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# Genetic Structure and Diversity of Brazilian Tree Species from Forest Fragments and Riparian Woods

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## 1. Introduction

Historical patterns of human occupation in Brazilian Neotropical Region, featured by deforestation for urbanization, economic exploitation and agriculture, have changed the Atlantic Forest landscape to a collection of fragments. Nowadays this biome is characterized for being highly fragmented but still possessing one of the highest rates of species diversity in the world.

Understanding the genetic structure of populations that occur in forest remnants is fundamentally necessary to establish efficient strategies for the re-composition, management, and conservation programs. For such, it is necessary not only to understand the genetic diversity of a species, but also, how this diversity is distributed within and between forest populations. Notably, a considerable part, if not the majority, of Brazilian Atlantic Forest fragments are linked to rivers or streams, once the policy applied in Brazil regarding conservation in agricultural areas favours the maintenance of legal reserves in proximity of water sources. The vegetation of river margins are subjected to flooding, a strong limiting factor which can lead to local adaptation. These ecological and landscape characteristics may have important outcomes to the genetic diversity of tree populations.

In this chapter, we assembled information from review and research papers of impact in this study area intending to raise knowledge to assist conservation initiatives of Brazilian Atlantic Forest fragments and riparian woods. We plan to broach fundamental concepts regarding the historical fragmentation process in Brazilian Neotropical Region, the effects of fragmentation upon the genetic diversity of forest remnants, and the local adaptation to seasonally variable river levels. This discussion is not intended to be a summary of the existing literature in the theme, but to address important information concerning genetic diversity of neotropical tree species, focusing in the results of eleven years of research on species frequently used in reforestation of legal reserves in Southern Brazil.

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## 2. The Neotropical floristic kingdom

The word *Neotropic* (from the Greek *neos* = “new”) refers to the tropical region of the American continent (Antonelli & Sanmartín, 2011), or “New World” - a term coined by Peter Martyr d’ Anghiera in 1493, shortly after Christopher Columbus’s first voyage to the Americas (O’Gorman, 1972). As currently defined (Schultz, 2005), the Neotropical kingdom extends from central Mexico, in the north, to southern Brazil, in the south, including Central America, the Caribbean islands and most of South America.

In the Neotropics, equatorial and tropical climates predominate with low climatic seasonality, when compared with kingdoms with cold and temperate climates. Precipitation and annual mean temperatures are generally high, but there is great regional variation (Antonelli & Sanmartín, 2011). Before human colonization, the rain forest of Amazonia accounted for about one third of the entire South American continent. There are, however, several other terrestrial biomes in the Neotropics that are noteworthy for their size and ecological importance, such as the Cerrado and the Atlantic forest of eastern Brazil (Antonelli & Sanmartín, 2011).

The outstanding species richness found today in the Neotropics has remained elusive in our understanding of the evolution of life on Earth (Antonelli & Sanmartín, 2011). Comprising around 90,000–110,000 species of seed plants, the Neotropics alone harbours about 37% of the world’s species, more than tropical Africa (30,000–35,000 spp.) and tropical Asia and Oceania combined (40,000–82,000 spp.) (Govaerts, 2001; Thomas, 1999). Sanmartín and Antonelli punctuated the factors that can explain this high species richness (Antonelli & Sanmartín 2011 and references therein). They are related 1) with the geographical position of Central and South America, resulting largely in tropical and equatorial climates; 2) edaphic heterogeneity; 3) biotic interactions that promote speciation mechanisms; 4) relatively stable environments over time, resulting in very ancient ecosystems that conserve niches; 5) adaptive radiation favoured by the great ability of dispersal of flowering plants; 6) geographic isolation (only 3.0 million years ago, South America became connected to North and Central America by the Isthmus of Panama); 7) climatic fluctuations of Pleistocene, leading to formation of refuges for many isolated populations and allopatric speciation; 8) uplift of the Andean cordillera, occurred largely in the last 25 million years; and 9) the profound change in the vast hydrological systems, especially in the Amazon region.

During millions of years there was a synergism between gradual and slow climate changes and speciation, giving time for natural selection and other evolutionary tolls to play their role. The final result of this long process of genesis and evolution of the Neotropical region, is that most of the Neotropical countries, such as Brazil, Colombia, Ecuador and Peru, are on the higher positions of any ranking of species richness. Brazil, in particular, occupies the first position in such rankings and is therefore considered the most Megadiverse country.

Neotropical kingdom is divided into Caribbean, Guayana Highlands, Amazonian, Brazilian and Andean region (Takhtajan, 1986). Brazilian region is, in turn, subdivided into the provinces of the Caatinga, the highlands of central Brazil, Chaco, Atlantic, and Paraná (Takhtajan, 1986). In the Brazilian territory, major biomes are spread over these provinces, such as the Caatinga, Cerrado, Atlantic Forest, Pantanal and Pampas. Even in the case of a predominantly tropical region, where, typically, there is less thermal seasonality and spatial climate variations than in temperate regions, there are important environmental variations

that create significant intra-regional heterogeneity. This fact can be explained by: 1) large latitudinal variation found, the northern boundary of the region is located around 3 ° S, and the south boundary, around 33 ° S latitude; 2) great altitudinal variation, with elevations ranging from sea level to mountainous regions that can reach approximately 2900 meters of altitude; 3) wide edaphic variation, the result of different soil genesis processes over time and space and 4) continentality, which determines a lower overall level of humidity and higher thermic amplitude, the most distant of the Atlantic Ocean. This great heterogeneity, combined with the inherent environmental characteristics of tropical regions that favor the development of life, and added to the climate and geological history of the entire Neotropic, which favored isolation and speciation, have provided to these biomes, in terms of floristic and physiognomy, a high species richness, high endemism and great structural complexity.

According to the Brazilian Institute of Geography and Statistics - IBGE (2004), Atlantic Forest biome constitutes the extra-Amazonian forest large set of South America, formed by rainforests (dense, open and mixed) and seasonal (deciduous and semideciduous). It comprises an environmental complex that includes mountain ranges, plateaus, valleys and plains of the entire eastern Brazilian Atlantic continental band. In southern and southeastern Brazil, it expands westward, reaching the borders of Paraguay and Argentina, also advancing on the southern highlands of Brazil, reaching the state of Rio Grande do Sul.

