



Genetic Consequences of Fragmentation in Tropical Forests: Novel Approaches to Assess and Monitor Critically Endangered Species

5

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Abstract

Home to a large number of species and indigenous communities, tropical forests across the world are a “melting point” of biodiversity and culture. Tropical forests provide several ecosystem services and form a treasure house for many pharmaceutically important products that have direct benefits to human well-being. However, increase in the anthropogenic activities in recent years has put tremendous pressure on these forests resulting in species extinctions, habitat loss, and fragmentation at a much large scale. Further, indiscriminate harvesting of forest resources has resulted in many economically important species being rendered rare, endangered, or threatened. In these fragmented and anthropogenically impacted populations, conservation action should consider the possible loss of diversity through drift and other microevolutionary processes. The recent developments in the field of conservation genetics and the rapid accumulation of genome-wide data from non-model organisms have enabled their applications in the conservation of these populations and species. However, to date, genetic methods have primarily focused on selected neutral loci to identify units of immediate conservation importance. Recently, next-generation sequencing (NGS) approaches and other statistical methods have been used to understand adaptive variations in fragmented populations. The ability to characterize detrimental and adaptive variation is expected to have tremendous importance for successful conservation efforts. In this chapter, we examine the impacts of forest fragmentation and habitat loss on species demography, fitness, genetic diversity, and evolutionary processes. In particular, we review the existing state of knowledge and discuss novel methods and approaches that could be employed to

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79

conserve genetic resources that would not only ensure the survival of the focal species but also maintain ecosystem integrity and stability.

Keywords

Conservation genetics · Genomics · Genetic diversity · Habitat fragmentation

5.1 Introduction

It is widely accepted that human-mediated habitat alterations have led to unprecedented loss of biological diversity. Curbing this drastic loss is one of the primary challenges faced by conservation biologists across the world (IPBES; Bongaarts 2019). Among these alterations, habitat fragmentation (dividing a continuous habitat into several smaller ones) poses direct threats to species and ecosystem survival and healthy functioning by disproportionately altering the structure, composition, and diversity. The effect of habitat fragmentation is further amplified with the loss of intra-specific genetic diversity within species. Such losses can often lead to irrecoverable outcomes, including inbreeding depression (Pavlova et al. 2017) and failure to adapt to future climate change (Gossmann et al. 2019; Alsos et al. 2012) and create extinction debts to species (Kuussaari et al. 2009) due to widespread decline in geographic distribution and population size of many species.

The effect of habitat fragmentation is severe in the tropics (Betts et al. 2019), which has a high biological diversity and supports most of the world's indigenous people, many belonging to the poorest communities (IPBES 2019). The tropical forests harbor a rich floral and faunal diversity comprising several ecologically and economically important species. The impact of forest fragmentation here is vast and direct, ranging from altering the forest structure and regeneration patterns to altering the ecosystem dynamics and human well-being (Lewis and Wu 2005). For instance, fragmentation results in increased habitat patches causing gaps in the canopy, bringing changes to forest structure and species composition and attracting colonization of invasive species. Among several detrimental effects of habitat fragmentation, loss in population connectivity, inbreeding depression, and associated genetic diversity reductions are of prime importance. Reduction in genetic diversity will eventually make species vulnerable to climate change (Bálint et al. 2011) and pest attacks (Stenberg 2017) and can even lead to local extinctions (Frankham and Ralls 1998). Recent studies also report the emergence of several zoonotic diseases including COVID-19 to increased human-wildlife interactions caused by habitat fragmentation (O'Callaghan-Gordo and Antó 2020).

The last decade witnessed a growth of several novel methods and approaches to identify the impacts of habitat fragmentation among plant species which led to the implementation of novel conservation measures. This included the development of several statistical methods, analyzing large genome-level datasets generated from next-generation sequencing (NGS) and combining disparate data types to unravel the natural and managed population's genetic structure. In this chapter, we discuss

the impact of habitat fragmentation on plant systems and highlight some methods and approaches used to measure the impacts of fragmentation and devise strategies for future conservation.

