d) recessive genetic load.

Genetic diversity was significantly negatively correlated with the latitude ($r = -0.58$) and significantly positively correlated with the longitude ($r = 0.45$) (Figure VI-S6). Pairwise- F_{ST} was significantly negatively correlated with the altitude ($r = -0.49$) (Figure VII-S6). No significant correlation was found between inbreeding and recessive genetic load with any of the geographical gradients (Figure VII-S6).

3.4. Current and future landscape of genetic adaptation to climate

3.4.1. Partitioning of the genetic variance

Together, climate and geography explained 31% of the total genetic variance for maritime pine in Corsica (Table VI-1). The pure effect of climate was significant even when controlling for

geography (p -value = 0.02) and explained 18% of total genetic variation (58% of the variation explained by the full model), suggesting association between genetic variation and climatic gradients (Table VI-1). In contrast, the pure effect of geography accounted for 9% of total genetic variance (28% of the variation explained by the full model), but the model was not significant (p -value = 0.13) (Table VI-1).

Table VI-1. Decomposition of the effects of climate (i.e., clim.), geography (i.e., geo.) or both, on genetic variation using redundancy analyses. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, not significant.

RDA models	% of explained variance (R ²)	% of relative explained variance	Adjusted R ² (%)	p -value
Full model: F ~ clim. + geog.	31	1	8	0.001***
Pure climate: F ~ clim. (geog)	18	58	3	0.015**
Pure geography: F ~ geog. (clim)	9	28	1.3	0.119 ^{ns}
Confounded climate/geography	4	14		
Total unexplained	69			

3.4.2. Identifying SNPs potentially involved in climate adaptation

The first axis, accounting for 3.72% of the variation, was primarily associated with annual precipitations (*bio 12*) and temperature (*bio 1*), while the third axis (2.03%) was driven by the precipitation seasonality (*bio 15*) and the isothermality (*bio 3*). We identified 30 loci showing extreme association with these two major axes of variation (Figure VII-S3).

3.4.3. Landscape of adaptive genetic variation to climate

Most of the variation was aggregated in the first axis of the adaptive enriched space (RDA1, 12.9%), which was associated with variation in temperature (*bio1* and *bio3*), and precipitation (*bio12*) (Figure VI-6a). Pinia (PIA) and Ventilegne (VEN) exhibited adaptive genetic variation for climates characterized by the hottest temperatures, while Utriolu (UTR), Calzatoju (CAL) and Bruscaju (BRU) exhibited adaptive genetic variation for dry climates, and the rest of the populations exhibited adaptive genetic variation for climates characterized by higher annual

precipitation and warmer, temperate climates (Figure VI-6a). The second axis, RDA2, was not significantly associated with any climatic predictor (Figure VI-6a) and was not retained for the extrapolation of the adaptive genetic turnover across the island (Figure VI-6b).

Extrapolation of the adaptive genetic turnover associated with the island's drivers of adaptive variation showed how RDA1 differentiated between areas of low altitude (positive scores) and high altitude (negative scores) (Figure VI-6b).

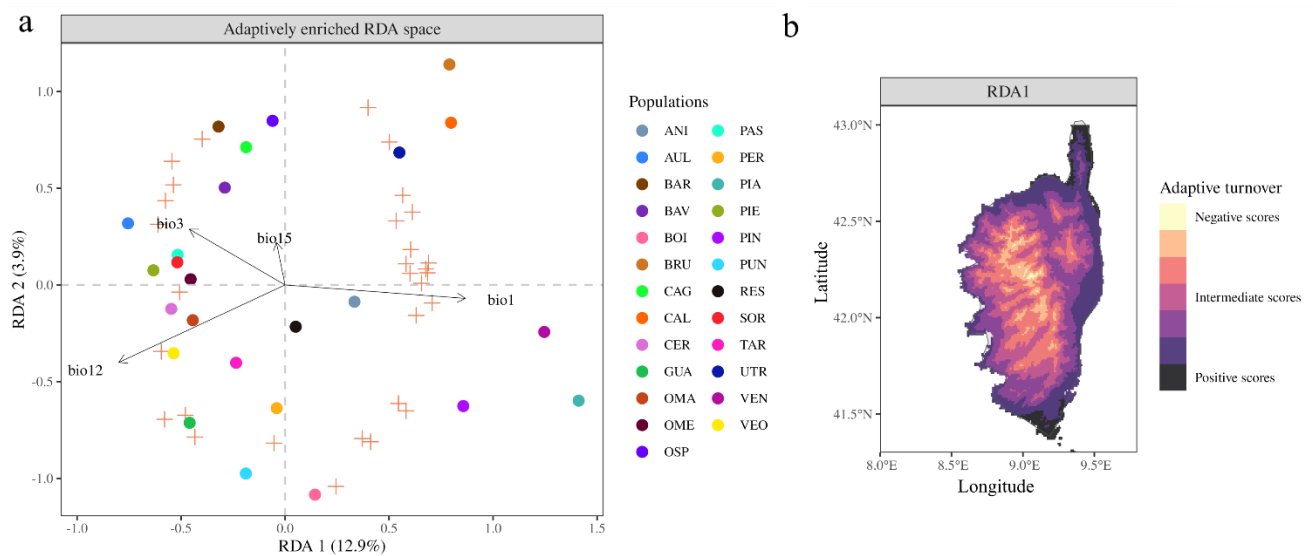


Figure VI-6. Maritime pine adaptive landscape with a) being the adaptively enriched genetic space showing association between potentially adaptive loci (orange crosses) with climatic drivers of adaptation, and the position of the populations (coloured dots) and b) being the spatial projection of adaptive genetic turnover across the island.

3.4.4. Future adaptive composition

Extrapolation of the adaptive genetic composition (enriched RDA1 scores) for current climate showed that areas of low altitude (i.e., coastal) characterized by hot and dry climates had the highest adaptive values (Figure VI-7a). Contrarily, high elevation localities (characterized by low temperatures throughout the year and increased annual precipitations) exhibited the lowest adaptive values in the current adaptive gradient (current adaptive RDA space) (Figure VI-7a). Interestingly, the future adaptive gradient (future adaptive RDA space) showed that, overall, all localities on the island of Corsica will experience an increase in adaptive values for maritime pine (Figure VI-7b). This observation is particularly true in areas where adaptive values are currently low, such as high-altitude localities. Finally, the comparison of predictions for current and future climate allowed us to identify the current climatic range of the adaptive gradient (the range of values representing 99% of the current adaptive composition) and the “outsiders” (i.e., the future values outside this range) (Figure VII-S4). This analysis showed a significant proportion (19%) of cells falling outside the current climatic range in the future, in particular in coastal locations, indicating locations whose climatic conditions have not been encountered by maritime pine in its current range on the island (Figure VI-7).

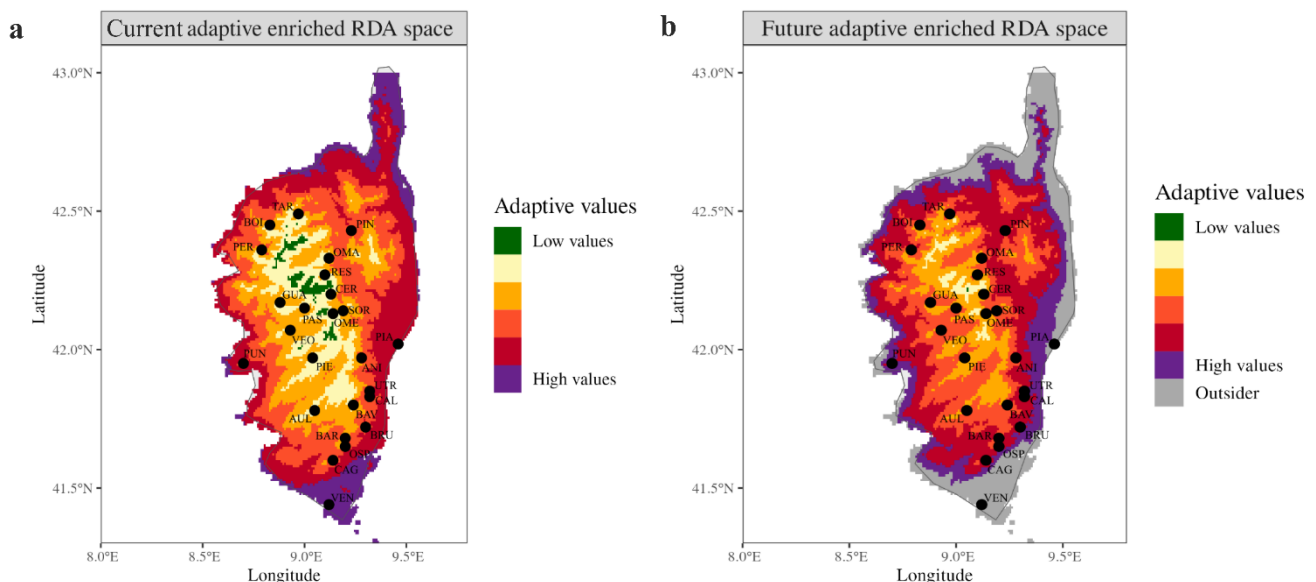


Figure VI-7. Projection of the predicted a) current and b) future adaptive compositions in Corsica. Colours represent the range of adaptive values as well as ‘outsiders’, and black dots represent populations.

3. Discussion

3.1. Low population genetic structure but significant impact of climate

We found no significant population structure, suggesting that maritime pines in Corsica form a single gene pool. Our results concur with those of Hurel (2019), Jaramillo-Correa et al. (2015) and Kerdelhué et al. (2014) who identified a single gene pool in Corsica using microsatellites (SSRs) and a high number of SNPs, respectively. However, although explaining a very low part of the variance (1.5% for PC1 and 1.2% for PC2), whose proportion of variance explained is comparable to that of Hurel et al. (2019), we identified three differentiated population clusters, as well as two isolated populations with the principal component analysis.

Tartagine (TAR), Bonifatu (BOI) and Perticato (PER) formed the first genetic group. These populations were located in the northwestern part of the sylvo-ecoregion (SER) K12 (Corsican mountains). However, they were not characterized by the same climate. TAR, despite peaking at the highest altitude of the three populations (960 m a.s.l.), was characterized by isothermality and low precipitation seasonality. BOI and PER were located at a lower altitude (440 m a.s.l. and 360 m a.s.l., respectively) and were characterized by a colder and wetter climate.

On the southeastern coast, Utriolu (UTR), Bruscaju (BRU) and Calzatoju (CAL) and, further south, Cagne (CAG), Barocaggio (BAR) and Ospedale (OSP) formed two different genetic and climatic groups. CAG, BAR and OSP were characterized by a cold and humid climate. The latter populations were located at high altitudes (1,040 m a.s.l., 950 m a.s.l. and 800 m a.s.l., respectively) and belonged also to SER K12, a region characterized by high annual precipitation and subalpine and montane vegetation. UTR, BRU and CAL were located at medium altitude (405 m a.s.l., 300 m a.s.l. and 130 m a.s.l., respectively) and were characterized by a warmer, drier climate. Although situated on the southeastern coast, these populations are assigned to SER K11 (Western Corsica), characterized by a dry, warm climate that fluctuates with altitude and marked by severe summer droughts and low water availability due to crystalline soils.