### 3. The history of fragmentation of the Atlantic forest biome

The Atlantic forest is the most uncharacterized Brazilian biome (IBGE, 2004). Since the beginning of European colonization, from 1500, several economic cycles of exploration occurred, generating successive impacts in a growing area (Dean, 1996). Brazil has the most diverse flora of the planet and also had its name inspired in a tree, Brazil-wood (*Caesalpinia echinata* Lam), a typical species of coastal forests of the southeast. The first cycle of the ancient Portuguese colony was the exploitation of this species, highly valued for producing a resin which conferred a reddish color to fabrics. Later, with the largest reserves of this wood already exhausted, other exploitation or agricultural cycles began, such as the sugar cane, gold, and ultimately, coffee. They all contributed strongly to clearance and degradation of new areas (Dean, 1996). From the late 19th century and throughout the 20th century, new development and national integration projects have come and settled a consistent process of industrialization and urbanization exactly in the area originally occupied by the Atlantic Forest. Nowadays, these urban areas have the highest population densities and lead the economic activities in the country (IBGE, 2004). An estimated 112 million people live in this area, which accounts for 61% of the population of Brazil (IBGE, 2007). The current results are the almost complete loss of primary forests and a continuous process of destruction of existing remnants, which place the Atlantic Forest biome in unworthy position in the world: as one of the most endangered ecosystems (SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais (INPE), 2011). In sum, predatory economic cycles and projects of development and national integration have led, throughout the biome area, to the expansion of the agricultural frontier, the establishment of industrial activities, mining and power generation and intense and disorganized urbanization process, causing the destruction of, approximately, 92% of the original vegetation, which had, in 1500, 1,315,460 square kilometers (Fundação SOS Mata Atlântica and INPE, 2011). The remaining 8% are highly fragmented, separated by a matrix that includes pastures, crops,

water reservoirs, industrial plants, mining and urban areas, especially on the margins of water bodies and mountain areas with highly tilted ground. Even so, one should not underestimate the importance of these fragments. For example, in terms of species richness, occur, even today, in the Atlantic Forest biome, about 20.000 species of vascular plants, of which 6.000 are endemic (Fundação SOS Mata Atlântica and INPE, 2011).

If on one hand the historical processes of economic development led to a predatory pattern of destruction with the formation of relictual fragments of sizes and levels of isolation and different anthropic impact, on the other, the Brazilian environmental legislation, considered one of the most advanced of the planet, through his last Forest Code, established in 1965 and improved in recent decades, defined areas of permanent preservation and legal reserve (Medeiros et al., 2004). The first has the function of conservation of ecosystem services, encompassing riparian forests, river headwaters, hills tops and mountains, hillsides with slopes greater than 45 °, "restingas" and mangroves. The second has the goal of biodiversity conservation and must have, at least, 20% of the property area in the southern and southeastern Brazil, reaching 80% of the area in the Amazon region. Thus, the historical process that led to the intense fragmentation of the Atlantic Forest biome has suffered, in recent decades, the influence of an environmental legislation more effective for conservation. The result is that most of the remaining fragments can be found in permanent preservation areas and legal reserves, especially in riparian areas and steep slopes with unstable soils.

At this time, Brazilian society is burned with a heated debate, in the Brazilian National Congress, on the proposed changes to the Forest Code. In one side, the sectors of society and policymakers linked to the economically strong Brazilian agricultural sector require the flexibility of code, aiming to reduce the need for recovery and conservation of areas of permanent preservation and legal reserve, in order to result in the release of more land for agriculture. In the other side, the Brazilian Society for Science Progress, urban sectors of society and policymakers linked to the environmental movement strongly oppose the proposed changes. There is a concern that, if these changes are approved, the fragmentation process of natural areas and the destruction of relictual fragments will be intensified, which would result in ecological and evolutionary consequences for populations of many species present in these natural areas.

## **4. Genetic diversity of tree species**

### **4.1 Fundamental concepts**

The genetic variability contained in plant species may occur in distinct levels: 1) species within ecosystems; 2) populations within species; and 3) individuals within populations of a species. The genetic structure of a species can be defined as the distribution of the genetic variability within and between its populations as a direct result of the combination among mutation, migration, selection and genetic drift. Also, many tree species harbor effective mechanisms that allow the dispersion of alleles, enabling them to maintain high levels of genetic variability within their populations (Hamrick et al., 1979; Hamrick, 1983; Loveless and Hamrick, 1987). Studying several natural tropical tree populations, Hamrick (1983), concluded that the genetic variability within natural populations is directly linked to their mating system, pollen dispersion syndrome, seed propagation and also by their effective



population size. These factors are also related to the geographic distribution and the type of community in which such species naturally occur.

As stated above, understanding the genetic structure of populations that occur in forest remnants is fundamentally necessary to establish adequate criteria in to which these populations will play a role in the re-composition of degraded ecosystems (Kageyama, 1987). For such, it is necessary not only to understand the genetic diversity of a species, but also, how this variability is distributed within and between their populations present in the disturbed areas. To such intention many statistical tools have since been developed to measure, qualify and partition this genetic variability.

In 1951, Sewal Wright established one of the main components of the distribution of genetic diversity in natural populations: the partition of the endogamy coefficient within and among populations. In his method Wright was able to determine how the endogamy coefficient determine not only the level of crossing between close related individuals within a population but also how it can be related to the differentiation of multiple populations and the overall adaptability of a metapopulation. Also he was able to demonstrate how this partition could be directly linked to the mating system present within each species. His method partitioned the components of the endogamy coefficient  $f$  into three distinct coefficients:  $F_{IS}$ , which is mainly used to measure the degree of crossing between closely related individuals within a population;  $F_{ST}$ , which can be considered an estimative of the endogamy level among populations. Although such concept might be strange, Wright was able to determine that this endogamy between populations was equivalent to determining the genetic relatedness among these populations; and  $F_{IT}$ , which represent the endogamy level present in the whole metapopulation and correspond to the overall adaptability measured for the sum of populations. We can also consider that  $F_{IS}$  represents the endogamy level related to the reproductive system present within a species,  $F_{ST}$  to be the endogamy level due to the partition of the population into subpopulations, and  $F_{IT}$  the endogamy level related to the reproductive system and the subdivision of all subpopulations.

This concept of partitioning the  $f$  statistic developed by Wright is highly important when we consider the genetic study of the fragmented population as it gives an overview of how the genetic variability is distributed within and among the subpopulations of a species in a determined area and permits us not only to infer the level of fragmentation within a metapopulation but also main type of reproduction present in a species.

When considering the genetic pattern of natural populations, we need also to know specific patterns of genetic richness within each population to answer a wide range of questions like: degree of conservation, percentage of variation within each specific population, differences in genetic diversity and degree of heterozygosity. This being said, we have to consider other important measures of population genetics.