5.2 Impacts of Forest Fragmentation and Habitat Loss on Species Demography and Fitness

Forest fragmentation (habitat fragmentation) is a landscape process often associated with the anthropogenic disturbance of a continuous forest. Fragmentations can occur due to logging, clearance of natural landscape for agriculture, or other anthropogenic activities. For example, construction of roads has led to fragmentation of forests into several patches that may get invaded by a mix of ornamental plants and other invasive species, affecting the local species composition of an area (Hardiman and Culley 2010). It is also shown that habitat fragmentation increases the vulnerability of invasion of exotic species (Primack & Rachel 2013).

The impacts of forest fragmentation and habitat loss on the demographic structure and plant fitness have been an important area of ecological research for many decades (Soule 1986, Wiegand et al. 2005). Habitat fragmentation has a serious impact on many species and threatens the survival of local populations. In general, habitat fragmentation seems to have two major genetic consequences. One, fragmentation results in the smaller populations becoming more isolated. And two, reduced population size and isolation increase extinction risks due to different stochastic events (such as genetic drift) and reduced gene flow between habitat patches as well as increased inbreeding, all of which can negatively affect population fitness. A plethora of published studies have demonstrated that offsprings in fragmented habitats suffer tremendous loss in genetic diversity in contrast to those in a contiguous habitat. Seedlings in fragmented habitats are shown to have reduced germination, higher mortality, and decreased growth rates (Tambat et al. 2005; Aguilar et al. 2019). Furthermore, a stronger negative effect on the progeny vigor of outcrossing plant species, except for vertebrate-pollinated species, has also been shown (Aguilar et al. 2019). The number of seedlings produced and its viability in a fragmented habitat is a key demographic parameter as it defines the density of individuals recruited in the next generation (Newman et al. 2013). Lower regeneration and higher seedling mortality, as a result of habitat fragmentation and overexploitation, could eventually reduce the overall population size of future generations.

Fragmentation also alters abiotic conditions (often known as edge effects) in the fragmented landscapes resulting in changes in the biotic interactions due to increased transitional area between habitats. For example, fragmentation directly influences the diversity and abundance of pollinators resulting in changes in plant mating patterns (see Aguirre and Dirzo 2008). The altered landscapes due to fragmentation are shown to disrupt pollinator movements resulting in reduced pollination services (Breed et al. 2013, Aguilar et al. 2006). A study by Winfree et al. (2009) has demonstrated a significant reduction in species richness and abundance among important pollinators like bees in fragmented habitats. In addition, habitat

modifications can also modify key pollinator behaviors such as foraging distances and time spent on individual flowers as well as the diversity of pollen sources (Delnevo et al. 2019), thus resulting in increased selfing, reduced fruit-set, low seed number, higher abortion, and overall reduced regeneration.

5.3 Impacts of Forest Fragmentation on Genetic Diversity and Evolutionary Processes

Fragmentation can result in a reduction in the genetic diversity of plant populations due to (a) reduction of total areas of habitat resulting in less number of breeding individuals, (b) isolation or separation of intact populations, and (c) creation of physical barriers for the gene flow between populations. The loss of continuous habitats due to anthropogenic fragmentation is considered one of the major causes of species extinction and the associated reduction in biodiversity (Sala 2000).

Reduction in population size will subsequently affect the total gene pool in the population as a result of genetic bottleneck (sudden decrease in population size resulting in severe genetic loss; Barrett and Kohn 1991, Fig. 5.1). Populations that remain isolated and are small in size over several generations often suffer from loss of allelic diversity (with loss of many rare alleles) and increased genetic differentiation (Barrett and Kohn 1991). Continued genetic drift in small populations can also result in deleterious alleles being fixed in the population (Bortoluzzi et al. 2019; Huenneke 1991). Reduced gene flow can alter both within and among-population genetic structure as well as increase mating among closely related individuals (inbreeding). Increased inbreeding results in increased individual homozygosity