Ventilegne (VEN) and, to a lesser extent, Pinia (PIA), were the most differentiated populations on the island, as revealed by the PCA and highlighted by the pairwise- F_{ST} estimates. Interestingly, Hurel et al. (2019) found a similar genetic differentiation for VEN, but not for PIA. The climatic envelope revealed that these two populations had a very marginal climate,

being the hottest and driest on the island. Despite being assigned to different SERs (VEN to SER K11 and PIA to SER K13), both are characterized by severe summer droughts. In addition, VEN was the southernmost population in our data set. This population was judged extreme by Durel & Bahrman (1995), because it was established “on a swampy soil” and exhibited “stunted trees”. PIA is a coastal population, located on the eastern coast of the island and it has the particularity of growing on the beach. PIA has been described by Durel & Bahrman, (1995) as a population in “a very special situation”. Currently, this population is affected by an outbreak of the pest *Matsucoccus feytaudi* Duc., which feeds exclusively on maritime pine. The first infestation of *Matsucoccus feytaudi* on the island was found at Pineto (PIN) in the northeastern mountains (Jactel et al., 1994), and has since spread throughout Corsica, causing considerable damage (Figure VI-8).



Figure VI-8. Maritime pine population a) Pinia (PIN) on sandy soil on the east coast of Corsica, b) dying forest and c), d) bark damage resulting from the combined weakening of the tree by the pest *Matsucoccus feytaudi* e) and the trunk borer *Dioryctria sylvestrella* which feeds on weakened trees. After hatching, the moth penetrates the inner zones of the bast and bores a gallery in which it feeds until autumn. This penetration is accompanied by an abundant secretion of resin c), d). Source: a) corseorientale.com, b) [S.C González-Martínez](#), c) chemindazur.org, d) forestal.cat, e) ephytia.inra

Interestingly, Pineto (PIN) as well as La Punta (PUN) in the southwestern coast were characterized by marginal climates, according to the climatic envelope (low precipitation seasonality for PIN and high precipitation seasonality for PUN), but were not identified as genetically distinct by the principal component analysis. Durel & Bahrman (1995) pointed out

that the PUN was devastated by fire. The island of Corsica is known to be subject to fires that have shaped plant succession at least since the Holocene (Carcaillet et al., 1997; Durel & Bahrman, 1995). The high frequency of fires on the island has created a favourable environment for the regeneration and expansion of maritime pine to the detriment of *Pinus nigra* ssp. *laricio* (herein *Pinus laricio*) (Carcaillet et al., 1997; Pimont et al., 2011).

Our results show significant isolation as a function of distance between maritime pine populations, indicating a reduction in gene flow as the geographical distance between populations increases. This result highlights that the island's specific orography (rugged topography) may have contributed to the emergence of genetically differentiated groups or populations (albeit weakly) that adapted locally and evolved in partial isolation in response to a contrasting climate. Our results are in line with those of Mariette et al. (2001), who hypothesized a reduction in gene flow between maritime pine populations to explain the species' genetic differentiation pattern on the island. As additional example, Mosca et al. (2014) and found that environment-driven selection, together with geographical isolation potentially due to rugged topography, may promote genetic adaptation for *Larix decidua* and *Abies alba* in Alpine ecosystems as well as for *Quercus longinux* in Taiwan, respectively.

3.2. The impact of geography in explaining the distribution of maritime pine genetic resources in Corsica

We observed a significant decrease in genetic diversity with increased latitude as well as a significant increase of genetic diversity with increasing longitudes. Bruscaju (BRU), located on the southeast coast, had the highest genetic diversity, while Tartagine (TAR), the island's northernmost population located in the west coast, had the lowest.

Latitudinal patterns of genetic diversity have been detected for some plant species (Hewitt, 1999; Petit et al., 2003), but are not generally widespread in plants. Hirao et al. (2017) and Kim et al. (2011) found a similar trend of decreasing genetic diversity with latitude for western white pine (*Pinus monticola*) and a widespread arctic-alpine plant (*Dryas octopetala*), respectively. In a Mediterranean environment, Fady & Conord, (2010) found a similar latitudinal trend for plant species in the Mediterranean basin, but it was not detectable if only gymnosperms or angiosperms were considered. In a more global context, De Kort et al. (2021) detected no significant latitudinal change in genetic diversity for plants across their range (including pine

species). In contrast, longitudinal clinal patterns on the distribution of genetic diversity in forest trees is reported in the literature. Fady & Conord, (2010) found a significant decrease in genetic diversity from east to west for gymnosperm species in the Mediterranean basin. Moreover, Conord et al. (2012) found similar longitudinal patterns of genetic diversity for a wide range of continental plant and animal species, but not for island species.

The latitudinal and longitudinal patterns of genetic variation across the island may be due to ancient historical events in the establishment of populations in the Mediterranean basin after the LGM (Hewitt, 2004). On a broader scale, south-to-north recolonization pathways and their significant role as structuring patterns of genetic diversity have been widely accepted for many European species, including species from the Mediterranean basin (Davis & Shaw, 2001; Petit et al., 2003). On a more regional scale, the island of Corsica may have undergone similar phylogeographic processes. During the Messinian Salinity Crisis, founding events from the Italian peninsula may have taken precedence over founding events from the Iberian Peninsula (which were probably two important *glacial refugia* for maritime pine during the LGM; Petit et al., 2003; Salvador et al., 2000) due to the proximity of the Italian peninsula to Corsica.

Interestingly, we found no significant correlation between genetic diversity and altitude within the island, unlike genetic differentiation, which was negatively related to altitude. This result suggests that elevation favours gene flow while coastal populations, often found in isolated valleys, are more genetically differentiated than high-altitude populations. Indeed, Ventilegne (VEN), the most southerly and genetically differentiated population was located on the coast (50 m a.s.l.), and Sorba (SOR), the least genetically differentiated population was located at the island's highest altitude (1,040 m a.s.l.). Corsica is characterized by steep altitudinal gradients, with strong environmental variation over short distances (temperature decreases by about 5.5°C per kilometre with altitude) (Körner, 2007). In fact, this species currently spreads at medium and high altitudes, where it may replace *Pinus laricio* (Häusser et al., 2019), resulting in more effective connectivity at these elevations.

Similarly to the latitudinal patterns of genetic diversity described above, altitudinal patterns of genetic differentiation are not widespread among forest tree species. Low genetic differentiation has been found along altitudinal gradients for European larch (*Larix decidua* Miller; Nardin et al., 2015) and sessile oak (*Quercus petraea*; Alberto et al., 2011), as well as for the Canary Island pine (*Pinus canariensis*; Navascués et al., 2008). This lack of differentiation with altitude may be explained by stepping-stone gene flow following tree

phenology along the altitudinal gradient (Navascués et al., 2008; Schuster et al., 1989). However, Kurt et al. (2012) found significant genetic differentiation with altitude for the Turkish red pine (*Pinus brutia* Ten.), as well as Castilla et al. (2016) for a Neotropical tree (*Miconia affinis*).

The level of genetic differentiation between populations is determined by the homogenizing action of gene flow against processes such as different adaptive responses to environmental conditions and genetic drift, which generate genetic differentiation (Bradburd et al., 2013). In our study, it should be noted that only four populations (i.e., Ventilegne - VEN, Bonifatu - BOI, Tartagine - TAR and Pinia - PIA, see Results) were characterized as having some level of genetic differentiation. These populations may exhibit highly specific genetic variation resulting from an adaptive response to extreme abiotic (e.g., temperature and summer drought for VEN and PIA, and highly specific locations in coastal sandy soil for PIA and swampy soil for VEN) and biotic (e.g., current *Matsucoccus feytaudi* infestation for PIA) pressures. In addition, VEN and PIA had some of the highest levels of recessive genetic load on the island, indicative of an accumulation of deleterious variants. It may be the result of their potentially small effective population size (Kimura & Ohta, 1969) and low genetic connectivity (Sachdeva et al., 2022). BOI and TAR may also be subject to extreme biotic or abiotic pressures that were not detected during sampling.

Altogether, we can hypothesize that the joint impact of demographic history and past climatic events, together with current higher connectivity at medium-high altitude, seem to play a major role in explaining the population genetic structure of maritime pine, as well as the distribution of its genetic resources. Furthermore, recurrent forest fires and significant anthropogenic impact (long-term deforestation and human-induced forest fires; Pausas et al., 2008; Vendramin et al., 1998) may contribute significantly to the formation of a heterogeneous, discontinuous forest, and may also have an impact on its genetic composition, a hypothesis worthy testing in future studies.

3.3. Current distribution of climate-associated SNP outliers and prediction for future climates

Exploring the effect of climate and geography on genetic variation in maritime pine, we found evidence of association between genetic variation and climate (18% of total genetic variation was explained by climate), indicating potential climate-related local adaptation for this species in Corsica. In this line, we identified 30 loci potentially involved in climate adaptation (“outliers”), driven by precipitation (i.e., annual precipitation and precipitation seasonality) and temperature (i.e., mean annual temperature and isothermality). These results support those of the climate envelope, which shows that temperature, isothermality and precipitation are important factors in the distribution of maritime pine on the island (Abad Viñas et al., 2016). Indeed, Condit et al. (1995) demonstrated that these climatic variables are critical for plant survival and both ecological (Walter, 2018) and evolutionary (Donoghue, 2008) theory suggest that temperature and precipitation are major determinants of plant traits at a global scale.

Maritime pine is an ecologically versatile tree. This thermophile species grows in areas characterized by average annual temperatures above 10°C and highly variable annual precipitation from 400 to 1,300 mm (Abad Viñas et al., 2016; Alía et al., 2009). Several studies highlighted the role of temperature and precipitation as important adaptive drivers in maritime pine across its range (Archambeau et al., 2024; Benito Garzón et al., 2011; Jaramillo-Correa et al., 2015; Wahid et al., 2006). For example, Jaramillo-Correa et al. (2015) found evidence of local adaptation to temperature and precipitation for this species, showing that the extreme climatic conditions (hot and dry) experienced by maritime pines in a common garden were strongly linked to the frequency of locally advantageous loci.

In addition, studies aimed at disentangling the drivers of genetic variation often found a high degree of collinearity between climatic and geographic gradients in widespread forest trees, preventing them to separate their relative effect (Capblancq & Forester, 2021). In our study, we detected a moderate (14%) correlation between climatic and geographic gradients, indicating that 14% of the variance was confounded between these factors. In comparison, Capblancq & Forester (2021) for lodgepole pine and Archambeau et al. (2024) for maritime pine, found that 48% and 50.5% of the genetic variance not be uniquely attributed to neutral genetic structure, geography or climate. This result highlights the difficulty to disentangle the environment from past demographic processes (Capblancq & Forester, 2021) and reflects, albeit to a moderate extent, the joint impact of past climates and demography in explaining the

current genetic variation of maritime pine in Corsica.

