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Tracking the origin of silver fir plantations along the boundary between different genetic clusters in central Apennines: Implications for their management

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ABSTRACT

Reforestation with native species determines that autochthonous populations and plantations are often within the reach of gene flow. To address efficient strategies for forest plantation management it is fundamental to track the origin of reforestation material, in order to limit potentially detrimental effects on the adaptive potential of autochthonous populations. The use of genetic information to determine the origin of plantations is very effective when historical data about reforestation programs are absent.

The main objectives of our study were to assess the origin of silver fir plantations in the Majella National Park (Central Apennines) and to compare genetic diversity parameters between plantations and natural stands. The latter objective is particularly relevant to evaluate the levels of genetic variation in plantations of local origin and to evaluate their suitability as already established reforestation stands. A comprehensive genetic dataset (1619 individuals from 33 natural silver fir populations genotyped at 16 nuclear microsatellite markers) was built to characterize potential seed sources for 10 plantations from the Majella National Park. Their genetic origin was assessed through combining the results of Bayesian assignment tests and analyses of genetic differentiation.

Based on the genetic structure characterizing natural populations, we were able to definitely assess the origin of most of the planted individuals. Five plantations were established using material which most likely originated in natural populations that are only 10–20 km distant. These plantations harbour levels of genetic variation similar to the surrounding natural populations and are, therefore, to be considered valuable local forest genetic resources. The other five plantations consist either partially or entirely of allochthonous individuals which are similar to Alpine and northern Apennine populations.

To avoid exotic gene flow to nearby autochthonous populations, we suggest the removal of plantations in which allochthonous individuals are present before they reach sexual maturity. However, before taking such action, we recommend the monitoring of the relative performance of different provenances, *i.e.* plantations entirely made by either putatively autochthonous or undoubtedly allochthonous material. Such an investigation would allow a thorough *ex post* evaluation of past reforestation programs.

To conclude, our results show that genetic data can provide essential information for general decision-making in forest plantations management and, considering the thorough characterization of silver fir genetic structure in this multi-refugial area, such information can be particularly useful for a correct management of Apennine plantations.

1. Introduction

Interspecific hybridization between native and allochthonous species has been widely recognized as a possible cause of native species' extinction (Mooney and Cleland, 2001). On the other hand, an aspect that has received little attention so far is the genetic introgression, at the intraspecific level, from plantations to autochthonous populations (Laikre et al., 2010; Steinitz et al., 2012; Thomas et al., 2014). Reforestation with native species is a common management practice, but this determines that autochthonous populations and plantations are often in the reach of gene flow (Byrne et al., 2011; Robledo-Arnuncio et al., 2009; Steinitz et al., 2012; Unger et al., 2014). Steinitz et al. (2012) quantitatively assessed gene flow between *Pinus halepensis* autochthonous populations and plantations. Their results indicated a large genetic introgression of exotic alleles in younger cohorts of autochthonous populations, providing evidence of rapid genetic homogenization. Foreseeing the effects of such introgression is not an easy task. Although exotic gene flow can lower inbreeding and increase genetic diversity, it may negatively affect fitness-related traits, in particular at the regeneration stage (Ramírez-Valiente and Robledo-Arnuncio, 2015; Unger et al., 2016). These findings indicate possible negative consequences of exotic gene flow on the adaptive potential of forest tree populations and suggest the importance of correct management practices, especially in areas where natural populations are fragmented and outnumbered by plantations.

Silver fir (*Abies alba* Mill.) is a widespread European conifer and Southern European massifs (*i.e.* the Balkans, the Apennines and the Pyrenees) represent the trailing edge of its distribution. Nowadays, Apennine beech-silver fir mixed forests are small and highly fragmented (Leonarduzzi et al., 2016; Piotti et al., 2017; Piovani et al., 2010) and are listed as priority habitats in the European Habitat Directive (*i.e.* 9220 and 9510, Natura 2000 Networking Programme). In the Apennines, a large number of silver fir plantations are present. Although an accurate estimate of their extension is not available, data about the distribution of conifer plantations (INFC, 2005) and the small size and isolation of most natural stands (Piotti et al., 2017) lead to the conclusion that plantations could have an important role in the future evolutionary dynamics of silver fir in the Apennines, influencing the distribution of its genetic variation.