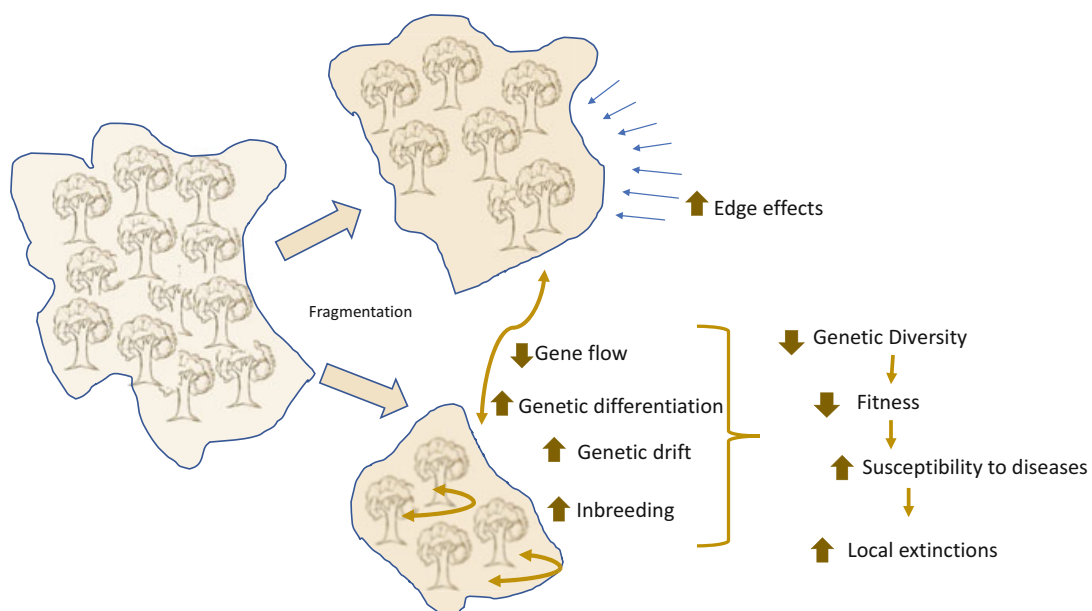


Fig. 5.1 A schematic diagram representing the potential impacts of fragmentation on plant populations

(reduced genetic variation within individuals) and leads to what is termed as inbreeding depression leading to a loss in individual fecundity, establishment, and survival (Keller 2002).

In tropical tree systems, habitat fragmentations are shown to pose detrimental effects in the long-term viability by opening grounds for inbreeding depressions and reducing gene flow across populations (see Vranckx et al. 2011; Finger et al. 2011; Jump and Penuelas 2006). The severity of inbreeding depression is particularly high in tropical trees which are historically outcrossing as the effects of deleterious recessive alleles are masked by their typically high individual heterozygosity. However, the consequence of fragmentation may vary according to species ecology and can magnify over time. Simultaneously, biological aspects such as the longevity of trees, mating systems, and effectiveness in seed or pollen dispersal are also shown to further resist fragmentation's detrimental effects. For example, temperate trees are less affected than tropical tree species by fragmentation due to their high density and seamless pollen-seed dispersals. It has also been shown that even several wind-pollinated trees such as *Fagus sylvatica* respond negatively to habitat fragmentation (Barbeta et al. 2011), adding more complexity to the existing state of knowledge.

5.4 Methods to Assess Fragmentation Impacts on Genetic Diversity

Several methods and programs are now available to assess the effect of habitat fragmentation on genetic diversity. Their applications range from assessing genetic diversity (e.g., Arlequin), gene flow between and across populations, to forward simulation of genetic data (e.g., SPLATCHE). These approaches are formulated to address the impacts of fragmentation on key genetic parameters among the isolated populations, vital to implementing effective restoration strategies for the future. These include (a) measuring gene flow via paternity analysis, seed dispersal patterns, and long-distance dispersals, (b) inbreeding depression, and (c) test for a fine-scale spatial genetic structure (FSGS) among fragmented populations. Some well-worked examples on these lines are discussed below.

