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## Genetic effects of forest management practices: Global synthesis and perspectives



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### ABSTRACT

Understanding the genetic impacts of forest management practices is crucial for conservation and management of forest genetic resources. Forest management practices based on selective and clear cut systems followed by natural or artificial regeneration can impact population structure and mating patterns, thus gene flow and genetic diversity. Survival and productivity of both tree and non-tree species can be compromised or, possibly, enhanced. The extent of genetic impacts depend on the management system applied, stand structure as well as species' distribution, demography, biological attributes and ecology. The impact of management practices is reviewed and synthesized for temperate, boreal and tropical forests based on experimental and simulation studies. In addition, the effects of genetically improved planting materials and establishment of large scale plantations on natural forests are examined. Recommendations are made for genetically sustainable forest management practices.

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## 1. Introduction

### 1.1. Forest management practices

Forest management aims at the sustainable provision of multiple goods and services from forests (Mendoza and Prabhu, 2000). Wood is often the most important product and its management is the subject of this review. Non-timber forest products and the provision of ecosystem services also need to be considered in sustainable silvicultural systems (Pearce et al., 2003). Long generation times of forest trees and rotation cycles often preclude the rapid adoption of changed management regimes on large forested areas.

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However, the role of biodiversity in forest ecosystems (Bengtsson et al., 2000) or impacts of global change and climate warming and the role of forests in this context (Bolte et al., 2009; Schlamadinger and Marland, 1996) are eventually reflected in forest management guidelines and recommendations (Lindner, 2000).

Forest management systems are manifold even though they do not fully reflect the enormous biodiversity within and among forest ecosystems (Günter et al., 2011). Different societal demands and different public pressures are important drivers creating a variety of silvicultural approaches to manage forests (Kimmings, 2008). The most important and universal aspects related to the regeneration, stand development and harvesting of managed forests which impact genetic diversity are described in this section.

Regeneration is the basic process that maintains forest ecosystem dynamics and, as such, is a key aspect of any sustainable forest management system (Ackzell, 1993). The fundamental distinction between natural regeneration based on seed and seedlings or veg-

etative propagules and artificial regeneration by planting or, less frequently by direct seeding, is particularly important for forest genetic resources (FGR). Artificial regeneration disrupts the continuous evolution of tree populations at a given site, but opens opportunities for increasing genetic diversity and enhancing productivity through the selection of superior provenances (White et al., 2005). Natural regeneration allows the transmission of genetic information to the next generation, but does not preclude adaptive and non-adaptive changes of genetic structures during the regeneration phase (Rajora and Pluhar, 2003). Silvicultural treatments such as enrichment planting, that mainly aim to enhance the value of secondary tropical forests (Schulze et al., 2008) by planting seedlings in patches where natural regeneration failed, exemplify options that combine artificial and natural regeneration in flexible silvicultural systems. The issue requires careful study since Schwartz et al. (2013) indicate positive effects when post-harvest silvicultural treatments are applied to increase the number of valuable trees. Another example that combines natural and artificial regeneration is the conversion of pure stands into mixed forests. The admixed species is frequently introduced by planting seedlings or by direct seeding, whereas the species to be converted contributes to the next generation by natural regeneration (Ammer et al., 2008).

Thinning operations are the main silvicultural techniques used for increasing the commercial value of forest stands during their development (Rötzer et al., 2010; Zeide, 2001). The growth of the most valuable trees within the stand is promoted and their spatial distribution optimized by removing trees of inferior quality. Since selective thinning is based on a phenotypic assessment of the trees in a stand, changes at a genetic level are expected when quantitative (e.g., height or diameter growth) and qualitative (e.g., stem form) traits used for selecting trees are at least partially under genetic control (Finkeldey and Ziehe, 2004).

Harvesting operations start after trees attain their target dimensions. Clear cutting after a stand reaches its rotation age followed by artificial regeneration is the most simple and widespread system. Partial harvesting systems such as shelterwood systems, seed tree cut, single or group selection or target diameter tree cuttings need to be combined with specific measures to enhance reproduction and survival of the next generation or to maintain pre-existing regeneration if economical or ecological reasons call for natural regeneration (Pommerening and Murphy, 2004). The number, spatial distribution and phenotypic criteria used for the selection of seed trees potentially influence the genetic structure of the next generation (Finkeldey and Hattemer, 2007).

## 1.2. Importance of genetic diversity

Without genetic diversity, evolution is impossible. Without adaptation, population size eventually declines, which can result in local extinction (Keller and Waller, 2002). At the ecosystem level, genetic diversity of keystone species (those whose effect is disproportionately large relative to their population size, such as many forest trees, see Mills et al., 1993) can affect species diversity in associated communities (Vellend and Geber, 2005; Whitham et al., 2006). As described below, the genetic diversity of trees species is a key component of forest ecosystem functioning.

Tree species are among the most genetically diverse organisms on Earth (Hamrick and Godt, 1992; Savolainen and Pyhajarvi, 2007). Natural selection can foster rapid local adaptation and thus can explain some of this diversity, often expressed as clines or mosaics across the distribution range of the species for key fitness-related traits such as survival, growth, phenology of growth and flowering, and resistance to drought and pests (Ducousso et al., 1996; Fallour-Rubio et al., 2009; Neale and Kremer, 2011; Savolainen et al., 2007).

Populations may also differ genetically for reasons other than responses to selection. Demographic processes, such as bottlenecks following catastrophic or founder events, and long distance migration during colonization, may imprint the genetic composition of populations just as (and often more) severely than natural selection (e.g., Conord et al., 2012; Liepelt et al., 2009; Magri et al., 2006 for Europe and the Mediterranean). Genetic drift may lead to extinction via inbreeding depression. Gene flow from other more diverse populations, via seed and pollen, can restore diversity, stop a decline to extinction and facilitate adaptation.

Thus, natural selection, genetic drift and gene flow collectively affect the genetic diversity of populations and either promote or hamper local and range-wide adaptation. In managed forests, silviculture can significantly modify the environment, and thus significantly affect both selection and demographic processes (André et al., 2008; Hawley et al., 2005; Lacerda et al., 2008; Oddou-Muratorio et al., 2004). Determining the thresholds and tipping points that truly affect FGR, however, remains a challenge.

## 1.3. Factors influencing genetic variability

Regeneration, from fecundation to seed dispersal and seedling recruitment, is a key stage affecting genetic diversity in natural forest tree populations. It is also a key stage in managed forests where foresters can modify the natural processes listed below. Demographic factors such as pollen and female flower quantity, flowering synchronicity, number, aggregation and density of congeners and their spatial distribution, act to modify the genetic diversity and structure of a forest population (Oddou-Muratorio et al., 2011; Robledo-Arnuncio and Austerlitz, 2006; Restoux et al., 2008; Sagnard et al., 2011; Vekemans and Hardy, 2004). The more adult trees are involved in reproduction, the higher the genetic diversity of the seed crop is likely to be. The mating system, whether it is predominantly outcrossed, mixed or selfed and whether long distance pollination is possible, also acts strongly on the genetic make-up of seedlings by supporting more or less gene flow into the population (Robledo-Arnuncio et al., 2004). Seed, whether they are dispersed near or far from seed trees, also affect gene flow among populations (Oddou-Muratorio et al., 2006; Bittencourt and Sebbenn, 2007). The higher the gene flow (via pollen and seed), the more genetically diverse populations will be. Consequently, different populations may be more similar when gene flow is high, with a negative trade-off for local adaptation when ecological gradients are steep (Le Corre and Kremer, 2003, 2012). Although there are exceptions, habitat fragmentation, on the other hand, will most likely reduce gene flow and promote differentiation (Young et al., 1996).

