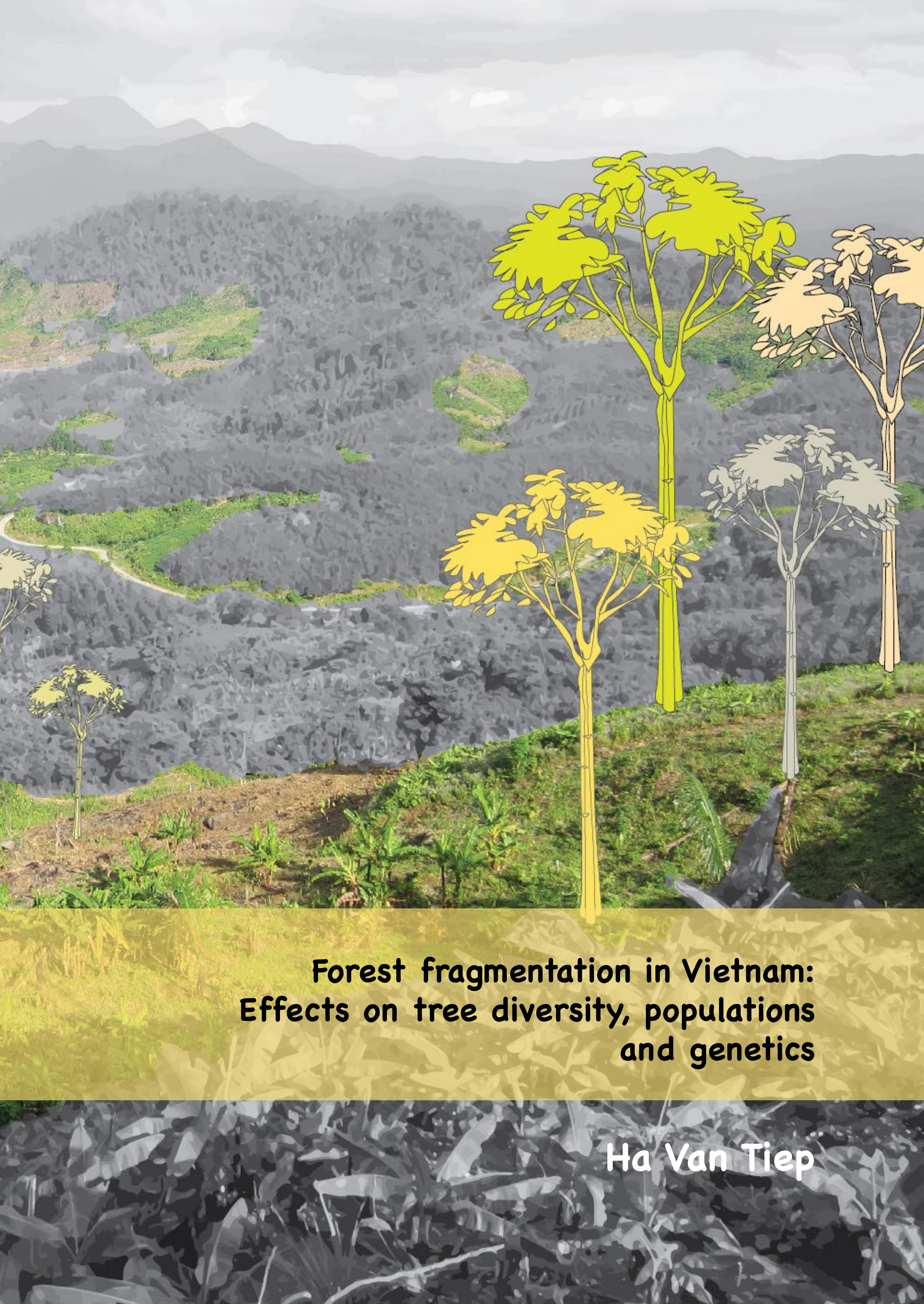

Forest fragmentation in Vietnam: Effects on tree diversity, populations and genetics

Ha Van Tiep

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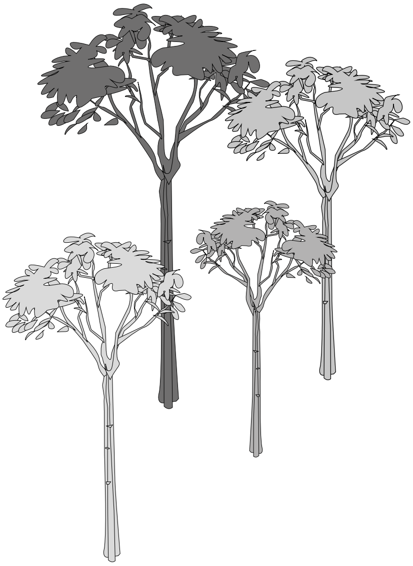

Ha Van Tiep

2015

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FOREST FRAGMENTATION IN VIETNAM: EFFECTS ON TREE DIVERSITY, POPULATIONS AND GENETICS

Bosfragmentatie in Vietnam: effecten op soortendiversiteit, populatiedynamiek en genetische diversiteit van boomsoorten

(met een samenvatting in het Nederlands)

Rừng phân mảnh tại Việt Nam: Ảnh hưởng đến đa dạng loài cây, quần thể và nguồn gien

(với một bản tóm tắt bằng tiếng Việt)

Proefschrift

ter verkrijging van de graad van doctor
aan de Universiteit Utrecht
op gezag van de rector magnificus, prof. dr. G.J. van der Zwaan,
ingevolge het besluit van het college voor promoties
in het openbaar te verdedigen
op woensdag 27 mei 2015 des middags te 12.45 uur

door

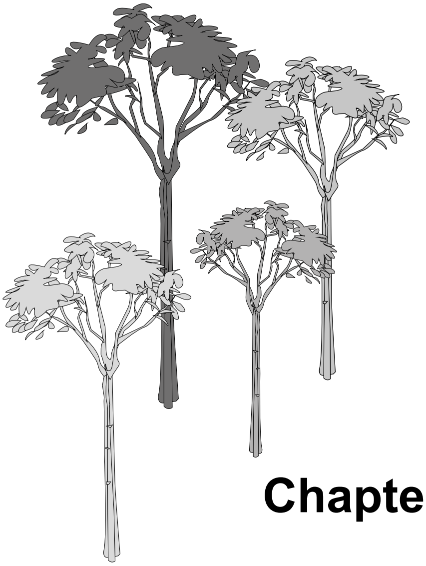
Ha Van Tiep

geboren op 10 oktober 1972 te Thai Binh, Vietnam

Promotoren: Prof. dr. R.G.A. Boot
Prof. dr. P.A. Zuidema

*“To my mother Hoang Thi Chung who passed away
before her dream came true”*

Contents



Chapter 1

General introduction

Forest Fragmentation in the Tropics

Forest fragmentation is a process whereby continuous forests are subdivided into smaller forest areas (forest fragments) mixed with non-forest land (Wilcove et al. 1986, Young et al. 1996). This is mainly caused by human activities converting natural forests into agricultural land for crop production, grazing and forest plantations or logging and road construction (Zuidema et al. 1996, Wade et al. 2003, Laurance et al. 2014b). Currently, forest fragmentation is common in most forest areas worldwide (Achard et al. 2002, Laurance et al. 2014b). Millions of square kilometers of the Earth's surface is covered by forest fragments (Pimm and Brooks 2013), and a quarter of the remaining tropical forest has been fragmented (Wade et al. 2003). Unfortunately, a lack of adequate data has made it impossible to measure the full extent of forest fragmentation in the tropics. Despite the lack of data, we do know that during the past decades, the tropical forest cover has been significantly reduced with approximately 6 million ha that have been lost and more than 2 million ha that are visibly degraded each year (Achard et al. 2002). About 280,000 ha/year of forests in Africa have been transformed into fragmented forests (Achard et al. 2002). Among tropical areas, Southeast Asia has the highest relative rate of deforestation, about 1.4% year $^{-1}$ (Sodhi et al. 2004), and about 650,000 ha/year of natural forests are fragmented into forest fragments (Achard et al. 2002). Consequently, three quarters of the original tropical forests may disappear by 2100, leading to a 42% loss of biodiversity (Sodhi et al. 2004). Rapid loss and fragmentation of old growth forests are considered to be the greatest threat to tropical forest biodiversity (Laurance and Peres 2006b) and to the integrity of forest ecosystems (Young et al. 2000).

Effects of Forest Fragmentation on Tree Population

Forest fragmentation has many negative effects on tree populations in various ways and through various processes as described in Figure 1.

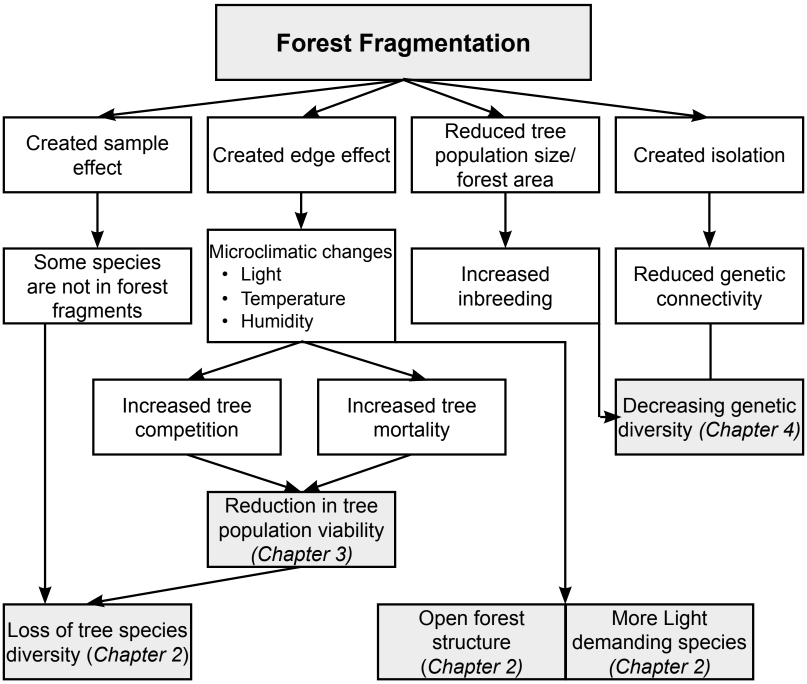


Figure 1. A conceptual representation of the theoretical ways in which four factors (sample effect, edge effects, reduced population size (forest area), and isolation) may cause reduction of tree population viability, loss of tree species and genetic diversity, and change of forest structure and tree species composition in forest fragments. Arrows indicate causal relations and research chapter indication.

Sample effect

Forest fragments are samples of the representative original forests, but they do not contain a complete species pool from the original forests. When forest fragmentation takes place, the size of tree populations will be reduced, only a small number of the natural tree species from the original forest is retained in the remnant fragments. Some species may therefore be absent in the fragments, not because their populations are extremely low, but because they were simply not present at the time of forest fragmentation (Laurance et al. 2011). Thus, forest fragmentation has caused the loss of local tree species in fragments (Turner 1996). In addition, the representativeness of the remaining fragments depends greatly on the amount of cleared forest area, the spatial location, the size of the fragments, and the spatial distribution of the original forests (Zuidema et al. 1996). Clearly, the deforestation area is not random because most of lowland forests are generally cleared before the forests in the upland, high slope areas. This was the case in the tropical dry forest in central Brazil (Bianchi and Haig 2013). As a result, forest fragmentation will cause tree species that are naturally distributed in lowland forests to be lost before tree species that are distributed in upland forests. In this thesis (Chapter 2), we present the results of a study on the sample effects by comparing tree species richness and composition in the research plots of forest fragments and those of continuous forests.

Edge effect

Edge effects refer to the changes in population or community structures that occur at the boundary of two habitats. In forest fragment ecology, edge effect is considered to be a crucial factor that negatively influences many aspects of tree population dynamics (Cochrane and Laurance 2002, Laurance et al. 2011). Edge effect changes microclimate conditions in fragments. Cleared boundaries surrounding fragments have resulted in lower humidity, higher temperature, and considerably more light compared to interior forests (Wright et al. 1996). In addition, wind turbulence is sharply increased in the forest edge areas (Laurance et al. 1998). Edge effect also creates a change in the surrounding vegetation composition with a high invasion of non-forest species, pest, and diseases from the matrix of vegetation surrounding the fragments (Laurance et al. 2011). These changes have affected tree population dynamics (Laurance et al. 1998), represented by the following three aspects. First, edge effect reduces tree species richness. Trees in small fragments have experienced a higher mortality rate due to stochastic events than those in large fragments and continuous forests (Laurance et al. 1998, Laurance et al. 2011). In addition, the number of seedling recruitments is reduced in small fragments (Benitez-Malvido 1998) due to a reduction in reproductive trees (Laurance et al. 2000) and an increase in mortality rate of seedlings (Zambrano and Salguero-Gómez 2014). The higher tree mortality rate (Laurance et al. 1998) combined with the lower number of seedling recruitments (Benitez-Malvido 1998) has resulted in a reduction in tree species richness in small forest fragments. Second, forest structure has also changed under driver of edge effect (Hill and Curran 2003, Echeverría et al. 2007). The large trees in small fragments are more vulnerable to climatic events such as wind turbulence and drought than the small trees (Laurance et al. 2000) due to their high stature and relatively thick crown (Laurance et al. 2000). As a result, the higher proportion of large dying trees has been observed more often in small fragments than in large fragments (Laurance et al. 2000, Pütz et al. 2011). The high mortality rate of large trees has resulted in an evident change in forest structure. The smaller fragments now contain a greater number of small trees than large trees. Finally, the edge effect has led to significant changes in tree species composition. The open gaps that have been created by dead trees near forest edge areas may create favourable conditions for pioneer seedling infestation (Popma et al. 1988). Consequently, the shade-tolerant seedlings may be dominated by the invaded pioneer seedlings, which would lead to a reduction in the number of shade-tolerant seedling species. As a result, a higher proportion of tree species in small forest fragments would be pioneer species (fast growing species) (Hill and Curran 2001).

A large number of studies about the effects that forest fragmentation has on forest structure, tree species richness, tree composition, and seedling recruitment have been conducted in the neotropic forest (Laurance and Bierregaard 1997, Laurance et al. 2011). However, such research is very scarce in Asia, and more specifically in Southeast Asia which has a high rate of deforestation and where forest fragmentation has become increasingly pervasive (Sodhi et al. 2004). Thus, more forest fragmentation studies in this region would offer a better understanding of the effects that forest fragmentation has on tree populations under different local circumstances and climates compared to the neotropic forest fragments. For instance, the differences in climate and land management patterns in Malaysian forest fragments have resulted in different patterns of forest fragment ecology compared to the neotropic forest fragments (Thomas 2004). This study (Chapter 2) will examine the effects of forest fragment size on remnants of natural forests. It is expected that the results of the study will show that forest structure, tree species diversity, and tree composition have significantly changed in forest fragments compared to the continuous forest.