5.4.1 Measuring Gene Flow Via Paternity Analysis and Seed Dispersal Patterns

Seed dispersal mechanisms play a primary role in expanding species ranges, recolonizing lost habitats, and thus improving the chance of their long-term survival. The wet tropical forest trees produce mostly fleshy fruits, i.e., >75% of the total tree species, and are actively dispersed by vertebrates (see Willson et al. 1989). Habitat fragmentations are shown to alter the existing dispersal mechanisms by affecting the magnitude of gene flow (Hamilton 1999; Young et al. 1996). A direct and accurate understanding of gene flow mechanisms will drastically improve the ongoing conservation efforts. Researchers have applied several non-genetic (e.g., setting seed



Fig. 5.2 (a) *Dysoxylum malabaricum* in the Western Ghats hotspot. (b) Seeding of *D. malabaricum* in the sacred groves. (c) The colorful seeds are dispersed by native birds such as hornbills. (d) Logging for economical uses and fragmentation have led to isolation of populations of *D. malabaricum* in the Central Western Ghats, and (e) bark of *D. malabaricum* is often used as an ingredient in the local medicine

traps) and genetic approaches such as maternal matching analysis using microsatellites to estimate gene flow via seed dispersals. Uniparentally inherited chloroplast and mitochondrial markers have been particularly useful to identify historical gene flow patterns, still these markers often fail to capture the contemporary gene flow due to their conserved nature. Interestingly, Ismail et al. (2012) used parentage analysis and a logical decision-based maternal tree assignment to identify the dispersal patterns in the tropical tree *Dysoxylum malabaricum* (Fig. 5.2). Their approach successfully identified the minimum distance where the seeds disperse. Such findings are shown to be highly useful for devising future conservation measures for *D. malabaricum* in its natural habitats.

5.4.2 Estimating Inbreeding Depression

Inbreeding depression is one of the initial consequences of habitat fragmentation. The increased spatial isolation and reduced population size of species due to fragmentation may result in mating within close relatives and results in reduced heterogeneity and fitness (Young et al. 1996). Habitats' discontinuity is shown to affect the quality of seed dispersals and pollination (Ferreira et al. 2020; Cunningham 2000, Aizen and Feinsinger 2003). Reduced seed dispersals and gene flow will further amplify the inter-population divergence. Inbreeding depressions can be calculated in several ways. Ideally, it can be calculated using pedigree-based indices (Pemberton 2004) or using the microsatellite-derived metrics to infer the

relative inbreeding between individuals by applying the formulae proposed by Ritland (1996), i.e.,

$$\text{Inbreeding coefficient (FIS)} \\ = \frac{1 - \text{intra population gene diversity}}{1 - \text{average expected heterozygosity of each population}}$$

Pedigree-based methods are quite impossible to apply in natural populations. In such instances, the individual inbreeding coefficients or the “kinship” of parent pairs (Loiselle et al. 1995) can be used as alternatives and has been successfully demonstrated by Ismail et al. (2012).

5.4.3 Test for a Fine-Scale Genetic Structure (FSGS) among Populations

Fine-scale population genetic structure (FSGS) is a non-random spatial distribution of genotypes in populations (Vekemans and Hardy 2004). Many empirical studies have shown that habitat fragmentation may lead to increased isolation by distance (limited gene dispersal) within a continuous population, altering its genetic structure at a finer scale. In population genetic terms, the neighboring individuals would be genetically similar compared to the distant ones. Such settings will further force an individual population to have unique genotypic makeup. A positive signal for an FSGS could indicate that the populations under study can be prone to inbreeding depressions due to reduced gene flow (limited seed and pollen dispersal), increased seedling mortality, altered regeneration patterns, etc. In any case, habitat fragmentations can exacerbate the detrimental effects of FSGS in a continuous population. This can be estimated by calculating the pairwise relatedness coefficient between samples and their relationships with the spatial distance separating individuals.

The three metrics listed above can be used to detect the effect of habitat fragmentation on natural populations. This information will provide important insights to manage and conserve the population from the adverse effects of fragmentation. With this understanding, future conservation goals can be achieved via assisted dispersal of seed and genetic enrichment (reintroducing genetically diverse seedlings back to the original habitats) to reduce mortality and the effect of inbreeding.

