

FPS COST Action FP1202
**Strengthening conservation:
a key issue for adaptation of marginal/peripheral
populations
of forest trees to climate change in Europe (MaP-FGR)**

SHORT TERM SCIENTIFIC MISSION REPORT

*Species distribution modeling of black pine (Pinus nigra Arn.): assessing
ecological marginality of genetic resources*

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STSM Start at 10/04/16 and End at 19/04/16.

Abstract

Pinus nigra belongs to the Mediterranean pine group and have a large distribution of 3.5 million hectares from North Africa to Turkey through the Balkans. It plays an important ecological and an economical roles. Two approaches are commonly used to assess the variability of tree functioning between subspecies. Both common gardens and species distribution modeling (SDM) are consequently useful to study the genetic variability, which is important for conservation and forest sustainability. The climatic niche of the species predicts a potential area slightly larger than the realized niche and the subspecies niches are differentiated. In this case, the intra-specific variation of niche occupancy at the subspecies level can't be explained by local adaptation which suggests that much of the variability observed between subspecies can be explained by phenotypic plasticity.

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1. Introduction

Pinus nigra belongs to the Mediterranean pine group and have a large distribution of 3.5 million hectares from North Africa to Turkey through the Balkans. It plays an important ecological and an economical roles. It is widely planted because of its durable wood, resin richness and easy to work. It experienced different glacial and inter-glacial periods leading to a fragmented distribution of the species (Isajev *et al.* 2004). Systematic botanical characteristics justify to consider it as a species, while its high intra-specific variation is a reason to subdivide it into several species. Indeed, the high morphological variation, as well as the physiological, chemical, ecological and genetic diversity had led to the creation of different subspecies (Scaltsoyiannes *et al.* 1994; Rafii, Dodd & Zavarin 1996; Barja *et al.* 2009). Despite the taxonomy is often questioned, different work of scientists recognize six subspecies linked to their geographical distribution (Quézel & Médail 2003; Bojovic *et al.* 2005). *P.nigra salzmannii*, is present in Spain and south of France. *P.nigra laricio*, is present in Sicily, Calabria and Corsica. *P.nigra nigra* which distribution goes from Italy to northern Greece leaving place to *P.n. pallasiana*, essentially present in Turkey and Greece. A population, *P.n. mauritanica* is also present in North Africa and another one in Croatia, *P.nigra dalmatica*. This wide and fragmented distribution area has produced a high genetic diversity between subspecies or provenances.

Two approaches are commonly used to assess the variability of tree functioning between subspecies. First, working with common gardens data make it possible to access to genotypic differences expressed by phenotypic traits of individuals of different geographic origins thanks to the control of the environmental conditions. In this study, we compared the radial growth strategies between the different provenances coming from the entire distribution area of *P. nigra* to estimate the part of the variation between population that are due to the genetic diversity from the part that are due to phenotypic plasticity .

Second detailed knowledge of species ecological and geographical distribution can also help to assess the ecological determinant of spatial patterns of biodiversity (Ferrier 2002; Funk & Richardson 2002; Rushton, Ormerod & Kerby 2004). Species distribution modeling (SDM) are an effective way to assess species spatial distribution over large spatial scale.

Both common gardens and species distribution modeling (SDM) are consequently useful to study the genetic variability, which is important for conservation and forest sustainability.

2. Objective of the STSM

Despite the proliferation of SDM, a limited number of studies have taken into account the intra-specific information based on morphologically defined subspecies (Pearman *et al.* 2010; Oney *et al.* 2013). Benito-Garzon *et al.* (2011) as well as O'Neill *et al.* (2008) have highlighted the importance of considering intra-specific variation when modeling species distribution. The first objective of the STSM will be to model the climatic niche of *Pinus nigra* as species and using one model by subspecies. The second objective will be to compare the different models and see if they differ between the whole model and the subspecies.

Finally, the third objective will be to characterize the ecological niche of the species and their different subspecies, to estimate the position of the common gardens studied otherwise within this niche. We will be able to explain the potential differences of radial growth as a function of the position of the individuals and of the common garden in the distribution area: central or marginal.

3. Links with Cost Action FP1202 MaP FGR

My project will contribute to the COST Action MaP-FGR, because it allows knowing if the studied genotypes are from the marginal part of the niche or not, and relating this information to the growth potential of the populations under study. We will therefore be able to provide information on the adaptation of forest tree populations to ecological marginal conditions.

