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Bruno Fady, Caroline Scotti-Saintagne

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Title:
# Why conserve genetic diversity? A perspective based on a case study with a European conifer

Short running title:
Why conserve genetic diversity?

Authors:
Bruno Fady[*1,2], Caroline Scotti-Saintagne[1]
[1]: INRAE, Ecology of Mediterranean Forests (URFM), Avignon, France
[2]: European Forest Institute (EFI), Barcelona, Spain

[*]: Corresponding author: Bruno Fady PhD, INRAE URFM, Domaine Saint Paul, Avignon, France. E-mail address: bruno.fady@inrae.fr

## Abstract

***Background*** - Biodiversity is the variability among living organisms that exists within species, between species and of ecosystems. Yet, genetic diversity, the within species component of biodiversity, is rarely considered as a conservation concern or goal in protected areas.

***Scope*** – In this perspective, we explore possible reasons why genetic diversity is poorly considered in conservation and ecological restoration. We also present the case study of a threatened forest conifer in France (*Pinus nigra* ssp. *salzmannii* (Dunal) Franco, Salzmann’s pine) that we offer as proof of how straightforward implementation of genetic diversity conservation goals can be in protected areas.

***Conclusions*** – Scientific studies in the fields of either conservation or biodiversity consider genetics in less than 10% of scientific productions. While genetic tools are used for taxonomic delineation, concerns about diversity within species at population level appear comparatively rare in conservation and biodiversity science or management. The use of genetic tools for the conservation of genetic diversity of Salzmann’s pine in France clarified its taxonomic status, identified populations relevant for in-situ conservation compatible with habitat conservation and made it possible to select genetically original individual trees that could be grafted as a core collection for dynamic ex-situ conservation. As threats on biodiversity increase worldwide, fully integrating genetic diversity in conservation demands that conservation adopts an evolutionary centered, nature for itself perspective, rather than either an anthropocentric, resource focused perspective or a bio-centered, emblematic species focused perspective.

## Keywords

Biodiversity, evolution, in-situ conservation, core collection, *Pinus nigra* Arnold, protected area, adopt evocentric model of conservation

## Genetic diversity is rarely a biodiversity conservation concern and goal

The Convention on Biological Diversity (CBD) of the United Nations defines biodiversity as the variability among living organisms that exists within species, between species and of ecosystems (United Nations, 1992). Nearly 200 countries have now signed this multilateral treaty entered in force in 1992 and are legally bound to conserve and sustainably use biodiversity as well as equitably share benefits from genetic resources.

Biodiversity is inherently complex and a holistic measure of biodiversity’s state and trends is a complex task. Simplified surrogate indicators are thus used. Traditionally, biodiversity monitoring globally has been done measuring trends in species diversity, their occurrence and richness (CBD, 2011). Although species richness measures have well-known flaws (Roswell et al., 2021), species have been described for a long time and benefit from widespread expertise, have a shared general even if fuzzy understanding (Sites and Marshall, 2004) and their protection is legally opposable in many jurisdictions (for example, under the Endangered Species Act of 1973 in the United States of America or under the Environmental Code (e.g. Article L411-3) in France). Habitat integrity and size are also often used metrics, particularly for measuring the efficiency of offset programs designed to compensate for human impact (Marshall et al., 2020). Habitats are often legally protected as well because of the remarkable species they contain and which define them, as in the European Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (commonly referred to as the Habitats Directive). The key elements that are monitored to provide evidence of risks of ecosystem collapse are also species (Bland et al., 2017).

Genetic diversity is a key ecological state and process. It is essential to adaptation and thus evolutionary potential, and supports key nature’s contributions to people (Hughes et al., 2008; Jump et al., 2009; Des Roches et al., 2021). Surprisingly, despite its importance for species and population sustainability, and despite being mentioned explicitly as a component of biodiversity in the foundational text of the CBD, genetic diversity is rarely considered and monitored as a conservation goal in protected areas (Frankham, 2010; Graudal et al., 2014; Laikre et al., 2020; Gumbs et al., 2023). Of the nearly 300,000 protected areas worldwide, only a small fraction includes genetic diversity as a conservation goal, and fewer than 10% - such as strict nature reserves or wilderness areas - have the conservation of genetic diversity as an indirect target (Fady and Bou Dagher Kharrat, 2024). Instead, almost all of the biodiversity conservation efforts implemented by countries in protected areas focus on species and their habitats (Dinerstein et al., 2019). Protected areas, thus, mostly aim at conserving the outcomes of past ecological and evolutionary processes, the biodiversity that was and that still is. In a climate-changing world where most of the Aichi Targets related to biodiversity have not been achieved (Secretariat of the Convention on Biological Diversity, 2020), this endeavor may be a lost cause in most places.