The projection of the genetic-based adaptive index across the landscape allowed us to visualize the spatial gradients of adaptive genetic turnover (i.e., change in adaptive allele frequency). The turnover of adaptive genetic variation was mainly driven by the annual temperature, isothermality and annual precipitation, as shown by the adaptive enriched space. The adaptive gradient differentiates low altitude (coastal) from high altitude (mountainous) populations. This result shows that the association between maritime pine genetic variation with temperature and precipitation factors is triggered by more complex environmental factors related to altitude, which is consistent with the island's altitudinal profile (Figure VI-9). Altitudinal gradients significantly influence numerous features of the physical environment, such as temperature, atmospheric pressure, moisture, radiation, wind and geology (Körner, 2007). In maritime pine, for example, Archambeau et al. (2023) found that the association of quantitative genetic variation (early growth in height) with climate (temperature of coldest month) was altitude-driven at large geographical scales.

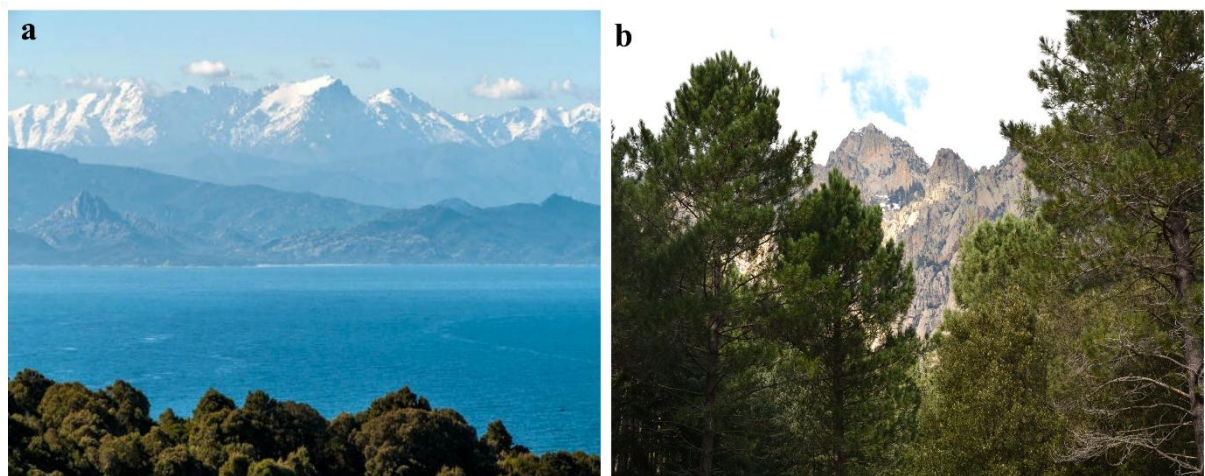


Figure VI-9. Specific orography of the Corsica Island: a) from coast to mountains, b) maritime pines at high altitude on the island. *Source: a) istockphoto.com, b) S.C González-Martínez.*

The projection of current and future adaptive composition as well as ‘outsiders’ (i.e., localities for which no insight into the future adaptive composition could be predicted) across the island made it possible to evaluate the impact of climate change on local adaptation for maritime pine in Corsica. The estimation of outsiders can improve our understanding of the extent to which future climate may be beyond the current adaptive range. In the future climate of Corsica (2041-2070, according to the SSP 3.7-0 scenario), we identified a significant part of

the island (19%) that will experience new climate, in response to predicted future increases in temperature and reductions in precipitation. This finding raises concerns about the short-term adaptation potential of coastal maritime pines in Corsica. Indeed, as an island, if the coastal populations are unable to migrate upwards, the possibilities of migrating to more suitable climates are limited.

To my knowledge, very few studies in the literature have identified ‘outsider’ localities for future adaptation. Hoste et al. (2024) delineated adaptive genetic units and projected the optimal distribution of these adaptive groups in the future for the northern chamois (*Rupicapra rupicapra*) in the European Alps. The authors identified ‘outsider’ adaptive units, defined as environmental conditions predicted for these locations that have not been encountered by the northern chamois in its current range. However, the authors did not give the relative proportion of ‘outsider’ units with respect to the current climatic range of the adaptive gradient. Francisco, (2023) examined the potential vulnerability to climate change of a mountain butterfly, the Apollo (*Parnassius apollo*), and found that 7.9% of its predicted adaptive composition in future climates was outside the current adaptive range of the climatic gradient. However, we do not have similar analyses for widespread forest trees to make solid comparisons with the proportion of ‘outsiders’ identified for maritime pine in Corsica.

Current and future projections of the adaptive composition of maritime pine across the island have revealed that this species is currently genetically well adapted to coastal localities (warm, dry climate) compared to high-altitude localities (cold and wet climate). Our future predictions clearly indicate that maritime pine will be genetically well adapted to higher altitudes. Maritime pines are currently spreading into forests previously dominated by *P. laricio* and are now overlapping in a broad elevation belt ranging from ca. 600-1,300 m a.s.l. (Zaghi, 2008). *P. laricio* is more water-demanding and vulnerable to fire than maritime pines (Pimont et al., 2011); as water availability is predicted to decline in future climate, the lower limit of the distribution range of *P. laricio* might move further upwards, further limiting the species’ distribution. Together with our genomic-based predictions, current demographic trends suggest that maritime pine might substitute *P. laricio* in the next decade (Häusser et al., 2019; Pimont, 2011). Conversely, at lower altitudes on the coast, our model predicts a shift in climatic conditions towards new conditions not currently encountered by the species on the island, and therefore beyond its currently occupied adaptive space. Facing the likely intensification of xerophilous conditions in these areas, forests and shrublands of *Quercus ilex* L. and *Rhamnus*

alaternus L. are expected to regress while other species such as *Pistacia lentiscus* L. and *Phillyrea angustifolia* L. may benefit from and a higher degree of openness and new climatic conditions (Garbolino et al., 2016). These predictions may increase the occurrence of fires in these areas (Garbolino et al., 2016), which could severely endanger the survival of maritime pine in the face of climate change. From the perspective of conservation of genetic resources, Ventilegne (VEN) and Pinia (PIA) (and to a lesser extent, Punta - PUN) may be particularly concerned given their coastal location. Even if we are unable to predict the relationship between adaptive variability and future climatic conditions for these populations, we can still point out that VEN and PIA showed high adaptive variation for temperature, underlining their potential for local adaptation to extremely hot and dry climates. Moreover, Archambeau et al. (2024) studied the change in allele frequencies required to maintain current gene-climate relationships under climate change (i.e., genomic offset) for range-wide maritime populations (including two Corsican populations, PIA and Pineta - PIE) and validated the predictions using mortality data from common garden experiments. The authors showed that Corsican populations were not predicted to be at risk of future climatic maladaptation, which might indicate that their current adaptive composition could be sufficient to maintain gene-climate relationships under climate change (especially towards an increase in temperature), at least for the period and scenarios considered.

4. Conclusion

Although our models can explore the distribution of current maritime adaptive composition along the studied area and predict its potential future disruption, our predictions are climate-limited. The future of maritime pine will depend not only on how the species adapts to changing climatic conditions, but also on competitive interactions (with conspecific or other species), human activities, the type of soil encountered during seedling establishment, as well as disease and pest epidemics (especially *Matsucoccus feytaudi* for Corsica). Besides, SNPs-environment correlations can only point to a (small) part of the real drivers of local selection and adaptation and miss the identification of other covarying factors (Jaramillo-Correa et al., 2015). Therefore, we suggest that a more integrative approach, including competition indices and soil types in GEA as well as phenotypic traits measured in common gardens, should provide us with valuable information on the driving forces underlying adaptive genetic variation of maritime pine in Corsica, and allow us to predict current and future adaptive composition more accurately.

5. Data availability

The data underlying this study will be made public and accessible to all on Data INRAE and scripts will be available on GitHub.

6. Acknowledgements

We thank Carmen García-Barriga, Francisco Auñón, Eduardo Ballester, Diana Barba, Maria Regina Chambel, Fernando Del-Caño and Rodrigo Pulido-Sanz for their contribution to genetic data production.

VII. Supplementary information – Chapter 3

1. The data

1.1. The populations features

Table VII-S1. Geographical location and sample size (N) of the 25 populations of *P. pinaster* included in the study; Abb.: Abbreviated population name.

Population	Abb.	N	Latitude (°)	Longitude (°)	Altitude (m)
Ania	ANI	12	41.97	9.28	630
Aullene	AUL	16	41.78	9.05	1105
Barocaggio	BAR	12	41.68	9.2	950
Bavella	BAV	16	41.8	9.24	1020
Bonifatu	BOI	16	42.45	8.83	440
Bruscaju	BRU	12	41.72	9.3	300
Cagna	CAG	12	41.6	9.14	1040
Calzatoju	CAL	12	41.83	9.32	130
Cervelio	CER	11	42.2	9.13	795
Guagno	GUA	12	42.17	8.88	500
Ominda	OMA	12	42.33	9.12	890
Omenino	OME	12	42.13	9.14	1080
Ospedale	OSP	9	41.65	9.2	800
Pastricciola	PAS	16	42.15	9	700
Perticato	PER	10	42.36	8.79	360
Pinia	PIA, stand1	13	42.02	9.46	10
	PIA, stand2	16	42.02	9.46	10
Pineta	PIE, stand1	10	41.97	9.04	750
	PIE, stand2	16	41.97	9.04	750
Pineto	PIN	12	42.43	9.23	365
Punta	PUN	12	41.95	8.7	650
Restonica	RES	16	42.27	9.1	700
Sorba	SOR	16	42.14	9.19	1040
Tartagine	TAR	12	42.49	8.97	960
Utriolu	UTR	12	41.85	9.32	405
Ventilegne	VEN	16	41.44	9.12	50
Vero	VEO	16	42.07	8.93	57

1.2. The climatic variables extracted for each population

Table VII-S2. Standardized climate variables extracted for the reference period 1901-1950 averaged over populations (*bio1*: mean annual temperature; *bio3*: isothermality; *bio12*: annual precipitation; *bio15*: precipitation seasonality). This set of climate variables was used to calculate the climate envelope and the current landscape of genetic adaptation to climate.