4. Materials and methods

The tools necessary for analysis are, for the most part, the programming language and statistics 3.1.0 R (R Core Team 2014) and QGIS (QGIS 2011) for mapping transformations.

Study area

The study area was created from a world map. It extends from east to west, from Portugal to the east of Turkey and from North to South, from France to North Africa. The study area was defined as to cover the natural range of the species by taking into account the distribution of the six subspecies studied coded as follow: *P.n. mauretana* (1), *P.n. salzmannii* (2), *P.n. laricio* (3), *P.n. nigra* (4), *P.n. pallasiana* (5) and *P.n. dalmatica* (6). The study area also corresponds to the area of distribution of different provenances studied during my internship (Table 1).

Data set

We extracted the distribution data from two different sources, the European Forest Genetic Resources Program (EUFORGEN) and the Joint Research Center (JRC). Euforgen provided two distribution maps of *Pinus nigra* (population and fragmented) based on existing bibliography and other information sources. The presences recorded correspond to the natural distribution of *Pinus nigra* in Europe and North Africa. Species presences were recorded in a Lambert Azimuthal equal-area projection. JRC provided the distribution map of all occurrences of the species, natural or planted. It is recorded percentage of the species within the grid cell.

in a raster according to the 1984 worldwide geodesic system (WGS84), with a 1km resolution. This data was reclassified with 0 coding for absences and 1 for presences. The delimitation of the subspecies on the distribution maps was done using a map produce by Quézel et Médail (Quézel & Médail 2003) and were coded from 1 to 6 according to the subspecies (Figure 1).

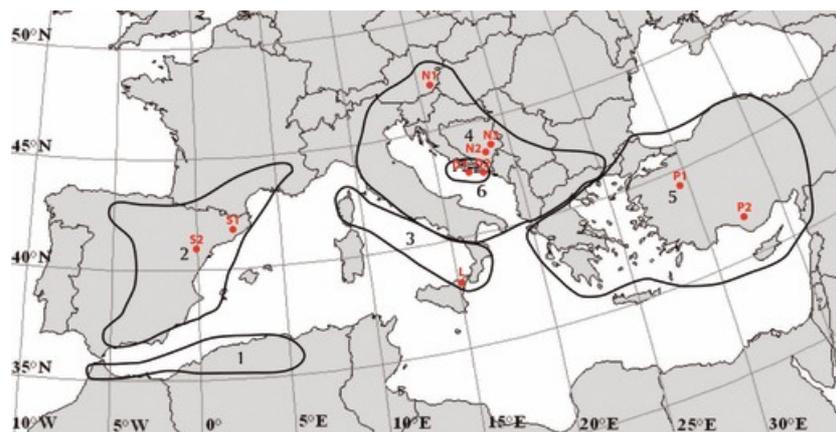


Figure 1: Geographic distribution of *Pinus nigra* subspecies: 1 = ssp. mauritanica; 2 = ssp. salzmannii; 3 = ssp. laricio; 4 = ssp. nigra; 5 = ssp. pallasiana; 6 = ssp. Dalmatica. .Quézel & Médail (2003)

To retrieve the coordinates of the presence of the species in the study area, maps from EUFORGEN and JRC have undergone several transformations. First, they were projected in the same coordinate system. Working across extended Europe, the different distribution maps have been projected according to the WGS84 coordinate system. Then, the resulting files were converted to raster and transformed to have the same dimensions. This approach ensures the alignment of the centers of the cells of each raster. The obtained raster have 6240 lines by 10,801 columns. The frame stretches from west -20.008 degrees to 70.00 degrees west longitude and 20 degrees north to 72.00 degrees north latitude. The resolution is 0.0083 decimal degrees per cell, less than one square kilometer.

In order to collect the coordinates of natural occurrence of the species, the two maps, EUFORGEN representing natural populations and JRC representing natural and planted populations, were overlapped. The map from the JRC database having a higher resolution was chosen to collect the coordinates of presences and absences. Furthermore, because the EUFORGEN map represents all natural populations of *Pinus nigra* and the JRC map represents natural and planted populations. Therefore, all the points in common between the study area, the JRC and EUFORGEN maps were considered as presences. In contrast, all the points that do not meet all these conditions were considered as absences. The climatic variables were then extracted for each point of presence. This operation was done for the whole species and for each subspecies.