The percentage of polymorphic loci is one of the simplest measurements of the genetic variation that can be used to evaluate the genetic variability present in a population. As the name says, it shows the number of polymorphic loci present in a population in relation to all the amplified loci obtained with the DNA-based Markers.

Another form to evaluate the genetic variability present within a population is to obtain information about its genetic diversity. Initially geneticist borrowed the method of

calculating such diversity from our friends Ecologists. The Shannon and Weaver (1949) index ( $H$ ) was employed in ecology to measure the diversity of species within a given area and later was adapted to measure the genetic diversity within the studied populations. Later on, a more specific index was developed to measure this genetic diversity eliminating some of the bias that was generated when adapting the Shannon index for the evaluation of the genetic data. The Nei's genetic diversity (1973) was developed as a specific way to measure the population genetic diversity using data obtained specifically with the DNA-based markers. This index was able to measure more accurately the degree of genetic variation within each population and presented different considerations when analyzing the data obtained by dominant (there is no way to differentiate the recessive alleles) codominant (all alleles are differentiated, and each pair of primers is considered to amplify only one molecular locus) markers. For dominant ( $H$ ) data Nei's genetic diversity is analyzed in terms of within population gene diversity ( $H_s$ ) and the total gene diversity present in the pool of populations studied ( $H_t$ ). But as said above, for codominant marker more detailed information can be given by this statistical index, dividing this statistic into observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosities, making it possible to calculate the excess or deficit of heterozygotes within each population, gene flow and inferences of genetic bottlenecks and genetic drift.

Considering that in the traditional method of calculation the genetic variability was based on the assumption that the populations were in Hardy-Weinberg equilibrium, some of the inferences obtained for this population presented a significant bias. As a good example we can consider the inference obtained with the Nei's statistic for genetic diversity, the observed heterozygosity ( $H_o$ ) was compared to the expected heterozygosity ( $H_e$ ) which was obtained as the pattern of distribution of all the alleles amplified if the population was in HW equilibrium. To eliminate this bias the Bayesian statistic method was adapted to the analysis of molecular data, promoting a revolution in the parameters that can be calculated using data obtained by the DNA-based markers. The Bayesian method is characterized by the use of the posterior probability to infer the likelihood of occurrence of a particular event. In this method all the assumptions, like HW equilibrium, are discarded and the obtained results with this method are compared with a chain (algorithms - Markov Chain of Monte Carlo MCMC and Metropolis Hastings) of results that come from the analyses of the same data. This method of chained analyses repeats itself in tandem until the obtained "chain" stabilizes and yields a result that come close to the real pattern of genetic variation present in natural populations. With this method some parameters like population bottlenecks, attribution of genotypes to specific populations, pattern of gene flow and migration, and attribution of individual paternity, allowing inferences on the population genetics based on DNA-based markers more complete and trustworthy.

#### **4.2 Consequences of habitat fragmentation to the genetic diversity of tree species**

Habitat fragmentation is one of the most important and well diffused consequences to the anthropic soil use dynamics (Brooks et al. 2002). It is characterized by the rupture of landscape unity that initially presented continuity, generating smaller parcels with different dynamics from the original habitat. Such parcels become disconnected from the original biological processes that occurred throughout the area (Dias et al., 2000), behaving like isolated "islands of biodiversity" surrounded by non forest areas (Debinsk and Holt, 2000).

For trees, degradation of primary habitat results from two main processes, fragmentation of forest into patches following clearance, and disturbance of habitat following extraction processes, such as selective logging. Tropical trees are thought to be particularly vulnerable to the effects of habitat degradation due to their demographic and reproductive characteristics (Lowe et al. 2005). Estimations made more than 10 years ago predicted that within fifty years, approximately, twenty-five percent of the vascular plant species would be extinct (Kala, 2000). This loss is still an ongoing process, which is not only linked to the loss of the number of individual plants of a species, but also to the loss of condition of the habitat in which they initially inhabited, as some species cannot persist in small fragments due to alteration in microclimatic conditions and to the intensification of the border effect in small fragments (Lovejoy, 1983).

Tropical trees are predominantly outcrossed, present extensive genetic flow and keep high levels of genetic variability. They frequently experience low density as a consequence of habitat fragmentation, are highly dependent upon animal pollination and present mixed mating systems, so they generally exhibit more genetic diversity among populations than temperate species (Dick et al. 2008).

For neotropical forest species, a reduction in habitat patch size or population density is usually equivalent to a reduction in population size (Lowe et al. 2005), or a genetic bottleneck. The genetic bottleneck leads to a very well known phenomenon in the evolutionary context of habitat disturbance, the genetic drift. Genetic drift can be defined as the sum of random changes in the frequencies of alleles within a population (Futuyma, 2005). This process has as principal outcome the decrease in genetic variability, which can be detected as a drop in the proportion of polymorphic loci and in the number of alleles per locus.

The reduced effective size of populations is also accompanied by the increase in endogamy levels. This can be a result of both the decline in pollen vectors and consequent raise of selfing in species with mixed mating systems, and the increased probability of crossing among relatives, given their close distribution and reduced potential mates. This can lead to a declined heterozygosity, augmented homozygosity and consequent fixation of alleles, independently of their effects over fitness.

The consequences of genetic drift and endogamy are maximized by the isolation of the remaining fragments, resulting in an increased genetic diversity among them. The loss of genetic variability can affect population viability and limit evolutionary opportunities to the populations: they are expected to suffer increased disease and pest susceptibility, loss of incompatibility alleles, fixation of deleterious alleles and decline in fitness (Young et al, 1996).

Lowe and coworkers, based in a computer simulation (Lowe et al. 2005), found that with even relatively low levels of gene flow between remnant populations, loss of diversity can be significantly mitigated by increasing effective population size. Changes in genetic diversity and differentiation following a decrease in population size take a number of generations to become apparent, which is not the case for inbreeding coefficient that increases immediately in the first generation following the occurrence of selfing. Long-lived, historically outcrossing species, such as neotropical trees, are expected to harbour a high genetic load, as deleterious recessive alleles will be masked at multiple heterozygous loci.



Also, although deleterious mutations are expected to be purged by selection over time in these species, mildly deleterious alleles can persist despite strong selection.

Some morpho-physiological and life-history traits could confer differences in plants' vulnerability to the effects of fragmentation. For example, species with long generation times will suffer weaker negative effects of fragmentation than the ones with short generation times. The same for species able to reproduce asexually, that will have an extended time between generations.