5.5 Empirical Pieces of Evidence for Genetic and Evolutionary Consequences from Tropics

As previously mentioned, tropical trees are particularly vulnerable to fragmentation threats (Ony et al. 2020, Degen and Sebbenn 2014, Farwig et al. 2007). Maintaining genetic diversity in tropical forest trees, especially in economically important, rare, and threatened species, has long-lasting implications for maintaining the ecological,

environmental, economic, and cultural significance within a landscape. The last decade witnessed a growing interest in population genetic approaches to study the impacts of habitat fragmentation in economically important tree species. As a result, it is now widely accepted that habitat fragmentation will eventually lead to high inbreeding and decline in genetic diversity and reproductive fitness in plant populations (Vranckx et al. 2011; Finger et al. 2011). Furthermore, the importance of genetic diversity for survival, adaptation, and evolution of individuals and populations, ecosystem stability, and functioning is also very well established. Thus, identifying the relative contribution of these effects on fragmented populations is of great conservation concern across the world (Frankham & Ralls 1998) and still remains an active research and development area.

In India, studies aiming to assess tree species' conservation genetics are comparatively less to that of animal systems. There are less than 50 published datasets with conservation genetics applications from the Indian subcontinent. Notable among these studies include a comprehensive analysis of the genetic structure conducted for the economically important tree species *Dysoxylum malabaricum* (white cedar) endemic to India's Western Ghats (Fig. 5.2). Due to its high demand for timber, *D. malabaricum* populations in the Western Ghats are heavily harvested. As a result, several populations are now fragmented and require immediate conservation attention. Several studies, using a combination of fine-scale population sampling and population genetic analysis, investigated the effects of habitat fragmentation and overharvesting and identified the patterns of natural gene flow and discussed future strategies for conservation (see Ismail et al. 2014, Bodare et al. 2013, Ismail et al. 2012, Bodare et al. 2017).

Ismail et al. (2012), based on a fine-scale sampling of adults and juveniles of *D. malabaricum* in the sacred groves of Central Western Ghats, found that the surviving trees contain substantial genetic diversity with similar levels in juvenile cohorts. There was also an instance of long-distance pollen flow; interestingly, they found low local tree density and a significant fine-scale genetic structure. Their findings point to an elevated mating between related individuals and a high probability of genetic drift, which will eventually erode genetic diversity in *D. malabaricum*. In a related study, Bodare et al. (2016) investigated the fine-scale spatial genetic structure in four fragmented patches in Northern Western Ghats and found significant differences in the allelic richness, observed heterozygosity, fixation index (F_{IS}), and relatedness ($P < 0.05$) between seedlings and adults. Their study concluded that the reduced genetic diversity and increased relatedness at the seedling stage might be due to fragmentation and disturbance. Their study also showed clear spatial genetic structure at the landscape level (<50 km), due to limited gene flow between forest patches.

In another study, Bodare et al. (2013) identified a spatial genetic structure of *D. malabaricum* across the Western Ghats, viz., a northern and southern genetic group using nuclear and chloroplast microsatellite makers. Their findings indicate a reduction in the diversity of the northern populations of Western Ghats. The study recommends a high conservation priority to northern populations and evaluates the regeneration dynamics of *D. malabaricum* in those regions.

5.6 Novel Tools and Methods to Conserve Genetic Resources

The rapid decline in sequencing costs now offers new opportunities to use novel genomic tools with increased accuracy to test population genetic questions, which was previously attempted using a limited set of selectively neutral markers. Genomic tools provide powerful support to develop intensive management practices for species that are threatened. It is possible to generate information from a large number of loci, which can further provide accurate population genetic parameters (Table 5.1). Substantial progress is being made in the field followed by applications of NGS methods. Notably, these advances include improved models and statistical tools for a better estimation of population genetic differentiation, proportion of admixture, and spatial distribution of variation.