The most effective species distribution models require data on both species presence and absences (Elith et al., 2006). As real absences are difficult to confirm, artificial absences data are created, usually called pseudo-absences. The dataset of pseudo-absences was created in three steps. First, a set of randomly selected points of absences was created corresponding to six times the number of presences. Afterwards, the climatic variables were extracted for each absences. Finally, the pseudo-absences data set was created from this new sample by selecting randomly five times the number of presences (Barbet-Massin et al. 2012).

Unlike EUFORGEN, the JRC map does not cover the whole study area by not including Turkey and North Africa. This should be taken into account during the analysis.

Climate data

Climate data are from the WorldClim database and extend BIO1 to BIO19 (WorldClim). The moisture index based (mind) on potential radiation and potential evapotranspiration after Turc (ETP) have been downloaded for each month of the year and assembled with the seasons. The explanatory variables are projected according to the World Geodetic System WGS84 and the same dimensions as the study area. These data correspond to the mean of the reference period 1950-2000 have a low spatial resolution (<1km). The rasters containing the climatic variables were transformed to have the same extent as the study area.

Satistical analysis

Selection of the explanatory variables

The choice of explanatory variables is critical for the analysis. The goal is to identify the climatic variables influencing the spatial distribution of *Pinus nigra* and its subspecies. Of

these variables, only significant variables are used in the model. To do this, 20% of the presence-absence points were randomly sampled and their climatic variables extracted. Correlations between variables were then calculated and the results shown in tree form in order to highlight correlated groups of variables. To select the variables explaining most the distribution, the explained deviance (D^2) of each variable were compared to each other. The highest D^2 of each group is selected.

Model

The projections were performed using BIOMOD2 (Thuiller *et al.* 2012). Models need both information about presences and absences. In the case of non-sufficient absent data, pseudo-absences were randomly selected. The presences and absences (or pseudo-absences) were given the same weight. This means that both of them have the same importance in the calibration process of the model. The presence-absences dataset has been split in two datasets to keep a part for evaluating the model. For all the data set of presence-absences, we used regression method GAM (generalized additive model) to build the model (Hastie & Tibshirani 1990). Binary transformation was carried out on the models to predict the suitability with values between 0 and 1. This transformation was done using the threshold that maximised the TSS, true skill statistics (Allouche *et al.* 2006). TSS corresponds to the sum of sensitivity and specificity minus one. The sensitivity is the proportion of presences correctly predicted, and the specificity is the proportion of absences correctly predicted. This threshold was assigned to 0.7 with which we could consider a species as present or absent. This threshold was shown to produce the most accurate predictions (Jiménez-Valverde & Lobo 2007). The obtained models were evaluated using the area under the receiver operating characteristic (ROC) curve (AUC) (Fielding & Bell 1997) and TSS.

In the end, each common gardens and provenances were localized in the output models and got their probability of suitability extracted. This will tell us if a provenance come from the center or peripheral part of the climatic niche and where the common gardens are situated in the niche.

5. Results

The variables selected for modeling climate niches are isothermality (bio3) which corresponds to the daily amplitude divided by the annual range of temperature, the temperature seasonality (bio4) corresponding to the coefficient of variation of average weekly temperatures, seasonality of precipitation (bio4) corresponding to the coefficient of

variation of average weekly precipitation (bio15) and the moisture index during the summer (mind_summer). These variables correspond to those with high explained deviance while ensuring the balance between the variables of temperature and precipitation and also, trying not to overload the model keeping maximum five variables explaining both the distribution of the species that each subspecies. This last condition forced to find a compromise between the need for explanatory variables common to models and the need of variables with strong explained deviance. The evaluation of the models (Table 1) shows good ability of models to predict the distribution of the species *Pinus nigra* and each subspecies. Descriptions of climatic niches are made on the basis of maps encoding presences and absences in a binary manner.

Table 1: Climatic niche models evaluation based on the species or subspecies. An AUC <0.5 and a TSS close to 0 means that the model does not predict better the distribution of individuals than a random model.

