

Review

Do Silviculture and Forest Management Affect the Genetic Diversity and Structure of Long-Impacted Forest Tree Populations?

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Abstract: The consequences of silviculture and management on the genetic variation and structure of long-impacted populations of forest tree are reviewed assessed and discussed, using Mediterranean forests as a working paradigm. The review focuses on silviculture and management systems, regeneration schemes, the consequences of coppicing and coppice conversion to high forest, the effects of fragmentation and exploitation, and the genetic impact of forestry plantations. It emerges that averaging genetic diversity parameters, such as those typically reported in the assessment of forest population genetics, do not generally present significant differences between populations under certain silvicultural systems/forest management methods and “control” populations. Observed differences are usually rather subtler and regard the structure of the genetic variation and the lasting adaptive potential of natural forest tree populations. Therefore, forest management and silvicultural practices have a longer-term impact on the genetic diversity and structure and resilience of long-impacted populations of forest tree; their assessment should be based on parameters that are sensitive to population perturbations and bottlenecks. The nature and extent of genetic effects and impact of silviculture and forest management practices, call for a concerted effort regarding their thorough study using genetic, genomic, as well as monitoring approaches, in order to provide insight and potential solutions for future silviculture and management regimes.

Keywords: genetic diversity; genetic structure; forest management; silviculture; resilience

1. Introduction

Genetic diversity is a crucial biodiversity component that allows species to adapt to local conditions and to evolve in new environments, while securing their long-term adaptive potential, especially under an era of global change. An understanding of the genetic impacts of silvicultural and forest management procedures, is essential for forest genetic resource management and conservation [1,2] and sustainable management in multipurpose forestry. Forest management and silvicultural practices, such as the harvesting system, artificial and natural regeneration, regulation of species mixtures, thinning, and harvesting operations, regeneration planting and management, forest conversion schemes, etc., may impact local environmental conditions and population spatial demographic structure [2,3]. In this respect, they could influence stand population genetics and exercise a potentially strong effect on the major evolutionary forces at microscale of selection, gene flow, mating systems and genetic drift [1,2,4]. As evolutionary forces in natural ecosystems can vary a lot and exert counter-acting effects on local genetic diversity, the impact of silvicultural and forest management practices may better be seen in long-impacted forest ecosystems that have been under constant human exploitation for thousands of years and where silviculture as well as forest management, have been used for a long period. In these conditions, the human management signal is high, and in case it

exerts an influence on the genetics of the populations of forest trees, it is more likely to be detected. Mediterranean forestry fits the above description. Forests have been continuously exploited since the last glaciation period, while Mediterranean forestry today carries the history of ancient and medieval management systems for coppice and high forest management, influenced by the “formal” forest management and silvicultural systems that have been developed originally in central and northern Europe since the 19th century.

Among planet Earth’s 34 biodiversity hot spots [5] is the Mediterranean basin. In the Mediterranean area that corresponds to less than 1.5% of the total land mass of the planet, more than 10% of the world’s biodiversity in higher plants is present. The Mediterranean higher plant biodiversity is mostly localized within forests which host more than 25,000 species of vascular plants, about 50% of which are endemics [6]. In fact, the total number of both forest tree species and endemic forest species is higher in the Mediterranean than in other Mediterranean type ecosystems, such as in California [7]. Forest tree species richness and endemism are also high (290 indigenous tree species and 201 endemics) and their genetic diversity is extraordinary [6]. Mediterranean conifers, for example, present a higher within population diversity than conifers of any other area [8]. Furthermore, Mediterranean populations of species with a continental distribution frequently are among the most variable in terms of their genetic diversity (e.g., [9]). All of the above have been the outcome of a complex geological, climatic, and anthropogenically influenced evolution of species, ecosystems, and landscapes that in this peculiar geographical setting is manifested even at a small spatial scale. The Mediterranean basin is characterized by an uneven forest distribution. The northern Africa and the Near East parts correspond to 35% of the total forest area, while the European Mediterranean part corresponds to the remaining 65%. Forest cover, as a percentage of the country area, differs among Mediterranean sub regions as well. It ranges from only 1–8% and 5–10% in Southern and Eastern countries, respectively, while in the northern Mediterranean countries it varies between 20% and 30% [10]. Humans populate densely the Mediterranean basin (currently more than 460 million people), while in eastern and southern Mediterranean, human populations are still deeply reliant on terrestrial ecosystem natural resources. Fifteen years ago Bariteau et al. [11], asserted that “the increasing severity of drought, climatic change and a series of anthropogenic influences, contribute to forest decline in the Mediterranean; there is a definite need for the protection of forest genetic resources of low elevation Mediterranean conifers especially in south and east Mediterranean countries”.