Because trees are long-lived, detecting which environmental factors affect most their genetic diversity is not straightforward. Selection at germination and recruitment stages may affect traits differently than at the adult stage. For example, early-stage shade tolerance for seedlings may be favored in dense populations whereas light tolerance will be important at later stages for the same tree (Poorter et al., 2005). Similar trade-offs can apply to disease and pest resistance (which can be ontogenic-stage-specific) or water use efficiency. At the population level, selection for light will favor fast growing and vigorous seedlings in dense stands, whereas in marginal stands resistance to drought might be a desirable trait.

## 1.4. Potential genetic impacts of forest management practices

Forest management practices which modify tree density and age class structure, at different stages during a forest stand rotation, can have strong effects on genetic diversity, connectivity and effective population size (Ledig, 1992). In essence, and depending on strength, the effect of silvicultural practices may be similar

to that of natural disturbances which are known to affect both selective and demographic processes (Banks et al., 2013). At one end of the silvicultural spectrum, clear cutting could have similar genetic effects as pest outbreaks, wild fires or storms (see Alfaro et al., 2014, this special issue). These may severely decrease population size and connectivity and thus increase differentiation, genetic drift and inbreeding in adult trees, but not necessarily at the regeneration stage (El-Kassaby et al., 2003). At the other end of the spectrum, with close-to-nature type forestry, management effects may be closer to those of localized dieback and browsing, which will probably not affect the overall genetic diversity of adult trees but could promote inbreeding and genetic drift at the regeneration stage, if the spatial pattern of adult trees is modified (Sagnard et al., 2011). The main difference between natural and silvicultural disturbances resides in the fact that forest managers choose the trees they remove and those that remain for regeneration at all stages during a forest stand rotation, and thus have the potential to exert a rational effect on forest genetic resources (Wernsdörfer et al., 2011). Within the same type of silvicultural practice, genetic responses may of course differ widely among species and populations depending on their biological attributes and ecological status, for example, their spatial distribution, shade tolerance and mating system. These differences as well as the general principles described above are discussed in Sections 2–4 dealing with regional challenges for forest management practices, where examples of genetic characterization undertaken using molecular markers that can facilitate the study of genetic impacts of alternative practices (Rajora and Mosseler, 2001a,b) are summarized (see also Table 1). Genetic impacts of large scale plantations on native forests are discussed in Section 5. In Section 6 of this review we conclude with key areas for research and recommendations for management based on genetic studies.

## 2. Genetic impacts of forest management practices in temperate and boreal forests

### 2.1. North America

North America has about 17% of the world's forest resources, with a forest area of about 679 million ha in 2010 (FAO, 2011a). Of this, 310 million ha resides in Canada, 304 million ha in USA and 65 million ha in Mexico. North American forests have been grouped into many forest regions based primarily on physiography, ecozone and forest cover types. Canada has 11 forest regions (Rowe, 1972). The boreal forest region is the largest of all, extending from Alaska to Newfoundland. Canada's boreal forest is one of the world's largest remaining intact forest ecosystems and forms two-thirds of Canada's total forest area. The boreal forest is dominated by a few spruce (*Picea*), fir (*Abies*), poplar (*Populus*) and birch (*Betula*) species. Forest fires have been an integral part of the boreal forest ecosystems, and boreal forest trees are adapted to fire disturbances, which facilitate stand replacement/ regeneration. Boreal forests are usually managed by clearcut harvesting followed by natural and artificial regeneration. Forest trees in other North American temperate forest regions are managed by both clearcut and partial-cut harvesting followed by natural and artificial regeneration systems. Several forms of partial-cut systems, such as shelterwood, seed tree, patch cut and group selection, are implemented. Of these, shelterwood and seed tree methods have been commonly used. The harvesting and tree retention intensities in partial-cut systems vary from species to species and region to region. Forest management practices based on clear and partial cuts can affect genetic diversity differently.

Studies on the genetic impacts of forest management practices in North American forest trees are limited and have focused only

on a small number of economically and ecologically important conifers (Krakowski and El-Kassaby, 2004), which have predominantly outcrossing mating system and strong inbreeding depression.

#### 2.1.1. Clearcut harvesting followed by natural or artificial regeneration

Variable results have been obtained for genetic impacts of clearcut harvesting and natural and artificial regeneration systems in boreal and temperate forest trees in the region. In white spruce (*Picea gaucha*) – a widely distributed transcontinental and late successional boreal species – genetic diversity of natural pristine old-growth and post-harvest young natural regeneration was significantly higher than that of the post-harvest plantations and phenotypic selections (Rajora, 1999) based on RAPD markers. The genetic diversity of post-harvest young natural regeneration was similar to that of unharvested old-growth. In a subsequent study, using microsatellite markers, similar patterns of genetic diversity among old-growth, young natural regeneration, plantations and phenotypic selections were observed (Fageria and Rajora, 2014). These studies, while differing in some conclusions, demonstrated that genetic diversity can be maintained by natural regeneration systems in white spruce. In a related study, post-clearcut natural regeneration had higher genetic diversity than post-clearcut artificial regeneration in shortleaf pine (*Pinus echinata*) (Raja et al., 1998).

In another widely distributed transcontinental boreal species, black spruce (*Picea mariana*), which is an early successional species (Hosie, 1979), post-fire natural mature, post-fire natural young, post-harvest natural young and post-harvest planted populations showed similar genetic diversity levels and latent genetic potential based on allozyme, c-DNA based sequence tagged site (STS) and microsatellite markers (Rajora and Pluhar, 2003; Rajora et al. unpublished data). The results suggested that forest fires, and clearcut harvesting and natural or artificial regeneration silvicultural practices, do not adversely affect genetic diversity of black spruce. The results are consistent with the reproductive biology and regeneration processes of the species. The cones of black spruce are semi-serotinous and trees can retain cones from several preceding seed years, providing a genetically diverse pool of seed. The semi-serotinous cones remain partially closed and disperse seed over a period of several years, providing an adequate supply for regeneration after fire or harvest (Fleming and Mossa, 1996; St Pierre et al., 1992; Viereck and Johnston, 1990). Furthermore, the seeds of black spruce remain viable in fallen cones for over 10 years (Schooley et al., 1979). Black spruce typically seeds promptly and regenerates well after both forest fires and clearcut harvesting (Fleming and Mossa, 1996; Sirois and Payette, 1989; St Pierre et al., 1992). All of these features would favor maintenance of high levels of genetic diversity in post-fire and post-harvest naturally regenerated stands. In another study, no significant allelic heterogeneity (allele frequency differences) was reported among mature and young naturally-regenerated, and young planted, black spruce from Ontario (Knowles, 1985).

Similar results were also reported for another early successional boreal-temperate species with semi-serotinous cones – lodgepole pine (*Pinus contorta* var. *latifolia*) – which has a distribution in western Canada and the north-west United States. Genetic diversity for microsatellite and RAPD markers was found to be similar in fire-origin unmanaged mature, post-harvest naturally regenerated young, and planted young, stands in Alberta (Thomas et al., 1999). However, in a subsequent enlarged study based on allozyme markers, harvest-origin stands were found to have significantly lower genetic diversity than the unmanaged fire-origin stands (Macdonald et al., 2001). There were no significant differences in genetic diversity between post-harvest naturally-regenerated and planted stands.