	AUC	TSS
<i>Pinus nigra</i>	0.936	0.749
<i>P.nigra mauretunica</i>	1	0.998
<i>P.nigra salzmannii</i>	0.973	0.896
<i>P.nigra laricio</i>	0.999	0.996
<i>P.nigra nigra</i>	0.988	0.942
<i>P.nigra pallasiana</i>	0.983	0.926

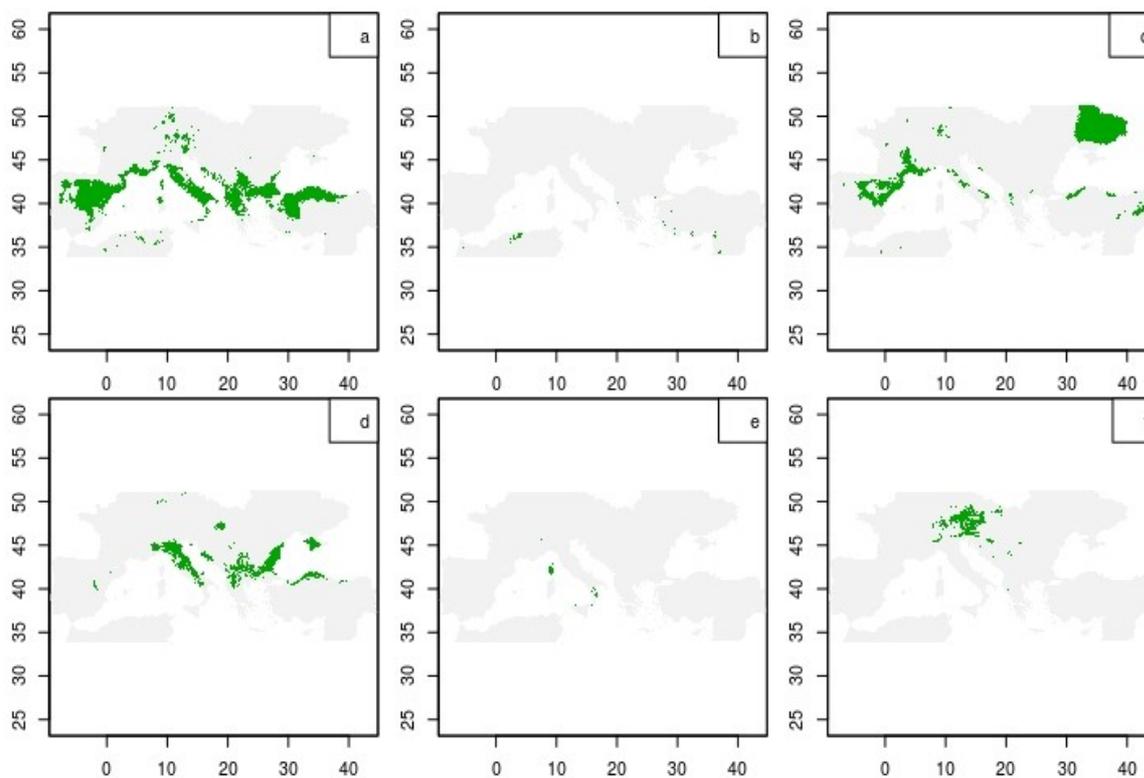
The comparison of the observed distribution of the black pine (Fig. 2) with the climatic niche of the species, without distinction of subspecies (Fig. 3a) shows that the observed individuals are in the potential distribution area. However, the model predicts a wider distribution area than it is observed. The species occurrences are recorded beyond the climatic niche and vice versa potential areas of occurrence are identified where the species has not been observed. Moreover, the limits of the potential distribution of the species are pushed to the north (southern Germany) and west (Portugal). Differences of predictions exist between the realized niche and the potential niche of the subspecies.

Figure 2: Map of observed distribution of *Pinus nigra* constructed from the points of presence of the EUFORGEN map and those in common between the JRC map and the EUFORGEN map.



The model of the subspecies *mauretanica* (Fig. 3b) describes an area favorable to the subspecies in Algeria, Greece and Turkey while the species is only referenced in Algeria and Morocco. The potential range of the subspecies *salzmannii* is very broad and extends throughout Europe to Ukraine and far beyond the observed distribution area (Fig. 3c). Its climatic niche overlaps with the one of the subspecies *pallasiana* (Fig. 3d). The latter is naturally present in Greece and Turkey (Fig. 2). The model does not predict the presence of the subspecies *pallasiana* in southern Turkey and on the contrary, predicted a strong presence in Italy (Fig. 3d). The subspecies *laricio* is observed in Corsica and Calabria, which is consistent with the projection of the subspecies (Fig. 3e). The observed distribution of the subspecies *nigra* extends from North to South, from Austria to the north of Greece and east to west, from Italy to Bulgaria. Finally, the model based on the species projects a small range in northern Europe corresponding to the subspecies *nigra*, while the model on the subspecies *nigra* (Fig. 3f) defines a larger area. However, the model predicts the subspecies *nigra* badly, if at all, in Eastern Europe and Greece.