Reduced population size (forest area)

Forest fragmentation has resulted in a reduction in tree population size (Ghazoul and Sheil 2010). The abundance of tree species with a patchy distribution depends on the location and the size of the fragments (Zuidema et al. 1996). In general, the larger fragments contain more species than the smaller fragments (Hill and Curran 2001, Hill and Curran 2003, Tripathi et al. 2010, Tripathi and Reynald 2010). This could be the reason that in the same census, a lower number of tree species have typically been recorded in small fragments than in large fragments and also in the areas of continuous forest (Turner 1996, Hill and Curran 2001). Tree species with a high-density population may not be critically reduced in number, but species with low numbers may be quickly reduced in population size, and species with a small population size may develop a high local extinction risk due to stochastic events (Zuidema et al. 1996). Therefore tree populations remaining in forest fragments at a given time may not be maintained in the future. This is known as “extinction debt” (Kuussaari et al. 2009). Thus, to efficiently conserve tree populations in forest fragments, study on the effects that forest fragmentation has on dynamics of tree populations is important for a better understanding of whether present tree populations can survive, grow, and the factors that determine their fate. However, very few studies have been conducted in the tropical forest fragments, only one just has been carried out in Mexican forest fragments (Zambrano and Salguero-Gómez 2014). Chapter 3 of this study will focus on how forest fragment size influences the remaining tree population dynamics. It has been hypothesized that tree population growth will be reduced in small fragments compared to those in large fragments and in a continuous forest.

Isolation

Forest fragmentation has resulted in increased spatial isolation among forest fragments (Young et al. 1996, Lienert 2004). According to the population genetic theory, isolation is expected to limit gene flow, seed dispersal, and species movement among fragments (Lienert 2004, Damschen et al. 2006, Laurance et al. 2011) due to artificial barriers such as plantation forest, agricultural field, grazing land, and road construction (Young et al.2000). Limitation of genetic exchange leads to increased inbreeding depression and reduced fitness of the progeny within population. Over time, these effects can cause genetic diversity degradation and reduce population viability of tree species (Young et al. 1996). However, the effects of isolation differ among tree species, depending on their seed and pollen dispersal mechanisms (Aparicio et al. 2012). Long-distance seed and pollen dispersal can be important for maintaining genetic diversity in fragmented populations by preventing inbreeding and limiting genetic drift (Hartl and Clark 1997). In addition, breeding system characteristics such as self-compatibility also contributes to the persistence of tree populations in the forest fragment (Levin 2010).

Currently, the genetic effects that forest fragmentation has on remnant tree populations, especially regarding gene flow and genetic mating systems are not fully understood (Kramer et al. 2008, Bacles and Jump 2011). Thus, further insight into the genetic effects of forest fragmentation on tree populations is vital to support science-based genetic diversity conservation. Chapter 4 of this study will focus on the effects of forest fragmentation on the genetic diversity of one critically endangered tree species in four small forest fragments. In that chapter, a hypothesis was formed which indicates that the genetic diversity of the studied tree species may have been degraded by forest fragmentation.

Vietnam Natural Forest and Forest Research Strategy

Vietnam natural forest changes

This study was conducted in Central Vietnam. The country has a surface area of over 32.12 million ha, three quarters of which is comprised of hills and mountains, and was originally covered by natural tropical forests. Thus, the forest sector of the Vietnamese government has been managing a much larger area of land than other sectors of the national economy, and has contributed significantly to the economic development and environmental protection in Vietnam. However, Vietnam has experienced substantial forest destruction at a rate of 6.9 - 14.6% y^{-1} (Koh 2007), and more than 5 million hectares of natural forests have been lost during the last 50 years (de Jong et al. 2006). Natural forest cover decreased from 68.1% to 30.9% between 1943 and 2005 (Meyfroidt and Lambin 2008). In 1943, the total forest area of Vietnam was 14.3 million ha, which accounted for 68.1% of the total land area, and the forests were completely natural forest (Meyfroidt and Lambin 2008). Since that time, forest cover has dramatically decreased, especially from 1976 - 1990. In 1990, it spanned only 9.2 million ha which accounted for only 28% of the total land area (de Jong et al. 2006). The causes of the decline in forest cover during this period are complex and diverse, and somewhat debated, but many researchers agree that the following factors could be the main causes; (1) Land conversion for agricultural production to meet the demand for food for domestic consumption, (2) Devastation by war, it is estimated that approximately 2 million ha of natural forests were lost, (3) Forest fire, mainly caused by human activities such as swidden agriculture, (4) Over harvesting of fuel wood and timber by both legal state organizations and illegal logging by individuals and units, (5) Poor management capacity of the forestry sector and a deficient institutional and legal framework (de Jong et al. 2006).

By 2012, the forest area in Vietnam had increased to 13.86 million ha, which covers approximately 39.9% of the total national land area. Of that area, natural forest amounted to 10.42 million ha and plantation forest was 3.44 million ha. Together, they were classified into 3 categories as defined by the Forest Protection and Development Law, 2003 (MARD 2013).

- Special use forest: 2.22 million ha, accounted for 16.0%
- Protected forest: 4.68 million ha, accounted for 33.8%; and
- Production forest: 6.96 million ha, accounted for 50.2%.

The main role of the special use forest is for natural conservation, protection of historical and cultural relics, tourism, and to some extent, environmental protection. Protected forests are maintained to protect water streams and soils and to prevent soil erosion and mitigate natural disasters. Production forests are mainly used for supplying timber and non-timber forest products, but they also provide environmental protection and biodiversity conservation.

In order to create a sustainable forest management program, the Vietnamese government has issued the National Forestry Development Strategy (NFDS) for the period 2006 - 2020 (MARD 2007), which serves as a basic orientation for the long term development of forest resources. On the one hand, the NFDS aims to sustainably utilize 16.24 million ha of forest land, increase forest cover to 35 - 43% by year 2010 and to 47% by 2020. On the other hand, it contributes to socioeconomic development, biodiversity conservation, as well as environmental services supply, and it reduces poverty and improves the livelihood of local farmers in mountainous areas (MARD 2007). Unfortunately, the small forest fragment conservation and restoration are not mentioned in this policy.

Vietnam forestry research strategy by 2020

The National Forestry Research Strategy (NFRS) for the period 2008 - 2020 has also been issued by the state (MARD 2008). It is a new phase in forestry research in Vietnam. The overall objective is to contribute and orient forest sector development, facilitate effective implementation of NFDS, and create a master plan for forestry research by 2020. The NFRS focuses on six forestry research aspects; (1) to increase the forest plantation yield by 1.5 times for tree species with a high economic value, (2) to develop production plantations focusing on the main tree species that have a high and sustainable productivity, (3) to maintain and promote the protective function of various types of forests, especially watershed production forests and coastal forests, (4) to conserve as well as sustainably utilize various sources of biodiversity and the genetic resources of forest trees including non - timber forest products, (5) to improve the technology used in exploitation activities to ensure reduced impact logging in natural forests, to develop timber processing technology at small and medium scale, and (6) to diversify raw material source utilization. To achieve these objectives, six priority research themes have been established; (1) Planning, monitoring, and assessing forest resources, (2) Forest policies and institutional arrangement, (3) Sustainable forest management, (4) Forest inventory and biodiversity conservation, (5) Silvicultural techniques, (6) Forest industry, forest product preservation and processing (MARD 2008). In order to efficiently implement the NFRS, there is a need to improve the research capacity both by training forest researchers at the masters and PhD levels by improving the infrastructure and the research facilities and by conducting pilot projects (MARD 2008).

In summary, NFRS is a basic strategy for forestry research in Vietnam, but there is no mentioning of forest fragmentation in terms of the threat to biodiversity and the potential contribution of existing forest fragments to biodiversity conservation, and the research on these aspects.

Forest fragmentation and study of forest fragmentation in Vietnam

Very little is known about the effects of forest fragmentation on tree populations in Southeast Asia, and only a few studies have been conducted in Singapore and Malaysia (Turner 1996, Turner and Corlett 1996, Thomas 2004). To our knowledge, no such previous study has been conducted in Vietnam. Because the country is known to have a high rate of deforestation in Southeast Asia, and land use changes quickly in Vietnam (Meyfroidt and Lambin 2008), forest fragmentation is common and pervasive where natural forest occurs, especially in the mountainous regions. In Vietnam, most of the remnant forest fragment areas, about 2,363,773 ha, have been legally allocated to household and community management (MARD 2013). Recently, in some areas in Vietnam, illegal conversion of old-growth forests into forest and rubber plantations have resulted in an increase in the number of forest fragments that are smaller in size and that have more spatial isolation (Meyfroidt and Lambin 2008). Thus, a study on the effects of forest fragmentation is crucial to understand the potential contribution of existing forest fragments to biodiversity conservation in multifunctional landscapes in Vietnam.

This Study

This study aims to improve our understanding of the effects of forest fragmentation on remnant forest tree populations. The specific objectives of this study are:

- To investigate the effects of forest fragment size on forest structure, tree diversity, and tree composition
- To analyze the effects of fragment size on the dynamics of three common large-stature tree species
- To assess the effects of forest fragmentation on genetic diversity of a critically endangered tree species.

Study site

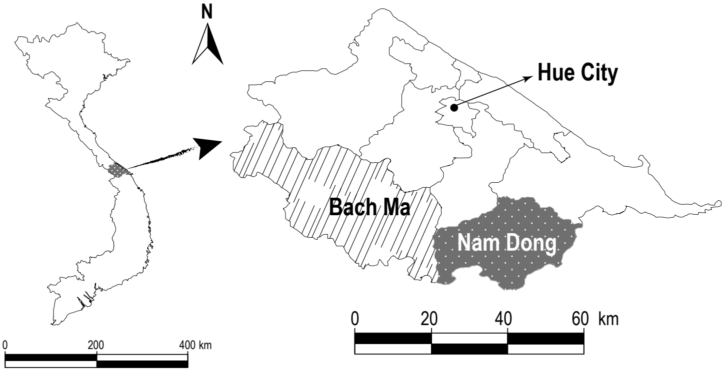


Figure 2. Study site

We conducted this study in the Nam Dong district and Bach Ma National Park, Thua Thien Hue Province, North Central Vietnam (16°15’N, 107°53’E, Figure 2). The district is an area of about 650.5 km^2. The climate is tropical monsoon with four seasons and two main windy seasons during the year. The annual average temperature ranges between 9.0°C and 39.0°C. The annual average rainfall varies between 1,500 mm and 4,000 mm with a high intensity rainy season from September to December. The topography is comprised of uneven and ragged mountainous highland, plains and deep gorges with a slope range of 200 - 400. The common soil types are alluvial soil, yellow-red soil in magma stone, and yellow - red soil in clay stone (Thang et al. 2010). The total natural forest cover is 3,996 ha, accounts for 61.4% of the total area (Thang et al. 2010) and decreased by about 6% from 1975 to 2004 (Thiha et al. 2007).The type of natural forest in this area is seasonal evergreen broadleaf forest (Dung and Webb 2008).

Forest fragmentation in this area has been caused by road construction for logging since the 1980s and land cover has changed by converting degraded natural forests to forest plantation since 1989 (Thiha et al. 2007). Most of forest fragments in the lowland areas have virtually disappeared and the only significant forest remnants are mainly found in the mountain slope. According to local inhabitants, remaining forest fragments have been allocated to their community management; therefore these fragments are well-managed and protected and provide some non-timber forest products such as bamboo shoot, mushroom, and herb plants for their livelihood. In recent years, with a high demand market for chip wood and resin rubber, most of the agricultural land area that has a high slope and poor soil has been converted into acacia and rubber plantations, leading to the remaining forest fragments mainly being surrounded by forest plantations.

In this study, we studied seven forest fragments that range in size of 1 - 150 ha and a piece of continuous forest in the Bach Ma National Park. We established 1 - ha permanent research plot in the center of each forest fragment and three 1- ha permanent research plots in the Bach Ma National Park.

Study species

We used various species sets in the studies reported in this thesis. First, for the study on the effects of fragment size on forest structure and diversity (Chapter 2), all tree species with diameter at breast high (dbh) ≥ 10 cm were studied. Second, for the study on dynamics of tree populations (Chapter 3), in the same research plots in the forest fragments and in a continuous forest, three large-stature tree species were selected; *Canarium bengalensis* (Burseraceae), *Palaquium annamense* (Sapotaceae), and *Parashorea stellata* (Dipterocarpaceae) to study their population dynamics. Finally, for the study on the effects of forest fragmentation on genetic diversity of remnant tree populations, one critically endangered species, *Parashorea stellata* (Dipterocarpaceae), found in four small fragments, was selected to investigate the effects of forest fragmentation on its genetic diversity.

Outline of the thesis

Chapter 1 will provide a general introduction to the research that was conducted.

Chapter 2 will give a quantitative analysis of the effects that forest fragment size has on forest structure, forest diversity, and tree composition. It is expected that forest fragmentation will lead to a change in forest structure and tree composition, and that it will reduce forest diversity in small fragments compared to those in large fragments and continuous forests overall. Seven forest fragments and a piece of continuous forest in the Bach Ma National Park were sampled to calculate the total basal area and the Shannon - Wiener Diversity index (H') and also to classify the fast and slow growing species based on their wood density. Based on these results, conservation measures will be discussed.

Chapter 3 will analyze the demography of three common large-stature tree species in different forest fragment sizes. A demographic field study in seven forest fragments and a piece of continuous forest in the Bach Ma National Park provided the basic data for constructing matrix models, which were used to project the population performances of three species and to determine the most important vital rate for the variation of tree population growth. It is expected that tree population growth will be reduced in the small forest fragments compared to the large fragments and the continuous forest. Calculations were done to determine the common asymptotic growth rate of the population (λ) and to conduct the Life Table Response Experiment (LTRE) analysis. Based on these results, conservation measures of fragmented tree populations will be suggested.

Chapter 4 describes the effects of forest fragmentation on genetic diversity of a critically endangered tree species (*Parashorea stellata*). It is expected that genetic diversity is more degraded in the seedling cohort than in the adult cohort. The leaf samples of all reproductive adult trees and 13 - 25 leaf samples of the seedlings were collected from four fragmented populations in four fragments with sizes ranging from 1 - 20 ha. The genetic diversity parameters including the observed heterozygosity (*Ho*), the expected heterozygosity (*He*), and the number of alleles (*Na*), the allelic richness (*Ar*), the pairwise levels of differentiation (F_{ST}), and the Wright's inbreeding coefficient (F_{is}) were calculated. Based on these results, conservation measures of this species will be discussed.

Chapter 5 provides an extensive discussion and summary of the main results and recommends further research on forest fragmentation in Vietnam.

Framework of this study

This study was financially supported by Tropenbos International (TBI), the Netherlands, through the project: “Capacity development and institutional support to the Vietnamese Academy of Forest Sciences through PhD and Postdoc research”. The project was undertaken by four partners; (1) Tropenbos International - Vietnam (TBI-Vietnam), (2) Ecology and Biodiversity Group, Utrecht University, (3) Forest Ecology and Forest Management Group (FEM), Wageningen University, and (4) Vietnamese Academy of Forest Sciences (VAFS).