Population	bio1	bio3	bio12	bio15
ANI	0.32	0.3	-0.34	-0.65
AUL	-1.08	0.92	0.87	0.05
BAR	-0.44	0.05	-0.21	0.84
BAV	-0.4	0.58	0.16	0.18
BOI	0.92	-0.57	1.16	0.18
BRU	1.39	0.03	-1.33	0.71
CAG	-0.23	-0.88	-0.57	1.37
CAL	1.34	0.24	-1.11	0.24
CER	-1.34	0.92	0.38	-1.02
GUA	0.19	-0.09	1.83	0.64
OMA	-1.51	0.86	-0.04	-1.42
OME	-0.91	0.84	0.46	-0.59
OSP	0.02	-0.27	-0.51	1.04
PAS	-0.74	0.58	0.62	0.01
PER	0.75	-0.65	1.11	0.81
PIA	1.85	-0.76	-1.48	-0.95
PIE	-0.66	0.72	1.11	0.18
PIN	0.41	0.6	-1.1	-2.31
PUN	0.28	-2.47	0.6	1.67
RES	-0.36	0.68	-0.12	-1.15
SOR	-1.55	0.94	-0.07	-1.12
TAR	-0.91	0.09	-0.05	-0.85
UTR	0.79	0.26	-0.95	0.05
VEN	1.9	-3.08	-2.05	1.41
VEO	-0.02	0.18	1.64	0.68

1.3. The population-level genetic indicators

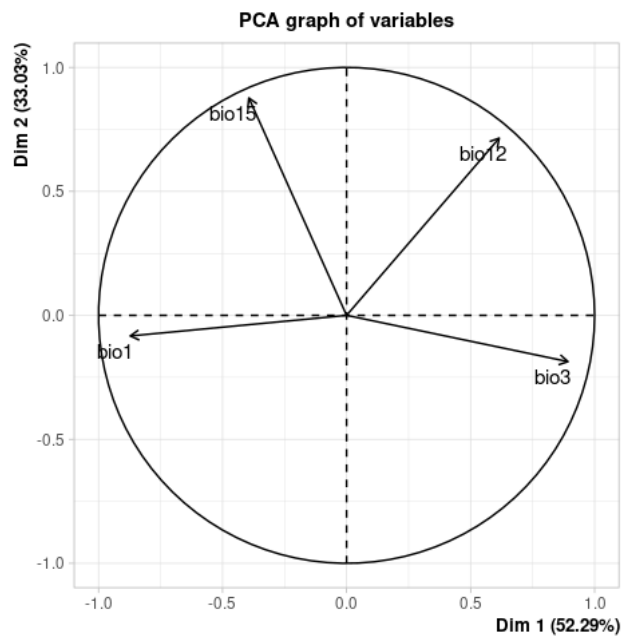
Table VII-S3. Genetic indicators for each of the 25 populations of *Pinus pinaster* included in the study. Values for stands within populations were averaged (see Table S1). Genetic diversity: genetic diversity estimated as $1-Q_{inter}$ using all SNPs and corrected for sample size (see main text for details); F_{IS} : population inbreeding; F_{ST} : population genetic differentiation; Recessive genetic load: number of predicted deleterious mutations in homozygosity standardized by synonymous mutations.

Population	Genetic diversity	F_{IS}	F_{ST}	Recessive genetic load
ANI	0.209	-0.084	0.022	0.453
AUL	0.203	-0.022	0.021	0.433
BAR	0.21	-0.027	0.029	0.441
BAV	0.212	0.024	0.02	0.447
BOI	0.198	0.038	0.038	0.449
BRU	0.228	-0.074	0.024	0.419
CAG	0.217	-0.018	0.025	0.43
CAL	0.206	0.004	0.025	0.425
CER	0.208	-0.044	0.018	0.43
GUA	0.204	-0.073	0.02	0.437
OMA	0.201	0.098	0.026	0.457
OME	0.205	-0.024	0.019	0.419
OSP	0.217	0.003	0.022	0.421
PAS	0.207	-0.051	0.023	0.429
PER	0.206	-0.113	0.026	0.45
PIA	0.215	-0.05	0.035	0.47
PIE	0.209	0.063	0.024	0.478
PIN	0.204	0.041	0.028	0.451
PUN	0.209	0.082	0.017	0.432
RES	0.206	0.06	0.022	0.434
SOR	0.218	0.105	0.015	0.451
TAR	0.195	-0.047	0.036	0.457
UTR	0.204	0.043	0.023	0.431
VEN	0.207	0.048	0.041	0.468
VEO	0.202	-0.009	0.028	0.447

2. The results

2.1. Correlogram and PCA of all climatic variables

Figure VII-S1. Pairwise correlogram based on Pearson's correlation coefficients between all standardized climatic variables (*bio1*: mean annual temperature; *bio3*: isothermality; *bio4*: temperature seasonality; *bio12*: annual precipitation; *bio15*: precipitation seasonality; *SHM*: summer heat moisture index). Blank cells represent non-significant coefficients using *p-values* at 5% significance level.



2.2. Redundancy Analysis (RDA)

2.2.1. Gene-environment association RDA biplot

Figure VII-S3. Results of the gene-environment association using redundancy analysis (RDA): projection of climatic variables, neutral (in grey) and outlier loci (in purple) into the two axis (RDA1 and RDA3) that explained most of the variance in the genetic RDA space.

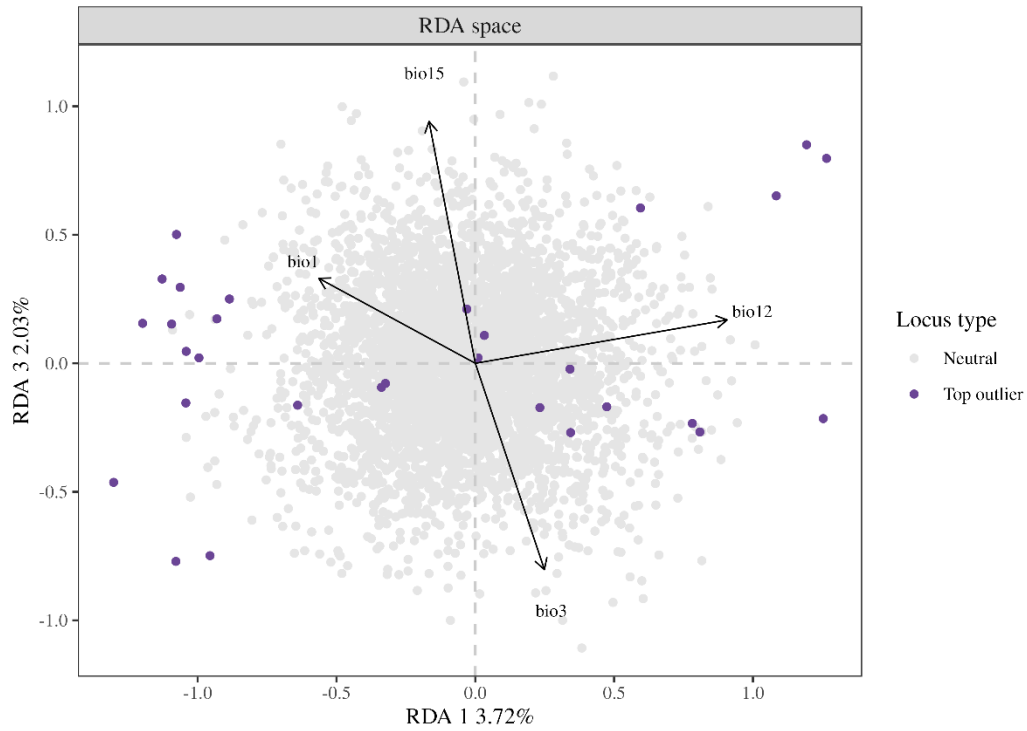
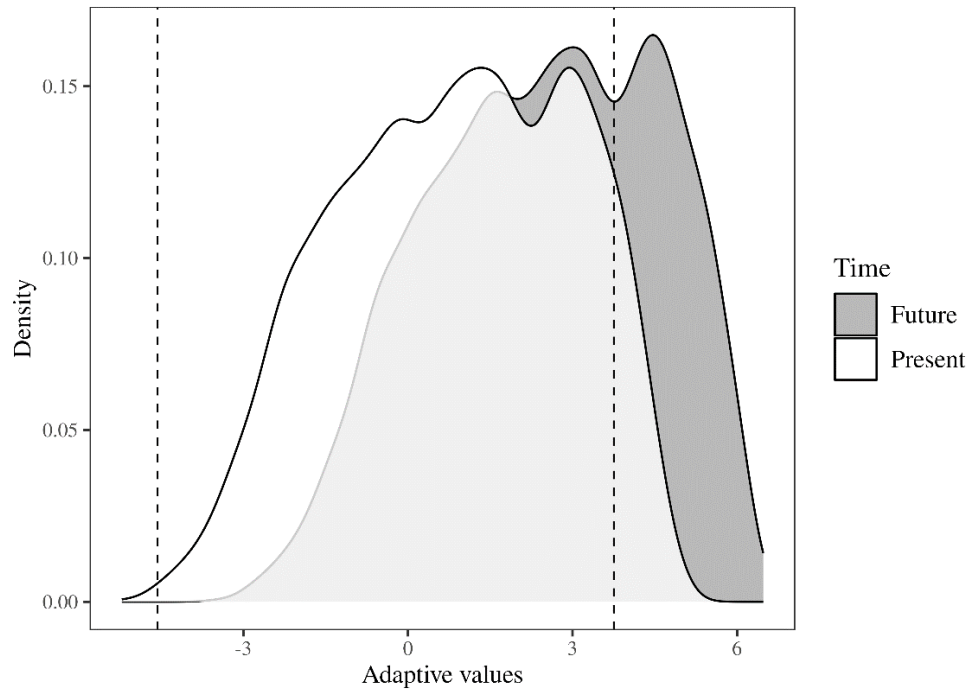
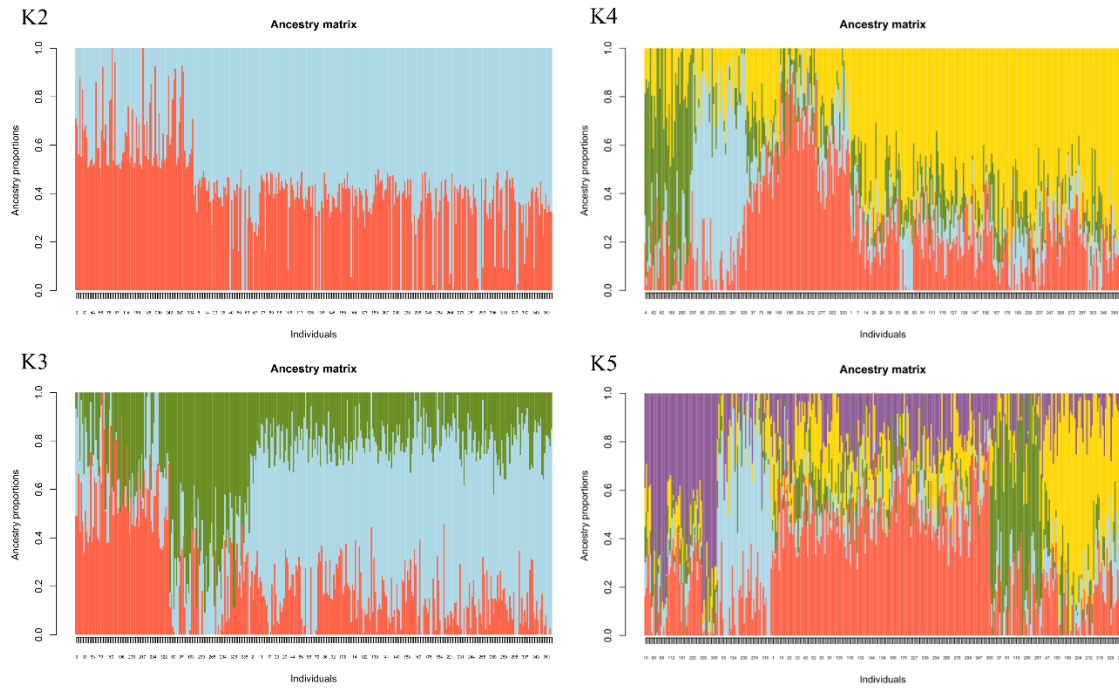


Figure VII-S4. Distribution of adaptive genetic composition (RDA1 scores) calculated for each cell in the study area (i.e., along the island's climatic range) for current (white) and future (grey) climates. The dotted lines represent the range of values where 99% of the current adaptive composition is present and is considered as the current climatic range of the adaptive gradient.



2.3. The genetic structure

Figure VII-S5. Barplot representation of ancestry coefficients obtained from LEA for $K=1$ to $K=5$ for the computation of maritime pine population structure in Corsica.