Figure 3: Map of the potential distribution of the species *Pinus nigra* (a) and the subspecies (b) *mauretanica*, (c) *salzmannii*, (d) *pallasiana*, (e) and *laricio* (f) *nigra*. The green areas correspond to climate zones favorable to the presence of the trees.



Each site was located in the climatic niche based on the species and on each subspecies. Hence, the probability of ability of the species to become established (PS: probability of suitability) was extracted (Table 1). Overall common gardens are located in areas with low probability of occurrence of the species (<50%). The sites of Levens and Verdun are in the margin of the climatic niche of the *salzmannii* subspecies. The site Pommet is both in the climatic niche of the *salzmannii* and *pallasiana* subspecies.

Table 4: Probability of the species and subspecies to become established (PS: probability of suitability,%) in each common .

site	<i>Pinus nigra</i>	<i>P. n.mauretanica</i>	<i>P. n. salzmannii</i>	<i>P. n. laricio</i>	<i>P. n. nigra</i>	<i>P. n. pallasiana</i>
Pomet	7,9	0	10,2	0	0	0,5
Cestas	0	0	0	0	0	0
Levens	36,7	0	26,8	0	0	0
Orleans	0,2	0	0	0	0	0
Verdun	0,9	0	0,1	0	0	0
Souiniet	31,1	0	0	0	0	0

During my Master thesis I studied the radial growth of *Pinus nigra*. The Figure 4 show the average ring width of the four subspecies studied in six common gardens. The average

ring width are not significantly different between the subspecies, but the subspecies *salzmannii* appears to be the less growing.

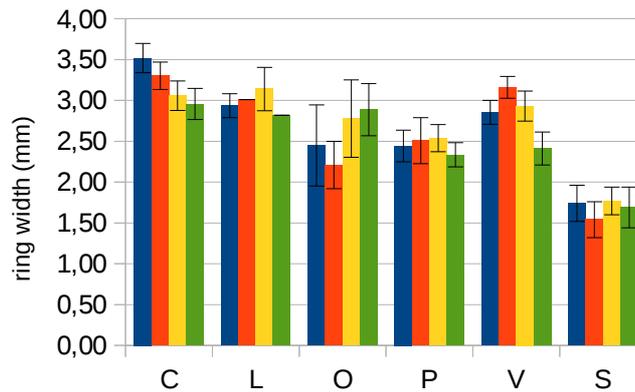


Figure 4: Mean ring width (mm) for the subspecies *laricio* (blue), *nigra* (orange), *pallasiana* (yellow) et *salzmannii* (green) in six common gardens 5 in France and the last in Tunisia : Cestas (C), Levens (L), Orléans (O), Pomet (P), Verdun (V) and Souiniet (S).

6. Discussion

The climatic niche of the species is consistent with the observed distribution of black pine, although it predicts a potential area slightly larger than the realized niche. Unrepresented areas by the models can be explained by the limitations of the climatic niche modeling. Only taking into account climatic variables, is to ignore the existence of other factors that can influence the distribution of individuals. These factors can be, soil type or land use (Coudun *et al.* 2006; Peterson & Nakazawa 2008), biotic interactions (Davis *et al.* 1998) the dispersion of species, phenotypic plasticity or local adaptation (O'Neill *et al.* 2008; Benito Garzón *et al.* 2011). In addition, since no map exists locating precisely the subspecies, the limits of distribution may not correspond to reality, especially for the subspecies *nigra* and *pallasiana* which borders are overlapping. Nevertheless, climatic niches of each subspecies are well differentiated. This differentiation can have ecological and historical explanations (Eckert *et al.* 2008). For example, the reduced range of the subspecies *salzmannii* in France is maybe the result of competition with other species such as *Quercus ilex* and *Pinus halepensis*, favored by human disturbance during the Holocene (Roiron *et al.* 2013). Moreover, dispersion may allow a species to occupy habitats that climatic niche consider as not suitable to the establishment of the species (Holt 1985; Pulliam 2000). However, barriers or constraints may also prevent dispersion of the species to occupy a habitat considered as favorable (Holt 2003). The species' history also affects its distribution. We know that past glaciation and deglaciation cycles have induced significant changes in species distribution (Davis & Shaw 2001). For example, during the last glacial maximum distribution of lodgepole pine was reduced to a number of