## Genetic diversity makes a small contribution to the conservation, biodiversity and ecological restoration scientific literature

One reason for the lack of consideration of genetic diversity in conservation may come from the scientific community itself. While genetic methods are now used widely in taxonomy to delineate species (Fujita et al., 2012; Antil et al., 2023), genetics as a science makes a very limited contribution to the field of either conservation or biodiversity. Scanning the scientific literature of the past decades using the Web of Science database for documents addressing the topics of either biodiversity or conservation, indicated that less than 10% of the total within each category included the topic of genetics (Table 1).

Across time, the 17,903 publications of topic “biodiversity and genetic*” increased from less than 1% in the 1990s to almost 8% in the 2020s. The trend is similar for the 54,932 publications of topic “conservation and genetic*” which increased from a maximum of 1% in the 1990s to 6% in the 2020s. These increasing trends completely match those of the two topics “biodiversity” and “conservation”. Thus, although macro- and micro-evolution was at the core of biological conservation when it was framed as a scientific field (Soulé, 1985), genetic diversity has had little importance in the scientific production of the fields of either conservation or biodiversity. In addition, half of conservation and biodiversity studies that do consider genetic diversity are concerned with endangered species or species with agronomic importance (Table 1), sustaining the claim that studies related to widespread or keystone species lag behind (Hoban et al., 2021; Willi et al., 2022).

The same scientific gap is true for the field of ecological restoration, which has attracted considerable interest internationally for reversing the loss of biodiversity (United Nations Decade on Ecosystem Restoration 2021–2030) and achieving several of the Aichi biodiversity targets of the Convention on Biological Diversity (Aronson and Alexander, 2013). Querying again the Web of Science over the same period, studies of ecological restoration that included a concern for genetics were less than 4% of all ecological restoration studies (Table 1), with a first occurrence in 1992 compared to 1976 for ecological restoration studies. Thus again, although genetic diversity is key to restoration success, it is seldom considered in this field of research (Thomas et al., 2014; Wei et al., 2023).

## The importance of ex-situ over in-situ conservation in the scientific literature

It would be false to say that genetic diversity has never been the focus of conservation. It is a strong concern for fragmented animal and plant populations where inbreeding is a direct cause of decline and restoring gene flow is advocated as a meaningful genetic management solution (Frankham et al., 2017; 2019). It has also been a strong focus of conservation for farm animals and crop and their wild relatives, where genetic diversity is considered as a resource to be used and is termed: genetic resources (Pilling et al., 2020). In this anthropocentric view of biodiversity (Mace, 2014), conservation is not done in natural environments (*i.e.* in-situ, letting natural selection and demographic processes shape genetic diversity over generations and changing environmental conditions), but rather as an ex-situ lineage management strategy, either in seed or sperm banks, or circa-situ on farm (Khoury et al., 2010). Countries tend to emphasize ex-situ conservation and legislation in their reporting of genetic monitoring (Hoban et al., 2021).

We performed a third query of the Web of Science, spanning the same time period as before, to confirm this inflated interest of ex-situ over in-situ conservation in the scientific literature. We took care to exclude terms related to the topics of medicine or archeology. The ex situ conservation literature search contained almost twice the number of references as in the in-situ conservation literature search (Table 1). The first ex-situ publication occurrence was in 1988 while the first in-situ occurrence was in 1993.

## How to conserve Nature with an evolutionary perspective? A case study with *Pinus nigra* Arnold, the European black pine.