Tropenbos International (TBI) is a non-governmental and non - profit organization, funded by the Dutch Government. It was established in 1988 as a Dutch response to increasing concerns about the disappearance and degradation of tropical rain forest worldwide. TBI aims to promote sustainable forest management and improve the sustainable livelihood of local inhabitants. TBI has facilitated multi -disciplinary research programs in cooperation with research institutions, governmental agencies, and other stakeholders in tropical countries. They currently oversee country programs in Colombia, the Democratic Republish of Congo, Ghana, Indonesia, Surinam and Vietnam (for more detail, see the website: www.tropenbos.org). TBI-Vietnam was established in 2001 as a representative country office of TBI in Vietnam and its main research site is located in central Vietnam. TBI-Vietnam aims to contribute to the successful implementation of the National Forest Development Strategy and to support the formulation of the National Forest Research Strategy. It also supports counterparts to conduct research project on the conservation and sustainable utilization of natural forest resources in Vietnam. In addition, TBI-Vietnam provides support for building research capacity in the forestry sector by providing short and long training programs, both in the country and overseas (for details, see the website: www.tropenbos.org).

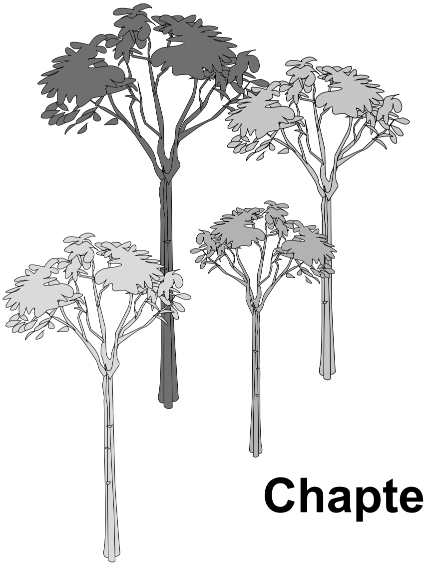
The Ecology and Biodiversity Group is part of the Department of Biology, at Utrecht University. The group focuses on the development, maintenance, and functioning of biodiversity. The group has conducted studies on different ecological scales that range from plants to population, ecosystem, and landscape, and they provide the guidelines for ecosystem management and restoration, as well as species conservation (for more detail, see the website http://www.uu.nl/faculty/science/en/contact/researchinstitutes/ioeb/research/groups/eb/pages/default.aspx).

The research of the Forest Ecology and Forest Management Group (FEM) is part of the C.T. de Wit Research School in Production Ecology and Resource Conservation (PE&RC). FEM focuses on finding a balance between the efficient use of forest services and the maintenance of the overall ecosystem. FEM has three main research themes (1) the ecology of forest regeneration, (2) biodiversity and functional diversity in relation to resource gradients, (3) sustainable supply of forest resources and environmental services. FEM has collaborated with various research organizations in Europe and other parts of the World, and published various papers in scientific journals (for more detail, visit the website: http://www.wageningenur.nl/en/Expertise-Services/Chair-groups/Environmental-Sciences/Forest-Ecology-and-Forest-Management-Group.htm).

The Vietnamese Academy of Forest Sciences (VAFS) was upgraded from the Forest Science Institute of Vietnam (FSIV) in 2010. Now, it is the leading research institution on forests in Vietnam. It has established a nationwide organizational system with its professional and regional research centers located throughout the country from North to South. The main tasks of the academy are to organize and implement academic research on different aspects of forestry ranging from ecology, silviculture, forest industry, and forest economics to forestry organization and management. It is also responsible for post-graduate training and the international research cooperation on forestry research (for more detail, visit the website: http://vafs.gov.vn/en).

Acknowledgements

I would like to thank René Boot and Pieter Zuidema for their valuable discussions and comments on this chapter.



Chapter 2

Effects of forest fragmentation on forest structure and tree diversity in central Vietnam

with R.G.A.Boot & P.A. Zuidema, submitted

Abstract

Forest fragmentation is an important cause of tropical biodiversity loss. Understanding the effects of forest fragment size on forest structure and diversity is essential for biodiversity conservation in fragmented landscapes. We studied the effect of fragment size on forest structure and species diversity in seven forest fragments in central Vietnam, ranging in size from 1 to 151 ha and embedded in a landscape of intensive *Acacia* and rubber plantations. A 1 - ha sample plot was established in the centre of each fragment and three similar plots were established at Bach Ma National Park, a continuous forest. All trees with a diameter at breast height (dbh) ≥ 10 cm were measured and identified. In total, 3,475 trees from 63 species were recorded, including individuals from 10 IUCN Red-listed species. The number of trees, basal area, and tree diversity increased logarithmically with fragment size, with fragments of >100 ha having similar values as continuous forest. Principal Component Analysis showed that tree species composition changed with fragment size, with small fragments containing more fast-growing species. Our results suggest that small (<100 ha) forest fragments retain high tree diversity and may thus significantly contribute to conserving forest biodiversity in intensively agricultural landscapes in the tropics.

Key words: Edge effect, forest fragmentation, forest biodiversity, forest structure, Vietnam.

Introduction

Forest fragmentation is identified as one of the crucial factors threatening tropical forest biodiversity (Turner 1996, Laurance and Bierregaard 1997, Bruna et al. 2009). Biodiversity loss in forest fragments may be caused by isolation and edge effects (Laurance and Bierregaard 1997, Laurance et al. 2011). When forest fragmentation takes place, the remnant forest fragment is first isolated and surrounded by different vegetation, such as agricultural fields, pastures, and tree plantations. Isolation reduces gene flow, seed dispersal, and species movement among patches of forests (Damschen et al. 2006), which may reduce genetic diversity and population viability of species (Laurance et al. 2011). Second, small isolated forest fragments are strongly affected by edge effects (Laurance et al. 1998), i.e. the influence of the change in surrounding vegetation on environmental conditions in the forest fragment (temperature, wind, and humidity) and the invasion of non-forest species, pests and diseases from the matrix surrounding forest fragments. These changes may decrease the survival of forest tree species (Laurance et al. 2000). For instance, strong reductions in tree survival and growth in Amazonian forest fragments have been mainly attributed to edge effects (Laurance et al. 2011). The changes in species diversity that are due to forest fragmentation depend on the area of the fragment. In general, larger forest fragments contain more species than smaller fragments (Hill and Curran 2001, Hill and Curran 2003, Tripathi et al. 2010, Tripathi and Reynald 2010), but this is not always the case (Haig et al. 2000, Ochoa-Gaona et al. 2004, dos Santos et al. 2007, Echeverría et al. 2007, Wassie et al. 2010). In addition to fragment size, species richness in forest fragments may also depend on the disturbance level, altitude, and spatial distribution of forest fragments (Wassie et al. 2010, Liu and Slik 2014). The positive relationship between species diversity and forest fragment area has important implications for conservation. On one hand, the positive diversity-area relation suggests that a large area is required (Laurance 2005) to maintain high diversity, but there is ongoing discussion about the recommended size that forest fragments should have if they are to contribute to species conservation (Zuidema et al. 1996, Laurance 2005). On the other hand, small forest fragments (< 100 ha) are much more numerous (Turner and Corlett 1996) and may still harbour substantial amounts of diversity (Arroyo-Rodríguez and Mandujano 2006, Arroyo-Rodríguez et al. 2009). These fragments can include rare species (dos Santos et al. 2007) and can maintain biodiversity for decades after isolation (Turner and Corlett 1996). Therefore, it has been stated that small forest fragments have made a significant contribution to tropical forest biodiversity conservation (Arroyo-Rodríguez et al. 2009), but studies in small tropical forest fragments are scarce.

One of the tropical regions that has experienced very high rates of deforestation and forest fragmentation is South - East Asia (Sodhi et al. 2004). In spite of the strong changes in forested landscapes in South - East Asia and the high diversity of these forest ecosystems, very little is known about the effects of fragmentation on forest structure and diversity in this region. Understanding the conservation value of (small) forest fragments that are embedded in fragmented landscapes is crucial for regional and national-scale efforts to conserve biodiversity in Southeast Asian countries. One of the countries that experienced strong deforestation in the region is Vietnam, where forest cover decreased from 68.1% to 30.9% between 1943 and 2005 (Meyfroidt and Lambin 2008). This change has resulted in strong forest fragmentation and has caused remnant pieces of natural forest in Vietnam to be surrounded by intensive plantations of fast-growing tree species (acacia, rubber) and agricultural fields (maize, cassava).

Here we report the results of a study on the effects of forest fragment size on forest structure and tree diversity in central Vietnam. Specifically, we ask the following questions: (1) Do tree density and basal area increase with forest fragment size? (2) Does tree diversity increase with forest fragment size? (3) Does the composition of tree species change with fragment size? We studied seven forest fragments that ranged in size from 1 - 150 ha, as well as a piece of continuous forest in a National Park.

Methods

Study area

We conducted the study in Nam Dong district and Bach Ma National Park, Thua Thien Hue province, in central Vietnam (16°15'N, 107°53'E). Nam Dong district covers an area of about 650,5 km^2 and with an altitude range of 40 - 1,700 m a.s.l. The climate is tropical monsoon with four seasons and two main windy seasons during the year. The north-west wind takes place in summer (dry and hot) from April to July and the south-east wind occurs in winter (wet and cold) from October to January. The annual average temperature ranges between 9.0°C and 39.0°C. The annual average rainfall varies between 1,500 mm and 4,000 mm, with a high-intensity rainy season from September to December. The topography comprises uneven and ragged mountainous highland, intensive plains and deep gorges with a slope range of 200 - 400. The common soil types are alluvial soil, yellow-red soil in magma stone and yellow-red soil in clay stone (Thang et al. 2010). The total natural forest cover is 3,996 ha, that accounts for 61.4% of the total area (Thang et al. 2010) and decreased by about 6% from 1975 to 2004 (Thiha et al. 2007). According to local inhabitants, forest fragmentation has taken place since the 1980s when the government started road construction for wood extraction. At that time, certain tree species with a high economic value such as *Hopea pierrei, Erythrophleum fordii, Madhuca pasquieri, Peltophorum pterocarpum, Dalbergia cochinchinensis, Dipterocarpus retusus, Parashorea stellata, Hopea hainanensis, Shorea guiso and Cinnamomum parthenoxylon*, were selectively logged from natural forests. Since 1989, the land cover changed because degraded natural forests were converted into tree plantations (Thiha et al. 2007). In addition, Agent Orange that was sprayed during the war in 1968 resulted in forest degradation (Westing 1971, Young et al. 2004). Bach Ma National Park is located in Nam Dong and Phuc Loc districts, Thua Thien Hue province. The park was established in 1991 and extended in 2008, covering an area of about 37,487 ha. The altitude ranges from 40 to 1.450 m and is hilly with a maximum slope up to 45 degrees. Annual average temperature is 25°C and annual rainfall amounts to 1,500 - 4,000 mm. Natural forest in Bach Ma National Park is classified as closed evergreen tropical rain forests, containing a high variety of tree species (Tordoff et al. 2003).

Data collection

We selected seven forest fragments that ranged in size from 1.1 to 151 ha (Table 1). They shared similar natural conditions (e.g. soil types, topography, altitude and time since fragmentation) and were located at 0.5

- 11.5 km from each other. Information about the surrounding habitat of each fragment was obtained from observation in the field and the age of the forest fragmentation as well as other related information from local people.

Table 1. Characteristics of studied forest fragments and continuous forest in Central Vietnam.

Plot code	Area (ha)	Location	Altitude (m)	Distance to edge (m)	Fragments surrounded by:
Fr1	1.1	N:107°35'15.8" E:16°6'36.6"	323.2	41.2	• Hybrid acacia and rubber plantations, on all sides
Fr2	4.8	N:107°40'23.3" E:16°9'45.4"	281.0	65.5	• Hybrid acacia and rubber plantation surrounded, on 3 sides • Shrubs, lianas, wild bananas and bamboo stands, on 1 side
Fr3	10.8	N:107°39'11.7" E:16°6'31.46"	336.0	74.3	• Hybrid acacia plantation, on 1 side • Shrubs, lianas, wild banana and bamboo stands, on 2 sides • Upland rice field cultivation, on 1 side
Fr4	22.5	N:107°40'10.58" E:16°9'39.18"	291.2	95.4	• Hybrid acacia plantation, on 2 sides • Shrubs, wild bananas, and bamboo stands, on 1 side • Upland rice field cultivation, on 1 side
Fr5	41.7	N:107°39'40.6" E:16°11'7.74"	371.0	167.2	• Hybrid acacia hybrid and rubber plantation, on 1 side • Shrubs, lianas, wild bananas and bamboo stands, on 3 sides
Fr6	101.0	N:107°38'32.7" E:16°9'18.18"	333.8	295.5	• Hybrid acacia plantation, on 1 side • Shrubs, lianas, wild bananas and bamboo stands, on 3 sides
Fr7	151.0	N:107°37'34.97" E:16°9'32.16"	384.4	525.6	• Hybrid acacia plantation, on 1 side • Shrubs, lianas, wild bananas and bamboo stands, on 3 sides
BM1	>1.000	N:107°39'55.8" E:16°3'26.2"	339.2	1,340.0	• Not applicable
BM2	>1.000	N:107°38'44.38" E:16°3'12.10"	333.5	1,370.0	• Not applicable
BM3	>1.000	N:107°39'13.40" E:16°2'11.6"	322.7	1,520.0	• Not applicable

Notes: Fr refers to plots in forest fragments, BM refers to plots in Bach Ma national park.

In order to determine fragment size, the boundary of each forest fragment was mapped and forest areas within the boundaries were calculated. The sample plot of 1 ha (100 × 100 m) was established at the centre of each fragment. In each sample plot we measured diameter at breast height (dbh) above buttresses for all trees ≥ 10 cm dbh. We also recorded the name of the species or collected a specimen for later identification. Furthermore, we also noted the co-ordinates of each sample plot and the distance to nearest edges.

Three similar sample plots were established in Bach Ma National Park, which is a continuous forest embedded in a national park that spans 37,487 ha. The distance among the plots in Bach Ma National Park was less than 5 km. The distance from these plots to those in the forest fragments was less than 17 km. Hereafter, these sample plots will be referred to as BM1, BM2, and BM3. They will be used as reference for the continuous forests (CF).

Data analysis

The inventoried species were categorized into two groups based on their wood density that was established by the Ministry of Agriculture and Rural Development of Vietnam (MARD 2004) and the morphology described in taxonomic literature (Chinh et al. 2009). We classified slow-growing species (SGS) as having a wood density of ≥ 0.6 g/cm^3 and fast-growing species (FGS) as having a wood density < 0.6 g/cm^3. Basal area (BA, m^2 ha^{-1}) and Shannon-Wiener Diversity index (H') (Shannon and Weaver 1949) were calculated for each sample plot. In order to estimate species richness among sample plots, rarefaction curves were calculated following the Chiarucci analytical formula (Chiarucci et al. 2008), by using the estimate S software program, version 8.0 (http://purl.oclc.org/estimates). The species composition was also ordinated by using variable number trees in a Principal Component Analysis (PCA). For this analysis, the CONACO 5.0 software was used. To investigate the status of a species, all inventoried species were checked in the online red list category of IUCN by using the link http://www.iucnredlist.org/search, which was accessed on October 15th, 2013. The Pearson and logarithmic regressions were used to analysis the relationship between the dependent and independent variables (at significance level $\alpha=0.05$) by using the IBM SPSS statistic software, version 19.