Many naturally outcrossed tree species frequently present selfing as a clear result of fragmentation, since low density/fragmented populations tend to be more autogamous than high density populations. In the hypothetical scenario of anthropogenic fragmentation ceasing and landscapes remaining as they are today, the effects on genetic diversity of plants will still be much stronger in the future if mating patterns continue shifting towards selfing (Dick et al. 2008, Aguillar et al. 2008).

Aguillar et al. (2008) showed that outcrossing species, such as neotropical trees, suffer greater losses of alleles and polymorphic loci than non-outcrossing species. For self-incompatible species in particular, this may result in the loss of low frequency self-incompatibility alleles (S) leading to mate limitation and further reduction of effective population size.

Animal pollinated outcrossed species are also strongly negatively affected in terms of effective pollination service and seed production by habitat fragmentation. Considering that more than 98% of tropical trees species are animal pollinated (Bawa 1990), these species are exceptionally vulnerable to fragmentation as a consequence of both, ecological and genetic mechanisms. Not only pollination but also seed dispersion in tropical forests is much more dependent in animals than in wind: more than 70% of all tropical tree species are animal dispersed (Howe and Smallwood 1982). These species share multiple agents and are generally understory (Dick et al. 2008).

For the majority of tropical trees, pollen flow transposes enormously the distances of the seeds flow. Pollen dispersion distances, although dependent on small animals in most cases, can be surprisingly as high as 500m and still higher, a few kilometers, in low density/fragmented populations (reviewed in Dick et al. 2008). Even if sufficient pollen reaches an isolated tree to fertilize all potential ovules, a reduction in diversity of the pollen cloud, due to fewer pollen donors, can reduce population fitness by allowing fertilizations from self, related, or maladapted parents. A reduction in seed set predicted from fragmentation may be due to one or a combination of a lack of pollination (e.g. from loss of pollinators), lack of compatible pollination (from increased self-pollination through restricted pollinator movement or a loss of incompatibility alleles owing to reduced population size), or inbreeding (Lowe et al. 2005).

Removal of primary habitat also usually decreases the probability that migrant seeds will find suitable sites for establishment. Under such circumstances, pioneers or invasive weeds will be favoured and will increase in occurrence. If a species' life history profile is characterized by frequent extinction and colonization events, the metapopulation is under threat of extinction if the two forces are not balanced. Even if site colonization does occur, founder bottlenecks can drastically reduce diversity (Lowe et al. 2005 and citations therein).

Species rarity can also determine its susceptibility to genetic erosion. Because common species have comparatively higher levels of genetic variability than naturally rare species, they are expected to lose more diversity due to recent fragmentation processes (Aguillar et al. 2008). Given the ubiquitous nature of anthropogenic habitat fragmentation in today's landscapes, this is important and of interest to conservation biology as they situate common species in potential risk of genetic erosion, which is counterintuitive to current conservation principles that almost exclusively emphasize efforts on rare or threatened species.

As discussed above, habitat fragmentation has the potential to erode genetic diversity of a species, and the magnitude of its effects is related to the state of several life-history traits. Among the several factors, deserve special attention the compatibility system, mating system, pollination vector, seed dispersal vector, vegetative growth capability, rarity, time elapsed in fragmentation conditions, (reviewed in Aguilar et al. 2008), and successional stage, as we are going to discuss below.

## 5. Local adaptation in tree species

An adaptation is a characteristic that enhances the survival or reproduction of organisms that bear it, relative to alternative character states, especially ancestral condition. The only way to an adaptation to evolve is by means of natural selection, so it can be also stated that adaptation is a characteristic that evolved by natural selection (Futuyma, 2005).

Local adaptation is the set of patterns and processes observed across local populations of the same species connected, at least potentially, by dispersal and gene flow. It is generally the case when resident genotypes in a deme have on average a higher relative fitness in their local habitat than genotypes originated from other habitats (Kawecki and Ebert, 2004 and references therein).

Local adaptation can be observed in a continuous population, in which sampling units are arbitrary, but is more commonly observed in fragmented populations, since they are discrete units of perennial populations in well delimited habitat patches (Kawecki and Ebert, 2004). Considering that the most existing neotropical tree populations have been fragmented by land use and urban occupation, local adaptation is a relevant area of study for neotropical tree species. Even though, most studies on local adaptation in plants are only available for herbaceous plants in temperate regions (Leimu and Fischer, 2008).

We aim to gather information on local adaptation in plants that can be used to evaluate its strength and outcomes for neotropical tree populations, considering their present fragmented character. Our understanding of this topic is mainly based on the papers of Kawecki and Ebert (2004), Savolainen and colleagues (2007), and Leimu and Fischer (2008).

The ability to adapt may be compromised in small populations because of reduced genetic diversity, caused by genetic bottlenecks or founder effects, which have as consequences an increase in genetic drift and inbreeding. In addition to reduced genetic variation and genetic drift, local adaptation can also be constrained by variation in natural selection. Temporal environmental variability may involve opposing selection pressures and thus constrain adaptation. In contrast, spatial heterogeneity of the habitats of plant origin favours selection for reduced dispersal and increases habitat fidelity, which may in turn favour the evolution of local adaptation (reviewed in Leimu and Fischer, 2008).

Reproductive traits have a role in determining the extent of local adaptation in natural populations. Gene flow, for example, can hinder local adaptation. This is true because protected polymorphism in a heterogeneous environment may be maintained even if dispersal results in complete mixing of the gene pool. In such a case demes will not differentiate genetically, i.e. there will be no local adaptation. Nevertheless, the existence of a pattern of local adaptation despite gene flow certifies to the strength of natural selection imposed by particular environmental factors (Kawecki and Ebert, 2004). Also, if local adaptation is constrained by lack of genetic variation, dispersal and gene flow between populations can enhance local adaptation by increasing genetic variation within populations and potential to respond to selection (Leimu and Fischer, 2008).

Spatial environmental heterogeneity favours reduced dispersal and habitat fidelity, which make conditions for local adaptation more favourable. It should be noted that environmental heterogeneity favours the evolution of adaptive phenotypic plasticity. In the absence of costs of and constraints on plasticity, a genotype that in each habitat produces the locally optimal phenotype would become fixed in all demes. Adaptive phenotypic plasticity would thus lead to adaptive phenotypic differentiation, but without underlying genetic differentiation. The failure of the metapopulation to evolve such ideal plasticity is thus a pre-requisite for local adaptation (Kawecki and Ebert, 2004 and reference therein).

Shortlived and self-compatible species tend to be more strongly differentiated at a smaller scale than long-lived and outcrossing species, and so the former are expected to show stronger adaptation to local conditions. Therefore, neotropical tree species, which are long-lived, outcrossing and as a group includes several examples of self incompatibility, are expected to have weak local adaptation (Leimu and Fisher 2008).