Conservation genetics has yet to attract the interest of the conservation and biodiversity scientific community. Biodiversity metrics including descriptions related to species functions and evolutionary history are more and more advocated as urgently needed in conservation (Moreno et al., 2017; Albassatneh et al., 2023). Yet, although they may help prioritization purposes, these more complex descriptions do not inform on adaptive potential or extirpation risks linked to genetic drift, and genetic diversity metrics are needed to monitor biodiversity threats and conservation actions in wild species (Laikre et al., 2020; Hoban et al., 2022).

We believe that the gap between biodiversity conservation and genetic resource conservation could and needs to be bridged. The efforts put in place in France for the conservation of the evolutionary potential and habitat of a subspecies of black pine (*Pinus nigra* Arnold) constitute a good example of how straightforward the use of genetic diversity can be as a method and how applicable genetic diversity is as a conservation goal.

The marginal habitats of this otherwise widespread and often planted conifer are protected in Europe under the Habitats Directive. In continental France, the “(Sub-) Mediterranean pine forests with endemic black pines” priority habitat concerns the sub-species *Pinus nigra* subsp. *salzmannii* (Dunal) Franco (Figure 1). Its main current threats are wild fires, habitat loss to competing introduced maritime pine (*Pinus pinaster* Aiton) and hybridization with planted black pines from other sub-species. Its small distribution area of currently less than 5 000 ha is the result of century-old land use changes to agriculture and grazing, and over-logging for mining lumber. The conservation status of this priority habitat for the period 2013-2018 was assessed as poor by the European Environment Agency, necessitating a change in management or policy to return the habitat to a favorable status although no danger of disappearance is expected in the foreseeable future (https://eunis.eea.europa.eu/habitats/10234).

While Salzmann’s pine is the keystone species of these habitats, and its small local population sizes can let suspect genetic drift, there is no specific management in place that safeguards the genetic diversity of its populations.

Salzmann’s pine is also regulated as forest plantation material in France. Under European Council Directive 1999/105/EC of 22 December 1999 on the marketing of forest reproductive material, genetic material used for planting must come from legally designated forests or orchards. In France, this taxon is seen as a diversification species for plantation as climate is warming and new pests (such as the needle blights *Dothistroma* sp. Hul. or *Sphaeropsis sapinea* (Fr .) Dyco et Sutton) are increasing their prevalence (Woods et al., 2016). Sales of seedlings for forest plantations in France have increased from almost zero in the early 2000s to over 100 000 in 2022 (https://agriculture.gouv.fr/statistiques-annuelles-sur-les-ventes-de-graines-et-plants-forestiers).

Both the existence of threats to its habitat and a renewed interest for its genetic resources warrant conserving its genetic diversity. It is best done in-situ, setting aside areas as vast as possible for natural selection to occur and shift phenotypic optima, tracking environmental changes. Because of threats such as wild fires that seem to not be realistically abatable given current climate adaptation plans (Fargeon et al., 2020; Roberts et al., 2020), ex-situ conservation is also advisable.

## *1- Taxonomic delineation and autochthony*

As with all taxa, and particularly those for which gene flow is strong and which have diverged recently from their most common recent ancestor (Scotti-Saintagne et al., 2019), the first step of this program was taxonomic delineation. *Pinus nigra* Arnold belongs to the *Pinus* clade which emerged within sub-genus *Pinus* some 50 million years ago during the Eocene. This clade also contains mountain habitat European pines such as *Pinus sylvestris* L. and *Pinus uncinata* Ramond ex DC. (Saladin et al., 2017). To our knowledge, there are no reports of interspecific hybridization between black pine and the other pines of its group.

Because of its large and discontinuous range extending over more than 3.5 million hectares of varied climatic and pedological conditions from western North Africa through southern Europe to Asia Minor, botanists, ecologists and foresters have always considered black pine as a collective species made of several subspecies with various ecological requirements and adaptive capacities of importance for conservation and use (Isajev et al., 2004). However, the identification of sub-species is challenging. While morphological taxonomic keys exist (Debazac, 1963; Rameau et al., 2008), among tree variation is high depending on habitat, and taxonomic authorities diverge on how many sub-species exist in *Pinus nigra*. Using a set of thirteen molecular markers (Giovannelli et al., 2017) and a phylogenetic approach, Scotti-Saintagne et al. (2019) were able to identify six genetic groups range-wide which they considered as six sub-species, splitting *Pinus nigra* subsp. *pallasiana* (Lamb.) Holmboe into two subspecies in comparison to the biogeography and morphology based Plant of the World Online nomenclature.