The three sample plots in the continuous forest (BM1, BM2, BM3) were excluded from the analyses that examined the effect of fragment size on forest structure and diversity, because the forest size is unknown and would have been uninformative. Therefore, these plots were used as reference points to represent the range of calculated variables in a continuous forest that has presumably been unaffected by edge effects or isolation.

Results

Forest structure

A total of 2,259 stems were recorded in the seven forest fragments and 1,216 stems were recorded in the three plots of the continuous forest. The number of stems per hectare increased from 202 stems (dbh >10 cm) in a fragment of 1.1 ha to 396 stems ha^{-1} in a 151- ha fragment. Plots in the continuous forest contained a maximum of 410 stems ha^{-1} (Table 2). A logarithmic regression showed a tight and positive relation between the number of stems and fragment size (Figure 1a).

Table 2. Forest structure and tree diversity in forest fragments and continuous forest in Central Vietnam.

Variables	Forest fragments							Continuous forest		
	Fr1	Fr2	Fr3	Fr4	Fr5	Fr6	Fr7	BM1	BM2	BM3
Total number of species (ha^{-1})	14	21	28	32	38	43	46	48	47	47
Number of SGS (ha^{-1})	3	8	10	10	16	20	23	27	25	29
Number of FGS (ha^{-1})	11	13	18	22	22	23	23	21	22	18
Proportion of SGS to total species (%)	21.43	38.10	35.71	31.25	42.11	46.51	50.00	56.25	53.19	61.70
Proportion of FGS to total species (%)	78.57	61.90	64.29	68.75	57.89	53.49	50.00	43.75	46.81	38.30
Total number of stems (ha^{-1})	202	316	323	331	345	346	396	398	408	410
Number of SGS stems (ha^{-1})	14	57	86	76	126	146	211	241	228	256
Number of FGS stems (ha^{-1})	188	259	237	255	219	200	185	157	180	154
Proportion of FGS stems to total stems (%)	93.07	81.96	73.37	77.04	63.48	57.80	46.72	39.65	44.12	37.56
Number of stems of 10 - 20 cm dbh (ha^{-1})	108	194	184	162	161	155	206	173	183	189

cont. Table 2.

Variables	Forest fragments							Continuous forest		
	Fr1	Fr2	Fr3	Fr4	Fr5	Fr6	Fr7	BM1	BM2	BM3
Number of stems of > 20cm dbh (ha^{-1})	94	122	139	169	184	191	190	225	225	221
Total basal areas (m^2 ha^{-1})	9.59	12.24	15.29	17.61	21.38	25.51	31.18	34.59	34.78	34.70
Shannon-Wiener index (H’)	2.30	2.79	3.12	3.37	3.54	3.62	3.59	3.67	3.67	3.61

Notes: Codes of fragments (Fr) and continuous forest (BM) as in Table 1, dbh = diameter at breast height, SGS = Slow Growing Species, FGS = Fast Growing Species, BA = basal area.

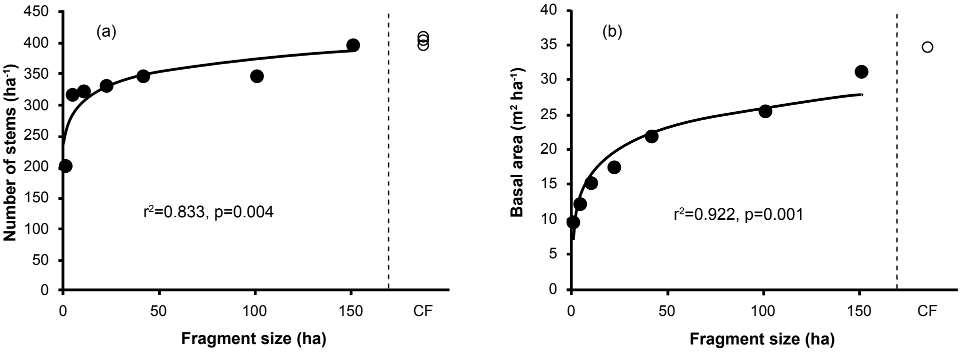


Figure 1. Relation between (a) stem density and fragment size, (b) basal area and fragment sizes, for forest fragments in Central Vietnam. Values for a continuous forest (CF) are shown for comparison. Logarithmic regressions were conducted.

The basal area ranged from 9.59 m^2 ha^{-1} in the 1.1- ha fragment to 31.18 m^2 ha^{-1} in a 151- ha fragment. In the continuous forest, the maximum basal area amounted to 34.78 m^2 ha^{-1}(Table 2). Here again, the basal area was strongly and significantly related to fragment size (Figure 1b).

We also evaluated whether the density of the small stems of recruiting trees (dbh:10 - 20 cm) was related to fragment size. While this density was quite variable, ranging from a low of 108 stems per ha in the 1.1- ha fragment to 194 stems ha^{-1} in the 4.8 - ha fragment, fragment size did not explain this variation (Figure 2a). For larger trees (dbh > 20 cm), a positive relation was found: tree density consistently increased from 94 stems per ha in a fragment of 1.1 ha to 190 stems ha^{-1} in a 151 - ha fragment (Figure 2b). In the continuous forest, the highest density of large stems was found; 225 stems ha^{-1} (Table 2).

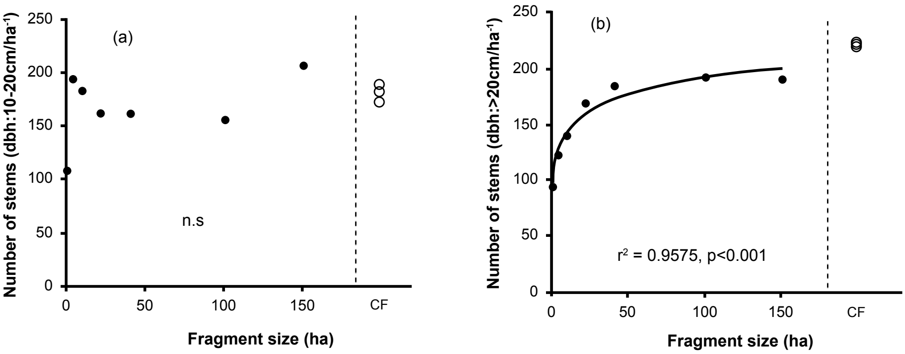


Figure 2. Relation between (a) density of stems of 10 - 20 cm dbh and fragment size, (b) density of stems of > 20 cm dbh and fragment size for forest fragments in Central Vietnam. Values for a continuous forest (CF) are shown for comparison. The logarithmic regressions were conducted, n.s = not significant, dbh = diameter at breast height.

Species diversity

A total of 63 tree species, representing 32 families were identified in forest fragments and the continuous forests (Table 3).

The species richness increased from 14 species ha^{-1} in a fragment of 1.1 ha to 46 species ha^{-1} in a 151 - ha fragment (Table 2). Plots in the continuous forest had a maximum of 48 species ha^{-1} (Table 2). A logarithmic regression showed a tight positive relation between species richness and fragment size (Figure 3a).

The estimation of species richness showed that the number of species had positively increased with fragment size (Figure 3b). This suggests that more species can be found in a larger fragment and in a continuous forest. The diversity index (H') value increased from 2.30 in a fragment of 1.1 ha to 3.62 in a 101- ha fragment, and to 3.67 in a continuous forest (Table 2). A logarithmic regression showed a positive relation between the diversity index and the fragment size (Figure 3c).

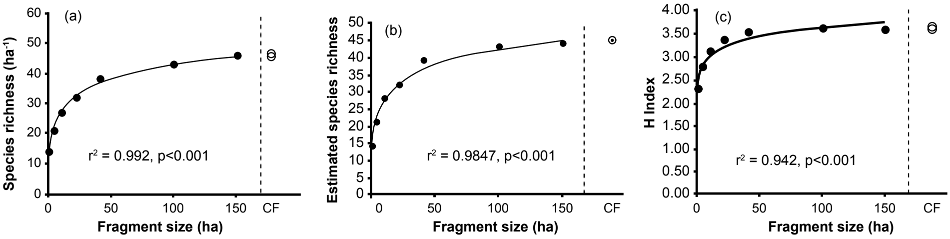


Figure 3. Relation between (a) species richness and fragment size, (b) estimated species richness and fragment size, (c) diversity index (H') and fragment size, for forest fragments in Central Vietnam. Values for a continuous forest (CF) are shown for comparison. A logarithmic regression was conducted.

Table 3. List of tree species located in sample plots in forest fragments and continuous forest in Central Vietnam.

No	Scientific name	Family name	IUCN code	No of stems	Number of stems per plots in forest fragment and continuous forest									
					Fg1	Fg2	Fg3	Fg4	Fg5	Fg6	Fg7	BM1	BM2	BM3
1	*Alangium chinense Lour*	Alangiaceae		71	8	11	14	13	6	6	2	3	4	4
2	*Alangium ridleyi King*	Alangiaceae		104	0	0	20	20	13	16	13	6	10	6
3	*Aphanamixix grandifolia Blume*	Meliaceae		49	0	6	12	3	8	6	2	0	4	8
4	*Aglaia roxburghiana Miq*	Meliaceae		39	0	0	7	0	9	8	7	3	1	4
5	*Aphanamixis polystachya (Wall) R.N.Parker*	Meliaceae	LR	27	0	0	8	0	7	4	4	2	0	2
6	*Artocarpus rigidus Blume*	Moraceae		70	0	11	0	7	13	9	5	10	7	8
7	*Artocarpus tonkinensis A.chev*	Moraceae		26	0	0	2	0	9	3	4	4	2	2
8	*Allospondias laknensis (Pierre) Stapf*	Anacardiaceae		62	0	24	6	11	7	5	5	1	3	0
9	*Actinodaphne cochinchinensis Meissn*	Lauraceae		41	0	0	2	7	12	5	2	2	5	6
10	*Acronychia oligophleibia Merr*	Rutaceae		13	0	0	0	0	0	0	0	11	1	1
11	*Amesiodendron chinense (Merr.) Hu*	Sapindaceae	LR	17	0	0	0	0	0	0	2	10	5	0
12	*Afzelia xylocarpa (Kurz.) Craib*	Leguminoseae		27	0	0	0	0	0	0	0	9	8	10
13	*Adenanthera microsperma Teijsm & Binn*	Mimosoideae		72	0	0	15	12	15	11	7	2	7	3
14	*Baccaurea sylvestris Lour*	Euphorbiaceae		142	23	23	18	15	12	12	8	14	9	8
15	*Burretiodendron hsienmu Ching & How*	Tiliaceae		3	0	0	0	0	0	0	0	2	1	0
16	*Cosmos bipinnalus Cav*	Asteraceae		124	13	16	18	9	7	6	10	9	16	20
17	*Castanopsis fissa Rehder&Wilson*	Fagaceae		165	34	35	26	14	9	6	8	9	13	11
18	*Canarium bengalense Roxb*	Burseraceae		96	7	7	5	6	7	11	17	17	8	11
19	*Canarium subulatum Guill*	Burseraceae		12	0	0	0	0	0	0	0	12	0	0
20	*Canarium album (Lour.) Raeusch*	Burseraceae		16	0	0	0	0	0	0	0	10	3	3
21	*Cinnamomum parthenoxylon (Jack) Meisn*	Lauraceae	CR*	48	0	8	0	0	0	2	0	7	14	17
22	*Cryptocarya lenticellata Lecomte*	Lauraceae		2	0	0	0	0	0	2	0	0	0	0

cont. Table 3.

No	Scientific name	Family name	IUCN code	No of stems	Number of stems per plots in forest fragment and continuous forest									
					Fg1	Fg2	Fg3	Fg4	Fg5	Fg6	Fg7	BM1	BM2	BM3
23	*Diospyros longibracteata Lecomte*	Ebenaceae		3	0	0	0	0	0	2	0	0	0	1
24	*Diospyros pilosella Lecomte*	Ebenaceae		4	0	0	0	0	0	0	2	2	0	0
25	*Engelhardtia chrysolepis Hance*	Juglandaceae		122	4	16	0	13	13	17	15	13	11	20
26	*Eurycoma longifolia Jack*	Simaroubaceae		9	0	0	0	3	1	0	4	1	0	0
27	*Endospermum sinensis Benth.*	Euphorbiaceae		76	0	0	0	8	9	10	9	7	11	22
28	*Enicosanthellum plagioneurum (Diels) Ban*	Annonaceae	LR	88	7	11	13	11	9	6	7	8	10	6
29	*Erythrophloeum fordii Oliv*	Leguminosae		61	0	0	0	0	0	12	9	13	16	11
30	*Gironniera subaequalis Planch*	Ulmaceae		240	36	49	23	24	18	15	19	15	19	22
31	*Garcinia oblongifolia Champ.ex Benth*	Clusiaceae		15	0	0	0	0	0	3	0	0	9	3
32	*Hopea hainanensis Merr & Chun*	Dipterocarpaceae	CR	80	0	0	0	6	11	9	19	14	12	9
33	*Knema corticosa Lour*	Myristicaceae		37	0	4	12	0	10	0	11	0	0	0
34	*Knema pierrei Warb*	Myristicaceae	VU	42	0	0	0	12	0	7	0	9	7	7
35	*Lithocarpus annamensis Hickel & A.Camus*	Fagaceae		50	0	0	0	0	0	0	16	12	14	8
36	*Lithocarpus amygdalifolia (Skan) Hayala*	Fagaceae		6	0	0	0	0	1	0	1	0	0	4
37	*Lithocarpus ducampii A.Camus*	Fagaceae		3	0	0	0	0	3	0	0	0	0	0
38	*Litsea seifera Pers*	Lauraceae		50	0	0	0	0	0	0	16	12	14	8
39	*Macaranga denticulate (Blume) Muell-Arg*	Euphorbiaceae		108	39	8	15	18	8	11	9	0	0	0
40	*Mischocarpus fuscescens Blume*	Sapindaceae		68	0	3	15	9	8	8	8	0	11	6
41	*Michelia balansae Dandy*	Magnoliaceae		74	0	0	0	12	8	8	12	15	10	9
42	*Madhuca pasquieri H.J.Lam*	Sapotaceae	VU	29	0	0	0	0	0	0	1	8	9	11
43	*Melannorrhoea laccifera Pierre*	Anacardiaceae		39	0	0	0	0	0	0	10	9	11	9
44	*Parashorea stellata Kurz*	Dipterocarpaceae	CR	135	3	10	13	7	7	11	5	29	26	24

cont. Table 3.