This notion that stresses the compounding current and anticipated stress in Mediterranean forests brings forward the issue of their resilience. Resilience is defined as the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks [12]. Forest ecosystem resilience can be defined as the capacity of an ecosystem to absorb disturbance and reorganize while undergoing change in order to retain essentially the same function (processes and properties), and ecosystem services. Genetic diversity is regarded as a component that can provide a basis for resilience, while forest management can affect ecosystem resilience, in fact management can be used to ensure ecosystem resilience (resilience-based management [13]).

Modern forest management and silviculture constitute an array of cultivation systems and distinct rules applied in the natural forest. They are widely applied in the Mediterranean region in the middle of the 19th century (in the northern part) and by the conclusion of the 19th century (in the southern and eastern parts). Forest management was principally an adoption of the predominant northern and central European forest management approaches and practices which have been used (with minimal modification) to the most productive temperate forests of the Mediterranean. Their focus is wood production in the realm of “multipurpose forestry”, the latter usually confined to the provision of beneficial externalities. Silvicultural management is using an array of guidelines targeted at the development of growing stocks, determining rotation periods and their chronological and spatial distribution, facilitating regeneration (reforestation) and controlling the structural pattern and tree density by thinning [14]. Forest management, as an anthropogenic activity, has been mainly exercised

to cover human needs. Upon its application, it has altered progressive forest succession and original forest composition and structure [14].

2. Genetic Impact of Silviculture and Forest Management Practices

2.1. Forest Management and Regeneration

Perhaps the most important issue in forest management and silviculture that may affect the genetic constitution of future forests, concerns the handling of the regeneration. Besides being the most obvious silvicultural practice, it may lead to possibly drastic changes of genetic structure for more than one generation. Natural regeneration may suffer by the potential employment of only a few set-aside trees that have been selected as seeders for the next generation. Such a practice would result in negative genetic consequences, namely the reduction of effective population sizes and the manifestation of genetic drift. Thinning and harvesting operations may also have a stern impact on adaptive and economically significant traits due to positive or negative selection regarding specific phenotypes. Moreover, there is a risk of carryover effects that relate to epigenetic memory regulation induced by temperature during post-meiotic megagametogenesis and seed maturation [15], or by climatic conditions during germination and early growth [16]. This epigenetic impact can have prolonged consequences for instance in (such as bud break, bud set and in the regeneration, and affecting adaptive traits [15,16]. Such phenomena, observed mainly in conifers, are attributed to complex epigenetic inheritance of DNA methylation patterns [17,18]. All of the above may head towards the loss of genetic variation and adaptive potential, particularly if gene flow via pollen is rigorously limited by differential (either considerably low, or high) population densities [4,19]. Such effects have been well documented in forest ecosystems [4,20–22] and are mainly prominent in age-class forestry. They are also apparent in the (common to the Mediterranean) conversion of coppice to seedling forest and regeneration after fire when only few mature trees are left. Continuous-cover forestry where a permanently irregular structure is maintained through the selection and harvesting of individual trees and close-to-nature silviculture where minimum necessary human intervention is used to accelerate the processes that nature would do by itself, rely fully on minimal selective cutting, and hence do not in theory modify genetic diversity, besides any underlying natural selection processes.