*Pinus nigra* subsp. *laricio* Palib. ex Maire and *Pinus nigra* subsp. *nigra* have been extensively planted in France since 1860 as part of a mountain erosion control program. We were able to confirm that hybrids between the local sub-species and these two exotics exist and represent 6 and 22% of seedlings selected in closed forests and open land habitats where the three taxa coexist, respectively (Fady and Scotti-Saintagne, 2018). Although hybridization is a natural process that can be beneficial for local adaptation, particularly in fluctuating environments (Barton 2001; Wachowiak et al., 2016), we consider that anthropogenic hybridization is detrimental in the case of Salzmann’s pine and, as argued by Allendorf et al. (2001), could lead to extinction. The local genotypes are much rarer than the exotics which demonstrate, among other traits, a higher susceptibility to needle blights (Perret et al., 2021; Vacek et al., 2023) and proof of increased resilience to warming temperatures or increasing drought is lacking (Giovannelli, 2017; Fkiri et al. 2018).

## *2- Evolutionary significant units and in-situ conservation*

For in-situ conservation of genetic diversity, identifying evolutionary significant units (ESU) have been the golden standard for several decades (e. g. Moritz, 1994; Crandall et al., 2000; Fraser and Bernatchez, 2001; Hoelzel, 2023). Initially relying on maternally inherited mitochondrial DNA, selecting populations that diverge from each other and thus originate from different genetic lineages can now be done using a much larger set of genetic markers, potentially reflecting both demographic and natural selection past events. In Salzmann's pine, using the same set of thirteen microsatellites markers, and despite sometimes extensive levels of individual admixture resulting from the recent evolutionary history of the species, we could identify five geographically distinct genetic groups (Figure 1) from different habitats (from mesic slopes in the Pyrenees to dry ridges in the Cévennes and cliffs in Gorges du Tarn as in Figure 2), which we considered as ESUs (Scotti-Saintagne et al., 2024).

An efficient genetic conservation strategy requires that at least one representative forest within each Salzmann's pine ESU should be a management unit devoted to conserving genetic diversity and fostering the process of adaptation. Populations should have minimum sizes large enough to harbor enough genetic variation (Le Corre and Kremer, 2012; Cubry et al., 2022), typically hundreds to a few thousand adult individuals. These management units require a long-term commitment, ideally with a legally or administratively recognized status (Koskela et al., 2013). This type of conservation, where the management emphasis is placed on natural regeneration under various environmental conditions, has been done in Europe since the early 1990s (Lefèvre et al., 2013) under the guidance of the European Forest Genetic Resources Programme (EUFORGEN) and currently includes 3.231 genetic conservation units for 113 tree species in 35 countries (http://portal.eufgis.org/).

However, and perhaps similarly to marine genetic conservation, long term commitments with a recognized status is a challenge for many jurisdictions as it eventually relies on stakeholders who may have other priorities (Taylor et al., 1999). For Salzmann's pine, a single in-situ genetic conservation unit was implemented so far out of the five other geographically distinct genetic units that would be required to effectively conserve the evolutionary heritage and potential of the taxon in France. Barriers to implementing more conservation management units include land tenure with multiple private owners in areas of importance, reluctance to add layers of legal protection where one already exists and lack of understanding of the importance of within-species diversity for long term adaptation.

### *3- Ex-situ dynamic conservation and defining a core collection*

When in-situ conservation is difficult because natural regeneration is scarce and cannot be increased by appropriate in-situ management, it is advisable to adopt a dynamic ex-situ conservation strategy where cloned trees can be planted and conserved outside of their original habitat in nearby environment less susceptible to anthropogenic disturbance, while encouraging natural regeneration. This strategy was deployed in the French Cévennes in an old stand, Col d'Uglas, the only representative of an ESU, where the remaining old trees produce few seeds. The strategy received strong support from local stakeholders, the general public and local media, providing visibility to both the planted collection and the remaining old founder trees.