2.4. The correlations among genetic indicators

Figure VII-S6. Pairwise correlogram based on Pearson's correlation coefficients between genetic indicators (F_{IS} : population inbreeding; pairwise F_{ST} : population genetic differentiation; Recessive GL: recessive genetic load) and geographical variables (latitude, longitude and altitude). Blank cells represent non-significant coefficients using p -values at 5% significance level.



VIII. Synthesis & Discussion

1. Molecular imprints of past demographic events at regional and range-wide scales

The spatial distribution of genetic variation across the range of a species is determined by the interplay of genetic drift, gene flow, mutation, and natural selection as well as anthropogenic activities, which fluctuate from historical times to present day (Brown, 1984; Holt, 2003; Slatkin, 1987). A current challenge in population and conservation genetics is to disentangle the relative effects of these processes, as a first step in predicting population response to environmental change. In this PhD, the spatial patterns of current genetic variation in maritime pine were studied along ecological and geographical gradients of marginality throughout the full maritime pine range (Chapter 1) and along clinal gradients at the regional scale in the island of Corsica, characterised by a specific orography and constituting valuable genetic resources for the species (Chapter 3).

At range-wide scale, we showed a trend towards decreasing genetic diversity and increasing genetic differentiation in geographically and demo-historically marginal populations (particularly in isolated populations on the southern margins) (Chapter 1), while at the regional scale we showed an increase in genetic diversity towards the south-eastern margins of the species' range (Chapter 3). Furthermore, contrary to the trends observed in Chapter 1, genetic differentiation did not follow any latitudinal trend towards the margins and was negatively associated with the altitude at the regional scale (Chapter 3). Consequently, the conclusion drawn in Chapter 1 suggesting that the processes underlying the spatial distribution of genetic diversity and differentiation in maritime pine may have operated in a similar way at both regional and range scales is called into question.

Post-glacial recolonisation and past climatic events during the Pleistocene are likely to have left significant imprints on the current spatial distribution of genetic diversity and differentiation within the ranges of forest tree species (Cheddadi et al., 2006; Hoban et al., 2010; Huntley et al., 2023; Petit et al., 2003), and it has been hypothesised to explain the spatial patterns of genetic diversity and differentiation of maritime pine across its range (Jaramillo-Correa et al., 2015; Bucci et al., 2007; Naydenov et al., 2014) (Chapter 1). Hewitt (1999) and Petit et al.

(2003) have highlighted the north-south pattern of genetic diversity for several woody angiosperm taxa across Europe but the authors underlined the difficulties to draw general conclusions from these patterns (Petit et al., 2003; Westergren et al., 2018 for *Picea abies* and Hoban et al., 2010 for *Juglans cinerea* L. in North America), suggesting that other factors than global past demo-historical processes may have shaped current genetic resources of forest trees.

We have shown in Chapter 1 the genetic proximity between the Corsican and North-East (made up of Italian and South-East French populations) gene pools, which corroborates the hypothesis of an Italian origin for the colonisation of maritime pine on the island of Corsica during the Messinian salinity crisis (Naydenov et al., 2014), and supports the west-to-east pattern of genetic diversity on the island (Chapter 3).

Chapter 1 provides relevant information on the spatial distribution of maritime pine genetic variation across its range as a function of ecological and geographical marginality, but we must bear in mind that it reflects both past demo-historical and ecological events. Past historical events have been shown to have the most important impact in explaining spatial patterns of genetic variation in widespread species (Hoban et al., 2010; Pironon et al., 2015) (Chapter 1). However, Chapter 3 revealed that other interrelated and potentially more recent processes than demo-historical ones, combined with the specificity of an island system, may have significantly shaped the current distribution of genetic diversity and differentiation patterns of Corsican maritime pines. Among them, restricted gene flow (i.e., specific orography and wind regimes originating from the Mediterranean Sea), the occurrence and severity of fires, human impact and biotic invasions (*Matsucoccus feytaudi*) may have been important drivers of current maritime pine genetic variation in Corsica, and may have mitigated to some extent the imprint of more global historical events. Furthermore, although not detected by our models in Chapter 1, we showed in Chapter 3 that the (albeit weak) genetic differentiation of maritime pine populations in Corsica may have been maintained to some extent by current habitat and climatic marginality, given that the most of the genetically differentiated Corsican populations were located in marginal habitats and climatic conditions.

Overall, we suggest that current spatial patterns of genetic diversity and differentiation in maritime pine at range-wide (Chapter 1) and regional scales in the Mediterranean basin (Chapter 3) may reflect the action of contrasting global demo-historical and climatic fluctuations. However, at finer spatial scales, we also suggest that more recent biotic,

anthropogenic or climatic events may have had a special importance in shaping current maritime genetic diversity and differentiation, as exemplified by our study in Corsica (Chapter 3), an island system with specific environment characteristics that may have dimmed, to some extent, the overall demo-historical patterns.

2. Evidence of climate adaptation in maritime pine at regional and range-wide scales

At a time when the climate is changing at an unprecedented rate, there is an urgent need to shed light on the factors that have historically shaped the current adaptive responses of forest trees populations and to clarify whether there is consistency at local and range-wide scales (Chapter 1, Chapter 3). Our ability to integrate current adaptive polymorphisms into predictive models could be decisive in better assessing the adaptive response of natural maritime pine populations under future climates (Chapter 1, Chapter 3). On the one hand, it has enabled us to gain a better understanding of which populations exhibit sufficient adaptive variation to perhaps have the potential to adapt in the short-term (Chapter 3) and, on the other hand, it helped to predict whether they are likely to maintain their gene-environment relationships or undergo maladaptation in future climates (Chapter 1). In addition, selection gradient analyses in two contrasted populations provided a better understanding of the real-time drivers of natural selection for maritime pine and allowed us to glimpse, to some extent, the patterns of ongoing local adaptation in such long-lived outcrossing species (Chapter 2).

2.1. Long-term past adaptation vs. real-time natural selection

Past climate fluctuations may have played major roles in influencing the adaptive potential of species through several bouts of climate-driven selection. During species range shifts in response to Quaternary climatic oscillations, local conditions may have acted as sieves, potentially sorting standing genetic variation unequally across the space (Guerrero & Hahn, 2017; Luqman et al., 2023). Maritime pine current geographic range is the outcome of a long history of range shifts from glacial refugia into new environments divergent from the ancestral habitat. Local adaptation (i.e., the selective sieving of genotypes across the landscape) implies

that populations inhabiting different areas of the species range may carry different genotypes and hence respond differently to changes in climate (Jump et al., 2006; Luqman et al., 2023).

We identified a set of putatively climate-adaptive alleles in maritime pine using different GEA methods potentially related to temperature (Chapter 1, Chapter 3) and precipitation (Chapter 3) at range-wide and regional scale, respectively. Our results are consistent with several studies in the literature that have found various outlier loci related to drought response in maritime pine at both range-wide and local spatial scales (Archambeau et al., 2024; Budde et al., 2024; Eveno et al., 2008; Grivet et al., 2011; Jaramillo-Correa et al., 2015; Scotti et al., 2023). Moreover, these climatic variables were also found as the main environmental constraints driving broadleaves and conifers tree species' distributions (e.g., *Fagus sylvatica*, Capblancq et al., 2023; and widespread Mediterranean species such as, *Pinus pinea* L., *Pinus halepensis* Mill and *Quercus ilex* L., Altieri et al., 2024).

The stronger importance of precipitation in driving maritime pine adaptive variation in the Corsica Island (Chapter 3) compared to the rest of the range (Chapter 1) tend to concur with Jaramillo-Correa et al. (2015) and Benito Garzón et al. (2011), who found contrasted regional patterns of adaptive variation between maritime pine populations in response to environmental heterogeneity. Corsican maritime pines are growing under highly contrasted environments following a steep temperature/precipitation gradient mainly driven by the altitude. In the island, we evidenced patterns of altitude-driven local adaptation, where potentially adaptive alleles related to precipitation may be beneficial to high elevation localities, while alleles related to temperature may be beneficial at lower altitudes and coastal localities (Chapter 3), which was not detected at the range-wide scale (Chapter 1).

In addition to the evidence for drought-related (i.e., temperature and precipitation) adaptive variation in maritime pine resulting from historical drivers of local adaptation (Chapter 1, Chapter 3), we found drought-related traits to be the targets of current population-level selection in both Mediterranean and Atlantic environments (Chapter 2) and showed that trees with higher drought tolerance are likely to confer a higher probability of efficient reproduction in the latter environment (Chapter 2). Drought tolerance has been shown to be a focal trait for future local adaptation of other tree species, such as Douglas-fir in North America (Bradley St Clair & Howe, 2007), and *Quercus* spp. (*Q. suber* in the Iberian Peninsula, Ramírez-Valiente et al., 2009; *Q. petraea*, *Q. pubescens* and *Q. robur* in Switzerland, Rellstab et al., 2016). However, a concerning result in the face of predicted increased drought is the trend towards stabilising

selection for resistance to cavitation (P_{50}) in the Mediterranean environment, together with strong selection for growth-related traits. Under increasing drought events and severity, Santos-del-Blanco et al. (2013) showed that, for Aleppo pine within the Mediterranean basin, growth plasticity (i.e., the capacity to display a high growth rate in good climatic conditions and a low growth rate in drought conditions) can be considered a very favourable trait, especially in dry and variable environments. I propose that trees with increased growth and reduced variance in P_{50} may be vulnerable to the predicted increase in drought in the Mediterranean due to climate change (Lindner et al., 2010).

Our results suggest that past climatic fluctuations, potentially acting in concert with historical range shifts, may have selected maritime pine genotypes along a gradient of temperature (Chapter 1) and precipitation, driven at the regional scale of the island of Corsica by steep altitudinal patterns (Chapter 3). This result highlights that past selective forces may have operated differently within a geographically discrete area (Jaramillo-Correa et al., 2015; Luqman et al., 2023). One has to keep in mind that these spatial patterns and drivers of adaptive variation represent the accumulation of adaptive polymorphisms resulting from past-climate selection, while the contemporary patterns of selection reflected in selection gradient analyses represent a snapshot of real-time selection in time and space. Our results show that past climatic fluctuations (Chapter 1, Chapter 3) may have resulted in similar climate-adaptive responses, to some extent, to the current drivers of selection in contrasting environments (Chapter 2). Moreover, we can highlight that current population adaptive responses (Chapter 2) not only reflect the complex and overlapping action of past selective pressures (Chapter 1, Chapter 3), but also shows the role of the current biotic environment (i.e., competition) in modulating the adaptive drivers and responses of maritime pine in the wild.

2.2. Future (mal)adaptation to changing climate

Under projected future climate scenarios, rising temperatures and reduced precipitation are likely to increase episodes of severe drought across maritime pine's range. The Mediterranean region is already experiencing intense and prolonged droughts (Peñuelas & Sardans, 2021) and could be particularly vulnerable to global change (Giorgi & Lionello, 2008). Salazar-Tortosa et al. (2024) showed that by 2070, most pine species (58%, including maritime pine) could face major reductions in habitat suitability, potentially leading to range losses and reduced species

richness particularly in the Mediterranean basin, raising serious concerns about the survival of maritime pine in this region. In this PhD thesis, I combined different genomic methods to gain insight into the spatial patterns of current and future adaptive genetic turnover and the potential for climate maladaptation in maritime pine at two different spatial scales, from the Mediterranean basin to the Atlantic coasts.