refuges in the United States and following the withdrawal of the ice, individuals have migrated from these refuges creating the current distribution (Wheeler & Guries 1982). Finally, a combined study of geography and genetic differences analyzed using microsatellite detected five barriers between the black pine into six groups corresponding to our six subspecies (Afzal-Rafii & Dodd 2007). The intra-specific variation of niche occupancy at the subspecies level can also be explained by differences due to availability of environments or local adaptation. For example, Murphy & Lovett-Doust (2007) shown that the niche occupancy of a *Fabaceae* varied according to the availability of regional environments. In contrast, several studies found differences in tree growth living in different environments because of local adaptation and a strong environment-genotype interaction (Rehfeldt *et al.* 1999; Savolainen *et al.* 2007).

During my master thesis I assessed the level of intra-specific variability of *Pinus nigra*. My study focused on the radial growth of the subspecies measured and provenances in six common gardens (5 in France and 1 in Tunisia). It allowed an evaluation of the genetic variability of the radial growth as well as its plasticity by comparing the growth of the subspecies between sites. When looking at the location of each comparative planting in the climatic niche of subspecies, it is expected that in a given site subspecies having the highest occurrence probability corresponds to the subspecies with the best radial growth of the site. If this relationship is observed it can be considered that there was a local adaptation of the subspecies and it would be an advantage compared to other subspecies (Kawecki & Ebert 2004). However, no such relationship was observed. In fact, the common gardens are found mainly in the climatic niche of *Pinus nigra salzmannii*, but the subspecies is on average the worst performing (Figure 4). This study does not demonstrate a local adaptation for black pine radial growth.

7. Conclusions

This study highlighted the differentiation of climatic niches of the subspecies of *Pinus nigra*. Generally the potential distribution of the species and subspecies is larger than the observed distribution. Only the subspecies *laricio* has a smaller potential distribution than the observed one. Moreover, these results coupled with those from my Master thesis have shown that despite a strong differentiation of the subspecies' climatic niches, there is a low genetic diversity across subspecies for the radial growth. This result suggests that much of the variability observed between subspecies can be explained by phenotypic plasticity.

8. References

- Afzal-Rafii, Z. & Dodd, R.S. (2007) Chloroplast DNA supports a hypothesis of glacial refugia over postglacial recolonization in disjunct populations of black pine (*Pinus nigra*) in western Europe. *Molecular Ecology*, **16**, 723–736.
- Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.
- Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3**, 327–338.
- Barja, A. del C., Borja, M.E.L., García, E.M., Serrano, F.R.L., Abellán, M.A., Morote, F.A.G. & López, R.N. (2009) Influence of stand density and soil treatment on the Spanish Black Pine (*Pinus nigra* Arn. ssp. *Salzmannii*) regeneration in Spain. *Forest Systems*, **18**, 167–180.
- Benito Garzón, M., Alía, R., Robson, T.M. & Zavala, M.A. (2011) Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*, **20**, 766–778.
- Bojovic, S., Jurc, M., Drazic, D., Pavlovic, P., Mitrovic, M., Djurdjevic, L., Dodd, R.S., Afzal-Rafii, Z. & Barbero, M. (2005) Origin identification of *Pinus nigra* populations in southwestern Europe using terpene composition variations. *Trees*, **19**, 531–538.
- Coudun, C., Gégout, J.-C., Piedallu, C. & Rameau, J.-C. (2006) Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. *Journal of Biogeography*, **33**, 1750–1763.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Davis, M.B. & Shaw, R.G. (2001) Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science*, **292**, 673–679.
- Eckert, C.G., Samis, K.E. & Loughheed, S.C. (2008) Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Molecular Ecology*, **17**, 1170–1188.
- EUFORGEN. EUFORGEN: Distribution maps. URL <http://www.euforgen.org/distribution-maps/> [accessed 11 June 2016]
- Ferrier, S. (2002) Mapping Spatial Pattern in Biodiversity for Regional Conservation Planning: Where to from Here? *Systematic Biology*, **51**, 331–363.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation*, **24**, 38–49.
- Funk, V.A. & Richardson, K.S. (2002) Systematic Data in Biodiversity Studies: Use It or Lose It. *Systematic Biology*, **51**, 303–316.
- Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized Additive Models*. CRC Press.
- Holt, R. (1985) Population-Dynamics in 2-Patch Environments - Some Anomalous Consequences of an Optimal Habitat Distribution. *Theoretical Population Biology*, **28**, 181–208.
- Holt, R.D. (2003) On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research*, **5**, 159–178.
- Isajev, V., Fady, B., Semerci, H. & Andonovski, V. (2004) *EUFORGEN Technical Guidelines for Genetic*