Additionally, trees can be cloned in a distant site to simply back the in-situ strategy or as an alternative to ex-situ dynamic conservation when the environment is too hostile or the causes of its destruction have not been suppressed. This strategy has also been deployed, concurrently for the five ESUs of Salzmann's pine, following the identification of a core collection based on allelic and differentiation coverage and the elimination of hybrids between Salzmann's pine and other black pine subspecies (Scotti-Saintagne et al., 2024). Cloned trees constitute a representative core-collection and can also be used to produce seed usable as forest reproductive material. This combined strategy benefiting both conservation and use can only be done if the perspective for forest reproductive material is increased genetic diversity, not breeding focused on specific traits. It might be a desirable perspective under climate change as a need for increased resilience is probably a more cautious management goal than increased productivity as would be desirable under management assuming stable climatic conditions (Holling, 1973; Lefèvre et al., 2014).

## Perspective: genetic diversity as a goal of conservation, and ecology as a concern for genetic conservation

Recognizing that genetic diversity is not sufficiently considered in conservation planning and monitoring of wild species, the Kunming-Montreal Global Biodiversity Framework (GBF) of the Convention on Biological Diversity, adopted late 2022, now includes indicators of genetic diversity state and trends for all species, both domesticated and wild ones (Hoban et al., 2022). Although these indicators are not perfect (Allendorf et al., 2024), particularly for forest trees (Fady and Bozzano, 2021; Santos-del-Blanco et al., 2022), this is a welcome change.

The French Salzmann's pine case study demonstrates that the conservation of genetic diversity is a perfectly compatible goal with that of habitat and biodiversity conservation in general. As classically done for nature protection, climate and biogeography were used for detecting meaningful ecological patterns, as genetic differentiation and local adaptation can be expected to follow vegetation, soil and bioclimatic landscapes (e.g. Potter et al., 2017). The French Salzmann's pine case study demonstrates that the use of genetic methods can significantly improve taxonomic delineation and spatial prioritization within taxonomic groups which should be transposable to most conservation endeavors focusing on species that are keystones of their ecosystems (Cottee-Jones and Whittaker 2012).

Integrating genetic diversity in conservation management is straightforward, valuable for conservation, and readily facilitated by how easily available and cost-effective genetic markers are now (Andrello et al., 2022). It can also significantly enlarge the portfolio of management options available for conservation, as genetic diversity within population, coupled with ground observations of habitat quality, adult population spatial structure, and number of adults and recruited juveniles, significantly correlates with population vulnerability and extinction risks (Koskela et al., 2013; Hoban et al., 2022). The methods we have used document demographic processes and not adaptive potential (but see Le Corre and Kremer, 2003 and 2012 for small populations). High throughput sequencing methods offer opportunities to scan genomes more completely, target genes putatively under selection and identify lags in adaptive potential (Allendorf et al., 2010; Rellstab et al., 2021).

Why is the vast majority of protected areas not incorporating objectives aimed at conserving genetic diversity and evolutionary potential within their conservation strategies? And, conversely, why are forests designated as genetic conservation units, such as those of EUFORGEN, not considered as protected areas? We are convinced that it is a recurring question of perspective (and thus vocabulary) on biodiversity and nature. In the case of forests for example, protected areas aim to conserve holistically what is the product of past processes while genetic conservation units aim to conserve specifically resources that have a value for adaptation now and under an uncertain, climate-changed future (Namkoong, 1992). Advocating for the conservation of genetic diversity of forest trees has been embedded in the framework of sustainable use rather than conservation of nature (Eriksson et al., 1993). In many countries, this narrative leads to a division of responsibilities, with protected areas under jurisdiction of authorities in charge of the environment while forest genetic (resource) conservation falls under the authority of a separate governmental jurisdiction overseeing forestry matters.

These diverging perspectives may be deeply rooted in the legacy of the original lack of integration of the scientific fields of ecology and evolution (Futuyma, 1986). Ecologists who are the main advocates of protected areas tend to consider genetic conservation secondarily because of their focus on conserving habitats. Conversely, geneticists who are the main advocates of genetic conservation, too often see protected areas as a model reluctant to embrace change as the driver of adaptation. While the ideas of ecologists and geneticists on how to best protect and conserve nature have recently aligned more, particularly when threatened species are concerned (Cook and Sgrò, 2017; Frankham et al., 2019; Gaitán-Espitia and Hobday, 2021; Willi et al., 2022), the multiple threats of the 21st century on biodiversity in general require stronger integration.