In the Mediterranean basin, our genomics-based predictions show that maritime pines currently appear to be genetically well adapted overall (Chapter 3), showing potential for short-term adaptation to projected climates (i.e., 2070) (Chapter 3). We did not detect strong climate maladaptation (Chapter 1), except for certain populations in the southern Mediterranean in specific environments (i.e., on the island of Pantelleria and on a promontory near the Straits of Gibraltar) (Chapter 1), which will be discussed in the next section. Temperature seasonality was the most important predictor contributing to the genetic turnover in genomic offset estimates and showed a steep slope between -2°C and 0°C . Increase in temperature seasonality results from amplified warming of summer temperatures compared to that of winter temperatures (Lee et al., 2021) and may be indicative of a loss of heat tolerance in populations characterized by a slight increase in exposure to warmer summer temperatures. Throughout the Mediterranean basin, maritime pines are showing some evidence of pre-adaptation to warmer climates, as shown in section 2.1, which may dampen, to some extent their vulnerability to the predicted warmer and drier climates.

High potential climate maladaptation was found for populations located in the Iberian Atlantic and French Atlantic coasts (Chapter 1), while the short-term adaptive potential for Corsican coastal localities remains uncertain (Chapter 3). Archambeau et al. (2024) found similar results, with a higher risk of maladaptation for maritime pine populations located in northwestern Iberian Peninsula and northern Brittany (France). The authors showed that the genomic offset predictions were positively associated with mortality rates in common gardens and natural populations (French and Spanish National Forest Inventories), thereby validating their results and suggesting that genomic offset predictions may be indicative of future fitness declines in maritime pine (Archambeau et al., 2024). Benito Garzón et al. (2011) also found low drought tolerance in maritime pine populations in the Atlantic Iberian Peninsula. This pattern has also been observed for *Quercus suber*, a broadleaf species widely distributed in the Mediterranean basin, where northern Iberian populations have been detected as being more vulnerable to climate change (Fréjaville et al., 2020). These results therefore suggest that

maritime pine in these localities may exhibit more climate adaptive variation related to colder and wetter climates than drought adaptive variants, leading to a strong disruption of current gene-environment relationships towards predicted warmer climates (Archambeau et al., 2024). Furthermore, our results indicate that local adaptation could also be detrimental to survival under future climates for populations that have evolved in response to local stressors other than increased drought and temperature (Benito Garzón et al., 2011; Frank et al., 2017).

Caution should be exercised when interpreting genomic offset (Chapter 1) and RDA-based adaptive turnover (Chapter 3) predictions. The limitations associated with these methods have already been discussed extensively in the literature, in particular for the genomic offset (Ahrens et al., 2023; Archambeau et al., 2024; Hoffmann et al., 2021; Lotterhos, 2024; Rellstab et al., 2021; and see Capblancq et al., 2018 and Capblancq & Forester, 2021 for RDA-based predictions) and I will only mention here the arguments that we consider to be particularly relevant to the interpretation of our predictions for maritime pine. The genomic offset calculation assumes that forest tree populations respond to environmental changes through non-adaptive processes. But the vulnerability of a population also depends on dynamic processes, such as the contribution of phenotypic plasticity, gene flow and adaptive potential, which are not integrated in the genomic offset approach (Foden et al., 2019). Therefore, under global warming, gene flow from southern populations locally adapted to warmer and drier environments may increase the fitness of northern populations living in colder and wetter environments by sharing adaptive drought-related allelic variants (Fréjaville et al., 2020), thus mitigating to some extent the predicted maladaptation of maritime pine in the northern parts of their range. Bontrager & Angert, (2019) showed that gene flow from core populations increases fitness in cold margin populations in an annual wildflower (*Clarkia pulchella*) and Isaac-Renton et al. (2018) highlighted that the introduction of pre-adapted alleles to warmer climates in cold margin populations of lodgepole pine may mitigate their physiological maladaptation to drought.

2.3. But what about marginal populations?

Marginal populations are expected to inhabit environments close to their physiological and ecological limits, and to exhibit low effective population size. They should therefore be more vulnerable to climate change due to limited gene flow and connectivity, leading to increased

drift and depauperate genetic diversity (Hampe & Petit, 2005; Eckert et al., 2008, Kawecki et al., 2008, see Section 2.1 and Chapter 1). Empirical evidence of adaptation lags in marginal populations in response to increased warming and droughts has recently been shown in European tree species (*Pinus nigra*, *Pinus pinea*, *Fagus sylvatica* and *Pinus pinaster* in Fréjaville et al., 2020; Leites & Benito Garzón, 2023), as well as in annual plants (e.g., *Arabidopsis lyrata*, Heblack et al., 2024).

In this PhD thesis, marginal populations were identified using different methods: quantitative indices aimed at distinguishing the geographical and climatic margins (Chapter 1), expert knowledge and a climatic envelope enabling us to locate climatically marginal populations in the landscape (Chapter 3). Geographically marginal populations at the southern edge of maritime pine range had low levels of overall and climate-associated genetic diversity (Chapter 1). In Corsica (Chapter 3), the most isolated and marginal populations in terms of climate and habitats, Ventilegne (VEN) and Pinia (PIA) (i.e., a southernmost coastal population and the population at lowest elevation, respectively) and, to a lesser extent, Pineto (PIN) (i.e., the population with lowest rainfall seasonality), displayed adaptive variation mostly associated with temperature on the island. No particularly high levels of potential future maladaptation, as shown by genomic-based methods, were observed for populations characterised by geographical marginality (Chapter 1), but no insight into the potential for short-term adaptation to future climates could be obtained for populations characterised by a marginal climate in Corsica (Chapter 3). To a lesser extent, Point-Cires (PCI, located on a promontory near the Straits of Gibraltar) and Pantelleria (PAN, located on the island of Pantelleria) showed moderate levels of predicted maladaptation to future climates (Chapter 1).

Given the arguments regarding the limitations of genomic offset (and related) predictions presented in section 2.2, these results should be interpreted with caution. Indeed, marginal populations have specific genetic features (e.g., small effective population size and restricted gene flow) that are not taken into account when modelling their potential for climate maladaptation. The geographically marginal populations in Chapter 1 showed low overall and climate-associated genetic diversity, in contrast to the climatically marginal populations in Chapter 3, whose adaptive variation was significantly linked to temperature. Despite the expected low vulnerability for future climates, geographically marginal populations may harbour locally reduced but regionally rare adaptive variations in response to strong selective pressures and on which selection may act (Chhatre et al., 2019), although not detected in our

study (Chapter 1). Therefore, I can hypothesise that, if past climate constituted strong selective pressures, rare and potentially climate-adaptive variants may allow them to adapt, to some extent, to predicted future climates. Moreover, maritime pine is already at its ecological limit in large parts of its southern range, and it is uncertain whether this species can cope with environments that will quickly become more arid in the near future (Alberto et al., 2013; Jaramillo-Correa et al., 2015). Fréjaville et al. (2020) evaluated the range-wide patterns of tree height variation in response to climate change for European trees, and found that the southern and warm margins showed the highest adaptation lags to either temperature or precipitation in future climate. Furthermore, northward migration for southernmost marginal populations (Chapter 1) will be challenged by the barrier created by the Mediterranean Sea, while populations inhabiting climatically marginal environments in Corsica may migrate to more suitable habitats at higher altitudes (Chapter 3).

Theory on the evolution of range limits predicts that gene flow from core populations may help adaptation at range margins by enhancing (potentially adaptive) genetic diversity and by reducing inbreeding depression (Antonovics, 1976; Kirkpatrick & Barton, 1997). However, Kottler et al. (2021) found little evidence of these positive effects of gene flow on population fitness at the range edge. Fréjaville et al. (2020) found that gene flow from core populations was maladaptive for European forest trees at the edge of their warm range. Sexton et al. (2011) drew similar conclusions for an annual plant, *Mimulus laciniatus*, where gene flow from the core to the warm edge was maladaptive by delaying development time, but the authors showed that gene flow could also improve fitness when taking place between populations at the same range limit (de Lafontaine et al., 2018; Morente-López et al., 2021). Finally, we found that marginal populations of maritime pine did not only have average levels of inbreeding but also that they had reduced genetic load (Chapter 1).

Overall, I can hypothesise that the geographically marginal populations of maritime pine at the warmer edge may be, at some extent, more vulnerable to climate change than core populations, but, as shown in the regional case study of Corsica, this may not be necessarily the case and more detailed population-specific and regional studies are needed.

3. Towards a conservation strategy for maritime pine

In this last section, I discuss the practical implications of our research on maritime pine genetic resources, adaptive potential and contemporary selection pressures, with a view to develop genomic-informed strategies for the conservation and appropriate management of this key species, in particular considering its fragmented range.

3.1. The risks of relying on single metrics

Millar et al. (2007) suggested that, regarding management approaches for forest trees “*no single solution fits all future challenges, especially in the context of changing climates, and the best strategy is to mix different approaches for different situations.*” This tenet also applies to how we use genetic information in order to build appropriate and integrative management strategies (Fady et al., 2020; Rodríguez-Quilón et al., 2016).

Genetic information is considered essential to assess the conservation status of populations (Laikre et al., 2020) and to design suitable strategies for the management and conservation of genetic resources (Aitken & Whitlock, 2013; Andrello et al., 2022; Fady et al., 2016). Climate change will cause multiple challenges for the conservation and management of forest genetic resources, notably under the assumption that future environments will be different from present without knowing with certainty about the specificity, the magnitude and the outcome of these changes (Millar et al., 2007). More specifically, the uncertainty regarding the magnitude of the change at different spatial scales makes difficult the development of appropriate forestry policy (Fady et al., 2016). For example, we showed that, function of their position within geographic (i.e., core *vs.* margins, Chapter 1; latitude and longitude, Chapter 3) or climatic ranges (i.e., Mediterranean *vs.* Atlantic) (Chapter 1 & Chapter 2), populations are not expected to experience climate change impact in a similar way (see also Hampe & Petit, 2005).

The development of genomic data has offered opportunities to characterise genetic resources with multiple analyses and metrics gauging for different processes, from classical Wright’s *F*-statistics to multivariate and predictive analyses, such as those in landscape genomics. In this PhD thesis, the assessment of overall genetic diversity (in the form of a heterozygosity metric) showed that it is not randomly distributed and that it varies according to

the geographical position of the population (peripherality) (Chapter 1) and clinal gradients (Chapter 3) at different spatial scales. While this metric has allowed us to detect populations with low or high levels of genetic diversity, giving some (rough) indication of its evolutionary potential, it does not allow us to assess the underlying processes responsible for its variability across the landscape (e.g., the role of inbreeding depression removing detrimental alleles) (Leroy et al., 2018). The use of this metric alone does not allow to distinguish between neutral and adaptive components of genetic diversity either, and therefore to gain better insights on maritime pine adaptive and evolutionary potential in the face of climate change in order to develop sound and comprehensive management guidelines.