The genetic systems of forest trees should be rather resilient to rational harvesting, given forest tree genetic and life history characteristics [23]. However, the practical evaluation of the results of silvicultural procedures on vital genetic processes of the main economically important species, is generally scarce. In the Mediterranean, the consequences of shelterwood and group selection cutting regeneration methods, on the mating systems and pollen movement in *Pinus sylvestris* L. natural populations in Spain, were studied by Robledo-Arnuncio et al. [24]. No significant effects of stand thinning on mating system parameters were found. It has been indicated that the *Pinus sylvestris* pollination system is well adapted to prevent an adverse influence of these regeneration methods. In fact, it appears that density reduction tends to upsurge the effective number of pollen donors and pollen flow, in line with the results of Karlsson and Örlander [25] who showed that *P. sylvestris* seed production increases, after cutting. Robledo-Arnuncio et al. [24] suggest that a raise in pollen donor number and seed production might somewhat counterweigh the decrease in maternal numbers, i.e., compensate for population reduction due to silvicultural thinning. A number of reports imply a minor deficit of low-frequency alleles among residual trees and natural regeneration, following to shelterwood harvesting (e.g., Adams et al. [26]), however, most analyses did not find any notable effects of silvicultural practices on the genetic variation parameters of regenerated stands [24]. Several factors may sustain population genetic structure under forest management and silvicultural measures, such as high gene flow from adjacent non-harvested stands and considerable effective population sizes. The results of Robledo-Arnuncio et al. [24] are in congruence to earlier findings which showed that stand density variation and different cutting methods did not result in substantial mating system parameter modifications, at least regarding wind-pollinated temperate tree species [27–29].

2.2. Post-Fire Natural Regeneration

One particular aspect of regeneration management in fire-prone ecosystems is regeneration after forest fires. Forest management and silvicultural measures aim to promote natural regeneration (usually through protection from grazing and use artificial reforestation only when natural regeneration seems to fail, typically 2–3 years after the fire event). Despite the general notion that forest fires have adverse effects in the forest gene pool, pertinent studies that examine this question are limited. Whenever basic genetic variation parameters that reflect the magnitude of genetic diversity in natural populations were examined, no significant differences between post-fire and control populations have been observed. Nevertheless, when the genetic architecture of post-fire and control populations were studied, it was found that relevant genetic parameters were generally lower in post-fire populations [30].

Forest fire effects on population genetics were studied in Greek populations of *Pinus brutia* and *Pinus halepensis*. The effects of differential forest fire history in the genetic diversity of regeneration after fire of *P. halepensis* were studied in a transect spanning from a general NE to SW direction, that presents significant differences in the frequency and severity of fires ranging from relatively low (NE end) to extremely high (SW end). *P. halepensis* populations presented high genetic variation, absence of inbreeding and Hardy-Weinberg equilibrium in areas with different fire incidence. Gene frequencies in areas with high and relatively low incidence of fires did not show statistically significant differences. High forest fire occurrence and damage (reflected by a forest fire damage index) was not correlated either positively or negatively with genetic diversity parameters [30], in congruence to relevant results by Krauss [31], England et al. [32] and Uchiyama et al. [33]. With regards to *P. brutia*, an assessment of genetic variation (observed heterozygosity and gene diversity) and structure (variation between mature populations that had survived ground fire events (“maternal” stands, or control populations) and populations of the regeneration (“progeny” stands, or post-fire populations), showed a lack of substantial changes in the amounts of genetic variation among the remaining post-fire populations and regeneration [34]. These results are similar to results reported in pertinent literature regarding *Picea* [35]. However, a shift was found in rare allele frequencies (including rare allele loss at a small scale), the occurrence of interspecific hybridization in the post-fire populations and the observation of some genetic bottleneck effects (rare allele frequency change and loss, changes in the frequency of heterozygotes) [34].

Hence, forest fires may not induce genetic erosion in forest tree populations per se, especially when population sizes are large and in reproductive maturity, natural distribution is continuous, and regeneration is abundant. However, there are indications that under particular circumstances, compounded in periods of high forest fire frequency and intensity, forest fires may have adverse consequences for the architecture of forest tree genetic variation and their long-term survival and existence.