**Table 1**  
Summary of key studies on genetic effects of forest management practices in different regions of the world.

| Region   | Species  | Mating system/<br>Pollen dispersal         | Other relevant traits                                       | Silvicultural practices  | Stand types studied  | Key results   | References  |
|--|--|--|---|--|--|---|---|
| North America  | <i>Picea glauca</i>  | Predominantly outcrossing, wind-pollinated | Boreal, late successional                                   | Clear-cut harvesting, tree improvement   | Natural old-growth, natural regeneration, plantations, tree improvement selections | Reduced genetic diversity ( $A$ , $A_e$ , $H_e$ , $H_o$ and genotypic diversity [ $G_A$ ]) in plantations and phenotypic selections as compared to natural old-growth and natural young regeneration                        | Rajora (1999), Fageria and Rajora (2014)                            |
|  |  |  |   | Experimental harvesting of increased intensities (green tree retention after 75%, 50%, 20% and 10%, and clear-cut) | Natural old-growth, natural regeneration harvesting of five intensities            | No negative impact of harvesting of five increased intensities on genetic diversity, inbreeding ( $F_{IS}$ ) and population structure   | Fageria and Rajora (2013)   |
|  | <i>Picea mariana</i>                                       | Predominantly outcrossing, wind-pollinated | Boreal, early successional semi-serotinous cones            | Clear-cut harvesting, artificial and natural regeneration, forest fires  | Natural mature, post-harvest and post-fire natural regeneration and plantations    | No adverse effects on genetic diversity ( $A$ , $A_e$ , $H_e$ , $H_o$ and genotypic diversity [ $G_A$ ]) and inbreeding levels  | Rajora and Pluhar (2003)  |
|  |  |  |   | Clear-cut harvesting   | Natural mature, natural young, plantations   | No significant allelic heterogeneity among different stand types  | Knowles (1985)  |
|  | <i>Pinus contorta</i>                                      | Predominantly outcrossing, wind-pollinated | Boreal, temperate, early successional semi-serotinous cones | Clear-cut harvesting   | Natural mature, post-harvest natural young regeneration, plantations               | No significant differences in genetic diversity of unmanaged mature, post-harvest naturally regenerated young and planted young stands  | Thomas et al. (1999), Macdonald et al. (2001)                       |
|  | <i>Pseudotsuga menzeisii</i>                               | Predominantly outcrossing, wind-pollinated | Temperate, shade tolerant                                   | Shelterwood, group selection, clear-cut  | Natural old-growth, residual trees, post-harvest seed, plantations                 | No negative impacts on genetic diversity and mating system; loss of rare alleles after shelterwood harvesting   | Neale (1985), Neale and Adams (1985), Adams et al. (1998)           |
|  | <i>Pinus strobus</i>                                       | Predominantly outcrossing, wind-pollinated | Temperate and boreal, early to late successional            | Seed tree (removal of 75% trees), shelterwood, pine release  | Natural old-growth, post-harvest residual and natural regeneration                 | Significant reduction in allelic and genotypic diversity after seed tree cut, loss of 20–90% rare and low-frequency alleles; no significant reduction in heterozygosity after any of the three harvesting systems practised | Buchert et al. (1997), Rajora et al. (2000), Marquard et al. (2007) |
|  | <i>Tsuga heterophylla</i>                                  | Predominantly outcrossing, wind-pollinated | Temperate montane, shade tolerant                           | Patch cut, shelterwood cut, green tree retention   | Natural mature, natural young regeneration   | No negative genetic impacts of patch cut and green tree retention; shelterwood system resulted in lower heterozygosity  | El-Kassaby et al. (2003)  |
|  | <i>Abies amabilis</i>                                      | Predominantly outcrossing, wind-pollinated | Temperate montane, shade tolerant                           | Patch cut, Shelterwood cut, green tree retention   | Natural mature, natural young regeneration   | No significant impacts of silvicultural treatments on genetic diversity   | El-Kassaby et al. (2003)  |
|  | <i>Tsuga canadensis</i>                                    | Predominantly outcrossing, wind-pollinated | Temperate, shade tolerant                                   | Selection and diameter limit cuts  | Natural mature, natural young regeneration   | Change in allele frequencies and genetic structure  | Hawley et al. (2005)  |
| <i>Pseudotsuga menzeisii</i> , <i>Tsuga heterophylla</i> , <i>Thuja plicata</i> , <i>Pinus monticola</i> , <i>Abies amabilis</i> | Predominantly outcrossing to mixed-mating, wind-pollinated | Temperate                                  | Commercial thinning   | Pre- and post-commercially thinned plantations   | Loss of 1–7 alleles  | El-Kassaby and Benowicz (2000)  |   |

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Table 1 (continued)

| Region                            | Species  | Mating system/<br>Pollen dispersal          | Other relevant<br>traits | Silvicultural<br>practices   | Stand types<br>studied   | Key results   | References   |
|-----------------------------------|--|---|--------------------------|--|--|---|--|
| Northern and<br>Central<br>Europe | <i>Pinus sylvestris</i>  | Wind-pollinated                             |                          | Shelterwood cut,<br>group selection cut  | Natural  | Non-significant increase in gene flow, outcrossing rate, and reduction in consanguineous mating   | Robledo-Arnuncio et al. (2004)                         |
|                                   | <i>Fagus sylvatica</i>   | Wind-pollinated                             |                          | Low vs. high management intensity  | Natural  | No effect, but slight increase in $F_{is}$ in less managed stands   | Buiteveld et al. (2007)                                |
| Mediterranean                     | <i>Pinus brutia</i>  | Wind-pollinated                             |                          | Over-exploitation  | Natural  | No reduction in genetic diversity. Slight increase in inbreeding  | Lise et al. (2007)                                     |
|                                   | <i>Castanea sativa</i>   | Wind-/insect-pollinated                     |                          | Natural regeneration/<br>coppice   | Natural/<br>coppice  | No reduction in genetic diversity by silvicultural practice   | Amorini et al. (2001)                                  |
|                                   |  |   |                          | Natural regeneration/<br>coppice   | Natural/<br>coppice  | No reduction in genetic diversity or change in mating system parameters by silvicultural practice   | Aravanopoulos et al. (2001),<br>Papadima et al. (2007) |
|                                   |  |   |                          | Natural regeneration/<br>coppice   | Natural/<br>coppice  | Some differences in within population genetic diversity and gene flow between the management systems  | Aravanopoulos and Drouzas (2003)                       |
|                                   |  |   |                          | Natural regeneration/<br>coppice   | Natural/<br>coppice  | Some differences in population genetic make-up between the management systems   | Mattioni et al. (2008)                                 |
|                                   | <i>Quercus pyrenaica</i>   | Wind-pollinated                             |                          | Coppice/coppice under conversion to seedling forest                                  | Coppice  | Intensive thinning in the populations under conversion resulted in significant losses of genetic diversity  | Valbuena-Carabana et al. (2008)                        |
|                                   | <i>Quercus ilex</i>  | Wind-pollinated                             |                          | Fragmentation  | Coppice  | Reduction of genetic diversity, increase of genetic differentiation   | Ortego et al. (2010)                                   |
| <i>Taxus baccata</i>              | Wind-pollinated  |   | Fragmentation            | Natural  | Demographic bottlenecks, high levels of inbreeding, strong genetic structure | Dubreuil et al. (2010)  |  |
| Australia                         | <i>Eucalyptus sieberi</i>  | Insect-pollinated                           |                          | Clear cut with sowing, seed tree retention with mechanical/fire disturbance, control | Natural  | No differences in genetic diversity parameters. Genetic homogenisation in sowing and bottleneck in seed tree retention  | Glaubitz et al. (2003b)                                |
|                                   | <i>Eucalyptus consideriana</i>   | Insect-pollinated                           |                          | Clear cut with sowing, seed tree retention   | Natural  | Significant reduction in genetic diversity parameters. Genetic drift in seed tree retention. No increase of inbreeding  | Glaubitz et al. (2003a)                                |
| South East<br>Asia                | <i>Scaphium macropodum</i>   | Insect-pollinated                           | Light demanding          | Selective logging  | Natural  | Genetic diversity not affected  | Lee et al. (2002a,b)                                   |
|                                   | <i>Shorea curtisii</i>   | Insect-pollinated                           | Shade tolerant           | Selective logging  | Natural  | Outcrossing rates reduced   | Obayashi et al. (2002)                                 |
|                                   | <i>Koompassia malaccensis</i> ,<br><i>Dryobalanops aromatica</i>   | Predominantly outcrossed, insect-pollinated |                          | Recent or past (50-yrs) selective logging  | Natural  | Reduction of genetic diversity of <i>K. malaccensis</i> by past logging. Increase of genetic diversity of <i>D. aromatica</i> (seedlings and saplings) immediately after logging                | Lee et al. (2007)                                      |
|                                   | <i>Shorea leprosula</i> , <i>Shorea ovalis</i>   |   | Shade tolerant           | Selective logging and simulation methods   | Natural  | Species with different breeding systems (outcrossing vs. apomictic reproduction) are affected differently by the same logging intensity; impacts to outcrossed being lower compared to apomicts | Ng et al. (2009)                                       |
|                                   | <i>Shorea leprosula</i> , <i>Scaphium macropodum</i> , <i>Parkia speciosa</i> , <i>Daemonorops verticillaris</i> , <i>Garcinia malaccensis</i> , <i>Calophyllum ferrugineum</i> var. <i>oblongifolium</i> , <i>Labisia pumila</i> , <i>Tectaria singaporeana</i> | Varied mating systems and pollinators       |                          | Selective logging  | Natural  | No decline in genetic diversity in regenerated stands. Loss of genetic diversity in mature trees and increase in genetic diversity in seedlings/saplings in immediately logged stands           | Wickneswari (2011)                                     |