Leimu and Fischer (2008) conducted the first quantitative review on local adaptation in plants, assembling papers that reported comparisons of the performance of plants from local and foreign populations. Among these studies, local genotypes performed on average better than foreign genotypes at their site of origin. However, divergent selection favoured locally adapted plants only in less than half of the pair-wise site comparisons. This suggested to them that local adaptation is less widespread than commonly believed. In this study, they also found that local adaptation appeared to be independent of some plant life-history traits, the degree of spatial and temporal habitat heterogeneity, and of the geographic distance between study populations, but was strongly affected by population size. This clear role of population size for the evolution of local adaptation raises considerable doubt on the ability of small plant populations to cope with changing environments. Thus, in the context of fragmentation process in the Neotropic small fragments, featured by low genetic variability as a consequence of genetic drift and endogamy, might not be able to respond to different selective pressures of changing environments and develop local adaptation.

## **6. Brazilian Atlantic forest fragments: Case studies of species from Tibagi River Basin**

### **6.1 The Tibagi project**

In this section of the chapter we intend to describe our experience in population genetic studies of neotropical trees remnants in Brazil. All species that we have studied have a high importance value index or IVI (the sum of relative dominance, relative frequency and

relative density) in the Tibagi River basin, Paraná, Brazil and, due to the rapid degradation of ecosystems associated with this river basin, its present occurrence was limited to highly impacted forest remnants. The Tibagi River Basin has a great importance in the economic and social development of one of the Brazilian states of greatest economic impact in the country, however, the degree of landscape devastation that has taken place since the beginning of the last century has been threatening the biodiversity of the ecosystem and even physical and chemical characteristics of its rivers. For these reasons, a group composed of around 51 researchers from the University of Londrina and other research centers, in partnership with COPAT (Consortium for Environmental Protection of the Tibagi River basin) and funded by Klabin S/A and Araucaria Foundation for the Support of Scientific and Technological Development of Paraná, developed the project "Aspects of Fauna and Flora of the Tibagi River basin" or Tibagi Project. The Tibagi Project produced a wealth of valuable information aimed at the recovery and conservation of the river basin as a whole. We limit ourselves here to present the knowledge gained about the influence of two factors on the genetic diversity of populations of neotropical tree species remnants: habitat fragmentation and local adaptation to seasonally flooded river banks.

The Tibagi River basin is composed of 65 direct tributaries and hundreds of sub-tributaries in an area of approximately 25,000 Km<sup>2</sup>, covering 54 counties in the Paraná State, Brazil. Its landscape, belonging to the Atlantic Forest biome, presents important climate and soil variations in the north-south axis that allows it to be divided into Upper, Middle, and Lower Tibagi. On the Upper Tibagi, the predominant vegetation is steppe grassy-woody also known as general fields, with patches of Araucaria forest. In the Middle Tibagi, there is a transition zone between rain forest and mixed semideciduous forest with some patches of fields and scrubs. In the Lower Tibagi, before fragmentation, the dominant vegetation was the semi-deciduous forest, which formed a continuum with the dense rain forest of the Brazilian coast. With massive deforestation due to lumber extraction, urbanization and expansion of the agricultural front, only small forest fragments remain in this area adding up to only 2.4% of the original forest cover in the lower Tibagi and 12.7% in the Tibagi River basin as a whole (Ribeiro, 2009).

The riparian forests are plant formations that surround bodies of water and for that reason, are deeply influenced by them. On the other hand, water quality and other physical characteristics of rivers are also heavily influenced by the presence and degree of conservation of the riparian forests. In river banks, where the vegetation is scarce or not present at all, events such as erosions can be up to 30 times more significant than in areas where the riparian vegetation is present. Moreover, it is estimated that 80-90% of sediments and pollutants generated in agricultural areas are filtered by riparian vegetation before reaching the bodies of water (Naiman & Decamps, 1997). From the ecological point of view, these forests work as ecological corridors, linking different ecosystems and thereby promoting gene flow, both by land, and across the river. These are environments in which the diversity is determined by the occurrence of flood events with consequent flooding of the river margins. These environments can be very heterogeneous when flooding events are short, sporadic and with little intensity; however, they can be slightly heterogeneous when these flooding events are constant or very prevalent and intense.

Flooding is the main limiting factor that acts on the riparian forest, since it changes dramatically the physical and chemical characteristics of the soil, which is the main



substrate for plant growth. In flooded soil, the diffusion of gases is severely reduced, with a sharp drop in oxygen levels, reduction of gas exchanges, accumulation of toxins, changes in pH and nutrient availability (Drew 1992). When flooding extends to total or partial submergence of the plants, the negative effects on vegetation are even greater due to reduced availability of light and carbon dioxide (Crawford, 1993). Once flood period is over, the soil becomes compacted and a series of injuries from re-aeration process arises due to the accumulation of reactive oxygen species in plant tissues during the flooding period (Crawford, 1993).

However, most of the riparian plant species survive the flooding stress through the development of morphologic, anatomic and physiological changes (collectively referred to as the low oxygen escape syndrome - LOES; Bailey-Serres & Voeselek, 2008) that re-established, at least in part, minimum energy levels for plant survival. Other plant species survive with avoidance strategies, completing their life cycles between periods of flooding. There are also those species that have better relative growth rates in flooded soil. The ability to tolerate periods of flooding gives plants a competitive advantage over those that do not tolerate this stress, which is evidenced by the example of the tolerant species *Cecropia pachystachya*, *Sebastiania commersoniana* and species of the genus *Inga*, which are most often found in areas affected by periodic flooding than in other plant formations, where inter-specific competition limits its distribution. In general, local adaptation in challenging environments may either favour the reduction of genetic variation through natural selection or lead to the expression of phenotypic plasticity of identical genotypes (Stöcklin et al., 2009).

In this light, it seems clear that the recovery strategies and/or conservation of genetic diversity of tree species of the riparian forests on the Tibagi River basin should consider: (i) knowledge about the history of fragmentation and its influence on the genetic structure of the affected populations, (ii) knowledge about the diversity of mechanisms of tolerance to flooding and their possible genetic determination, (iii) and the influence of local adaptation to flooding events on the distribution of genetic variation within and among populations. In order to answer these questions, many common species from Tibagi river basin were studied, regarding flood tolerance and occurrence of morphological, anatomical and physiological changes in response to it. For eight of these species, we used DNA-based molecular markers (RAPD, AFLP and SSR) to obtain estimates of population genetic parameters such as polymorphic loci, total genetic diversity and genetic differentiation within and among populations. The eight sampled species have high importance value index (IVI) in Tibagi River basin (five are among the ten species with highest IVI by region) and cross-pollination system, but vary in regard to gender distribution and dispersal mechanisms for pollen and seeds (Table 1).