2.3. Artificial Regeneration

The need for artificial regeneration (post-fire failure of stand establishment, forest destruction, overgrazing, etc.) is usually considerable, especially in fire-prone areas. The issue of the genetic quality of the plant material used for artificial regeneration is an emerging topic in research and in forest management. Artificial regeneration may suffer by a non-autochthonous origin of the seedlings and a potentially restricted genetic base. Using an allochthonous genetic resource may in theory enrich the local gene pool, but at the same time it may result in outbreeding depression. The use of genetically improved material in reforestations (depending on the protocols used) does not necessarily alleviate the above problems. The major question of concern is the use of certified forest reproductive material (FRM) “source identified, selected, qualified, or tested” [36] (the latter potentially genetically improved) over local randomly chosen seeds and the associated issues of genetic quality, amount of genetic diversity, and adaptive potential of the material chosen. Besides the choice of the material used, the potential adverse genetic implications of nursery practices have long been known [37]. Every step in FRM production, from mother tree phenotypic selection and stand seed collection to

artificial planting that includes seed processing and storage, nursery conditions and operations [37], mass production and grading of seed and seedlings, as well as breeding operations and potential FRM transfer, can have an effect on genetic diversity mainly by directional selection [38].

The quality of the genetic material used in artificial regeneration of *Quercus suber* was investigated in Portugal [39], where dwindling reforestation success was attributed to inferior genetic quality of the reproductive material used in reforestation [39,40]. Observable effects of artificial regeneration have also been detected in conifer populations. In a study of *Pinus brutia* in Turkey, Kandedmir et al. [41] reported considerable genetic variation within and among forest stands, but no distinctive genetic variation patterns according to elevation, geography, or breeding zones [42]. They suggest that this finding can be ascribed to intensive forest management and to the substantial use of artificial regeneration [41].

The effects of using genetically improved material in artificial regeneration were investigated by Bouffier et al. [43] and by Içgen et al. [44]. Bouffier et al. [43] studied in successive breeding populations of *Pinus pinaster*, the evolution of genetic variation regarding selected traits in France. By using as a base line the forest where selected trees originated, they have found a notable reduction of quantitative genetic variation in the population of selected plus trees (especially for height and diameter). They further compared the genetic diversity of the latter “plus trees” to the genetic variation of the population that comprised of plus tree progenies (second step of artificial selection). In this case, genetic variation was not significantly altered [43]. Içgen et al. [44] studied the probable influence of forest management and use of artificially selected and genetically improved plant material on established *Pinus brutia* plantations in Turkey. They conveyed that seed source (seed stands, orchards, plantations originating from the same area) genetic relationships differed with respect to seed source locations. In line with Bouffier et al. [43], Içgen et al. [44] reported the presence of genetic changes between initial selection at the seed orchard (plus tree selection phase) level and established plantation level (selected seed/seedling production phase). Generally, it is apparent that the use of genetically improved material for artificial regeneration which has resulted from typical artificial selection and breeding processes may reduce the genetic base of the planting material. It is up to the forest manager to decide the advantages and disadvantages of the use of genetically improved material over a restriction of the genetic base.

3. Management Systems: Seedling vs. Coppice Forests

Coppicing is a traditional vegetative regeneration system which takes advantage of the resprouting ability of many tree species. Coppicing has been prevalent as an ancient forestry practice, in particular in areas where special wood products are needed (wood poles of small dimensions, firewood). Modern forest management and silviculture have been attempting to limit this system and convert coppice forest to seedling high forest. Nevertheless, a considerable amount of coppice forests is still present (for instance more than 8 million ha in the Mediterranean). Stand structure and density differs in the two systems, potentially affecting gene flow and mating patterns, while in rapidly changing environments, local adaptation of lasting coppice forests may be compromised due to the absence of sexual reproduction. These issues reflect a biological basis for investigating genetic differences in differentially managed populations.