The combination of standard population-genetic metrics with more complex genomic approaches such as landscape genomics allowed us to uncover spatial patterns of adaptive variation resulting from adaptive processes that are not detected by traditional population genomic approaches (Rellstab et al., 2015). Landscape genomics simultaneously examine the effects of demographic history, migration, and selection by combining information on the phenotype, the genotype, and the local environment of large numbers of geo-spatially referenced samples collected across the landscape (Rellstab et al., 2015; Sun et al., 2024). With these approaches, we evidenced that populations expected to be the most maladapted to future climates showed also high levels of climate-adaptive genetic diversity (Chapter 1). We hypothesised these populations to be potentially less vulnerable to climate change than peripheral populations, which exhibited the lowest levels of potentially climate-adaptive genetic diversity, although no significant maladaptation was detected (Chapter 1). Furthermore, we could demonstrate that climate was the main driver of maritime pine adaptive variation at range-wide and regional scales (Chapter 1 & Chapter 3) (see Rellstab et al., 2019 for a similar pattern for *Pinus cembra*), therefore highlighting the importance of past-climatic conditions in shaping maritime pine adaptive processes. However, the development of precise management and conservation guidelines relies not only on predictions of the extent to which climate change may impact neutral and adaptive genetic resources, but also on the investigation of the real-time drivers and targets of contemporary selection that may lead to local adaptation in response to current selective pressures (Chapter 2).

Ouborg et al. (2006), Reed & Frankham (2001) and Rodríguez-Quilón et al. (2016) pointed out the difficulties to quantify accurately forest trees adaptive genetic variation and evolutionary potential. Population adaptive potential depends on the additive genetic variance of relevant

traits for fitness (Frankham, 2010). In response to heterogeneous biotic and abiotic conditions, natural selection can cause local populations to exhibit divergent phenotypic trait values, resulting from a complex interplay between environment and genome (Fady et al., 2020; González-Martínez et al., 2006; Le Corre & Kremer, 2012; Love & Ferris, 2024). Thus, the identification of individuals with adaptive trait values allowing them to persist under future climates is of major importance to define conservation strategies (Rodríguez-Quilón et al., 2016). Rodríguez-Quilón et al. (2016), de Miguel et al. (2022), González-Martínez et al. (2002) and Archambeau (2022) found high levels of adaptive trait differentiation for maritime pine across its range (Figure VIII.1). It is therefore essential to disentangle the relative roles of environment and genetic variation that has shaped past and present phenotypic variation, so that we can characterise the underlying genetic architecture of adaptive quantitative traits and predict the effect of future climate change (Fady et al., 2020).

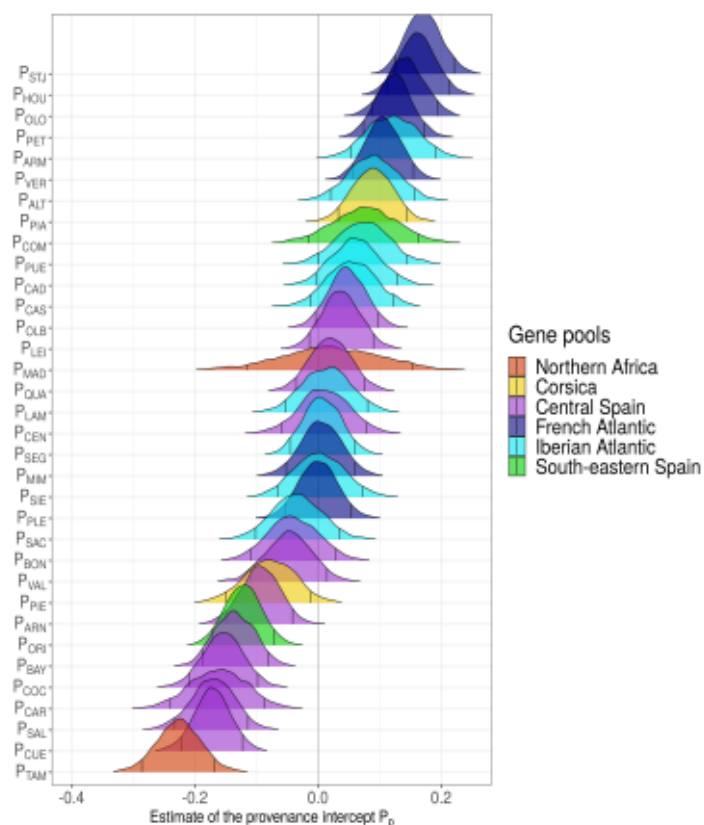


Figure VIII.1. Differences in height growth among maritime populations (i.e., provenance) from different gene pools. These results were obtained from hierarchical Bayesian models inferring variations in maritime pine height growth as a function of climatic and genomic variables, using height measurements from 34 populations planted in the five communal gardens of the CLONAPIN network. *Figure extracted from Archambeau (2022).*

Combining standard population genetic metrics with more integrative genomic-based approaches along with quantitative genetics and ecological data would increase our understanding of the molecular basis of adaptation and short-term evolutionary potential of maritime pine, and on a larger scale, on forest ecosystems (Avanzi et al., 2024; Fady et al., 2020; Porth & El-Kassaby, 2014; Rodríguez-Quilón et al., 2016). With this PhD thesis, I showed that it is necessary to understand how different processes may impact maritime pine genetic resources at different time (past *vs.* current) and spatial scales, from population-level (Chapter 2), to regional (Chapter 3) and range-wide scales (Chapter 1), in order to develop adapted and integrative spatiotemporal management guidelines (Fady et al., 2016). I therefore suggest that jointly considering different types of information will help in the refinement of hypotheses and the recognition of potential mechanisms not considered when using single-metric approaches (Leroy et al., 2018).

3.2. Identification of populations with conservation value in maritime pine

Conservation strategies depend on many parameters describing the full range of population genetic, demographic and ecological features (Aravanopoulos, 2016; Rodríguez-Quilón et al., 2016; Willi et al., 2021). As shown in the section 3.1 and supported by Gradl et al. (2022) and Hughes et al. (2008), evaluating conservation priorities on the basis of population genetic diversity alone is known to be insufficient. In this PhD thesis, I combined genetic indicators assessing different processes potentially linked to populations' evolutionary resilience and vulnerability to climate change (Chapter 1 & Chapter 3) and investigated current local adaptation trends (Chapter 2) at different spatiotemporal scales, enabling us to identify a number of populations with conservation interest from different perspectives.

One issue continues to be the subject of extensive debate in the field of conservation genetics. Should priority be given to marginal populations because of their unique allelic composition or should the focus be on core populations that carry the bulk of allelic diversity? On the one hand, peripheral or island populations, due to their small size, geographical isolation, frequent occurrence in sub-optimal habitats and higher prevalence of extinction, have often been considered of little importance to overall species conservation (Hoffmann & Blows, 1994; Millar & Libby, 1991). Vaxevanidou (2006) found a mixture of highly diverse and depauperate

marginal populations in Canary Island pine, an endemic pine species from the westernmost Canary Islands, and suggested that diversity-poor marginal populations have reduced conservation value due to a possibly recent origin via colonisation from nearby core populations. However, Petit et al. (1998) suggested that for conservation purposes, the level of divergence of a population in terms of allelic composition would be at least as important as its allelic diversity *per se*. In the same line, Lesica & Allendorf (1995) and Vucetich & Waite (2003) stated that including peripheral populations in conservation strategies would depend on their evolutionary potential as well as their genetic divergence from other conspecific populations. González-Díaz et al. (2020) showed that a relict population of mountain pine (*Pinus uncinata* Ram.) in northern Spain, potentially resulting from a long-isolation from the rest of the range, was genetically depauperate but exhibited private (i.e., unique) haplotypes compared with population in the continuous distribution of the central Pyrenees. The authors therefore considered this relict population to be of great value as a genetic reservoir for future restoration efforts (e.g., assisted migration).

As a complementary analysis to those presented in the three main Chapters of this PhD, I used the 83 range-wide populations of maritime pine with the set of 1,325 SNPs from Chapter 1 to explore each population's contribution to total allelic diversity. Allelic diversity can provide complementary information for the development of conservation plans of forest genetic resources, as it is highly sensitive to population bottlenecks and more related to long-term selection response than heterozygosity (López-Cortegano et al., 2019). I decomposed the average allelic diversity into three components: the total (AT), within- (AS) and between- (DA) population allelic diversity, using the rarefaction method implemented in METAPO2 software (López-Cortegano et al., 2019). Then, following Petit et al. (1998), population's contributions to total allelic diversity were obtained by removing sequentially each population and calculating the change in total allelic diversity. This analysis revealed that throughout the range of maritime pine, many populations, particularly marginal populations located in the southernmost part of the range, harbour population-specific alleles that may constitute valuable genetic resources for the species (see Figure VIII-2; Fady et al., 2016, 2022; Provan & Maggs, 2012).

Southernmost populations in Morocco, Tunisia and in the island of Pantelleria (e.g., Adeldal - ADE, Sidi-Meskour - SID, Aïn Babouch - ABA, and Pantelleria - PAN) showed the highest contributions to allelic divergence, with ADE population in Morocco also showing a positive contribution to allelic diversity. Wahid & Bounoua (2013) suggested that Moroccan marginal

populations of maritime pine are more likely to contain unique alleles and may therefore contribute strongly to maintaining the overall level of genetic variation of the species.

Interestingly, two populations that constitute unique genetic clusters (see Chapter 1, Figure II-1), Point Cires (PCI) and Fuencaliente (FUE), showed no positive contribution to total allelic diversity, either through its diversity or its differentiation component. We found these populations to display among the lowest overall genetic diversity and potential adaptation to the climate throughout their range, without, however, showing any recessive genetic load or maladaptation to future climate (Chapter 1). Long-term isolation and small N_e in these populations (e.g., the population of FUE, ~12 ha, consists of only ~1,200 trees and it is located more than 100 km away from the closest native stand; Charco-García, 2016; Unger, 2021) may have resulted in depauperate overall and potentially climate-adaptive genetic diversity (Chapter 1). However, historical records for FUE (Charco-García, 2016) and the presence of an endemic population of the co-evolved pest *Matsucoccus feytaudi* in PCI (Burban et al., 1999; Burbán & Petit, 2003) suggest that both are ancient populations that had larger distributions in the past.

Other remarkable populations with conservation interest were found in Southeastern Spain (e.g., Estepona - EST) and North-East (e.g., Arenzano - ANO, La Bisbal - GIR) gene pools, which is relevant given the potential status as glacial refugia during the LGM of these parts of the maritime pine range. It is interesting to note that Corsican populations showed a negative contribution to allelic diversity, although they displayed potentially climate-adaptive genetic diversity (Chapter 3).