Table 1 (continued)

| Region        | Species  | Mating system/<br>Pollen dispersal  | Other<br>relevant<br>traits | Silvicultural<br>practices                         | Stand types<br>studied | Key results  | References                                       |
|---------------|--|---|-----------------------------|--|------------------------|--|--|
| Latin America | <i>Dicorynia guianensis</i> , <i>Sextonia rubra</i> , <i>Symphonia globulifera</i> , <i>Voucapua americana</i> | Large bees, small insects, perching birds, hummingbirds, small bees, and trips as pollinators |                             | Selective logging (Reduced Impact Logging – RIL)   | Natural                | Small differences in genetic parameters between control and logging scenarios  | Degen et al. (2006)                              |
|               | <i>Carapa guianensis</i>   | Moths, small bees as pollinators  |                             | Selective logging – RIL                            | Natural                | Similar levels of genetic diversity and allelic richness between pre- vs. post-logging; no difference in out-crossing rates, as well as no significant levels of biparental inbreeding. Low levels of pollen pool differentiation were found between pre-vs. post-harvesting | Cloutier et al. (2007)                           |
|               | <i>Carapa guianensis</i> , <i>Sextonia rubra</i>   | Moths, small bees as pollinators  |                             | Selective logging – RIL                            | Natural                | High levels of pollen flow and no significant levels of biparental inbreeding  | Cloutier et al. (2007)                           |
|               | <i>Hymenaea courbaril</i>  | Bat-pollinated  |                             | Selective logging – RIL                            | Natural                | RIL affected the gene pool and spatial genetic structure of the reproductive population  | Lacerda et al. (2008)                            |
|               | <i>Bagassa guianensis</i>  | Wind/thrips-pollinated  |                             | Selective logging – RIL                            | Natural                | No significant differences observed for genetic diversity and spatial genetic structure  | Silva et al. (2008)                              |
|               | <i>Manilkara huberi</i>  | Insect-pollinated   |                             | Selective logging – RIL                            | Natural                | High and consistent inbreeding level and significant genetic spatial structure due to limited seed and pollen flow   | Azevedo et al. (2007)                            |
|               | <i>Symphonia globulifera</i>   | Bird- and insect-pollinated   |                             | Selective logging – RIL<br>Selective logging – RIL | Natural<br>Natural     | Outcrossing rate and level of correlated mating not affected<br>Mating system not affected   | Carneiro et al. (2007)<br>Carneiro et al. (2009) |
|               | <i>Bagassa guianensis</i> , <i>Hymenaea courbaril</i> , <i>Manilkara huberi</i> , <i>Symphonia globulifera</i> | Several pollination systems   |                             | Selective logging – RIL                            | Natural                | Loss of alleles, genotypes and increased genetic distances observed for all species, but effective number of alleles, expected and observed heterozygosities and fixation index little affected  | Sebben et al. (2008)                             |
|               | <i>Swietenia humilis</i>   | Insect-pollinated   |                             | Fragmentation                                      | Natural                | Lower spatial genetic structure  | White et al. (2005)                              |
|               | Review of 23 neotropical species   | Various pollination mechanisms  |                             | Fragmentation                                      | Natural                | No general effect on genetic diversity, but sometimes significant increase of inbreeding and decline of reproductive output and fitness  | Lowe et al. (2005)                               |

### 2.1.2. Selective (partial) harvesting systems followed by natural or artificial regeneration

Genetic impacts of selective harvesting in temperate North American species depend upon the species and the harvesting system. Shelterwood and group selection harvesting systems showed no negative impacts on genetic diversity and mating system in Douglas-fir (*Pseudotsuga menzeisii*) (Neale, 1985; Neale and Adams, 1985; Adams et al., 1998). However, rare alleles were lost after shelterwood harvesting. In eastern white pine (*Pinus strobus*), with the harvesting of about 75% of the trees (close to seed tree cut), allelic diversity was reduced by about 25%, and most other genetic diversity parameters were reduced by 25–60% in the post-harvest residual gene pool (Buchert et al., 1997; Rajora et al., 2000). Between 20% and 90% of low frequency and rare alleles were lost after harvesting. However, heterozygosity was not found to be sig-

nificantly reduced by harvesting as it is not as sensitive to bottlenecks and perturbations in populations as allelic richness. The shelterwood cutting of about 20% of trees in eastern white pine resulted in genetic diversity reductions of about 7% for the number of alleles in postharvest residual stands (Rajora et al. unpublished data), while there was no reduction in heterozygosity. In another study, shelterwood harvesting appeared to have had no negative impacts on genetic diversity (Marquard et al., 2007). Therefore, shelterwood harvesting appears to have less drastic effects on genetic diversity than an approximate seed tree cut in eastern white pine.

Genetic impacts of patch cut, shelterwood cut and green tree retention were evaluated in western hemlock (*Tsuga heterophylla*) and amabilis fir (*Abies amabilis*) in coastal montane forest using allozyme markers (El-Kassaby et al., 2003). No significant impacts

of silvicultural treatments on genetic diversity of amabilis fir were detected, whereas the shelterwood system resulted in lower heterozygosity in western hemlock. Selection and diameter limit cuts also changed the genetic structure in eastern hemlock (*Tsuga canadensis*) (Hawley et al., 2005).