No	Scientific name	Family name	IUCN code	No of stems	Number of stems per plots in forest fragment and continuous forest									
					Fg1	Fg2	Fg3	Fg4	Fg5	Fg6	Fg7	BM1	BM2	BM3
45	*Palaquium annamense Lecomte*	Sapotaceae		107	0	3	0	5	8	10	33	9	15	24
46	*Pygeum arboreum (Bl.) Blume*	Rosaceae		2	0	0	0	0	0	0	0	0	2	0
47	*Quercus poilanei Hickel & A.Camus*	Fagaceae		8	0	0	8	0	0	0	0	0	0	0
48	*Randia oxyodonta Drake*	Rubiaceae		60	8	20	6	7	2	4	3	2	4	4
49	*Swintonla pierrel Hance*	Anacardiaceae		19	0	0	0	0	0	0	0	1	10	8
50	*Scaphium macropodum Miq*	Sterculiaceae	LR	124	2	25	12	12	9	13	7	11	17	16
51	*Sterculia foetida Linn*	Sterculiaceae		28	0	0	13	0	0	0	0	8	3	4
52	*Shorea guiso (Blco) Blume*	Dipterocarpaceae	CR	24	0	0	2	0	0	6	7	4	0	5
53	*Styrax annamensis Guillaumin*	Styracaceae		54	0	0	0	8	11	8	8	7	7	5
54	*Sapium discolor (Champ.) Muell-Arg*	Euphorbiaceae		34	0	0	0	0	13	12	9	0	0	0
55	*Schefflera octophylla (Lour) Harms*	Araliaceae		123	8	21	25	9	13	6	10	6	10	15
56	*Sandoricum indicum Cav.*	Meliaceae		52	0	0	2	14	9	8	3	10	6	0
57	*Shorea roxburghii G.Don*	Sapotaceae		13	0	0	0	0	0	0	0	5	5	3
58	*Syzygium cuminii (L.) Skeels*	Myrtaceae		6	0	0	0	0	0	3	2	0	0	1
59	*Trema orientalis (L.) Blume*	Ulmaceae		68	0	0	0	13	14	19	22	0	0	0
60	*Tarrietia javanica Blume*	Sterculiaceae		51	0	0	0	7	9	6	11	6	6	6
61	*Vitex quinata Williams*	Verbenaceae		79	10	5	10	5	9	12	7	9	6	6
62	*Wrightia annamensis Eberh.&Dubard*	Apocynaceae		56	0	0	0	11	8	7	5	10	6	9
63	*Wrightia tomentosa Roem & Schult*	Apocynaceae		2	0	0	1	0	0	1	0	0	0	0

*Notes: Codes of fragments (Fr) and continuous forest (BM) as in Table 1, IUCN code = species status in IUCN's Red-List; LR= Lower risk, VU = Vulnerable, CR = Critically endangered, * refers to status for Vietnam.*

Species composition

Our results revealed changes in tree species composition as a function of fragment size. The number of slow-growing species (SGS) increased from 3 species ha^{-1} in a fragment of 1.1 ha to 23 species ha^{-1} in a 151 - ha fragment (Table 2). Plots in the continuous forest contained a maximum of 29 species ha^{-1} (Table 2). In addition, the number of fast-growing species (FGS) slowly increased from 11 species ha^{-1} in a fragment of 1.1ha to 23 species ha^{-1} in a 151- ha fragment (Table 2), and decreased to 18 species ha^{-1} in the plot in the continuous forest (Table 2). A logarithmic regression showed that the proportion of fast-growing species per ha significantly decreased with increasing fragment size (Figure 4).

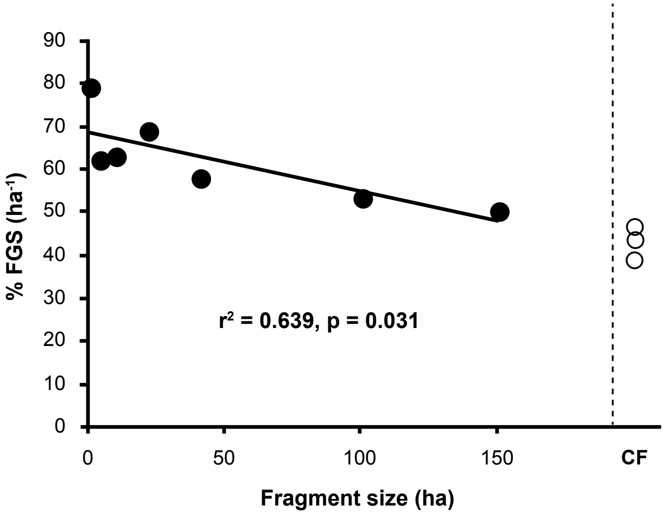


Figure 4. Relation between proportion of fast growing species (FGS) and fragment size for forest fragments in Central Vietnam. Values for a continuous forest (CF) are shown for comparison. A linear regression was conducted.

The PCA analysis clearly separated the slow growing species such as *Cinnamomum parthenoxylon, Hopea hainanensis, Madhuca pasquieri* and *Melannorrhoea laccifera* from the fast growing species such as *Alangium chinensis, Baccaurea sylvestris, Cosmosbipinnalus, Castannopis sp, Enicisanthellum plagioneurum* and *Schefflera octophylla* (Figure 5). The first PCA axis explained 42% variation in species composition and its scores were significantly related to fragment size (Figure 6). The second PCA axis explained 24% variation in species composition but its scores were not significantly related to fragment size.

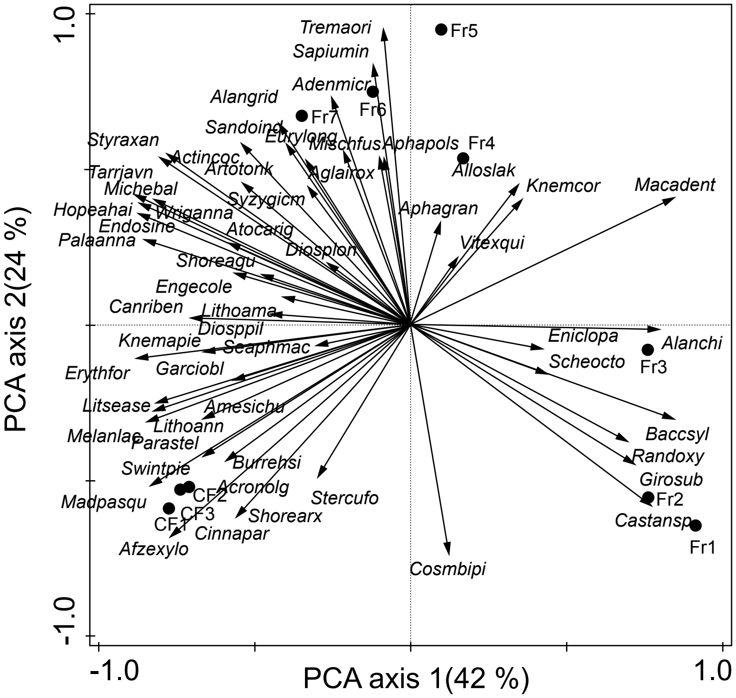


Figure 5. Results of a principal component analysis for species composition of forest fragments and continuous forest. The first PCA axis explained 42% and the second PCA axis explained 24% of total variance in tree species composition. CF = continuous forest and Fr = forest fragments. Numbers following 'Fr' are in order to fragment size (see Table 1).

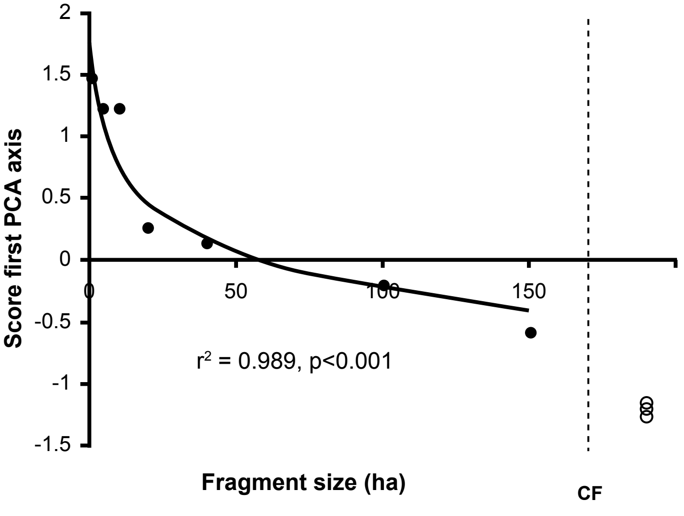


Figure 6. Relation between scores of first PCA axis and fragment size. Values for a continuous forest (CF) are shown for comparison. A logarithmic regression was conducted.

Discussion

Overall, our results show that compared to a reference forest, forest fragments have changed in forest structure, tree diversity and tree species composition. However, in the large forest fragments (≥ 100 ha), forest structure, tree diversity and tree species composition were comparable to that of the reference forest.

Effects of forest fragmentation on forest structure

Tree density, basal area and the density of large trees (> 20 cm dbh) were substantially lower in small fragments (< 100 ha). An increase in tree density and basal area with increasing fragment size was also found by Tripathi & Reynald (2010) and Tripathi et al. (2010) in India. In a study in Chile, Echeverria et al. (2007) reported that the basal area of trees (dbh > 5 cm) significantly increased with increasing fragment size but that their density was not related to fragment size. In contrast, Wassie et al. (2010) did not find a relationship between tree density or basal area with fragment size because of the strong effect of disturbance and the different altitude gradients of church forests in Ethiopia. The higher number of large trees in large forest fragments that we found was also reported by Arroyo - Rodriguez & Mandujano (2006) for a study in Mexico.

There are two possible causes for the decline in the number of trees and basal area in small fragments. The first reason that there is a strong occurrence of edge effects in small fragments (Laurance et al. 1998, Laurance et al. 2011). Edge effects are considered to exert their greatest influence on tree survival within 100 m of the forest edge (Laurance et al. 1998). Most of the small sample fragments in this study (≤ 100 ha) (Table 1) did not have relatively unaltered interior habitats. Therefore, in these fragments, the remaining tree population may have experienced environmental changes due to edge effects (Laurance et al. 2001, Laurance et al. 2011). As a consequence, the tree mortality rate in the small fragments may have been higher than that in large fragments (Laurance et al. 1998). In addition, within small forest fragments, large and emergent trees may have been more vulnerable to wind strike and drought compared to large fragments (Laurance et al. 2000, Laurance et al. 2001), potentially leading to the observed lower abundance of large trees with in small fragments.

The second reason for a decrease in tree density and basal area in small fragments is related to human disturbance. Some studies have reported that human disturbances affect forest structure (Hitimana et al. 2004) and reduce tree density and basal area in forest fragments (Sagar et al. 2003, Wassie et al. 2010). In the study area for this research, the traditional swidden agriculture was still practiced by local farmers; therefore fire may cause tree mortality in the margins of forest fragments. Standing dead trees with fire scars were indeed observed along the edges of the forest fragments studied.

Effects of forest fragmentation on tree diversity and composition

We observed that tree species richness positively increased with increasing fragment size, and that the tree species composition was changed with a higher proportion of fast-growing species than slow-growing species in small fragments. The positive relationship between species richness and fragment size was also found by Tripathi et al. (2010) in India, Hill & Curran (2001, 2003) in Ghana, and Zhu et al. (2004) in China. In stark contrast, no significant relationship between fragment size and tree species richness was found by Santos et al. (2007) in Brazil, Haig et al. (2000) in Canada, and Arroyo-Rodriguez & Mandujano (2006) in Mexico. As far as species composition is concerned, some researchers also reported changes in species composition as a function of fragment size (Hill and Curran 2001, Zhu et al. 2004, Echeverría et al. 2007). For instance, in Chilean forest fragments, the abundance of fast- growing species decreased in large fragments (Echeverría et al. 2007) which was similar to the findings from this study.

There are three possible reasons that could explain why the decrease in species richness is lower in small fragments and slow-growing species are lost from those fragments. The first reason is that there could have been a strong invasion of fast-growing species into small fragments. The increase of tree mortality near forest edges results in higher light conditions that may foster the establishment and growth of fast- growing species. In this study, we indeed observed that there was a high density of fast growing species such as *Alangium chinensis, Cosmos bipinnalus, Castannopis sp, Enicosanthellum plagioneurum, Schefflera octophylla, Baccaurea sylvestris*, etc., in the small fragments (Figure 5). Moreover, naturally regenerating individuals of fast- growing species may outcompete slow-growing species within small fragments, leading to a loss of the slow-growing species. We indeed observed that most slow growing species such as *Cinnamomum parthenoxylon, Hopea hainanensis, Madhuca pasquieri, Melannorrhoea laccifera*, etc., were absent in the small fragments (Figure 5). Second, the number of recruiting seedlings may be lower in small forest fragments than in large fragments due to a loss of seed-dispersal agents. High pressure from hunting leads to a reduced number of fruit-eating animals. Animal-dispersed tree species have indeed been found to decline in small forest fragments (Cordeiro and Howe 2001). Moreover, small forest fragment size and its edge effects have negative impacts on the tree fecundity (Núñez-Ávila et al. 2013) that reduces the seed sources for seedling establishment. Because there was a lack of information on seed dispersal modes for many of the tree species included in our study, it was not possible to evaluate whether animal-dispersed species were disproportionately lost from the community in the studied forest fragments. Finally, human disturbances may reduce species richness of slow growing species in small fragments. After fragmentation, illegal logging activities may have been more intensive in small fragments than in large fragments due to easier accessibility. As slow growing species such as *Afzelia xylocarpa, Cinnamomum parthenoxylon, Hopea hainanensis, Madhuca pasquieri, Parashorea stellata, Erythrophloem fordii, Shorea guiso, Shorea roxburghii*, etc., are more attractive for illegal logging than fast-growing species, this may lead to a reduction in their density in small forest fragments.

Implications for conservation value of small fragments

There is an ongoing discussion about how large a forest area should be to contribute significantly to forest biodiversity conservation (Zuidema et al. 1996, Laurance 2005, Zhang et al. 2014). One view is that forest biodiversity can only be preserved in very large forest areas, with sizes of over one million ha in order to include the habitat required for viable populations of large-bodied species (Laurance 2005). Another opinion is that a protected area as small as 1000 ha can play an important role in forest biodiversity conservation (Heywood and Stuart 1992). In stark contrast, some scientists argue that small forest fragments can also play an important role in tropical forest biodiversity conservation (Turner and Corlett 1996, Arroyo-Rodríguez et al. 2009), by acting as stepping stones to increase connectivity among fragments and harbouring a relatively high plant diversity (Arroyo-Rodríguez and Mandujano 2006, Arroyo-Rodríguez et al. 2009, Tripathi et al. 2010, Tripathi and Reynald 2010, Liu and Slik 2014).