To conclude, I believe that the genetic uniqueness, low recessive genetic load and low predicted maladaptation to future climates of maritime pine marginal populations could largely outweigh their low overall genetic and potentially climate-adaptive diversity for long-term conservation purposes (Lesica & Allendorf, 1995; Hampe & Petit, 2005; Sexton et al., 2014). Most European marginal populations seem adequately protected in the framework of the European Forest Genetic Resources programme (EUFORGEN, see asterisks in Figure VIII-1). Still, there is an urgent need to establish transcontinental conservation efforts to protect valuable genetic resources from the southernmost part of the range in North Africa, as also suggested by Fady et al. (2022) and highlighted in the recent Forest Genetic Resources Strategy for Europe (2021) (Alía et al., 2021). In addition, we lack detailed information on adaptive traits and fitness of marginal populations, in particular in parts of the range characterised by contrasting selective pressures or potentially maladapted to future climates, in order to develop robust and

appropriate conservation strategies. Therefore, establishment of new common garden experiments, where quantitative traits can be assessed, are urgently needed (see also Sampedro & Alía, 2023). Furthermore, to our knowledge, contemporary selection has not been assessed in marginal populations of maritime pine, and only a few studies have sought to examine its current drivers and targets in a limited part of the species range (González-Martínez et al., 2006; Alía et al., 2024, 2014 ; Chapter 2). Consequently, we are currently lacking information to understand how contemporary selective pressures are shaping maritime pine phenotypes outside a few core populations of the species, and what are the current targets of natural selection that may contribute to local adaptation and potential short-term evolution in the face of climate change.

Finally, in agreement with Petit et al. (1998) and Hoban & Strand (2015), for better “genetic capture” of *in situ* diversity and potentially specific adaptation, I suggest focusing conservation efforts on a combination of natural populations from different gene pools, contrasting spatial scales and environments, with genetic and quantitative population features relevant to conservation in current and future climates. This combination could enable us to preserve most of the genetic resources and adaptive potential of maritime pine, which will undoubtedly determine the fate of the species in the face of contemporary climate change. In this PhD thesis, I pointed out to some populations with conservation interest; selection does not claim to be exhaustive but we hope that it will help to prioritize populations for conservation of genetic resources.

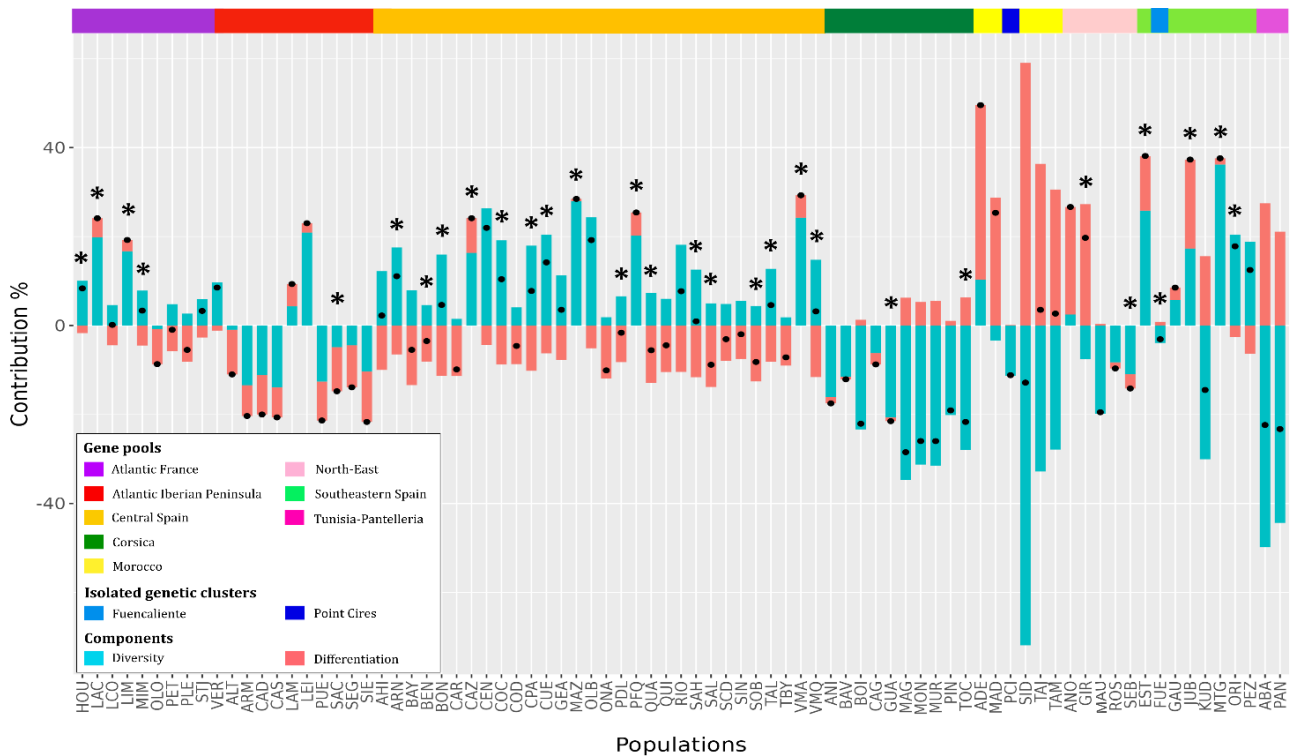


Figure VIII-2. Percentage contribution (Contribution %) to total allelic diversity through the components of allelic differentiation and allelic diversity, for maritime pine populations across its distribution range. Populations are grouped by gene pool (i.e., by the gene pool that contributes >50% of population ancestry), denoted by a bar colour legend. Black dots represent total allelic diversity. Populations that are part of the European network of Genetic Conservation Units (GCU) are marked with an asterisk (www.euforgen.org/species/pinus-pinaster).

3.3. *Ex situ* conservation strategy: the special case of marginal populations at both regional and range-wide scales

Because of their specific location in the periphery or in suboptimal environments, marginal populations are characterized by a high degree of fragmentation and isolation, often resulting in small N_e . These unique conditions are likely to be the cause of low genetic connectivity and increased genetic drift, resulting in low genetic diversity (Chapter 1) and potentially stronger inbreeding, that may compromise their responses to climate change (Serra-Varela et al., 2017). In turn, marginal populations may exhibit unique adaptations to some contrasting and potentially strong pressures that is of specific interest for the conservation of forest genetic resources (Lesica & Allendorf, 1995; Hampe and Petit, 2005; Sexton et al., 2014; Fady et al., 2020). Given the pace and magnitude of climate change increasing the risk of genetic erosion in their original location, *in situ* conservation of maritime pine marginal populations is

potentially no longer an option (Cavender et al., 2015; Fernández & González-Martínez, 2009).

In the Mediterranean basin, the southernmost part of maritime pine range, comprising Northern Africa and Tunisia, southern Spain as well as the Pantelleria and Corsica islands, is expected to be particularly vulnerable to future climate change. In this part of the range, maritime pine populations were geographically isolated from the core (Chapter 1) and potentially under harsh environmental pressures and marginal habitats (Chapter 3). Interestingly, we found that southernmost marginal populations at range-wide scale were not specifically threatened by maladaptation to future climates compared with populations along the Atlantic coast (Chapter 1), probably due to their higher altitude. In addition, although we could not predict short-term adaptive potential of Corsican populations due to the limitations of our model, they showed good overall potential for altitudinal range shift in response to global warming (Chapter 3). However, marginal populations showed low overall (Chapter 1, Chapter 3) and potentially climate-adapted (Chapter 1) genetic diversity, at both range and regional scales. An important point to bear in mind is that our predictions are based solely on climate. For more realistic predictions, we would need to take into account dispersal capacity and constraints, available habitat and soil types, as well as present and future (expected) biotic pressures. At a regional scale on Corsica Island, strong biotic pressures such as the increasing presence of *Matsucoccus feytaudi*, as well as harsh habitat conditions (e.g., swampy soil in the southernmost population of Ventilegne - VEN) and its specific ecological situation (i.e., island populations), likely influenced maritime pine genetic resources and local adaptation (Chapter 3). I can hence assume that the combined effects of climate change, together with increased biotic pressures, availability of suitable habitat and dispersal capacities will likely drive some of these populations to extinction in the wild.

In such cases, *ex situ* conservation measures will be necessary (Ducci & Donnelly, 2018; Fady et al., 2020; George et al., 2024; Kelleher et al., 2015). *Ex situ* conservation preserves populations or individuals as ‘copies outside of their natural habitat’ (Fady et al., 2016 and see article 2 of the Convention on Biological Diversity). *Ex situ* collections include samples of target populations conserved either as living collection in the field (e.g., botanical gardens, clone collections or gene banks, and even repurposed planted stands, provenance tests and seed orchards) or as reproductive material (e.g., seeds, pollen, tissues or DNA) maintained under artificial conditions (Murray, 2017). The establishment of *ex situ* collections is of utmost importance because it addresses the need for long-term genetic rescue in species which are

potentially under immediate threat (George et al., 2024).

Ex situ collection of living samples in the field allow the maintenance of a dynamic situation from an evolutionary perspective, in which natural processes such as gene flow and natural selection are taking place (Kelleher et al., 2015). The importance of *ex situ* genetic conservation has been mainly recognized for species which are characterized by scattered and discontinuous occurrence. In Finland, for example, being the northern range margin for many tree species, distribution ranges are characterized by a high degree of fragmentation and isolation among subpopulations (George et al., 2024). Consequently, *ex situ* genetic conservation (mostly dynamic) has been adopted by the Finish National Genetic Resources Program (2020) as a justified conservation measure for broadleaves and coniferous species such as *Fraxinus excelsior*, *Juniperus communis*, *Quercus robur* and *Tilia cordata*. Vaxevanidou et al. (2006) established in situ genetic reserves for the conservation of Canary Island pine genetic resources and highly recommended the development of complementary multifunctional *ex situ* collections, such as seed orchards, for those populations who's in situ conservation efforts seemed challenging. Serra-Varela et al. (2017) recommended *ex situ* conservation for maritime pine populations from eastern and southern Spain genetic groups.



Figure VIII-3. Maritime pine seedlings. *Source: Fôret Gascogne Bois.*

In maritime pine, I suggest dynamic *ex situ* conservation should be preferred, in particular for marginal populations already living close to the species physiological limits, in order to preserve the relevant processes shaping genetic diversity and adaptive potential at different scales within tree populations, so they can continue to evolve and adapt to ongoing global changes.

X. Conclusion

The different PhD chapters converge on the key role of drought-related climatic variables in determining the current and future adaptive capacity of maritime pine populations throughout its range. Despite a general trend towards increasing vulnerability to climate change in the warmer and drier part of the range, I have shown the challenges in drawing general conclusions when considering different spatial scales, therefore highlighted the need for more detailed regional and population-specific studies. Indeed, not only past selection but also current selection drivers may affect maritime pine differently in different parts of the range, as shown by contrasted selection gradients across Mediterranean and Atlantic maritime pine populations. Integrative genomic-based approaches have shown promise for improving predictions of short-term population responses to environmental change and for developing genomic-based strategies for the conservation and appropriate management of this keystone forest tree. Although geographically marginal populations are of conservation interest for different reasons, I suggest that conservation efforts should focus on a selection of natural populations from different gene pools and contrasting environments that display genetic and phenotypic traits relevant for adaptation under current and future climates. Apart from demographic historical factors, I argue that conservation practices should also include more recent factors such as anthropogenic impact, microclimate and biotic interactions, particularly when selecting populations for conservation in particular systems such as island populations. Finally, I propose that *ex situ* conservation strategies need to be developed for maritime pine, particularly for marginal populations located in fragmented ranges and in environments that may no longer be suitable for this species in the near future. More broadly, this work contributes to a better understanding of maritime pine adaptive processes and selection drivers at different spatial and temporal scales, and to strengthens the knowledge needed to develop robust and integrative management strategies in response to the urgent challenge of ongoing climate change.

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