Among the large-scale sequencing approaches for conservation genetics, restriction-site associated DNA sequencing (RAD-seq) and genotyping by sequencing (GBS) approaches have been widely used to generate high-quality population

Table 5.1 Genomic approaches with applications for population genetic studies

Sl No.	Sequencing approach	Applications	References
1	RAD-seq	Identifying conservation units, developing ex situ conservation plans, identifying populations for reintroduction, genetic rescue for inbred populations	Basak et al. (2019); Brandrud et al. (2017)
2	Genotyping by sequencing (GBS)	Assessing adaptive potential, identifying conservation units, population structure and demographic analysis, molecular marker discovery, reference genome is not required	Chung et al. (2017)
3	Transcriptome sequence in association with genome sequence data	Assessing adaptive potential and population genetic analysis	Gasc et al. (2016)
4	Environmental DNA	Understanding historical special legacy and species movements when combined with paleoecological datasets	Bálint et al. (2018); Stewart and Taylor (2020)
5	Bait STR	Assemble massively parallel sites of short tandem repeats. Recover several introns region in the genome which has applications for population genetics	Kistler et al. (2017)
6	Pool-seq	Pooling samples before library preparation, cheaper	Hivert et al. (2018)
7	GRAS-Di (genotyping by random amplified sequencing, direct)	Genetic differentiation patterns, population structure and demographic analysis	Enoki and Takeuchi (2018)

genomic data in plant species (Parchman et al. 2018; Cai et al. 2020). Their main advantage is in rapid marker discovery and genotyping many individuals, even in the absence of a reference genome. RAD-seq and GBS methods are increasingly used in tree species studies and are expected to become the most common methods for generating genome-wide datasets (Parchman et al. 2018).

A recent genetic analysis of *Cryptomeria japonica* based on RAD-seq data revealed a low diversity and structure within the ancient populations (Cai et al. 2020). The datasets identify the role of strong genetic drift caused by climate fluctuations and intense anthropogenic disturbance as the major driving factors. Yet another study by Ahrens et al. (2017) used the microsatellite genotyping and GBS approach to study the population structure of four rare terrestrial orchids in Australia. This study is particularly of interest as these four co-occurring species exhibit low morphological diversity. While microsatellites could only detect the out-groups, the GBS data recovered a strong population structure among these species. These studies indicate the potential use of new NGS approaches in capturing genetic patterns that failed to be detected by the conventional molecular markers.

5.6.1 Measuring Adaptive Potential

The adaptive potential of a species to novel challenging environmental conditions determines the probability of long-term survival and persistence of a species. A study by Abebe et al. (2015) used GBS approaches to identify genomic signatures of local adaptation in *Hordeum vulgare* populations in Ethiopia. The study identified the genetic structure and diversity of populations under study and identified its association with climatic variables. Besides the climatic variables explaining the observed genetic variation, the study further identified putative adaptive loci in *H. vulgare* populations. By uncovering the genetic footprints of barley adaptation to landscape and climatic variables, the study offers unlimited options for future exploration, cultivation, and conservation of specific genotypes. Similarly, a genome-wide scan on *Handroanthus impetiginosus* by sampling 75,838 SNPs identified highly diverse and structurally conserved genes related to plant development and primary metabolic processes (Collevatti et al. 2019). The study pinpoints adaptive sweeps leading to a polygenic model, implying that the adaptive traits are under polygenic control in natural populations of *H. impetiginosus*.

Overall, these studies highlight the power of sequence-capture through SNP genotyping in detecting loci under selection, which can inform future conservation strategies in non-model organisms, and applying such methods can add to a deeper understanding of the future adaptive potential of plant populations in the wild (see Table 5.2). The genome-based approaches can further target species and populations with unique features such as the potential to survive in extreme environmental conditions.