Our results suggest that small forest fragments (1-10 ha) still retain a significant amount tree species richness, and that large forest fragments (≥ 100 ha) are similar to continuous forests in terms of forest structure, species richness, and species composition. In addition, we recorded 55 tree species in the studied forest fragments, of which 10 species are included in IUCN Red List with four (*Cinnamomum parthenoxylon, Parashorea stellata, Hopea hainanensis*, and *Shorea guiso*) having the status ‘critically endangered’. The presence of these tree species in small forest fragments clearly shows that small fragments can be crucial in conservation of threatened species. Thus, we strongly affirm that even small forest fragments that are rich in biodiversity, and are important complementary elements for tropical forest biodiversity conservation. However, small forest fragments by themselves cannot provide sufficient habitats for a viable population of many species, therefore the conservation value of these fragments may also decline over time because extinctions may occur during the next generation after fragmentation (Tilman et al. 1994). Some tree species identified in this study may not naturally regenerate by themselves because of the poor habitat quality and the micro-environmental changes. In this study, the time since fragmentation was about 30 years and may be too short to completely evaluate the change of forest structure and tree diversity in the fragments that were studied. Therefore, conducting population dynamics studies of tree species in remnant forest fragments is needed to better understand whether tree species have a viable population and whether sufficient recruitment is taking place to maintain populations in the future.

Increasingly, tropical landscapes in South-East Asia and elsewhere will consist of a mosaic of land uses and vegetation types with (often) small remaining or re-growing patches of forests. The conservation of tropical forest biodiversity in these landscapes will therefore depend heavily on the conservation value of (small) forest fragments. Our study shows that such forest fragments provide important nature values and deserve to be actively conserved.

Acknowledgements

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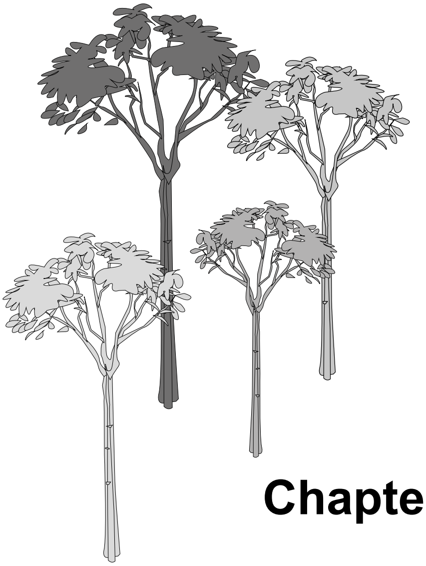


Chapter 3

Effects of forest fragment size on tree population dynamics: a demographic modelling study on three species in Central Vietnam

with R.G.A. Boot & P.A. Zuidema

Abstract

Forest fragmentation is widespread in tropical forest regions. The consequences of fragmentation for tree diversity and species composition are caused by changes in the demography of tree species in forest fragments. So far, little is known about the potential shifts in populations of tropical tree species. We investigated the demographic effects of forest fragmentation on three large-stature tree species in Central Vietnam: *Canarium bengalensis* (Burseraceae), *Palaquium annamense* (Sapotaceae), and *Parashorea stellata* (Dipterocarpaceae). Using integral projection models (IPMs), we compared tree population dynamics between a continuous forest and different-sized forest fragments. We conducted a 3-year monitoring study to quantify seedling recruitment, growth and survival of the study species in 10 permanent 1-ha plots in small fragments (< 20 ha), large fragments (> 20 ha and < 150 ha), and a continuous forest. While all three species were regenerating naturally in forest fragments, the rate of seedling recruitment was lower in small fragments than in large fragments and continuous forest. Growth in diameter at breast height (dbh) was not significantly different among fragments and continuous forest, but mortality rate was higher in small fragments than in large fragments and continuous forest. For all three species, the asymptotic population growth rate (λ) was slightly below 1 (0.98 - 0.99) in small fragments and above 1 (1.02 - 1.04) in large fragments and continuous forest. The 95% confident interval of λ did not include the value of 1 for all three species in small fragments, indicating that populations are projected to slightly decline in small fragments, while remaining stable in large fragments and continuous forest. Life Table Response Experiments (LTRE) analysis showed that differences in λ between forest types were mainly attributed to differences in survival (71 - 97.3%), followed by seedling dynamics (0.4 - 25.1%), and in fecundity (1.1 - 11.3%). These results suggest that small fragment size limits the viability of our study species, but that these species have rather good prospects to survive in fragments of > 20 ha.

Key words: Forest fragmentation, forest fragment size, integral projection models (IPMs), Life Table Response Experiment, population growth rate, Vietnam.

Introduction

Forest fragmentation is one of the main threats to tropical forest biodiversity (Laurance and Bierregaard 1997, Laurance et al. 2011). These fragmentation-induced shifts in diversity and composition of tree species are caused by changes in the demography of individual tree species in forest fragments. Tree population growth is expected to decline in forest fragments due to a reduction in recruitment (Benitez-Malvido 1998, Benitez-Malvido and Martínez-Ramos 2003), in survival (Laurance et al. 1998, Laurance et al. 2000) and growth (Zambrano and Salguero-Gómez 2014). A reduced recruitment and survival may potentially result in a loss of tree species richness over time (Turner 1996, Turner and Corlett 1996, Laurance et al. 2006a). The rate of tree species loss likely depends on fragment size (Turner 1996, Laurance et al. 2006a), with small fragments likely losing species at a faster rate than large fragments (Turner 1996, Laurance et al. 2006a, Stouffer et al. 2009). Hence, the tree species present in fragments at a given time may not be maintained in the future. This phenomenon is called "extinction debt" (Kuussaari et al. 2009), referring to the number or proportion of species that is likely to go extinct in the future but is currently still present in fragments. To what extent the magnitude of the extinction debt depends on fragment size is under debate (Wearn et al. 2012, Halley et al. 2013, Wearn et al. 2013).This is a very relevant debate for biodiversity conservation, because if extinction debt does not or only slightly increase when fragment size reduces, this would show the conservation value of small fragments (Arroyo-Rodríguez et al. 2009).Thus, it is important to evaluate the viability of tree populations in forest fragments. To do so, studies on population size distributions, species diversity and genetic diversity are not sufficient because they do not provide information on likely changes in populations over time. Projections from demographic models do provide such information and have shown to be useful to evaluate the viability of tree populations (Salguero-Gómez and De Kroon 2010, Zuidema et al. 2010, Merow et al. 2014). So far, demographic modelling studies in small tropical forest fragments are rare (Zambrano and Salguero-Gómez 2014).

We investigated the demography of three large-stature tree species in forest fragments of different size as well as a continuous forest in central Vietnam. Natural forest cover in Vietnam has decreased from 68.1% in 1943 to 30.9% in 2005 (Meyfroidt and Lambin 2008), causing widespread forest fragmentation. In this study, we answer three questions. (1) What are the effects of forest fragment size on vital rates (survival, growth, and fecundity) of our study species? (2) What is the effect of forest fragment size on population growth rate of our study species? (3) Which vital rates are most important in explaining the effect of fragment size on population growth rate? We also compare vital rates and population growth rates between forest fragments and continuous forest.

Methods

Study species

We studied three large-stature tree species, to which we will refer with their generic name in the remaining text.

- *Canarium bengalensis Guill* (Burseraceae) is a large-stature deciduous tree, with a straight and cylindrical trunk, attaining 30 - 40 m in height and 50 - 120 cm in diameter. Its wood is used for construction and furniture. Flowering takes place in June, and fruiting occurs from July to December. Fruits are edible and measure 3 cm long and 1.5 cm wide, containing hard seeds. Seeds are dispersed by animals such as monkey and squirrel. The species is naturally distributed in India, Myanmar, Laos, and Vietnam at elevations below 300 m.a.s.l. This is a light demanding species with abundant natural regeneration (Chinh et al. 2009).

- *Palaquium annamense Lecomte* (Sapotaceae) is a large-stature evergreen tree with a straight trunk and high-positioned branches. It attains 12 - 40 m in height and 20 - 120 cm in diameter. The wood is used for construction and furniture. Flowering takes place from July to August, and fruiting occurs from August to October. Fruits are ellipsoid, 2.0 - 2.5 cm long and contain seeds of 1 - 2 cm long. Seeds are dispersed by animals such as monkey, wild pig and squirrel. The species is naturally distributed in India, Malaysia, Myanmar, Thailand, Cambodia, Indonesia, and Vietnam at elevations of 300 - 800 m.a.s.l. This is a light and moisture demanding species with poor natural regeneration (Chinh et al. 2009).
- *Parashorea stellata Kurz* (Dipterocarpaceae) is a large-stature evergreen and critically endangered tree species. Trunk is straight and cylindrical and the species can reach 30 - 50 m in height and 80 -120 cm in diameter. Wood is used for construction and furniture. Flowering takes place from April to June, and fruiting occurs from August to October. The fruit is small, 1 cm in diameter, possesses 5 wings and is wind dispersed. The species is naturally distributed in Cambodia, Myanmar, Laos, and Vietnam at elevations of 300 - 800 m.a.s.l. This is a light and moisture demanding species with good natural regeneration (Chinh et al. 2009).

Study site

We conducted the study in Nam Dong district and Bach Ma National Park, Thua Thien Hue province, in central Vietnam (16°15'N, 107°53'E, Figure 2, Chapter 1). Nam Dong district covers an area of about 650.5 km^2, where altitude ranges from 40 to 1,700 m. The climate is tropical monsoon with total annual precipitation of 1,500 - 4,000 mm, which mostly falls from September to December. Summers (April to July) are dry and hot with prevailing northwest winds; winters (October to January) are wet and cold with prevailing southeast winds. The annual average temperature is 25.3°C. The topography comprises uneven and ragged mountainous highland, intensive plains and deep gorges with a maximum slope up to 40 degrees. The common soil types are alluvial soils, yellow-red soils on magma stone and yellow-red soil on clay stone (Thang et al. 2010). The total natural forest cover in Nam Dong district is 3,996 ha and accounts for 61.4% of the total area (Thang et al. 2010) and has decreased by 6% from 1975 to 2004 (Thiha et al. 2007). According to local inhabitants, forest fragmentation has taken place since the 1980s when the government started constructing roads for timber extraction. At that time, certain tree species with a high economic value such as *Hopea pierrei, Erythrophleum fordii, Madhuca pasquieri, Peltophorum pterocarpum, Dalbergia cochinchinensis, Dipterocarpus retusus, Parashorea stellata, Hopea hainanensis, Shorea guiso*, and *Cinnamomum parthenoxylon*, were selectively logged from natural forests. Since 1989, land cover in the district changed radically when degraded, logged natural forests were converted into plantations of fast growing tree species such as hybrid acacia and rubber (Thiha et al. 2007). Bach Ma National Park is located in Nam Dong and Phuc Loc districts, Thua Thien Hue province. The park was established in 1991 and extended in 2008, covering an area of about 37,487 ha. The altitude ranges from 40 to 1,450 m and is hilly with a maximum slope up to 45 degrees. Annual average temperature is 25°C and annual rainfall amounts to 1,500 - 4,000 mm. Natural forest in Bach Ma national park is classified as closed evergreen tropical rain forests, containing a high variety of tree species (Tordoff et al. 2003).

Study design and data collection

We selected seven forest fragments that ranged in size from 1.1 to 151 ha, representing common fragment sizes in the study area (Appendix 1). They shared similar natural conditions (e.g., soil types, slope, climate, topography, and age of fragmentation) and were located at 0.5 - 11.5 km distance from each other. Altitude of the studied fragments ranged between 280 to 390 m.a.s.l. The matrix of surrounding vegetation consisted of tree plantations of fast growing species (hybrid acacia and rubber) and agricultural field (maize, cassava, and banana).

To estimate fragment size, the boundary of each fragment was mapped and the area within these boundaries was calculated. In 2011, a permanent 1 - ha plot (100 × 100 m) was established in the centre of each fragment and three additional 1-ha plots were established in Bach Ma National Park, a continuous forest spanning 37,487 ha. The three plots in Bach Ma National Park (hereafter ‘continuous forest’) were located at < 5 km from each other and at less than 17 km from the plots in the forest fragments.

At first measurement, in July 2011, we searched, mapped, tagged, and measured all juveniles and adult trees with diameter at breast height (dbh) ≥ 5 cm of three study species in all permanent plots. We repeated this measurement in 2012 and 2013. We re-measured dbh and total height and recorded reproductive status of all tagged individuals. During re-censuses, we evaluated mortality of tagged individuals. To study seedling dynamics and quantify natural regeneration, we established five subplots with a total area of 800 m^2 within each 1 - ha plot. One subplot of 400 m^2 (20 × 20 m) was located in the centre of the plot, and four smaller subplots of 100 m^2 (10 × 10 m) were located in the corners. At the first measurement in July, 2011, we searched, tagged, and measured all seedlings and saplings of three study species in all subplots. We measured total height and diameter at stem base or dbh (dbh ≥ 2 cm, if possible). We conducted the same measurements during re-censuses in 2012 and 2013, and then also recorded seedling mortality and searched, tagged and measured newly recruited seedlings.

Statistical analysis

In our statistical tests we choose to pool data from the three plots in continuous forest (‘CF’), after testing for differences in vital rates between these plots (ANOVA, $p > 0.05$). Furthermore, we choose to construct two categories of fragments: the category of ‘small fragments (SF)’ contained the study fragments of 1.1, 4.8, 10.8 and 22.5 ha; the category of ‘large fragments (LF)’ contained the fragments of 41.7; 101.0 and 151.0 ha.

For each study species, we tested for differences in dbh growth between small fragments, large fragments and continuous forests by using a linear model (gl). As no effect of forest type was found for the three study species ($p > 0.05$), we used the Hossfeld IV equation (Zeide 1993) to relate dbh growth to dbh. This equation realistically describes the initial increasing growth rate with dbh for small trees, followed by a phase of decreasing dbh growth. We related the probability of survival and fecundity to dbh and forest type using a generalized linear model (glm). We used an ANOVA to test for differences in seedling recruitment among small fragments, large fragments, and continuous forest, followed by post hoc Tukey multiple comparisons. To construct IPMs, we selected models that had the lowest AIC scores. We conducted all statistical analyses using the R environment (version 3.0.3, http://www.r-project.org), and used IPMpack version 2.0 (Metcalf et al. 2013) to perform the fits for the Hossfeld equation.

Construction of Integral Projection Models (IPMs)

We constructed Integral Projection Models for our study species. Each IPM describes how a continuous population changes in discrete time. An IPM is presented by a kernel K, which contains probabilities of transition based on vital rates (growth, survival, and fecundity). The population dynamics simulated by an IPM can be written as (Metcalf et al. 2013):

$$n(y, t+1) = \int_{L}^{U} K(y, x) n(x, t) \mathrm{d}x$$

where n(y, t+1) is the distribution of individuals over all possible sizes y, including both already established and newly recruited individuals, at time t +1; n(x, t) is the distribution of individuals over all possible sizes at time t; L and U are the lower and upper observed size, respectively; and K is the kernel that describes the changes in size during from time t to time t+1. K can be broken into two sub-kernels, P and F (Metcalf et al. 2013), which results in:

$$n(y, t+1) = \int_{L}^{U} [P(y, x) + F(y, x)] n(x, t) \mathrm{d}x$$

where sub-kernel P presents the transitions among sizes due to survival and growth, and sub-kernel F describes the per capita contribution of reproductive trees to recruitment of seedlings. After discretizing kernel K, using a large number of fine categories, K can be considered as a very large transition matrix, and can be analyzed using tools developed for matrix modelling (Metcalf et al. 2013).