In Tibagi River basin, the analysis of the pluviometrical events from 1932 to 1990 showed that there were ten significant flood events in the region in this period, while the fragmentation of the vegetation was more pronounced between 1920 and 1960 (Medri et al., 2002). Considering that the first study published by the group comprised a minimum of 76 years between the collection of plant material and the first pronounced flooding event registered in the region and 83 years in relation to the beginning of the fragmentation process; in the meantime, the considered species advanced at least three generations (Table 1). It was expected at first that: (i) the genetic diversity of populations of degraded areas



might have been reduced compared to preserved areas, (ii) the pioneer species have been less affected by the effects of fragmentation than the species of late successional stages, (iii) there has been significant genetic differentiation between fragments and (iv) local adaptation to flooding has caused genetic structure, probably by reducing the diversity in populations that regularly experience stress.

Tree Species	Ss <sup>1</sup>	Ra	MS (SD) <sup>2</sup>	Pd	Sd	Long	Mm	Np	Pp(%)	Ht	Fst	Fis	Ref.
<i>A. sellowiana</i>	Pi/Si	2-4	Ou & Vp (Di)	Bi	Bi	25	SSR	5	77.78-100	0.32-0.48	0.197	0.03(-) 0.33	Oliveira, 2010
							RAPD	2	66.67-67.48	0.17-0.18	0.059	-	Medri et al., 2011
							RAPD	9	35.32-52.38	0.09-0.14	0.495	-	Medri et al., 2011 <sup>4</sup>
<i>A. polyneuron</i>	St	50	Ou (He)	Bi	Ab	1200	AFLP	2	88.5-99	0.31-0.37	0.265	-	Damasceno et al., 2011
<i>C. xanthocarpa</i>	St	6-8	Ou (He)	Bi	Bi	60	AFLP	2	92.27-92.82	0.32-0.33	0.180	-	Ruas, 2009
<i>C. gonocarpum</i>	St/Cl	-	Ou (He)	Bi	Bi	-	AFLP	2	79.5-92.1	0.28-0.31	0.300	-	
<i>L. divaricata</i>	Pi	2	Ou (He)	Bi	Ab	60	RAPD	2	80.69-86.9	0.9	0.104	-	De Carvalho et al., 2008
<i>M. aquifolium</i>	St/Cl	2	Ou (Un)	-	Bi	60	RAPD	3	72.80-84.51	0.17-0.21	0.218	-	Sahyn et al., 2010
<i>P. rigida</i>	Pi	10	Ou (Mo-Si)	Bi	Ab	100	RAPD	2	91.95	0.94	0.063	-	Silva et al., 2010
							AFLP	8	48.44-82.81	0.17-0.30	0.228	-	Souza, 2011
<i>S. terebinthifolius</i>	Pi	2-4	Ou (Di)	Bi	Bi	10-15	RAPD	2	64.64-70.72	0.168-0.20	0.137	-	Ruas et al., 2011
							SSR	6	87.5-100	0.48-0.62	0.199	0.04(-)0.03	Ruas et al., 2011 <sup>4</sup>

<sup>1</sup> Pi: Pioneer; Si: Secundária inicial; St: Secundária tardia; Cl: Clímax.

<sup>2</sup> Ou: Outcrossing; Vp: Vegetatively propagated; Mo: Monoecious; Mo-Si: Monoecious, Self incompatible; Di: Dioecious; He: Hermaphrodite; Un: unknown.

<sup>3</sup> Bi: Biotic; Ab: Abiotic.

<sup>4</sup> In press.

Table 1. Biological features and genetic parameters of the tree species studied in the Tibagi Project initiative. Information on biological traits was obtained in the literature and by personal communications of experts. When more than two populations of a given species were studied, the Fst values are represented as an average of those populations. Ss: Successional stages; Ra: Reproductive age, in years; MS (SD): Mating system (Sex distribution); Pd: Pollen dispersal; Sd: Seed dispersal; Long: Longevity, in years; Mm: Molecular marker; Np: Number of populations; Pp: Percentage of polymorphic loci; Ht: heterozygosity or genic diversity, when either codominant or dominant markers are respectively applied; Ref: references.

## 6.2 Local adaptation of tree species to flooding

In the Amazonian floodplain forests there are some regions where the water column reaches up to 7m with submersion of trees for long periods, and regions where this stress is less intense. Comparing the different areas of flooding, it is possible to observe a significant variation in the occupation pattern of these areas ranging from monospecific to over 150 species ha<sup>-1</sup> (Wittmann et al., 2007 and references therein). It is clear that the stress intensity and duration of flooding periods determine the diversity of species occupying these areas. In the Tibagi River basin, the most critical flooding period is the three wettest summer months (December-January-February), with areas that may remain flooded for a few days to several months depending on the intensity of the phenomenon. Torezan & Silveira (2002), conducted several phytosociological studies in forest fragments along the Tibagi River Basin

comparing areas under different intensities of occasional floodings. It was observed that the higher intensity, duration and size of the flooded area, the lower species richness was found. In a fragment with 100% of flooded area, there were 42 species/ha, while in fragments located in non-flooded areas, or with an insignificant area subject to flooding, the number of tree species was often greater than 100/ha, reaching up to 127 in one single area. Thus, we consider as a starting point the hypothesis that the stress of flooding, typically observed in the region, should determine the occupancy of the periodically flooded banks, favoring the establishment of species tolerant to this stress.

Several studies with species that are found in the Tibagi River basin were conducted in a greenhouse to answer this hypothesis. Plant species not found in the wetlands and the species most often found in the wetlands have been challenged in artificial flooding treatments with different intensities and durations. Briefly, the results showed that some tree species naturally distributed in this river basin but that do not occur in flooded areas, did not tolerate the stress of artificial flooding; also, there was a great variation in the response of the species from wetlands. In addition to this information, the provenance trials, conducted to compare the performance of populations of the same species from areas periodically flooded and non flooded, showed that for the studied species, *Luehea divaricata* and *Parapiptadenia rigida*, the plants that originated from populations naturally flooded were more efficient in responding to waterlogging stress (De Carvalho et al., 2008) or tolerated higher levels of stress, which was not tolerated by the plants of the other provenance (Silva et al., 2010). In a similar study with the tree species *Aegiphila sellowiana*, Medri et al. (2011) used plants regenerated from seeds collected in four regions that presented occasional flooding, showing a variation in the response of individual tolerance to waterlogging. In this experiment, 46.7% of the plants died, while the remaining individuals developed morpho-anatomical alterations common to tolerant species, supporting up to 80 days flooding (Medri et al., 2011).