To assess the consequences of exotic gene flow on the adaptive potential of autochthonous populations the performance of native, planted and hybrid individuals should be compared (Unger et al., 2016). A fundamental prerequisite for such an investigation is to exactly determine the origin of the material used for reforestation, which also implies a detailed knowledge about the genetic structure of the species at the biogeographical scale. Throughout silver fir distribution range, distinct genetic clusters are present due to a complex Quaternary history (Liepelt et al., 2002, 2009; Piotti et al., 2017). A recent study has intensively surveyed Apennine silver fir populations identifying three differentiated genetic clusters likely determined by the presence of different glacial refugia during the last glacial cycle (Piotti et al., 2017). In particular, a steep genetic barrier separating central and southern Apennine genetic clusters at the latitude of Gran Sasso and Majella massifs in central Apennines was found.

In the present work, ten silver fir plantations of unknown origin from the Majella National Park (hereafter MNP) were sampled and genetically characterized with the set of nuclear microsatellite markers (hereafter nSSRs) used by Piotti et al. (2017). To improve the genetic characterization of natural populations from which the planted material could have been collected, nine new natural populations were added to the 24 collected by Piotti et al. (2017). Overall, genetic data from 33 natural populations were used to describe the species' genetic structure in an area comprising all potential sources for silver fir reforestation material, which is a key step to assess the provenance of plantations. The main objectives of our genetic survey were: (*i*) to track the origin of silver fir plantations in the MNP, and (*ii*) to compare genetic diversity between natural populations and plantations. The latter objective is particularly relevant because comparing levels of genetic variation between plantations of local origin, if any, and surrounding natural populations allows to select already established reforestation stands to which priority should be given for conservation and re-naturalization programs. In fact, the ultimate goal of our genetic survey was to provide essential information for the correct management of silver fir plantations in the MNP to the light of a thorough evaluation of the distribution of genetic diversity in surrounding Apennine populations.

2. Material and methods

2.1. Sampling and genotyping

The study area is located in the central Apennines within the MNP which covers an area of 74.095 ha, 62% of which represented by forests (Andrisano et al., 2016). In the MNP, conifer plantations cover 4850 ha. Several silver fir plantations are present, covering about 80 ha and that were probably established during the mid 20th century from unknown seed sources. No silver fir populations of natural origin are nowadays present in the MNP since the species has been completely eradicated in this area during the XIX century (Tenore, 1827; Zecca, 1858). Conversely, natural silver fir populations belonging to two well-differentiated genetic clusters are present immediately north and south of the MNP (Piotti et al., 2017).

The ten largest silver fir stands in the MNP were sampled (Fig. 1 and Appendix A, Table A1). Nine were undoubtedly classified as plantations, given their peculiar structural characteristics (even age distribution and regular spatial distribution of individuals) and information gathered from interviews to local forest managers. In each of these plantations, needles from 25 adult individuals at least 20 m apart were sampled. The "Fossa di Pentima" stand (FOS) has a more irregular structure, with individuals up to 130 cm dbh and more than 120 yrs old (T. Andrisano and G. Ciaschetti, personal communication, 2016). As for the other stands, no documentation is available about its establishment. Considering that a natural origin of this stand could not be excluded *a priori*, 50 individuals were sampled in FOS to spatially cover the entire stand.

To determine the origin of planted individuals, we took advantage of the extensive genetic characterization of silver fir natural populations that was carried out by Piotti et al. (2017). The available dataset was enriched by adding nine natural populations from areas that represent potential seed sources for MNP plantations (Fig. 1 and Appendix A, Table A1). In particular, six Apennine populations located immediately south (RSL and CME) and north (SEG, LVE, LAG and RPM) of the study area, two populations from central Alps (SMO and VBR), and a population from Sumava Mountains, in Czech Republic (SUM), were added. As in Piotti et al. (2017), 50 adult individuals at least 20 metres apart were sampled in each natural population. All sampled individuals were genotyped at 16 unlinked and null allele free nSSRs (Aag01, Aat01, Aat02, Aat03, Aat04, Aat05, Aat06, Aat08, Aat09, Aat10, Aat11, Aat13, Aat14, Aat15 and Aat16, Postolache et al., 2014; NFF7, Hansen et al., 2005). The multiplexing and amplification procedures are reported in Postolache et al. (2014).

2.2. Data analysis

Standard genetic parameters describing within-population genetic diversity (number of alleles, *Na*; observed and expected heterozygosities, H_O and H_E; fixation index, F_{IS}) and differentiation (Hedrick's G'_{ST}) were calculated using GenAlEx (Peakall and Smouse, 2012). Allelic richness (Ar_{34}) based on rarefaction at 34 gene copies was estimated for all natural populations and plantations by FSTAT (Goudet, 1995). Differences in genetic diversity parameters between plantations and natural stands were tested with a two-way ANOVA in R (R Core