The genetic effects of this management method has been studied primarily in Fagaceae species that historically have been managed as coppice forests for hundreds of years, namely chestnut (*Castanea sativa*) and oak (*Quercus* spp.). Various studies have contrasted typical genetic variation parameters (percent polymorphic loci, allelic richness, gene diversity, and observed heterozygosity) between coppice forest and (usually geographically proximal) seedling high-forest. With regards to *C. sativa* there is a general agreement that the genetic diversity parameters between seedling high forest and coppice forest do not differ significantly [45–48]; a result that has been established by using different genetic markers. Nevertheless, a more in-depth analysis of genetic data identified some differences between these management systems. Aravanopoulos and Drouzas [47] have studied high forest-coppice pairs, each of them situated in the same geographical area. Geographic proximity is

essential in such comparisons in order to exclude possible provenance effects. The chestnut high forest populations studied were true old-growth seedling populations and the coppice populations have been managed as such for centuries. It was found that the distribution of genetic diversity differed between the two management systems. Coppice populations appear to retain a higher percentage of within population genetic diversity compared to seedling high-forest populations. Some young seedling recruits are also found within coppice forests, but gene flow is clearly higher in the latter. As original stools were old (aged at 250 years on the average) and records suggest that coppice management has been employed since antiquity, these results may indicate a potential for higher within population differentiation and slower evolutionary response for coppice populations in a contemporary time of rapid environmental change [47]. Mattioni et al. [48] have identified weak (nonetheless significant) differences in two-locus allelic correlations between naturalized stands (“natural” stands which originated from abandoned anthropogenically managed populations, most likely old orchards) and coppice forests in a linkage disequilibrium analysis. They suggested that long-standing management methods could affect the population genetic composition, although their results may have possibly been inflated by one-locus disequilibria that could not be assessed by the dominant inter simple sequence repeat (ISSR) markers that they used. In fact, the clonal (to a varying extent) nature of the coppice forest (several ramets originating from the same genet) may increase the global allelic correlation among loci of the forest and decrease effective population size [48,49]. Genetic differences were also found between standards and coppice shoots in a *Quercus cerris* coppice forest under conversion [50]. Therefore, all studies indicated some differences in the genetic structure between natural (seedling) high forest and coppice populations, despite the absence of differences in averaging genetic diversity statistics.

Mating systems were studied in a pair of an old-growth natural seedling *C. sativa* population and one coppice population located in the same geographical area in Greece by Papadima et al. [51], as mating systems parameters are important when planning coppice conversion to high forest. Parental stands were evaluated based on an analysis of 16 codominant loci in 27 trees per population. Twenty seeds per tree from eight of the above trees were also genotyped for the same loci in order to derive mating system parameters. Inbreeding was very low in both population types with an upper bound somewhat higher in the coppice population and was solely attributed to consanguineous mating and bi-parental inbreeding. Pollen and ovule allele frequencies did not show marked differences. Overall, results indicated the absence of strong differences in the mating system parameters of the two population types [51]. A quantitative genetics comparison between an old-growth seedling high forest chestnut population and a coppice population located in the same area was attempted by Alizoti et al. [52]. The genetic structure (variance between and within these populations) of seven seedling quantitative traits was investigated. Heterogeneity was higher within than between the old-growth and coppice populations growing in the same environment. High genetic correlations among all quantitative traits were found in the coppice population in contrast to the seedling one, where a high genetic correlation was observed for seedling height and leaf length only [52]. These results may imply a higher genetic uniformity for the coppice population for quantitative adaptive traits.

The genetic diversity and clonality levels in the oak *Quercus pyrenaica* were studied in Iberian high forest and coppice populations by Valbuena-Carabaña et al. [53]. Results showed that the considerable genetic diversity levels detected were comparable under these different silvicultural systems [53]. Results are in concordance to similar investigations presented above regarding *Castanea sativa* (e.g., [47–49]). Nevertheless, in a preliminary comparative study on the genetic diversity of standards compared to coppice shoots in *Quercus cerris* under conversion, [50] found a reduced genetic variation in the standards. The latter reports differences in averaging genetic statistics among different management components in a Fagaceae species. All other pertinent studies identified subtler disparities among populations. Clearly, more studies are needed in this area.