When these results were obtained (2000 - 2002) we believed that there should be a genetic background related to flood tolerance, but the variation in responses observed between the tolerant species pointed to the existence of a large number of genes and/or a strong effect of genotype-environment interaction in determining the tolerance. With these in mind, we used Random Amplified Polymorphic DNA (RAPD) to see if there was a reduction in genetic variation in populations tolerant to flooding, and whether it was possible to detect variation between populations that respond differently to the stress. In our experiments of performance comparison, the percentage of polymorphism observed *in situ* among adults of *Luehea divaricata* and *Parapiptadenia rigida* was greater (approximately 6%) in the areas subjected to periodic flooding than in the highest regions, which is never affected by stress. The studied populations of *L. divaricata* and *P. rigida*, showed genetic differentiation of 10.48 % for the first species and of 6.00% for *P. rigida* (while about 90% of the observed variation was attributed to the variation found within populations). These results suggested that perhaps the expected reduction in genetic diversity of riparian communities has been masked by the balance between different evolutionary forces that could be occurring *in situ*. Considering the proximity of the sampled areas and the fact that both are crossbreeding species, there certainly is gene flow between the flooded and non flooded populations, which in turn must ensure the re-establishment of genetic diversity in each generation. Possibly, the lower inter-specific competition and greater light availability on the river banks may represent, for the pioneer species studied, a more important factor than natural

selection caused by flooding, enabling the maintenance of higher levels of diversity in wetlands.

We needed a model that would allow us to access the isolated effect of flooding on the genetic diversity of populations of plants tolerant and intolerant to stress. In this experimental model we use the tree species *A. sellowiana*, which displays a gradation of responses to flooding, ranging from death to survival periods of up to 80 days of stress. When comparing plants of *A. sellowiana* which survived the stress of artificial flooding (tolerant), with plants which died (intolerant), the genetic differentiation around 6% was detected between the two groups and it was not possible to detect important variation in the percentage of polymorphism between both of them (Medri et al., 2011). Given these results, it became clear that the vast phenotypic variation between tolerant and intolerant plants of *A. sellowiana* can be, at least in part, related to the genetic patterns observed when using the DNA-based marker RAPD. A similar situation was found by Bekessy et al. (2003) who used RAPD markers to study genetic variation in populations of the South American tree *Araucaria araucana*. Even though we have yet to acquire the knowledge of which genes determine the stress tolerance of flooding on tree species it is possible that this character is directly influenced by many genes as suggested by Sairam et al. (2008) in their review entitled "Physiology and biochemistry of waterlogging tolerance in plants".

Interestingly, considering the results obtained by the group, especially with the local adaptation experiment, carried out *ex situ* with *A. sellowiana*, it becomes clear that the genetic diversity within and between populations cannot be considered the only factor in the election of sources for the recovery of degraded riparian forests. In short, the RAPD markers used in these studies allowed us to detect consistent results for the three species studied since more than 94% of genetic variation detected can be attributed to variation found within populations, following the pattern usually observed for pioneer species, with preferably cross-fertilization. In the absence of knowledge on the mechanisms of inter-specific diversity of tropical trees on response to flooding, we may conclude, erroneously, based only on estimates of distribution of the genetic diversity, that both the populations that occupy the margins of the flooded rivers and those never flooded could be used as seed sources for the recovery of degraded riparian areas. However, the difference in performance between plants, as measured by morphological parameters, indicate that populations locally adapted to the stress would provide a better material for the recovery of degraded riparian areas.

### 6.3 Effects of fragmentation in natural populations from Tibagi River Basin

In several years of studies observing the effects of fragmentation and local adaptation on the genetic diversity of the remaining tree populations of the Tibagi River Basin, eight species were evaluated mostly with dominant molecular markers (Table 1). The information gathered here reflect observations for post-fragmented populations, and the number of generations elapsed since the beginning of the fragmentation process is equal to one or two for centenary species, and no more than ten generations for the species with longevity from 20 to 25 years.

As seen among tropical species (Matallana et al., 2005), all species present higher frequencies of cross-fertilization and animals play an important role in pollination and/or seed dispersal. These characteristics can be readily related to the high levels of genetic diversity (or heterozygosity) observed in the sampled populations (Table 1). In addition, pollen and

seed dispersal by animals, often observed in tropical species, should provide high gene flow between nearby populations in a continuous gradient, while favouring the genetic differentiation over long distances (Givinish, 1999 and references there in). In such cases, the observed genetic distance between populations was positively correlated with their geographic distances. This hypothesis could be verified from the combined analysis of two studies conducted with *P. rigida*, where two nearby populations (Silva et al., 2010) and eight populations distributed over a long geographic scale (Souza et al., 2011) were evaluated. For nearby populations, the  $F_{ST}$  value obtained was only 6.2%, whilst the average  $F_{ST}$  between the eight populations was 22.8%, and the correlation between genetic and geographic distance was positive and significant. Similarly, the observed values of  $F_{ST}$  between geographically close and distant populations of *A. sellowiana* ranged from 9.56% to 50.26%, respectively (Medri et al. 2011; Oliveira, 2010). For this species in particular, the genetic differentiation between distant populations may be even more pronounced than the one seen for *P. rigida* due to the occurrence of vegetative propagation.

When the genetic diversity among populations is compared between the studied outcrossing species, one can see that there are significant variations among the observed values of  $F_{ST}$  (6% - 30%, Table 1), which is suggested to be related to successional stage that each species occupies.  $F_{ST}$  values for the initial or secondary pioneer species vary between 6% - 19% and the values for the late secondary or climax species vary between 21% - 30%. In both cases, genetic differentiation among populations assume moderate to high values, which is, in principle, expected to occur among tropical species. Tropical species are often pollinated by animals or have their seeds dispersed by them, often have mixed breeding system in which selfing rates can be changed depending on the environment and are represented by low-density populations (Dick et al. , 2008). These characteristics, together, make the tropical species more dependent on the quality of the ecosystem where they are inserted than the temperate species, and therefore more susceptible to the effects of fragmentation. Under the effect of fragmentation, tropical species suffer a reduction in the availability of pollinators and/or seed dispersers with the reduction in the number of individuals, experiencing a higher proportion of inbreed crosses and genetic drift, with a resulting increase in genetic differentiation between populations.