The gap between nature conservation and genetic diversity conservation may also be rooted in practice. Awareness of the importance of diversity within species is increasing among different stakeholders as worries about the damaging effects of climate change increase, but how to use this awareness remains a challenge (Vinceti et al., 2020; Heuertz et al. 2023). Lack of expertise has been identified as a barrier for the use of genetic data and implementation of conservation genetic practice, and so have costs (Taylor et al., 2017). While costs have gone down significantly and may only be perceived as too high, lack of expertise remains rather unsolved despite repeated calls for increasing training in genetics and communication channels between researchers and managers (e.g. Schiebelhut et al., 2024). As the case of Salzmann’s pine has shown us, a strong co-designed conservation project integrating academia, managers and policy makers can be a success. And when genetic data uncover hidden biological facts such as highly divergent and unique or genetically endangered populations, interest for genetic tools and conserving genetic diversity increases strongly in management agencies, forest owners and the general public.

Recognizing different values of nature is also needed (Mace, 2014; Milot et al., 2020; Pereira et al., 2020; Pascual et al., 2024) so that, rather than objects such as species or genes, conservation can successfully focus on the processes that sustain biodiversity and long-term adaptation (Bowen, 1999; Brum et al., 2017). Genetic diversity (at least of keystone species, thus trees in the case of forests) needs to be included both in the design and conservation goal of protected areas, optimally as part of legally enforceable objectives. Beyond using genetic tools to select representative evolutionary significant units and relevant protected areas within them, management must concentrate on facilitating and fostering natural regeneration emerging from as large as possible number of adults. Conversely, for forests which are genetic conservation units, to be recognized as protected areas, management must embrace an ecological perspective. This includes, *a minima*, a long term legally recognized commitment to conservation and excluding the plantation of exotic tree species.

Adopting a common protection framework for genetic diversity, species, habitats, and ecosystems is highly desirable in the Anthropocene as threats on the biosphere are extremely high and increasing (Schierenbeck, 2017; DeWoody et al., 2021; Antonelli et al., 2023). Conservation of genetic diversity needs to change its perspective and adopt a non-anthropocentric perspective of nature (Muradian and Gómez-Baggethun, 2021; Taylor et al., 2020). Conversely, the management of protected areas needs to change its management perspective from biocentric to evocentric, one that considers evolutionary trajectories (Sarrazin and Lecomte, 2016). Relying on evolutionary processes is possibly the only option available for protecting all aspects of biodiversity under a very uncertain future with an irremediably changed climate.

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Table 1: results of different search queries in the Web of Science (from Jan. 01, 1955 to Nov. 11, 2024). All terms are from the field “Topic”.

| Query terms | Number of documents |
|---|---|
| Biodiversity | 220,680 |
| Conservation | 545,912 |
| Biodiversity AND genetic* | 17,903 |
| Conservation AND genetic* | 54,932 |
| Conservation AND genetic* AND (rare) OR (rarit*) OR (crypt*) OR (threat*) OR (endanger*) OR(agro*) OR (agri*) OR (resource*) | 27,140 |
| Biodiversity AND genetic* AND (rare) OR (rarit*) OR (crypt*) OR (threat*) OR (endanger*) OR(agro*) OR (agri*) OR (resource*) | 9,059 |
| “Ecological restoration” | 29,134 |
| “Ecological restoration” AND genetic* | 1,143 |
| "in-situ conservation" or "in situ conservation" NOT archeolog* or medic* NOT "on-farm" or "on farm" NOT "circa situ" or "circa-situ" NOT "ex-situ conservation" or "ex situ conservation" | 1,248 |
| "ex-situ conservation" or "ex situ conservation" NOT archeolog* or medic* NOT "in-situ conservation" or "in situ conservation" | 2,363 |

Figure 1. Geographic distribution of the five subspecies of *Pinus nigra* Arnold recognized by Plant of the World Online (https://powo.science.kew.org/) and of the five genetic groups identified in France within subspecies *salzmanii*. From Isajev et al. (2004), Scotti-Saintagne et al. (2019) and EUFORGEN (https://www.euforgen.org/species/pinus-nigra).