### 2.1.3. Experimental harvest of variable retention followed by natural or artificial regeneration

Most of the studies on genetic impacts of forest harvesting and renewal practices are based on existing operational harvesting treatments, as controlled experimental harvesting and regeneration experiments are long-term and very expensive. There are three such experiments reported so far in North America; of these EMEND (Ecosystem Management Emulating Natural Disturbance) is the most comprehensive, large-scale and elegant (EMEND, 2014). At the EMEND project site, genetic diversity, inbreeding levels, and population genetic structure of white spruce in conifer-dominated and mixedwood forest, were similar between unharvested control or preharvest old-growth and post-harvest natural regeneration after five harvesting treatments (green tree retention of 75%, 50%, 20%, and 10%, and clearcut), with clearcut showing no negative genetic impacts (Fageria and Rajora, 2013). Adams et al. (1998) examined the effects of shelterwood, group selection and clearcut harvesting in Douglas-fir in a replicated experiment. There was no negative impact of any of the three management systems and natural and artificial regeneration on overall genetic diversity. However, rare alleles were lost after harvesting in the shelterwood system. El-Kassaby et al. (2003) conducted their study as a part of the partially replicated MASS (Montane Alternative Silvicultural Systems) project involving shelterwood, patch-cut, and clearcut harvesting systems. As already noted above (Section 2.1.2) these silvicultural treatments did not show any negative impact on the genetic diversity of amabilis fir, but heterozygosity was reduced in western hemlock following the shelterwood system.

### 2.1.4. Commercial thinning

Very little information is available on the impacts of commercial thinning on the genetic diversity of North American forest trees. Although genetic diversity was not significantly reduced after commercial thinning in two Douglas-fir plantations in British Columbia, there were losses of 1–7 alleles after thinning in Douglas-fir and the associated species western hemlock, western red cedar (*Thuja plicata*), western white pine (*Pinus monticola*) and Pacific silver-fir (*A. amabilis*) (El-Kassaby and Benowicz, 2000). No negative impacts of pre-commercial thinning were observed in fire-origin and harvest-origin stands of lodgepole pine (Macdonald et al., 2001).

## 2.2. Northern and Central Europe

The forests of Northern and Central Europe are comprised of comparatively few woody species. The low species diversity of the region is intimately linked to the effect of the strong climatic oscillations (glaciations) during the Quaternary, with large parts of the region covered by glaciers or permafrost during cold periods (Hewitt, 2000). Thus, the woody vegetation retreated to refugial regions mostly in the south of Europe during glacial periods. Genetic variation patterns of most native European woody plant species were strongly influenced by their respective refugia and recolonization routes during the Holocene (Petit et al., 2003). In addition, efficient gene flow between populations of different origin and population history (Kremer et al., 2002), and rapid local adaptation (Ennos et al., 1998) during the recolonization process, shaped natural genetic variation patterns.

Central Europe has a long history in forest management. Over-exploitation resulted in severe forest degradation and losses of for-

est cover during the medieval and early modern periods (Hosius et al., 2006). Sustainable forest management systems were developed and successfully applied in response to this situation with the main objective to meet the strong societal demand for wood. Today, most Central and Northern European forests are intensely managed, and almost no primary natural forests are left in Europe (Lorenz et al., 2005). Thus, virtually all genetic resources of Northern and Central European tree species have been shaped by a combination of natural processes such as postglacial recolonization and local adaptation, and human impacts including seed transfer, fragmentation and silviculture.

Europe is one of the few regions with a moderate increase in forest cover over the last decade. Most Central European forests are managed to produce wood, to provide services such as water of high quality or habitat for multiple plants and animals, and to serve as recreation areas. Thus, forest functions are rarely segregated in Europe and most forests are managed to meet both production and conservation goals (Bengtsson et al., 2000).

Conifers, in particular Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), dominate boreal forests in Northern and Eastern Europe, but are also important species in managed temperate forests in Europe. Broadleaved trees, mainly beech (*Fagus sylvatica*) and oaks (*Quercus* spp.), dominate the potential natural vegetation in Central Europe and are also intensely managed in this region (Hemery, 2008). Non-native 'neophytes' such as the North-American Douglas fir (*Pseudotsuga menziesii*) have been planted in Europe only to a limited extent, but are regionally important; their role is likely to increase in future in response to climate change (Bolte et al., 2009).

The most important stand-forming trees in Northern and Central Europe (beech, oak, spruce, pine) share important life history characteristics: their reproduction starts late after several decades of vegetative growth, they are long-living and rarely harvested before an age of 80–100 years, they form dense stands of low species diversity even under natural conditions, and they are wind-pollinated enabling effective gene flow over large distances.

Both artificial and natural regeneration are commonly practiced in Central Europe's forests (Geburek and Müller, 2005). The areas of forests established by means of artificial regeneration are often small, and the rotation period in planted forests is similar to the average age of harvestable trees in naturally regenerated forests. Accordingly, it is difficult and not appropriate to strictly separate artificial 'plantations' from 'natural' forests in Central and Northern Europe (Geburek and Turok, 2005), and both regeneration systems are reviewed with regard to their genetic implications. Losses of genetic variation are observed if critically low population sizes are encountered during the regeneration of stands (Hilfiker et al., 2004). Negative impacts of genetic drift on intraspecific diversity patterns were observed in species-rich forests (Chybicki et al., 2011). The management of forest stands appears to have only minor impacts on overall levels of genetic diversity in most temperate and boreal forests (Rajendra et al., 2014). However, the genetic consequences of phenotypic selection during thinning and harvesting operations are largely unknown. Strong impacts are expected mainly at loci controlling important economic traits (Finkeldey and Ziehe, 2004).

The marketing of forest reproductive material is legally controlled in the member states of the European Union. Comparable regulations exist in most other industrialized countries following a voluntary scheme of the Organization for Economic Co-operation and development (Ackzell and Turok, 2005; Nanson, 2001).

### 2.3. Mediterranean

The Mediterranean basin constitutes one of the planet's 34 biodiversity hot spots (Biodiversity Hotspots, 2010). More than 10% of

the world's biodiversity in higher plants is encountered in the Mediterranean region, an area that corresponds to less than 1.5% of the total land mass of the planet. The originality of the Mediterranean lies in its climate, which is transitional between temperate and dry tropical. It is characterized by a dry and hot summer period of variable length, which imprints a strong water stress on vegetation during the growing season. Mean minimum temperatures of the coldest months and intra-annual distribution and amount of precipitation define climatic subdivisions and shape forest types. Mediterranean forests represent 1.8% of world forest area with more than 80% of their total tree standing volume in Southern Europe (Fady and Médail, 2004). The Mediterranean basin is heavily populated (more than 460 million people) and on its eastern and southern rims inhabitants are still heavily dependent on the natural resources of terrestrial ecosystems. The history of human effects on Mediterranean forests is one of long term depletion. Sporadic until the advent of the Bronze Age 6500 years ago, deforestation for agronomic activities, wood fuel, timber and other purposes increased through Antiquity and peaked during the Renaissance. By the end of the 19th century, the Mediterranean forest had lost 75% of its initial post glacial area although forest cover is now increasing (Fady and Médail, 2004). Forest management and silviculture in the Mediterranean region have applied a set of well-defined rules since the mid 19th century on the northern rim and towards the end of the 19th century on the eastern and southern rims. Largely this involved the adoption of the prevailing Central European management strategies and techniques applied with little adaptation. The focus is wood production within the context of "multipurpose forestry". Silvicultural management employs a set of rules that plan growing stocks, determine rotation periods and their spatial and temporal distribution, promote regeneration (reforestation), regulate tree density and structural patterns by thinning, and reduce conflict between multiple uses (Fabbio et al., 2003). Practice has been modified, according to the prevailing economic purpose and the successions in progress since original enforcement (Fabbio et al., 2003).