Conservation and Use for European Black Pine (Pinus Nigra). Bioversity International.

- Jiménez-Valverde, A. & Lobo, J.M. (2007) Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica*, **31**, 361–369.
- JRC. Index de ftp://mars.jrc.ec.europa.eu/Afoludata/Public/DS66/. URL
ftp://mars.jrc.ec.europa.eu/Afoludata/Public/DS66/ [accessed 11 June 2016]
- Kawecki, T.J. & Ebert, D. (2004) Conceptual issues in local adaptation. *Ecology Letters*, **7**, 1225–1241.
- Murphy, H.T. & Lovett-Doust, J. (2007) Accounting for regional niche variation in habitat suitability models. *Oikos*, **116**, 99–110.
- O’Neill, G.A., Hamann, A. & Wang, T. (2008) Accounting for population variation improves estimates of the impact of climate change on species’ growth and distribution. *Journal of Applied Ecology*, **45**, 1040–1049.
- Oney, B., Reineking, B., O’Neill, G. & Kreyling, J. (2013) Intraspecific variation buffers projected climate change impacts on *Pinus contorta*. *Ecology and Evolution*, **3**, 437–449.
- Pearman, P.B., D’Amen, M., Graham, C.H., Thuiller, W. & Zimmermann, N.E. (2010) Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change. *Ecography*, **33**, 990–1003.
- Peterson, A.T. & Nakazawa, Y. (2008) Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. *Global Ecology and Biogeography*, **17**, 135–144.
- Pulliam, H. r. (2000) On the relationship between niche and distribution. *Ecology Letters*, **3**, 349–361.
- QGIS, D. (2011) Quantum GIS geographic information system. *Open Source Geospatial Foundation Project*.
- Quézel, P. & Médail, F. (2003) *Ecologie et Biogéographie Des Forêts Du Bassin Méditerranéen*. Elsevier.
- R Core Team. (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2013.
- Rafii, Z.A., Dodd, R.S. & Zavarin, E. (1996) Genetic diversity in foliar terpenoids among natural populations of European black pine. *Biochemical Systematics and Ecology*, **24**, 325–339.
- Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L. & Hamilton, D.A. (1999) Genetic Responses to Climate in *Pinus contorta*: Niche Breadth, Climate Change, and Reforestation. *Ecological Monographs*, **69**, 375–407.
- Roiron, P., Chabal, L., Figueiral, I., Terral, J.-F. & Ali, A.A. (2013) Palaeobiogeography of *Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco in the north-western Mediterranean Basin: A review based on macroremains. *Review of Palaeobotany and Palynology*, **194**, 1–11.
- Rushton, S.P., Ormerod, S.J. & Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology*, **41**, 193–200.
- Savolainen, O., Pyhäjärvi, T. & Knürr, T. (2007) Gene Flow and Local Adaptation in Trees. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 595–619.
- Scaltsoyiannes, A., Rohr, R., Panetsos, K.P. & Tsaktsira, M. (1994) Allozyme frequency distributions in five European populations of black pine (*Pinus nigra* Arnold). (I) Estimation of genetic variation within and among populations. (II) Contribution of isozyme analysis to the taxonomic status of the species. *Silvae Genetica*, **43**, 20–30.

Thuiller, W., Georges, D., Engler, R., Georges, M.D. & Thuiller, C.W. (2012) Package "biomod2."

Wheeler, N.C. & Guries, R.P. (1982) Biogeography of lodgepole pine. *Canadian Journal of Botany*, **60**, 1805–1814.

WorldClim. WorldClim - Global Climate Data | Free climate data for ecological modeling and GIS. URL <http://worldclim.org/> [accessed 8 July 2016]

Annexe 1 : List of the provenances used.