The genetic effects of coppice conversion to high forest have been insufficiently studied thus far and the few relevant studies reported non-concordant results. Valbuena-Carabaña et al. [53] advice against intensive conversion practices of *Q. pyrenaica* coppice into seedling (high) forest due to the anticipated significant reduction in genetic variation when unique genotypes were taken away. Ortego et al. [54] found an extensive clonal structure of *Quercus ilex* coppice with high number ramets constituting a single genet and reached similar conclusions. The arguments against intensive thinning of Valbuena-Carabaña et al. [53], may be regarded as somewhat in contrast to those made by Mattioni et al. [48], concerning their observation that the coppice management system may increase the total allelic correlation among loci and decrease effective population size, while thinning operations in (over-mature) coppice will reverse these trends. Indeed, fundamental genetic theory suggests that population inbreeding is a function of effective population size [55] and therefore thinning of old coppice may offset genetic drift, and assist ultimately in the preservation of the inherent genetic variation diversity [48].

Overall, genetic diversity between seedling high forest and coppice forest does not appear to differ significantly, while there is also absence of strong differences in mating system parameters. On the other hand, long-term management techniques have an impact as coppice populations, present high clonality and higher genetic uniformity for quantitative adaptive traits and appear to present a slower evolutionary response. From a genetics and ecology perspective coppice conversion to high forest is a favorable prospect, as coppice management may potentially reduce the evolutionary rate of local adaptive potential. Conversion to high forest may reinstate natural succession in forest ecological dynamics and restore a more typical course of evolution and adaptation in an era of rapid environmental change [47]. In addition, it may reduce genetic drift and increase effective population sizes. However, thinning intensity must be moderate in order not to result in unique genotypes being lost [53].

4. Forest Management: Fragmentation and Over-Exploitation

The genetic outcomes of forest fragmentation and overexploitation are not well known. Forest fragmentation is the emergence of spatial discontinuities that break large, contiguous, forested areas into smaller pieces of forest causing population fragmentation and ecosystem destruction. Forest exploitation refers to the long-term intensive mis-management of forests that result in forest ecosystem degradation and inability to provide forest products and ecosystem services. In theory, forest fragmentation may cause a reduction or loss of genetic connectivity. Both forest fragmentation and overexploitation may lead in a reduction of effective population size and inbreeding depression, which will eventually result in a decrease in species genetic variation and fitness.

Certain studies report a notable deficit of genetic diversity and enlarged genetic differentiation after forest fragmentation and reduction of tree density, while others fail to establish such effects [56,57]. Contrasting results may be expected for perennial organisms like forest tree species which exhibit vastly different life history characteristics, temporal scales of sampling and time-frame that has elapsed since fragmentation [57]. Recent studies of Mediterranean species, such as in *Taxus baccata* [58] and *Plantago brutia* [59], point towards the negative genetic consequences of forest fragmentation as an outcome of intensive management. Ortego et al. [54] suggested that intensive management leading to long-term population fragmentation induces negative genetic consequences, such as reduced pollen exchange, augmented genetic differentiation between different management units, erosion of resident genetic diversity and the prevalence of asexual over sexual reproduction. An ample volume of empirical data indicates that forest trees are sensitive to fragmentation [60], however, the available evidence has been a matter of debate, principally regarding temperate forests [61], since in numerous situations fragmentation might have been rather new and fragments may encompass notable remaining forests. Particular reports have even indicated that fragmentation will create open landscapes and facilitate pollen movement which may counterweigh anticipated adverse genetic consequences [57].

Over-exploitation effects in the genetic structure of forest tree populations were explored in a study of *Pinus brutia* in Turkey [42]. Over-exploited populations under intensive forest management were compared to natural populations that provided a background benchmark of genetic diversity.