We constructed nine IPMs: one for each combination of species and forest type (small fragment, large fragment and continuous forest). Each IPM consisted of a part for seedling dynamics and one for tree dynamics. Seedlings were classified into three categories based on total height (Sl1: 0.1 - 0.5 m, Sl2: 0.51 - 1.0 m, Sl3: >1.0 m tall and ≤ 2 cm in dbh). In the IPM, seedling dynamics were simulated among these discrete classes (Zuidema et al. 2010). As the number of seedlings in the Sl3 category was very low, this caused transition probabilities from Sl3 to trees to be hard to quantify realistically. For each species, we therefore pooled data from all forest types to obtain a more realistic value of the transitions in the Sl3 category.

We used 600 mesh points for the continuous part (for dbh) of each IPM. When constructing the kernel, we modified the values for certain vital rates as these were not realistically described using the statistical model. First, as none of the trees > 20 cm in dbh of *P. annamense* and *P. stellata* died in the study plots in continuous forest, this resulted in unrealistically high survival rates predicted by logistic regressions. We therefore assumed annual survival rates of these trees to be 99% (Clark and Clark 1996) and applied this rate in the kernel. Second, the logistic regressions for reproductive status predicted small trees to have a reasonable chance to being reproductive. As the smallest trees that were observed to be reproductive measured 17 cm dbh (*C. bengalensis*) or 20 cm dbh (*P. annamense* and *P. stellata*), we set the probability to be reproductive to zero for trees smaller than these dbh values.

IPM analyses

We calculated population growth rate (λ) (Caswell 2001) to compare the population growth rates of three species in small fragments, large fragments, and continuous forest. If $\lambda > 1$, populations are projected to grow, if $\lambda < 1$, populations are projected to decline. To calculate the 95% confidence intervals around these average values, we applied bootstrapping method (Jongejans and De Kroon 2005). For each bootstrap estimate, we resampled with replacement from the data set, recalculated regression coefficient, established the kernel and calculated λ. This was repeated 400 times and the 95% confidence intervals for λ were obtained from the frequency distribution of these values. Finally, to determine the degree of similarity in order to examine how far the observed size distribution was from the expected size distribution, the stable size distribution that resulted from IPMs were compared to that of the observed population.

We conducted Life Table Response Experiment (LTRE) analyses (Caswell 2001) to investigate the contributions of components of the IPMs to the observed variation in λ between forest types. We performed one way LTRE analysis (Merow et al. 2014). First, we set the IPM of continuous forest as control and calculated the differences in λ for small fragments and large fragments with respect to this control. In addition, we did an analysis in which the IPM of large fragments was used as control to examine what caused the differences in λ between small and large fragments. Then, for each of these two LTRE analyses, we calculated a mid-way IPM as:

$$K^* = (IPM_{(treatment)} + IPM_{(control)})/2$$

Next, we calculated the IPM of the differences between IPM treatment and IPM control as:

$$IPM_{Difference} = IPM_{(treatment)} - IPM_{(control)}$$

Then, we calculated the contributions of transitions in the kernel to differences in population growth rate by weighting the IPM of the differences by the sensitivity (S) of the mid-way IPM K* as:

$$IPM_{Contribution} = IPM_{Differences} \text{ x } SK^*$$

Finally, we grouped the contributions into three parts of the kernel: seedling dynamics, survival and growth (P part of the kernel) and fecundity (F part of the kernel), the contribution of seedling dynamics was calculated as the sum of the $IPM_{Contribution}$ for the 3 discrete seedling classes. The contribution of survival and growth was calculated as the sum of the P-part of $IPM_{Contribution}$ over all dbh categories. And the contribution of fecundity was calculated as the sum of the F-part of $IPM_{Contribution}$ over all dbh categories. We conducted all IPM analyses in the R environment, using IPMpack version 2.0 (Metcalf et al. 2013).

Results

Vital rates in relation to forest fragment size

For all species, tree survival rate was lower in small fragments than in large fragments or continuous forest (Figure 1, Appendix 2). For trees, survival probability ranged across species from 74.4 - 76.5% in small fragments, 92.5 - 95.9% in large fragments, and 94.4 - 99.1% in continuous forest (Figure 1).

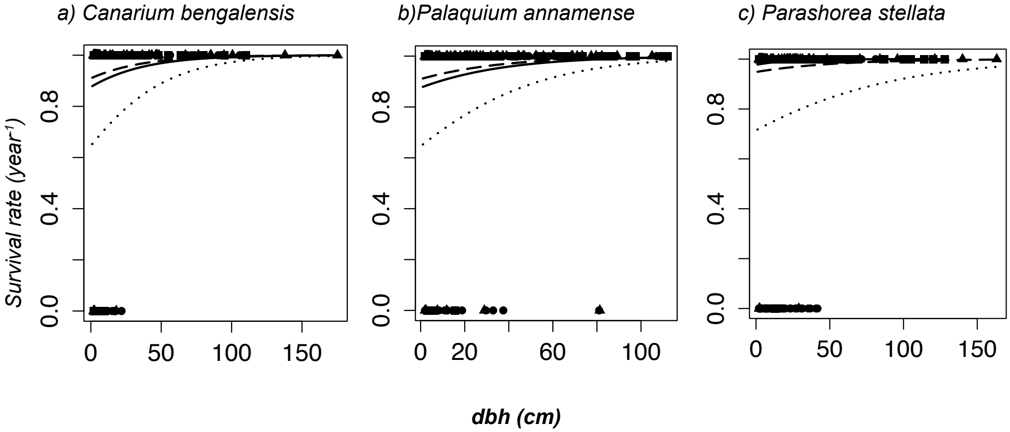
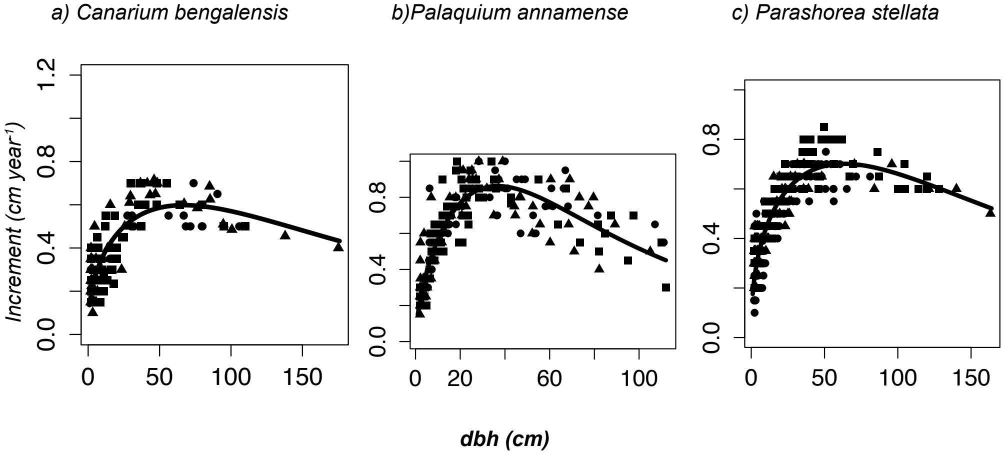


Figure 1. Tree survival rate in relation to tree diameter (dbh) and forest type for three large-stature tree species in central Vietnam. Lines are fitted logistic regression. Dotted lines for small fragments (SF), long dash dotted lines for large fragments (LF), and continuous lines for continuous forest (CF). Symbols are observed values for survival probability, small fragments (●), large fragments (▲), and continuous forest (■).

For small seedlings (Sl1), survival probabilities were 56.3 - 78.1% (range for the three species) in small fragments, 71.0 - 78.5% in large fragments, and 69.1 - 7 6.7% in continuous forest. For medium-sized seedlings (Sl2), survival probabilities were 77.8 - 84.8% in small fragments, 81.5 - 86.7% in large fragments, and 84.0 - 93.1% in continuous forest. And for large seedlings (SI3), survival probabilities were 64.0 - 85.7% in small fragments, 83.7 - 87.0% in large fragments, and 88.9 - 95.5% in continuous forest.

The dbh growth of all three species showed similar patterns across fragments and continuous forest. It increased from the low value 0.1 - 0.4 cm y-1 for the small trees to the high value (0.6 - 1.2 cm y-^{1}) for the mid-sized trees (20 - 50 cm dbh), and it then gradually decreased to lower values again (Figure 2). There were no significant differences in dbh growth across fragments and continuous forest (p > 0.05) suggesting that forest fragment size had no effect on tree growth rate.



a) Canarium bengalensis *b)Palaquium annamense* *c) Parashorea stellata*

Figure 2. Relation between dbh growth and dbh for three large-stature tree species in central Vietnam. Lines are fitted Hossfeld IV curves. Symbols are observed values for small fragments (●), large fragments (▲), and continuous forest (■).

In all species, the reproductive status was related to dbh (Figure 3). The smallest reproducing trees measured 17 cm dbh (*C. bengalensis*) and 20 cm dbh (*P. annamense* and *P. stellata*). The probability of reproductive trees did not depend on fragment size (p > 0.05). For all three species, flowering occurs at irregular intervals, causing many individuals to be reproductive in one year and not in the next. In spite of this, we found newly recruited seedlings for all three species in both study years, in fragments of all sizes as well as in continuous forest.

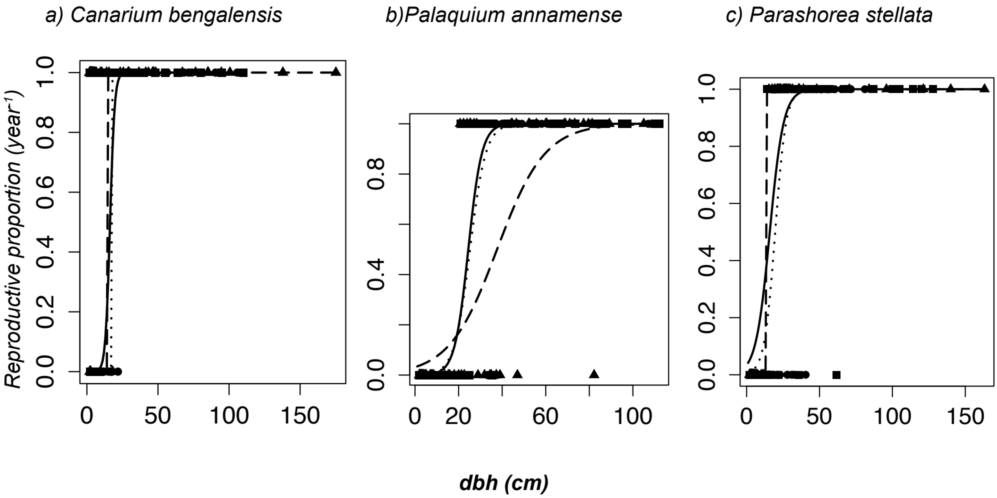


Figure 3. The probability of being reproductive as a function of dbh and forest type for three large-stature tree species in central Vietnam. Lines are fitted logistic regression. Dotted lines for small fragments (SF), long dash dotted lines for large fragments (LF), and continuous lines for continuous forest (CF). Symbols are observed values for probability fecundity: small fragments (●), large fragments (▲), and continuous forest (■)

In all three species, seedlings recruitment in large fragments and continuous forest was significantly higher than that in small fragments (ANOVA, p < 0.01), but did not differ significantly between large fragments and continuous forest (ANOVA, p > 0.05).

Population growth rate and stable structure

We found that population growth rate (λ) slightly varied across fragment sizes and continuous forest. The values of λ was below 1 (range across species: 0.986 - 0.998) in small fragments (Table 1) and above 1 (1.018 - 1.042) in large fragments and continuous forest for all three species (Table 1). The 95% confidence intervals of λ did not include the value of 1 in any of the three species in small fragments (Figure 4), suggesting that tree populations will slightly decline in small fragments. In contrast, it included the value of 1 for all three species in large fragments and continuous forest (Figure 4), indicating that tree populations are projected to remain stable over time.

Table 1. Population growth rates (λ) and 95% confidence intervals of three large-stature tree species small fragments (SF), large fragments (LF), and continuous forest (CF) in central Vietnam.

Fragment	*C. bengalensis*	*P. annamense*	*P. stellata*
SF	0.998[0.996, 0.999]	0.996[0.992, 0.997]	0.986[0.982, 0.998]
LF	1.029[1.027, 1.030]	1.018[1.020, 1.026]	1.033[1.031, 1.048]
CF	1.031[1.032, 1.037]	1.026[1.024, 1.027]	1.042[1.041, 1.042]

For all species, the stable population structure resembled the observed size structure better in large fragments and continuous forest than in small fragments (Appendix 3). In large fragments and continuous forest, both observed and simulated values were characterized by a high proportion of seedlings and small trees in the first category for the three species.

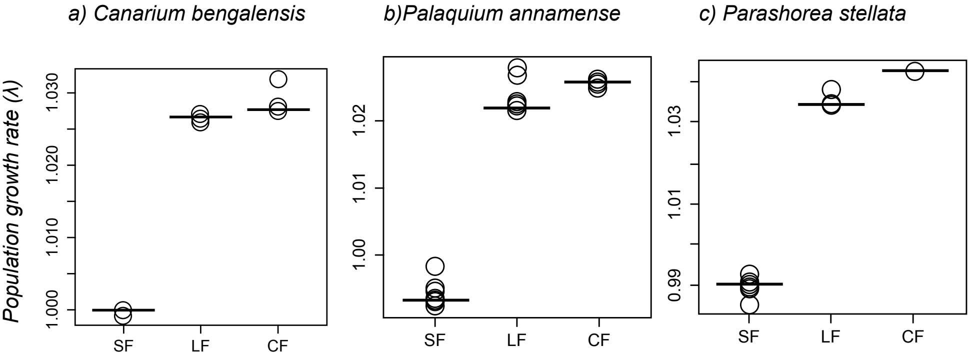


Figure 4. Box plot of population growth rates (λ) of three large-stature tree species in small fragments (SL), large fragments (LF) and continuous forest (CF) in central Vietnam. The box- and-whiskers are not visible because the 95% confidence interval is very marrow. The line shows the median value of λ.

In small fragments, the simulated values were remarkably high for large trees (Appendix 3), suggesting that future populations may contain a high proportion of large trees, likely because of insufficient recruitment.

Life Table Response Experiments (LTRE)

Our LTRE analysis revealed that vital rates did not contribute equally to the observed differences in population growth rates (λ) between forest fragments and continuous forest. For all species, the strong variation in λ cross forest types was mainly attributed to survival and growth, and to a lesser extent to differences in seedling dynamics and fecundity (table 2).

Table 2. Results of the Life Table Response Experiment (LTRE) analyses of three large-stature tree species across forest types in central Vietnam. For each species the values of λ are compared between three forest types. The final three columns indicate the contributions of different parts of the kernel to the difference in λ.