Table 5.2 Examples of popular programs and variant calling pipelines capable to handle genomic data for conservation genetics applications

Sl No	Packages/ pipelines	Applications	References
1	SimAdapt	Simulate forward time evolutionary process of adaptation and population dynamics in changing landscapes	Rebaudo et al. (2013)
2	GRAINSCAPE	Modelling landscape connectivity	Chubaty et al. (2020)
3	inbreedR	Large-scale SNP datasets	Stoffel et al. (2016)
4	POLYGENE	Genetic analysis of autopoloids	Huang et al. (2019)
5	ResistanceGA	Effect of landscape features on gene flow	Winiarski et al. (2020)
6	SAMtools	Variant calling	Li et al. (2009)
7	GATK	Suite of tools for variant discovery and genotyping	https://gatk.broadinstitute.org/hc/en-us
8	BayPASS	Genome-wide scans, identifying markers subjected to selection	
9	Fast-GBS	Reference bases assembly	Torkamaneh et al. (2017)
10	Stacks	De novo and reference-based assembly, common population genetics summary statistics	Catchen et al. (2013)
11	SimRAD	Prediction of number of loci expected under RAD-seq/GBS, when a reference genome is available	Lepais and Weir (2014)

5.6.2 Simulating Genetic Data to Design Process-Based Conservation Plans

Plants are sessile organisms where the movements occur via seed or pollen dispersal or asexual reproduction through clonal propagation. Direct estimation of their movement patterns can be challenging. These inferences are crucial to test hypotheses such as whether the current-day distribution of a species results from its long-term historical distribution or such patterns evolved in response to human disturbances. Integrating population genetic/demographic inferences to conventionally disparate datasets as global climate datasets (Espíndola et al. 2012) and population connectivity models (see Roffler et al. 2016) can establish a reliable picture of past changes in landscape leading to the current population distributions. The application of these approaches is straight, by modeling the landscape features affecting dispersal through time inputs the current human-induced disturbance of populations into its historical context (Iverson and McKenzie 2013). Furthermore, these approaches can also facilitate future conservation decision-making by modeling the future impacts of anthropogenic effects on forest habitats.

A notable advancement is the possibility of using ancient DNA techniques to decipher genetic information from herbarium collections. The applications of having genome information from stored specimens range from bringing back some species from extinctions (see <https://reviverestore.org>) to the incorporation of extinct phenotypic variation to the present day (Exposito-Alonso et al. 2020).

5.6.3 Common Challenges

The DNA sequencing approaches are getting extremely popular, allowing inexpensive and massively parallel sequencing of short DNA reads. However these massive dataset can also pose several methodological challenges namely 1. Complexities associated with assembling and annotating full genomes, while using short-fragment sequencing approaches, are still a major bottleneck. It requires a reference genome from a related taxon, which is still a severe lacuna in many cases. 2. Recent studies have also raised substantial concerns about the environmental impact of the ongoing sequencing efforts such as the 1000 Genomes Project. and 3. Accurate information on ploidy and chromosome numbers in many naturally hybridizing allopolyploids are lacking. Moreover, the chances of genotyping errors and sample contaminations pose additional threats for successfully executing a population genomics project.

5.7 Summary and Conclusions

Despite longstanding research, the impact of habitat fragmentation and anthropogenic disturbance on forest genetic diversity remains poorly understood. The need to find an acceptable balance between natural forests and their function amidst the ongoing anthropogenic effects is one pressing challenge for conservationists worldwide. It is also important to understand that there are several instances where imperial evidence tends to violate theoretical expectations. For example, it is likely that fragmentation may not always deplete the genetic diversity among plant populations. Since tree species vary widely with respect to their life history, ploidy levels, and existing genetic variability, the responses to fragmentation too are likely to vary. Thorough knowledge and understanding of the historical population structure and the ecology and the biology of the species and embracing insights from natural history and breeding may help develop biologically meaningful inferences. Appropriate usage of genome sequencing tools in connection with ecological datasets aka considering a “trees perspective” in understanding fragmentation genetics (see Bacles and Jump 2011) has the potential to develop solutions for curbing the ongoing effect of habitat fragmentation. Furthermore, it is imperative to continue research to understand how forest resources especially non-timber forest products that are quite widely harvested in the tropics can be sustainably used, conserved, and restored in a changing environment. There is also a need to employ multidisciplinary approaches considering the impacts of climate change besides fragmentation and include ecological niche models and molecular tools as well as large-scale

comparative studies to draw up general principles accompanying forest fragmentation genetics. The findings may have positive implications on societal development by protecting and sustainably using the world's remaining plant species and their habitats.

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