<i>Code prov</i>	<i>Name provenance</i>	<i>Country</i>	<i>Species</i>	<i>Latitude</i>	<i>Longitude</i>	<i>Altitude</i>
PRIE	Priego (Sierra de Cuenca)	Spain	<i>Pinus nigra salzmannii</i>	40° 15' 12.05" N	1° 52' 15.06" O	850
FRES	Fresneda (Sierra de Cuenca)	Spain	<i>Pinus nigra salzmannii</i>	40° 55' 42.6" N	0° 04'28.3" E	1000-1050
GAGN	Gagnières	France	<i>Pinus nigra salzmannii</i>	44° 07' N	4° 17' E	200-500
PO-LV	Popova-Livada (Macédoine sud)	Yougoslavia	<i>Pinus nigra pallasiana</i>	41° 10' N	21° 55' E	1450
DOBL	Doblhoff	Austria	<i>Pinus nigra nigra</i>	48° 00' 22.83" N	16° 13' 49.77" E	280
THASII	Ile de Thassos II (Forêt communale de Prinós)	Grece	<i>Pinus nigra nigra</i>	40° 40' N	24° 40' E	600-1100
AYAN I	Ayanick I	Turkey	<i>Pinus nigra pallasiana</i>	41° 43' N	34° 31' E	1400
TZAR	Tzarvaritza (Kustendil Forêt de Gabra)	Bulgaria	<i>Pinus nigra nigra</i>	42° 1' 39"N	22° 50' 49" E	950-1150
KUST	Kustendil	Bulgaria	<i>Pinus nigra nigra</i>	42° 16' 37"N	22° 41' 29" E	900-1100
STUD I	Studenica I (Serbie)	Yougoslavia	<i>Pinus nigra nigra</i>	43° 30' N	20° 33' E	930
ASPR	Aspromonte (Cafalo-Pantonizzi)	Italy	<i>Pinus nigra laricio</i>	38° 05' N	16° 00' E	1300
PERT	Perithorion	Grece	<i>Pinus nigra nigra</i>	38° 05' N	22° 15' E	1300
YILA	Yilanli (Mugla)	Turkey	<i>Pinus nigra pallasiana</i>	37° 20' N	28° 24' E	-
MUGL	Mugla	Turkey	<i>Pinus nigra pallasiana</i>	37° 20' N	28° 24' E	900-1050
CRIM IV	Crimée IV (Aluchtin)	Russia	<i>Pinus nigra pallasiana</i>	44° 33' N	34° 17' E	500
VALD III	Valdoniello (Valdu Niellu) 3 (triage n°35)	France (Corse)	<i>Pinus nigra laricio</i>	41° 51' N	9° 06' E	1100
COSE II	Cosenza	Italy	<i>Pinus nigra laricio</i>	39° 15' N	16° 17' E	1300
CANT	Catanaro (Manouso)	Italy	<i>Pinus nigra calabrica</i>	38° 54' N	16° 34' E	-
CAZO	Cazorla (Segura)	Spain	<i>Pinus nigra salzmannii</i>	37° 50' N	3° 00' O	1500
SGUL	(Hérault) - Saint-Guilhem-le-Désert	France	<i>Pinus nigra salzmannii</i>	43° 41' N	3° 35' E	350-400
ALAC	Alaçam	Turkey	<i>Pinus nigra pallasiana</i>	39° 35' N	28° 35' E	800-1000
GRAN	Grancia (Sila Greca)	Italy	<i>Pinus nigra calabrica</i>	39.41° N	16.58° E	850
MARG	Marghèse	France (Corse)	<i>Pinus nigra corsicana</i>	41° 39' N	9° 12' E	1000
TRCO	Trenta Coste (Sila Greca)	Italy	<i>Pinus nigra calabrica</i>	39.4° N	16.58° E	1050
ALES	Brougatles Ales	France	<i>Pinus nigra salzmannii</i>	44° 07'35.4" N	4°05'09.0"E	-
PUGET	Puget Theniers	France	<i>Pinus nigra austriaca</i>	43°57'24.1"N	6°53'53.0"E	-
TAVO	Macchia della Tavola (Sila Greca)	Italy	<i>Pinus nigra calabrica</i>	379°16'45"N	16°26'59.4"E	950
OLET	Olette (Pyrénées orientales)	France	<i>Pinus nigra salzmannii</i>	42°36'01.0 » »N	2°14'25.8"E	-