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The effect of silvicultural management on the genetic diversity of a mixed *Nothofagus* forest in Lanín Natural Reserve, Argentina

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ABSTRACT

Knowledge of the impact of forest management practices is crucial to allow the use of natural resources while ensuring the sustainability of genetic variation, which is essential for the potential adaptive capacity of forests. The main objective of this work was to study the effects of a seed cut on the genetic diversity of a mixed *Nothofagus* forest in northwestern Andean Patagonia. Silviculture based on the shelterwood system was carried out in stands composed of *Nothofagus dombeyi*, *Nothofagus nervosa* and *Nothofagus obliqua*, located in Lanín Natural Reserve (Neuquén province, Argentina). Through intensive sampling of pre (mature trees) and post (regeneration) harvest populations of all three species from a 3-ha plot established after 20 years of the silvicultural intervention, in combination with microsatellite genotyping (more than 2000 individuals with 15 markers), we determined that modification of relative abundance of species in the post-harvest population that followed the implemented management had altered the global genetic diversity of the mixed forest; however, no impact was detected at species level in the entire plot or in two subplots with different species proportions. Pollen and seed dispersal from the surrounding areas may have contributed significantly to maintaining both genetic diversity in the post-harvest natural regeneration and the low differentiation between this and the pre-harvest gene pool in all species. The use of species-specific markers allowed us to determine that the level of introgressive hybridization was not changed by management; however, further studies are required to evaluate whether this practice influences the directionality of introgression.

1. Introduction

Forest management practices, altering environmental conditions and forest stand structures, may impact genetic diversity and population genetic structure in harvest populations (Finkeldey and Ziehe, 2004). The development of management strategies that foster self-sustaining forest requires an understanding of the impact of these practices on the diversity of forest ecosystems (it ensures the availability of favorable ecological conditions for a wide variety of species), species diversity (it provides security when facing unpredictable environmental conditions), and genetic diversity (it facilitates adaptation to changing environments) (El-Kassaby, 2000). Hence, comprehension of the consequences of disturbances to within-population genetic structure can be crucial to the conservation of forest genetic resources through appropriate management (Piotti et al., 2012).

Silvicultural selection represents an anthropogenic force through which sometimes large numbers of trees, and the genes they contain, are removed from a natural system (Schaberg et al., 2008). The cleaning of young stands of inferior phenotypes or the removal of high value trees (phenotypes with commercially important traits such as growth, and stem straightness) may impact genetic diversity in mature tree populations if the phenotype is correlated to a particular genotype, and also in the next generation, if the forest is regenerated naturally (Finkeldey and Ziehe, 2004; Paffetti et al., 2012). The impact of management could also be seen in species diversity if it modifies the abundance of different species among the mature trees or the environmental conditions that selectively influence the establishment of different species, which

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in turn is expected to determine the global genetic constitution of the managed forest. Management activities may have an impact on the genetic diversity of the next generation (post-harvest regeneration) due to the reduction in effective population sizes, thus limiting dispersal of genes through seed and pollen. Variance in the contribution to regeneration among mature trees is one of the main factors affecting genetic diversity and inbreeding in finite populations. Another factor that affects genetic diversity in the seeds is the spatial distribution of the reproductive trees after selection (Lefèvre, 2004). Mixed forest management could also modify patterns of inter-specific hybridization or force new inter-specific crosses (Gallo et al., 1997) through modification of the relative abundance of species, stand densities and spatial distribution of the reproductive trees, which all have an impact on the mating system (Lefèvre, 2004). With regard to all these factors, the same silvicultural system applied in sites with different species proportions could have different effects on the genetic diversity of the populations. Genetic variation in natural regeneration also depends on the amount of gene flow from surrounding forests, and therefore the effects of reduced population size on levels of genetic variation may be balanced by gene flow for species with efficient dispersal means for pollen and diaspores (Finkeldey and Ziehe, 2004).

Thus, silvicultural practices involving natural regeneration, regulation of species mixtures, thinning, and harvesting operations could have a strong influence on the evolutionary forces (drift, mating systems, gene flow and selection) that shape the genetic variation (Finkeldey and Ziehe, 2004), essential for forests to have the potential to adapt to climate change (Lefèvre et al., 2012). Contrasting evidence for the effect of management on genetic diversity in tree populations has been reported, and depending on the tree species and silvicultural methods used, this ranges from negative (El-Kassaby et al., 2003; Glaubitz et al., 2003; Paffetti et al., 2012; Rajora, 1999) to none (Buiteveld et al., 2007; Fageria and Rajora, 2013, 2014; Marquardt et al., 2007; Rajendra et al., 2014; Westergren et al., 2015). Therefore, the effects depend upon the species, its life-history traits, demography, geographic distribution, ecological characteristics and harvesting and regeneration regimes (Ratnam et al., 2014). This controversy, coupled with a lack of information concerning the impact of silvicultural management on genetic diversity in mixed forests (only 20% of the 39 studies reviewed for Ratnam et al., 2014 included more than one species), calls for further evidence. New knowledge in mixed forests analyzing the impact on genetic diversity, at community (mixed forest) and species level for all comprised species, should help to conserve genetic variation for forest sustainability, ecosystem stability and the continued adaptation and survival of forest trees (Fageria and Rajora, 2013; Rajora, 1999).