Forest management and silvicultural practices in the Mediterranean have an impact on the genetic diversity of tree populations as can be deduced from the relatively few studies available in the literature (Table 1). Besides a few inconclusive or apparently contradictorily studies, it appears that standard genetic diversity parameters do not generally differ significantly between populations under particular forest management approaches and controls (Amorini et al., 2001; Aravanopoulos et al., 2001; Aravanopoulos and Drouzas, 2003; Mattioni et al., 2008). For example, the genetic diversity and mating systems parameters of natural and coppice forests (coppicing being a typical management system for Mediterranean broadleaves) do not differ significantly (Papadima et al., 2007; Mattioni et al., 2008). Nevertheless, differences in the amount of within population diversity, the levels of gene flow and the levels of linkage disequilibria, indicate that long-term management may influence genetic makeup (Aravanopoulos and Drouzas, 2003; Mattioni et al., 2008). Genetic impact seems to be more apparent under intensive forest management (Aravanopoulos and Drouzas, 2003; Ortego et al., 2010). Overall, the possibility of negative genetic impacts by management in the delicate Mediterranean forest ecosystems calls for careful approaches in the realm of sustainable multi-purpose forestry.

#### 2.4. Australia

Australia has approximately 147 million hectares of native forest which represents 19% of total land cover. Eucalypt forest accounts for 79% of natural forest, with *Acacia*, *Melaleuca* and other types accounting for the rest. Exploitation from natural forest dropped by 40% from 1999–2000 to 2009–2010 (ABARES, 2011),

but temperate natural eucalypt forests are still important sources of wood. Harvesting and natural regeneration policies mandate the conservation of local species' genetic diversity (Commonwealth of Australia, 1992).

Glaubitz et al. (2003a,b) examined the effects of harvest and regeneration practices on the genetic diversity of regenerated cohorts of two taxonomically close *Eucalyptus* species in the natural forests of Victoria, south-east Australia (Table 1). They compared genetic diversity measures (e.g., expected heterozygosity, allelic richness) among different regeneration methods after harvesting, but did not find consistent results across studies. For the dominant *Eucalyptus sieberi* no significant differences in genetic diversity measures were observed even between adult trees in nonharvested stands and saplings in harvested stands (Glaubitz et al., 2003b). In the case of the less dominant *Eucalyptus considiana* a decline in genetic diversity in harvested stands was observed (Glaubitz et al., 2003a). In the latter study, the decline in genetic diversity was larger in the seed tree retention system than under aerial sowing. These results suggest that less dominant species are more susceptible to genetic erosion.

Mimura et al. (2009) compared gene flow, outcrossing rates and the effective number of pollen donors between highly fragmented (with 3.3–3.6 trees per hectare) and continuous (with 340–728 trees per hectare) forest of *Eucalyptus globulus* in Victoria and Tasmania. The results showed some impact of fragmentation on mating pattern and gene flow. Outcrossing rates and the effective number of pollen donors per tree declined slightly, while correlated-paternity increased in fragmented sites. On the other hand, an increase in long distance dispersal in fragmented sites was also observed, which may mitigate the other potentially negative effects of fragmentation. Slight reductions in outcrossing rates at fragmented sites were also reported in other *Eucalyptus* species (Millar et al., 2000).

### 3. Genetic impacts of forest management practices in tropical forests

#### 3.1. Southeast Asia

Rapid socio-economic development in Southeast Asia, particularly in agriculture and industrial infrastructure, has affected the level of timber production and forest ecosystem services. At the end of 2010, it was estimated that the total forested area in South East Asia was 214 million hectares which covers 49% of the total land area. The forest cover ranges from 26% in the Philippines to 68% in Laos PDR. In terms of forest cover loss there has been a reported decrease from 1.0% per annum in the 1990s to 0.3% per annum during the period 2000–2005 followed by an increase to a 0.5% annual rate from 2005 to 2010 (FAO, 2011b). Generally there are two types of management system practiced in Southeast Asian tropical rain forest, monocyclic and polycyclic. The monocyclic system comprises of uniform tropical shelterwood and irregular shelterwood approaches. The polycyclic system is mainly selective cutting of crop trees with different minimum cutting limits for dipterocarp and non-dipterocarp tree species. The choice of a particular silvicultural system for a production forest depends on a host of factors, economic and ecological, of which economic considerations are paramount. In most countries of Southeast Asia where commercial logging is undertaken, some form of selective felling as opposed to a uniform system is adopted with the aim of conserving stock for future use.

The impact of logging on the population structure of tree species depends strongly on the degree of disturbance and the intensity of logging (Ho et al., 2004). The threat to genetic diversity posed by commercial logging is correlated with the abundance of a species in a particular forest management unit (Wickneswari et al.,



2000; Wickneswari et al., 2004; Wickneswari and Boyle, 2000). Tree density of a species can therefore be a useful indicator reflecting risk to genetic viability rather than simply the overall disturbance level based on reduction in basal area of all trees (Lee et al., 2002a,b). Ng et al. (2009) showed that species with different breeding systems (outcrossing vs. apomictic reproduction) are affected differently by the same logging intensity, with impacts to outcrossed species being lower compared to apomicts. Since mating and gene flow patterns tend to be similar in species with similar ecological characteristics (Turner, 2001), information collected on the most important commercial species may be applied to related more minor ones in informing management approaches.

### 3.2. Latin America

Currently, about 31% of tropical forest in Latin America remains intact, and 55% of this is Brazilian forests. Although forest management operations are practiced in several countries in the region, the results and discussion herein focus on specific cases of the Dendrogene project, which provides the largest body of information on model species of different ecological, genetic and commercial interests (Kanashiro et al., 2002a). Concerns and policies focus on reducing impacts of management for given forestry products, but, as elsewhere, impacts at inter-specific and intra-specific levels are difficult to evaluate. The Dendrogene project aimed to apply scientific knowledge on species composition, reproductive health and genetic diversity to support enabling legislation for sustainable rainforest management in the Brazilian Amazon. The project focused on three fundamental areas: (1) the correct identification of species; (2) the development of reliable models for predicting the long-term impacts of selective logging on tropical tree species; and (3) the application of scenario analysis to guide policy and management decisions.

Correct and careful species identification at field inventory level is crucial as mistakes may lead to several negative unintended consequences in product markets and for forest health (e.g., unintentional destruction of unknown species) (Martins-da-Silva et al., 2003). An example of the issue of misidentification is illustrated by a study on the genus *Couratari*, where 112 individuals recorded as *Couratari guianensis* were revealed to be *Couratari oblongifolia* or *Couratari stellata* (most abundant), while 6 specimens described as *Couratari* sp. included both *Cariniana micrantha* and *Carinana decandra* (Procopio and Secco, 2008). Other studies of complex genera including *Copaifera* (Fabaceae, Martins-da-Silva, 2006), *Tabebuia* (Bignoniaceae, Costa, 2004), and *Microphollis* (Sapotaceae, Silva, 2004) have found similar mis-identification. Lacerda and Nimmo (2010) reported that at least 43.5% of all species identified after botanical checking did not appear in the forest inventory and the common practice of matching vernacular names to scientific ones proved to be severely deficient.

Considering the high importance of correct botanical identification and the uncertainty of forest inventory data which provide the basis for selective logging operations, community and rural extension training in identification is important. Hence, Dendrogene and follow-up projects have provided training course and written guides on this (Ferreira et al., 2004; Procopio et al., 2005).