No significant differences between the two population types were found in genetic polymorphism and heterozygosity [42]. However, a homozygosity excess was observed (about 6% higher) in over-exploited populations, suggesting the potential influence of inbreeding in these populations. Intensive forest management, fragmentation, reduction of standing wood, and reduction of crown closure did not seem to result in drastic changes in the amount of genetic diversity [42]. The authors warn though that genetic diversity may gradually diminish over subsequent generations, if over-exploitation pertains [42,57].

Overall, case studies do indicate that both fragmentation and overexploitation may have adverse effects on genetic diversity, but generalized conclusive statements cannot be made given the variety of forest ecological conditions, field situations during sampling, study approaches and species life history characteristics.

5. Genetic Impact of Forestry Plantations

Plantation forestry is a major form of forestry practice that is expected to increase in the future in terms of land use, wood volume produced, and socio-economic importance. Worldwide, planted forests constitute almost 7% of the total forest area [62], exceeding an area of 250 m ha worldwide [63], while at least 33% of the planet's industrial round-wood derived from plantations by 2012 [64]. Plantation forestry may also impact the genetic diversity of forest species [65]. Plantation germplasm is precisely selected for the optimal performance of economically important quantitative traits, a selection procedure that could result in a more restricted genetic base for ensuing generations and in the weakening of local adaptation in natural forests. Clearly in the choice between genetic gain and genetic diversity, the number of parental seed trees (e.g., from a seed orchard or arboretum) used to provide the FRM is crucial: a low number will cause inbreeding among progeny, while a large number will increase genetic diversity and reduce differentiation among plantations. Forestry plantations are the first step in forest tree domestication, a process where the choice, nursery production and transfer of FRM may affect genetic diversity and future local adaptation [36,37,66] (see also Section 2.3).

Plantation forestry is usually spatially proximal to natural forest and employs in many cases the same species or genera as the natural forest, a result of tuning species selection to local ecological, edaphic and climatic requirements. Plantation to natural forest gene flow, forms an essential (however, not yet well studied) threat of genetic introgression from exotic conspecifics into indigenous populations. Large scale plantation forestry is frequently associated with a mechanized plantlet production from seed sources unrelated to the planting site. From the population genetics perspective the most important harmful consequence is artificial genetic homogenization, namely the progressive upsurge in genetic similarity between introduced and native gene pools through gene flow [67]. In this respect, anthropogenically brought gene flow of exotic origin may ultimately overwhelm locally adapted genotypes in natural populations.

An excellent relevant case study is the work of Steinitz et al. [68] on the results of forest plantations on the genetic constitution of conspecific native *Pinus halepensis*, a highly resilient species to stressful environments. The study considered natural *Pinus halepensis* populations with diverse levels of spatial separation from neighboring conspecific plantations approximately 40 years after plantation establishment. Results showed that native populations in two locations were significantly different from their respective surrounding plantations. Allele frequency changes (presence of novel alleles, common cohort allele frequency alterations), among different age classes (mature tree age classes, natural regeneration) were observed. Changes in allele frequencies were due to considerable gene flow from the plantations as was an increase in the genetic variation of the young age class. A notable result of forest plantations on the genetic variance within and between native proximal conspecific populations has been detected, resulting in a modification in the genetic constitution of the natural population younger age classes. Steinitz et al. [68] demonstrated that even in cases of highly isolated natural populations, elevated aggregate rate of gene flow over a period of many years will result in a strong long-term genetic contamination from plantations. Changes in allele frequencies produced by incoming gene flow may have potentially adverse effects in native populations. Plantations comprised

of faraway provenances exert a gene flow that could result in a migration load (outbreeding depression) in the recipient population [69]. Even a small genetic difference between native and non-indigenous populations may endanger widespread local adaptations [70] for multilocus quantitative traits [71].