Nothofagus dombeyi (Mirb.) Oerst. (coihue), *Nothofagus nervosa* (Poepp. et Endl.) Oerst. (raulí) and *Nothofagus obliqua* (Mirb.) Oerst. (roble pellín) (Nothofagaceae) are forest trees of southern South American temperate forests; which can occur in pure or mixed forest. They are wind-pollinated, outcrossing, and anemochorous trees with limited seed dispersal (c.a. 100 m, Donoso, 1993). Among South American beeches, seed production was studied for several species (e.g. *Nothofagus nitida*, *Nothofagus glauca*, *N. dombeyi*, *Nothofagus pumilio*, *N. obliqua* and *N. nervosa*) revealing that this is a discontinuous and irregular phenomenon, characterized by mast events (more than 15 million viable seeds per ha) that usually occur every two or three years (Donoso, 1993; Marchelli and Gallo, 1999). *N. nervosa* and *N. obliqua* are deciduous species belonging to the subgenus Lophozonia, whereas the evergreen *N. dombeyi* belongs to the subgenus *Nothofagus*. According to the revised classification of Heenan and Smissen (2013), the subgenera are actually considered as genera; but this change does not alter the phylogenetic relationships between Nothofagaceae species. Natural hybridization has been reported in mixed forests between species belonging to the same pollen type (e.g. Donoso et al., 2004; Marchelli and Gallo, 2001; Premoli et al., 2012; Stecconi et al., 2004), which strongly correlates with phylogenies within Nothofagaceae (Heenan and Smissen, 2013; Manos, 1997).

The relevance of these species lies in their broad distribution area, abundance and timber production. In Argentina this forest covers 313.000 ha, ranging from 39° 29′ and 40° 22′ S and 71° 15′ and 71° 40′ O (Lara et al., 1999). Silvicultural management of mixed *Nothofagus* forests has been carried out within Lanín Natural Reserve jurisdiction (40° 9′ S and 71° 21′ O) since late 1980, mainly following the shelterwood system. This system consists in successive regeneration fellings which retain partial forest cover until the regeneration phase is complete (approximately 20 years). The purpose of the cuts is to leave a homogeneous canopy cover of around 30–40% pursuing homogenous distribution of the residual trees, maintaining the original relative species composition of the mixed forest, to produce seeds for natural regeneration and to provide shelter for the young seedlings (Chauchard, 1989). However, its impact on the genetic diversity of these forests is still unknown. Thus, the main objective of this work was to study the effects of a seed cut on the genetic diversity of a mixed *Nothofagus* forest in northwestern Andean Patagonia (Argentina). Hybridization dynamics between *N. obliqua* and *N. nervosa* was also evaluated since new inter-specific crosses could occur through modification of demographic structure (e.g. relative abundance of species, spatial distribution of the reproductive trees) due to management of mixed forest (Gallo, 2004). So based on mentioned information we hypothesized that harvesting practices would influence patterns of intra and inter-specific crosses, modifying the genetic diversity of the post-harvest natural regeneration of mixed *Nothofagus* forests, although we could not predict the direction of the change as management consequences have combined effects on the mating system (e.g. reduction in stand density could increase inbreeding and gene flow which decrease and increase genetic diversity respectively). We also hypothesized that the impact would vary depending on the relative abundance of species in the managed populations.

2. Materials and methods

2.1. Study area

The study area is located on Cerro Quilanlahue (40° 8′ S and 71° 28′ O), at 930 m a.s.l., and lies within Lanín Natural Reserve (Neuquén province, Argentina). This is a mixed stand composed entirely of *N. dombeyi*, *N. nervosa* and *N. obliqua* with an understory dominated by a Bambuseae (*Chusquea culeou*). The area is north facing, lies across an elevation range of 40 m and the soils are classified as Andisoles (Ferrer et al., 1991). The climate is humid temperate, with a mean annual temperature of 9 °C and total annual precipitation of 1800 mm (dataset 1998–2013 from the Quechuquina weather station, Autoridad Interjurisdiccional de Cuencas de los ríos Limay, Neuquén y Negro).

In 1993, a seed cut was carried out in the study area. After that intervention it was unmanaged, because the canopy cover reached the value pursed by management strategy (c.a. 40%; see Introduction). A 3 ha rectangular plot was established in this area in 2009. The structure of the stand was previously characterized by dendrometric parameters, such as number of stems per hectare, basal area per hectare, diameter and tree heights and ages of mature trees and regeneration (Sola et al., 2015), indicating that: (a) the forest was at a mature stage, and (b) matures and pre-harvest regeneration was dominated by *N. nervosa,* while this species represented a minority of post-harvest regeneration. Age of post-harvest