#### 3.2.1. The Eco-gene model and case studies

The Eco-gene model has been used to elucidate genetic processes and the consequences of logging and forest fragmentation in the long term (Sebben et al., 2008). In this model, data on genetic structure, gene flow and the reproductive biology of Amazonian timber species before and after logging were integrated with data on growth, regeneration and ecology under different scenarios and intensities

of logging. The expectation was that these results would help to guide and create new criteria for sustainable logging in the region.

Seven species with contrasting ecological and reproductive characteristics were selected for incorporation in the model. The species fit into three ecological groups (pioneer, climax of fast growth/light demanding and climax of slow growth/shade tolerant categories) and have different reproductive systems (dioecious, monoecious, hermaphrodite), with different pollinators and seed dispersers. The seven species investigated were *Bagassa guianensis* (Moraceae), *Carapa guianensis* (Meliaceae), *Jacaranda copaia* (Bignoniaceae), *Dipteryx odorata* (Fabaceae), *Hymenaea courbaril* (Fabaceae), *Symphonia globulifera* (Clusiaceae) and *Manilkara huberi* (Sapotaceae).

*Dipteryx odorata*, *J. copaia* and *M. huberi* are hermaphrodites and pollinated by insects, while *B. guianensis* is dioecious and mainly wind-pollinated, with the participation of trips, a tiny insect. *Hymenaea courbaril* is hermaphrodite and pollinated by bats, while *S. globulifera* is hermaphrodite and pollinated by birds, moths and butterflies. *Dipteryx odorata* and *B. guianensis* occur at low density in the study area (0.17 and 0.34 individuals per hectare, respectively), while *H. courbaril* and *S. globulifera* occur at somewhat higher density (0.58 and 0.88 individuals per hectare, respectively, the latter being for trees >10 cm dbh), and *J. copaia*, *M. huberi* and *C. guianensis* at 1.75, 3.35 and 6.33 individuals per hectare, respectively. *Jacaranda copaia* and *B. guianensis* are typical gap colonizing species, while *M. huberi*, *S. globulifera*, *H. courbaril*, *D. odorata* and *C. guianensis* are climax species, of low growth rate except for the last (medium growth rate). *Dipteryx odorata* is a tetraploid while the rest are diploid species.

The experimental area is the 546-hectare Dendrogene plot, called the Intensive Study Plot, located in the Floresta Nacional do Tapajós (FLONA), Belterra. The sampling method varied for adults and progenies. For adults, cambium samples from all trees greater than 20 cm dbh were collected (with the exception of *J. copaia*, for which samples from all trees greater than 10 cm dbh in a smaller 200 ha plot were taken). Progeny arrays comprised 20–40 fruits collected from each of 10–30 randomly selected ‘mother’ trees from 2002–2004 (pre-logging) and 2007–2008 (post-logging). Polymorphic microsatellite loci for the different species as described by Azevedo et al. (2007), Carneiro et al. (2011), Cloutier et al. (2007), Lacerda et al. (2008), Silva et al. (2008) and Vinson (2009) were used for characterization.

Logging led to a range of losses in the total number of alleles for the adult trees for the species for which estimates were made; 10% for *D. odorata*, 8.3% for *B. guianensis*, 8.7% for *H. courbaril* and 11.6% for *M. huberi*, respectively (Carneiro et al., 2011, Lacerda et al., 2008, Silva et al., 2008, Vinson, 2009). Whilst these alleles may be lost from the adult population, they were found in juveniles and progenies. Furthermore, there was a compensation for the loss of some alleles by the immigration of alleles from outside the plot. These results illustrated the importance of the area surrounding the logging operation, since trees may reproduce with those outside the plot, mitigating the effects of logging. The field site used in these studies was surrounded by pristine forest and represented 0.001% of the total area of the Tapajós FLONA. However, if the field site had been a fragment, with no gene flow from outside, alleles would be lost with every logging event, and as more logging cycles are conducted there would be a further decline in the number of alleles over time.

*Jacaranda copaia* and *C. guianensis* are out-crossed species with no inbreeding either before or after logging, results in accordance with the weak spatial genetic structure observed among adult trees. Co-ancestry values for *J. copaia* were:  $F_{ij} = 0.1$  and 0.03 up to 100 m and biparental mating ( $t_m - t_s$ ) = 0.029 and 0.030, before and after logging, respectively (Vinson, 2009). Values for *C. guianensis* were:  $F_{ij} = 0.07$  and 0.04 and  $t_m - t_s = 0.015$  and 0.028, before and after

logging, respectively (Cloutier et al., 2007). These results can be explained by these species having high gene dispersal, high genetic diversity, large effective population sizes, and undisturbed (never previously logged) populations surrounded by pristine forest.

The estimated multi-locus outcrossing rate ( $t_m$ ) for *M. huberi* was high ( $0.98 \pm 0.111$ ) suggesting that the species is predominantly allogamous. *M. huberi* showed high levels of genetic diversity, however this species also presents a high rate of endogamy, i.e. a deviation from Hardy–Weinberg equilibrium, most likely caused by crossing among related individuals ( $t_m - t_s = 0.277$ ) and a high spatial genetic structure up to 450 m. Pollen flow was the most restricted among the studied species. These results suggest that *in situ* conservation management programs for the species should include large areas, avoiding fragmentation to minimize isolation by distance effects. Azevedo et al. (2007) recommended reduced impact selective logging, and that removal of trees should be randomized to avoid fragmentation and sub-population losses. The significant spatial genetic structure observed in the population (as a whole) at a radius of 450 m was not detected after exploitation, with the genetic structure observed in commercially exploited trees lost. There appears to be a significant difference in the pattern of genetic diversity and endogamy in the new generation. The fixation index of 0.26 in seedlings before logging was decreased to 0.06 after logging (unpublished data).

*Dipteryx odorata* pollen from inside the plot originated from relatively few pollen donors per mother tree (2.6 trees pre-logging, 1.7 post-logging) relative to the total number of potential pollen donors (pre-logging 66, post-logging 39). Strong asynchrony in flowering is likely to be limiting reproduction, and this aspect has serious consequences for species being managed by selective logging due to the possibility of a mother tree having no breeding partners if the area being managed is a 500 ha (or smaller) fragment with no possibility of pollen flow from other fragments (Vinson, 2009).

*Hymenea courbaril* showed high pollen flow movement with low biparental inbreeding ( $t_m - t_s = 0.096$ ), however, a high spatial genetic structure was observed ( $F_{ij} = 0.227$  up to 100 m and  $F_{ij} = 0.139$  up to 300 m), possibly as a consequence of gravity seed dissemination (Lacerda et al., 2008). The results suggest that logging produced an increase in the number of pollen donors and further pollen dispersal. Logging may also result in a significant reduction in the genetic diversity within the progeny of the species and an increase in self-fertilization (Carneiro et al., 2011).

*Symphonia globulifera* showed a distinct spatial genetic structure ( $\theta_{xy} = 0.119$  up to 50 m; comparable to that of half sibs with  $\theta_{xy} = 0.125$ ) possibly as a consequence of gravity seed dissemination (Carneiro et al., 2007). Although *S. globulifera* has a low number of pollen donors ( $N_{ep} = 2.4\text{--}4.0$ ), low selfing and biparental inbreeding rates ( $t_s = 0.0\text{--}0.11$  and  $t_m - t_s = 0.063\text{--}0.093$ , respectively) were detected. High levels of pollen immigration from outside of the study area (49%) and long distance pollen dispersal inside the study area consistent with hermaphrodite and bird-pollinated species were observed (Carneiro et al., 2007, 2009).