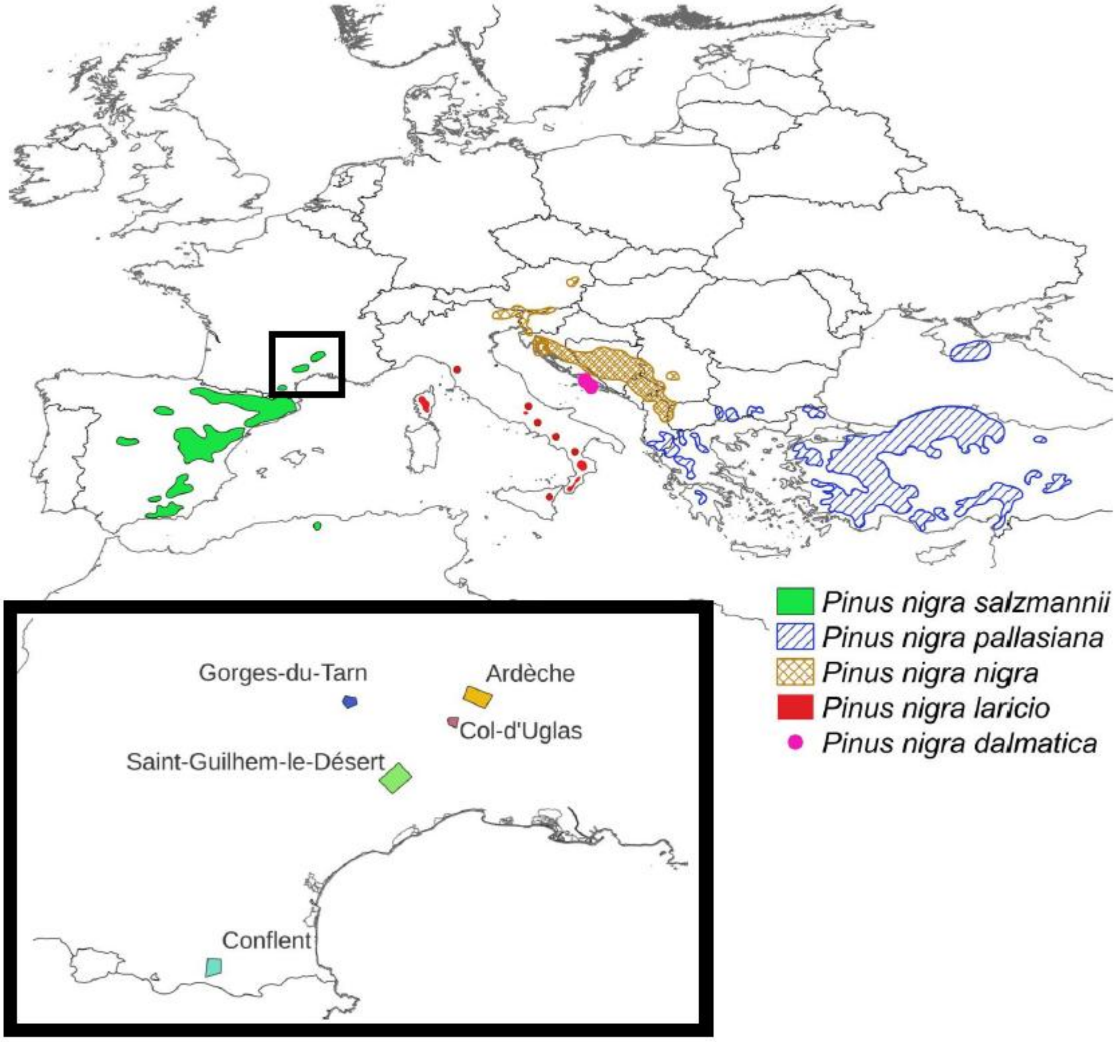

Figure 2. Example of a Salzmann’s pine priority habitat, Gorges du Tarn, southern France.