It is suggested that the observed tendency of lower values of  $F_{ST}$  between the pioneer species than among the secondary is a reflection of the life history of these species. The pioneer species represent the first successional stage of the forest, being able to invade areas not yet occupied, including harsh environments and forest edges. Thus, given the ecological role they play, the pioneers are heliophyte, experience rapid growth, lower inter-specific competition, increased investment in reproduction (r selection), a higher number of generations per unit time and aggregate distribution. Fragmentation, therefore, does not cause too negative effects on the pioneer species. In fact, while fragmentation reduces the number of individuals of the species of later successional stages and completely alters the environment they occupy, the pioneer species can be instead favored by this process. Also, the pioneer species from the fragments of the Tibagi River Basin have advanced several generations (10 -15 generations) since the beginning of the fragmentation process. So, after several cycles of cross-fertilization, gene flow between populations may have indeed come relatively high to overcome the effects of fragmentation, allowing lower levels of genetic differentiation among populations.



Unlike the pioneers, the late secondary and climax species tend to have less aggregated spatial distribution, to be ombrophilous and to occupy more specialized niches. These species spend their energy more in the inter-specific competition than in reproduction ( $k$  selection) and have slow growth and far fewer generations per unit time. The species of late successional stages, considered here, represent the first or second generation post-fragmentation and thus are believed to reflect the immediate consequences of the fragmentation process. Interestingly, one of the secondary species studied, *Aspidosperma polyneuron*, was found in a continuous distribution, in a plateau followed by a high declivity (Damasceno et al., 2011), and the other, *Maythenus aquifolium*, was found in fragments separated by up to 30 km (Sayhun et al., 2010); however, the  $F_{ST}$  values observed in the two situations were similarly high, suggesting that part of the genetic differences found between the populations of these species also linked to adaptive characteristics (Sayun et al. 2010; Damasceno et al., 2011).

Another important information that we could extract from the obtained results for the sampled populations in these regions of lower, middle and upper Tibagi (Ruas et al. 2011 In press; Ruas et al. 2011; Medri et al. 2011 In press; Oliveira et al, 2011) is that the intense fragmentation towards middle-lower Tibagi has provided a significant increase in inbreeding coefficient ( $F_{IS}$ ), loss of alleles and reduced genetic diversity compared to populations from the upper Tibagi (Table 1). These factors also influenced the genetic differentiation between populations of the upper Tibagi (where fragmentation is less evident) and the others. The only exception to this result was observed in *A. sellowiana*. When analyzing the species *A. sellowiana* with microsatellite markers we also observed the formation of two distinct groups of populations (Dendrogram using Nei's genetic distance, 1978), one comprised of populations from the middle Tibagi region and the other pertaining to lower Tibagi (Oliveira, 2011 submitted). Even though *A. sellowiana* is able to perform vegetative reproduction and also its propagules can reach as far as 10m distance from mother tree, we evidenced highly significant negative values of  $F_{IS}$  indicating excess of heterozygosity in tree of the five populations. When considering the effect of recent genetic bottlenecks in these populations, the values obtained by the software bottleneck indicated that four of the five populations showed significant values of heterozygosity excess, when considering the Infinite Allele Model, and only one population presented significant levels of heterozygosity excess for all tree models (Infinite Allele Model, Two-phase Model and Stepwise Mutation Model). Migration rates calculated for these populations demonstrated that exchange of 30% of migrants between two populations from the middle Tibagi region. Such results demonstrate that some of these populations are suffering more than others, the impact of fragmentation and also founder effect and gene flow are playing a key role in the shaping of the genetic variability within these populations of *A. sellowiana* promoting a weak balance between the evolutionary forces of genetic drift and migration in this post fragmentation period landscape.

Lately, this research group has been engaged in the development and inter-specific transference of microsatellite primers (SSR) for the species *L. divaricata* (Ruas et al., 2009), *A. sellowiana* (Ruas et al., 2010), *P. rigida*, *A. polyneuron*, *C. xanthocarpa*, *C. gonocarpum* and *A. polyneuron*. The use of SSR markers will allow more accurate estimates about the distribution of genetic variation and the effects of fragmentation and local adaptation between the species of the Tibagi River basin. Such is possible due to the codominant nature of these markers, allowing to access allelic information and thus to estimate the number of



alleles, heterozygosity, inbreeding and gene flow among natural populations. Although much work is yet to be done with these and other species of the Tibagi River basin, the present studies certainly represent a great step for the comprehension of the present availability of genetic resources and of its relation to the life history of species from forests fragments pertaining to the Tibagi River basin.

## 7. Conclusion

In summary, the knowledge we have accumulated so far on the genetic structure of the studied populations allows us to infer that the large genetic differentiation that has been maintained between natural populations, especially among those of late successional stages, makes it imperative to conserve all forest remnants. One of the strategies that we believe can be effective for the conservation and restoration of these ecosystems is the establishment of green corridors to restore communication of pollinators and dispersers between forest fragments of the Tibagi River basin. Moreover, the development of SSR markers for tropical tree species would first increase our knowledge on those species genome and help the investigation of the genetic determination and evolution of some important adaptations, such as flooding tolerance. Second, it would advance our understanding of the effects of habitat fragmentation over the riparian forests' diversity.

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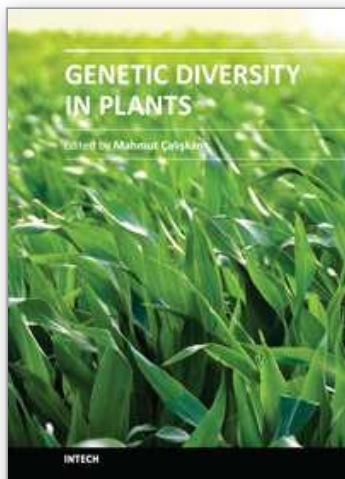
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## **Genetic Diversity in Plants**

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Genetic diversity is of fundamental importance in the continuity of a species as it provides the necessary adaptation to the prevailing biotic and abiotic environmental conditions, and enables change in the genetic composition to cope with changes in the environment. Genetic Diversity in Plants presents chapters revealing the magnitude of genetic variation existing in plant populations. The increasing availability of PCR-based molecular markers allows the detailed analyses and evaluation of genetic diversity in plants and also, the detection of genes influencing economically important traits. The purpose of the book is to provide a glimpse into the dynamic process of genetic variation by presenting the thoughts of scientists who are engaged in the generation of new ideas and techniques employed for the assessment of genetic diversity, often from very different perspectives. The book should prove useful to students, researchers, and experts in the area of conservation biology, genetic diversity, and molecular biology.

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