As *B. guianensis* is a dioecious species, outcrossing values were very high. However, differences between the multilocus outcrossing rate and single locus outcrossing rate were significantly different from zero ( $P < 0.05$ ), suggesting the occurrence of bi-parental inbreeding within the population. Significant structure up to 300 m before logging was detected, with the coancestry coefficient between individuals close to values expected between cousins (0.063). However, after logging the total population (reproductive trees and juveniles) did not show spatial genetic structure, suggesting that logging has disrupted it (Silva et al., 2008). The combination of wind and thrip pollinators of *B. guianensis* form 'thrip clouds' that visit neighbouring trees, with three pollen donors per mother tree from a narrow geographic range. The non-random

crossing of *B. guianensis* has important implications for conservation and seed collection programmes (Silva et al., 2008).

### 3.2.2. Eco-gene simulation results: A quick overview

The Eco-gene simulation model was developed to study silvicultural impacts on temperate forests (Degen et al., 1996) and then adapted to be applied in tropical forest management (Degen et al., 2003, Degen et al., 2004, Kanashiro et al. 2002b). Considerable effort was taken to collect the information needed to run the model, and below we present some of the results.

Sebben et al. (2008) provided results for the four species, *B. guianensis*, *H. courbaril*, *M. huberi* and *S. globulifera*, with the model parameterized using empirical data from field studies in FLONA. Included data were genotypes at microsatellite loci, demography, ecology and growth for each species. Several scenarios, combining two different cutting diameters (45 and 60 cm dbh) and two different cutting cycles (30 and 65 years) as used in Brazil and French Guiana were tested. Logging scenarios were applied for six cutting cycles, and final genetic and demographic data were compared to baseline data from corresponding control scenarios. At the end of the simulated period the basal area was strongly reduced under all conditions in *B. guianensis*, *H. courbaril* and *M. huberi*. *Symphonia globulifera*, however, was able to recover its basal area following logging in two scenarios. Based on these results, a Minimum Cutting Diameter (MCD) of 60 cm diameter at breast height was recommended.

Simulations studies for *D. odorata* and *J. copaia* were undertaken by Vinson et al. (2013), which confirmed the importance in modelling of considering population density, growth patterns and breeding systems. Results in terms of basal area recovery were consistent with concerns stated by van Gardingen et al. (2006) who evaluated yield regulation options in the region. While the current Brazilian forest management regulations are sustainable for *J. copaia*, they are not for *D. odorata* in the long term. A recommended scenario for *D. odorata* is to increase the MCD from 50 cm to 100 cm over a 30-year logging cycle.

## 4. Parkland management systems

Parklands are field-fallow land-use systems in which trees are preserved by farmers in association with crops and/or animals where there are both ecological and economic interactions between trees and other components of the system (Bonkougou et al., 1994). The length of the fallow period (3–4 to 25–30 years) depends on each farmer according to the land they possess, the needs of their household and the way they manage the land. Very often one or two tree species are dominant in the system.

The impact of human practices is particularly marked in the agroforestry parklands where alternating fallow and cultivation periods, tree selection, annual crop cultivation, and other field activities, affect the regeneration, growth, spatial distribution and phenology of tree species. The most extensively researched parkland tree genetically and ecologically is the economically important species *Vitellaria paradoxa* (seed oil used for food and cosmetics) from the Soudano-Sahelian zone (shea tree; Hall et al., 1996; Boffa et al., 2000).

Research conducted on *V. paradoxa* has shown that parkland management has favored regeneration and growth, and increased ability to flower and fruit (Kelly et al., 2004; Kelly et al., 2007). Parkland management appears to have favored gene flow at local and regional levels and has created the conditions to support high genetic diversity within the species and good adaptation to local environment (Allal et al., 2011; Logossa et al., 2005; Sanou et al., 2005). Parkland management has not reduced the variability of economically important traits such as lipid seed constituents in the species (Davrieux et al., 2010).

## 5. Impacts of plantation forests on native forests

Increasing areas of the world's forests are composed of planted as opposed to native forest (Puyravaud et al., 2010; FAO, 2012). This is in part because planted forests are often more productive than native forests resulting from targeted site selection and the use of improved genetic stock as well as the adoption of modern silvicultural techniques. Establishing plantations of native tree species on previously degraded pasture is one strategy to reduce logging pressure on native forests (Brockherhoff et al., 2008; Plath et al., 2011). Plantation forestry is often associated with the use of seed sources not native to the planting site. Gene flow between plantation and natural forest constitutes an important (but yet overlooked in the literature) threat to native populations.

Plantation forests may impact either positively or negatively on adjacent native forest. Positive impacts may arise because the planted forest: (1) provides corridors allowing the movement of biota between forest fragments (Bennett, 2003); (2) provides habitats for forest birds, insects and other species that experience difficulty inhabiting small forest remnants (Neuschulz et al., 2011; Mazzoli, 2010); and (3) increases genetic diversity through either seed or pollen dispersal into inbred remnant tree populations (Byrne and Macdonald, 2000). Negative impacts may include: changing the abiotic environment, such as lowering the water table (Kagawa et al., 2009); changing fire frequency or increasing temperature (do Nascimento et al., 2010); damage to native forest remnants during harvesting (do Nascimento et al., 2010); changing the biotic environment, such as increasing the pest (mammal, invertebrate, fungal, bacterial) load (Jairus et al., 2011); and changing native gene pools through the invasion of native forest by introduced seed (Potts et al., 2003). Anthropogenically induced gene flow of alien provenance may eventually swamp locally adapted genotypes in the natural forest if plantation areas occur over wide areas. A typical example of this concerns black pine in southern France, where the local subspecies *Pinus nigra salzmann* covers just over 5,000 ha, while planted non-native *Pinus nigra* currently covers over 200,000 ha (Fady et al., 2010). Sampson and Byrne (2008) indicated that forest fragmentation can increase the level of deleterious contamination of natural stands by plantations by increasing gene flow distances.

## 6. Conclusions and recommendations

Both the EMEND and DendroGene projects conducted in North America and Latin America, respectively, serve as good approaches to understand the long-term genetic effects of logging for sustainable forest management. Silvicultural practices should take the population size, reproductive biology and growth rate of a species into account to ensure that genetic diversity and evolutionary processes are maintained in forest populations. For a comprehensive view of genetic impacts of forest management practices, more than one molecular marker type (and perhaps more than one genome type) is advisable to be used, as different markers may provide complementary results. Allelic diversity measures are more suitable than expected heterozygosity ( $H_e$ ) in assessing the genetic impacts of forest management practices because  $H_e$  is not very sensitive to bottlenecks and perturbations in populations. The identification of genes directly involved in traits controlling productivity and quality is urgently needed to further explore the consequences of selective cutting.

Density of a species can be a useful indicator of risk of genetic viability, rather than the overall disturbance level based on reduction in basal area of all trees. Mating and gene flow patterns tend to be similar in species with similar ecological characteristics.

Therefore, information on mating system, gene flow and inbreeding depression from major species may be relevant to closely related taxa for management strategies. Hence, knowledge of the biological attributes of species including the main pollinators, flowering phenology and synchrony can be used to develop field guides for management to maintain genetic diversity.

Correct botanical identification in forest inventories is an important issue, since it is related directly to the conservation of species and the sustainability of forest management. Certainly, the better the understanding at the species level, the better the possibility of using species models for simulations to develop more robust scenarios for evaluating the sustainability of the forest management. Given the importance of forests for the maintenance of ecosystem balances and livelihoods, it is the responsibility of everyone to use and conserve these natural resources for this generation and those to come.

## Contribution of authors

All authors contributed equally to the conceptualization, preparation and revision of this review paper. W.R. assumed the responsibility to compile and edit the various sections as lead and corresponding author.

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