An additional outcome of widespread gene introgression from plantations bearing exotic material is the genetic homogenization of the various native populations. The anthropogenically induced gene flow by plantation establishment may disrupt local adaptive complexes and induce genetic homogenization in natural populations, especially if they are small compared to plantation size. In *P. halepensis* it was found that genetic divergence among natural forests was lower at the younger age class which indicates a genetic homogenization process [67,68]. These results are concordant to other reports concerning brutia pine (*P. brutia* Ten.) [41] reported considerable genetic variation within and among *P. brutia* stands in Turkey, but no distinct diversity patterns according to elevation, geography, or breeding zones. It has been suggested that the extensive use of artificial regeneration from non-local sources homogenized genetic diversity patterns in natural populations [41,42]. Another characteristic example is with regards to *Pinus nigra* var. *salzmanni* in southern France, where natural populations cover about 5000 ha (non-native planted *Pinus nigra* covers >200,000 ha), putting the integrity of the indigenous genetic resources at risk of contamination [72].

Plantation genetic diversity was studied in Syria where plantations constitute most of the forest cover. *P. brutia* plantations exhibited a notable decrease in mean genetic variation parameters compared to natural populations and were more genetically differentiated [73]. The stronger genetic differentiation in plantations may reflect the low number of seed trees from only a few populations that contributed to planted progenies [73]. In the same study, plantations of *Cupressus sempervirens* did not manifest a significant decline in mean genetic diversity, but were also more differentiated. The former result may be associated to an elevated gene flow among natural source populations and an overall uniform genetic variation present in natural forests.

Overall, the reduction of genetic variation found in plantations, may be regarded as an expected outcome of the selection process during domestication. Moreover, the demonstrated genetic introgression from non-local plantations (as well as introgression from artificial regeneration based on non-local sources within the natural forest) and the ensuing genetic homogenization of natural indigenous forests calls for a thoughtful reassessment of silviculture, afforestation, and forest management strategies and guidelines. Genetic homogenization results in a reduction of spatial gene diversity and variation in quantitative traits, and could reduce the capacity for adaptation to environmental change, weakening the resilience of biological communities [67,68]. These results clearly show once more that the prerequisite for the preservation of the needed elevated levels of genetic variation among forest plantations, is a well-planned seed collection from a large number of trees originating from well-established populations.

6. Conclusions and Perspectives

Silviculture and forest management systems have an influence on the genetic variation and structure of the populations of forest trees. Silvicultural and management systems, such as those referring to the management of natural regeneration systems, artificial regeneration using plant material of various origin, seedling, coppice and under conversion forest, fragmentation and overexploitation, as well as the establishment of plantations, influence genetic parameters. Nevertheless, forest tree populations appear to be generally highly resilient to forest management practices. Averaging genetic variation parameters, do not present significant differences between populations exposed to specific forest management methods and “control” populations. Observed differences are rather subtler and regard primarily the structure of the genetic diversity. Potentially negative differences of forest management approaches for instance refer to gene flow, effective population size, rare allele frequencies, founder effects, and disruption of local adaptive complexes. An adverse influence on genetic diversity and structure appears to be more noticeable in intensive forest management situations.

Because of environmental change and anthropogenic impact, species and ecosystem resilience in Mediterranean forests needs to be high. Neutral and adaptive genetic diversity provides a mechanism reinforcing both population perseverance and persistence of ecosystem functions [74], and loss of genetic diversity may reduce resilience [75]. As the impact on genetic diversity of silviculture and forest management practices used in the Mediterranean does not generally appear to be substantial, resilience associated to genetic diversity is not largely expected to be compromised in the immediate future as an upfront result of management practices. To the level that genetic diversity affects species resilience [75,76], there is no direct cause of concern for species resilience by the silviculture and forest management practices used. However, some of the finer genetic changes found, especially those dealing with genetic connectivity and effective population size, may eventually decrease fitness [74,77] and exert some unfavorable influence on the long-term resilience of Mediterranean forests.

Overall, the silviculture and forest management genetic impacts on long-impacted ecosystems, call for cautious methodologies, practices and policies at the strategic and operational levels, under the scope of sustainable multi-purpose forestry.

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