Species	Forest types compared	Differences of λ	Contribution to variation in λ		
			Seedling dynamics	Fecundity (F kernel)	Survival and growth (P kernel)
C.bengalensis	SF vs CF	-0.0312	0.011	0.029	-0.072
	LF vs CF	-0.0021	-0.006	-0.016	0.021
	SF vs LF	-0.0298	0.004	0.022	-0.056

Species	Forest types compared	Differences of λ	Contribution to variation in λ		
			Seedling dynamics	Fecundity (F kernel)	Survival and growth (P kernel)
P.annamense	SF vs CF	-0.0306	0.057	0.027	-0.121
	LF vs CF	-0.0083	-0.193	0.108	0.077
	SF vs LF	-0.0222	0.169	0.114	-0.301
P.stellata	SF vs CF	-0.0559	0.049	0.036	-0.1359
	LF vs CF	-0.0092	0.251	-0.393	0.1231
	SF vs LF	-0.0466	0.010	0.012	-0.0532

Notes: SF = Small fragments (< 20ha), LF = Large fragments (> 20 ha and < 151 ha),
CF = Continuous forest.

As growth rates did not differ among forest types the contribution to explaining variation of λ was the difference in survival between forest types. Comparing fragments and continuous forest, the difference in survival and growth between populations explained 91 - 99% of the difference in λ, variation in seedling explained 1.0 - 25%, while fecundity contributed just 2.6 - 11%. The difference in survival and growth between populations explained 71 - 97% of the difference in λ, and seedling 0.4 - 17%, fecundity 1.0 - 11% when comparing among fragments.

Discussion

For all three study species we found that (1) survival rate is lower in small fragments than in large fragments and continuous forest; (2) seedling recruitment is lower in small fragments than in large fragments and continuous forest; and (3) tree population models project slightly declining populations in small fragments (λ <1) and stable population sizes in large fragments and continuous forest.

Effects of fragment size on vital rates

The higher tree mortality rate in small fragments found in this study is comparable with results obtained from previous studies of tree population dynamics in Amazonian forest fragments (Laurance et al. 1998, Laurance et al. 2006a) and in Mexican forest fragments (Zambrano and Salguero-Gómez 2014). In these and other studies, a higher tree mortality rate was indeed recorded in small forest fragments than in large forest fragments and continuous forest (Laurance et al. 1998, Laurance et al. 2000, Laurance et al. 2011, Zambrano and Salguero-Gómez 2014). The main factor, which could reduce tree survival in small fragments, is the strong influence of edge effects. Edge effects are known to be a dominant cause of tree mortality (Laurance et al. 1998, Laurance et al. 2011), but this depends on time since fragmentation and the forest structure of the surrounding vegetation (Laurance et al. 2011). In our case, the sampled forest fragments are surrounded by forest plantations (hybrid acacia and rubber) and crop fields (maize, cassava), which are completely cleared at intervals of 1-5 years. This implies that the magnitude of edge effects in the studied fragments has probably not diminished over time. Furthermore, considering that edge effects are strongest within 100 m of the forest edge and increased tree mortality is recorded within 60 m of the forest edge (Laurance et al. 1998), most of our small fragments (≤ 20 ha) have little or no unaltered interior habitats (Appendix 1). In the large fragments and continuous forest, the permanent plots were located at >100 m from the edges, causing much smaller influence of edge effects (Laurance et al. 1998), and likely resulting in the higher survival rates in large fragments and continuous forest.

The second finding is that seedling recruitment was lower in small fragments than in large fragments and continuous forest. Similar results were obtained in studies on seedling dynamics in Amazonian forest fragmentation (Benitez-Malvido 1998, Benitez-Malvido and Martínez-Ramos 2003). Low seedling recruitment in small fragments may be caused in two ways. First, recruitment can be limited if the abundance of seed dispersal agents is reduced in forest fragments (Michalski and Peres 2005, Stouffer et al. 2009, Boyle and Smith 2010). Lower disperser abundance may in part result from a lower abundance of animal-dispersed tree species (Cordeiro and Howe 2001, Núñez-Ávila et al. 2013) or by a reduced reproductive output of trees in small fragments (Aguilar et al. 2006) due to pollen limitation (Ghazoul and McLeish 2001). Disperser abundance may also be reduced by hunting. We have indeed observed many animal traps along trails in the studied fragments. Among our study species, *C. bengalensis* and *P. annamense* are animal-dispersed species and recruitment in these species could therefore have been affected by lack of dispersers. The second factor that could have reduced seedling recruitment rates in small fragments is a high competition between the seedlings of pioneer species and the seedlings of our study species, which are shade-tolerant. Small fragments, which are made up by a more open and dynamic 'edge habitat' (Laurance et al. 1998, Laurance et al. 2000) may be more favorable for establishment of pioneer and liana seedlings than shade-tolerant seedlings (Popma et al. 1988). The high abundance of seedlings belonging to pioneer species such as *Alangium chinensis, Cosmos bipinnalus, Castannopis sp, Enicisanthellum plagioneurum, Schefflera octophylla* and *Baccaurea sylvestris* in small fragments suggest this explanation for the low recruitment rate of our study species.

We did not find an effect of forest fragment size on dbh growth of our study species. This result is in contrast with that of a recent demographic study on fragmentation effects in Mexico (Zambrano and Salguero-Gómez 2014), which revealed higher dbh growth rates in continuous forest compared to forest fragments (Zambrano and Salguero-Gómez 2014). These reduced growth rates in fragments may be related to the drought sensitivity of the Mexican study species. Our study species are not particularly drought-sensitive (Chinh et al. 2009), and may therefore be less affected by drier conditions in fragments.

Differences in population dynamics across forest fragment sizes

We found lower population growth rates in small forest fragments (< 20 ha) compared to large fragments and continuous forest. All three study species in large fragments and continuous forest showed stable population growth rates (confidence intervals of λ include 1), but populations in small fragments are projected to decline over time (mean $\lambda < 1$ and confidence intervals do not include 1). The only other study that we know on tree population dynamics in forest fragments yielded somewhat comparable results: in both continuous forest and 'large' fragments (≥ 19 ha) populations of *Poulsenia armata* were projected to grow ($\lambda > 1$) (Zambrano and Salguero-Gómez 2014). Studies on the population dynamics of understory herb in Amazonian forest fragments (Bruna and Kress 2002) showed declining population growth rates in small forest fragments but continued reproduction and recruitment (Bruna and Kress 2002). The asymptotic population growth rates (λ) reported here and in the two mentioned published studies represent the deterministic demographic effects of fragmentation. In addition, there can be stochastic events such as disturbances, climatic extremes, or demographic stochastic processes which cause sudden changes in population dynamics and may result in local extinction. Clearly, such events may have profound effects on small remnant populations in forest fragments, and their effects need to be evaluated in future studies on demographic implications on forest fragmentation. A second recommendation for fragmentation studies is to explicitly study the genetic diversity and degree of genetic exchange between remnant populations in forest fragments (Chapter 4).

What caused the considerable differences in population growth between forest fragments and continuous forest? Analysis of Life Table Response Experiments revealed that variation in population growth was mainly caused by differences in survival between small fragments on the one hand and large fragments or continuous forest on the other. This result contrasts those of a demographic study on Mexican forest fragments (Zambrano and Salguero-Gómez 2014) which showed that the largest contribution to differences in λ between forest fragments and continuous forest was adult fecundity (Zambrano and Salguero-Gómez 2014). In forest fragments, the variation of λ was likely due to variation in mortality rate which is known to be a critical driver of the dynamics of tree populations (Laurance et al. 1998, Laurance et al. 2011). The high mortality rates of both seedlings and large trees which we observed in forest fragments could have caused the differences in tree population growth rates between forest types.

In this study, the Integral Projection Models (IPMs) proved to be suitable for our comparative demographic studies, as it allows to work with small sample sizes and demographic data. In addition, the significant forest fragment size effects evaluated in regression models can be directly included in the kernels.

Implications for conservation

There is a discussion about the degree to which extinction debt results in apparent high levels of diversity, which are doomed to decline over time. The results of this study suggest that viable population can be maintained in fragments of > 20 ha. In small fragments, populations are projected to decline, but natural recruitment continued and it will take a long time before these populations disappear. In the meantime, small fragments may serve as stepping stones for pollen or seed exchange among fragments. Large fragments may thus contribute to conserving tree species, including threatened species such as *Parashorea stellata* in fragmented landscapes. However, to efficiently conserve these fragments, a primary goal is to create conditions that can ascertain population maintenance. For large-stature tree species in the forest fragments we studied, it usually takes considerable time for seedlings to grow into large adults and the chance that they reach that stage may be rather low due to edge effect and stochastic events. Survival of large adults is therefore important for population maintenance, and a slight change in adult survival may have a large impact on population dynamics. Thus, to maintain a viable population, the management measure should be controlled at a level that does not threaten the survival of adults. Strictly protected adult trees, specially threatened species in forest fragments is therefore highly recommended.

The contribution of relatively small forest fragments to conserving tree species, especially threatened species in fragmented landscape deserves more attention from conservation organizations, both in Vietnam and throughout the tropics. In view of the fact that tropical landscapes will be increasingly fragmented and that part of the conservation efforts need to take place in these landscapes and in these relatively small fragments.

Appendix 1. Characteristics of the studied forest fragments and continuous forest in central Vietnam.

Plot code	Area (ha)	Location	Altitude (m)	Distance from plot to closest edge (m)	Fragment surrounded by:
SF1	1.1	N:107°35'15.8" E:16°6'36.6"	323.2	41.2	• Hybrid acacia and rubber plantations, on all sides
SF2	4.8	N:107°40'23.3" E:16°9'45.4"	281.0	65.5	• Hybrid acacia and rubber plantation surrounded, on 3 sides • Shrubs, lianas, wild bananas and bamboo stands, on 1 side
SF3	10.8	N:107°39'11.7" E:16°6'31.46"	336.0	74.3	• Hybrid acacia plantation, on 1 side • Shrubs, lianas, wild banana and bamboo stands, on 2 sides • Upland rice field cultivation, on 1 side
LF1	22.5	N:107°40'10.58" E:16°9'39.18"	291.2	95.4	• Hybrid acacia plantation, on 2 sides • Shrubs, wild bananas, and bamboo stands, on 1 side • Upland rice field cultivation, on 1 side
LF2	41.7	N:107°39'40.6" E:16°11'7.74"	371.0	167.2	• Hybrid acacia hybrid and rubber plantation, on 1 side • Shrubs, lianas, wild bananas and bamboo stands, on 3 sides
LF3	101.0	N:107°38'32.7" E:16°9'18.18"	333.8	295.5	• Hybrid acacia plantation, on 1 side • Shrubs, lianas, wild bananas and bamboo stands, on 3 sides
LF4	151.0	N:107°37'34.97" E:16°9'32.16"	384.4	525.6	• Hybrid acacia plantation, on 1 side • Shrubs, lianas, wild bananas and bamboo stands, on 3 sides
BM1	>1.000	N:107°39'55.8" E:16°3'26.2"	339.2	1,340.0	• Not applicable
BM2	>1.000	N:107038'44.38" E:1603'12.10"	333.5	1,370.0	• Not applicable
BM3	>1.000	N:107039'13.40" E:1602'11.6"	322.7	1,520.0	• Not applicable

Notes: SF and LF refer to plots located in small and large forest fragments respectively; BM refers to plots located in the continuous forest, Bach Ma National Park.

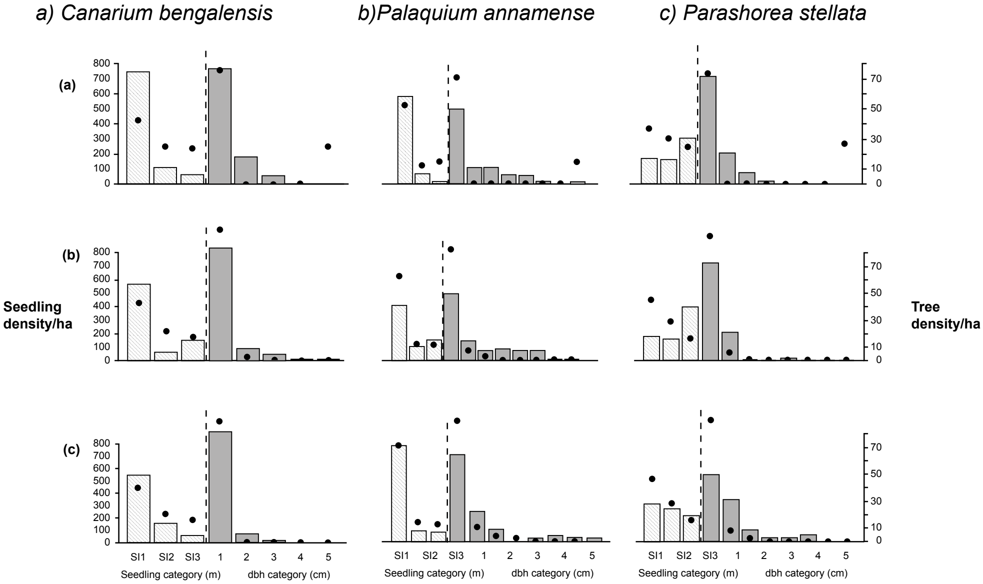
Appendix 2. Statistical models and fitted parameters that were used to construct kernels for Integral Projection Models of three large-stature tree species in forest fragments and continuous forest in central Vietnam.

Species	Fragment	Model
C. bengalensis		
Survival	SF	Survival = 1/(1+Exp(- (0.031*dbh + 0.477))), R^2 (Nagelkerke) = 0.09
	LF	Survival = 1/(1+Exp(- (0.029 *dbh + 2.702))), R^2 (Nagelkerke) = 0.06
	CF	Survival = 1/(1+Exp(- (0.208*dbh + 1.236))), R^2 (Nagelkerke) = 0.02
dbh growth	SF	$\Delta_{dbh} = [3.802 * 1.316 * dbh^{(1.316 - 1)}] / [3.802 + (dbh^{1.316})/744.392]^2$ (n = 482)
	LF	$\Delta_{dbh} = [4.555 * 1.427 * dbh^{(1.427 - 1)}] / [4.555 + (dbh^{1.427})/396.796]^2$ (n = 464)
	CF	$\Delta_{dbh} = [7.938 * 1.535 * dbh^{(1.535 - 1)}] / [7.938 + (dbh^{1.535})/379.607]^2$ (n = 497)
Fecundity	SF	Fecundity = 1/(1+Exp(- (56.11 *dbh -976.13))), R^2 (Nagelkerke) = 0.7
	LF	Fecundity = 1/(1+Exp(- (20.440*dbh -299.350))), R^2 (Nagelkerke) = 0.62
	CF	Fecundity = 1/(1+Exp(- (0.625 *dbh - 10.182))), R^2 (Nagelkerke) = 0.6
P. annamense		
Survival	SF	Survival = 1/(1+Exp(- (0.037*dbh + 0.483))), R^2 (Nagelkerke) =0.06 , $p < 0.05$
	LF	Survival = 1/(1+Exp(- (0.006*dbh + 2.364))), R^2 (Nagelkerke) = 0.02, $p > 0.05$
	CF	Survival = 1/(1+Exp(- (0.133*dbh + 1.395))), R^2 (Nagelkerke) = 0.02, $p > 0.05$
dbh growth	SF	$\Delta_{dbh} = [4.727 * 1.557 * dbh^{(1.557 - 1)}] / [4.727 + (dbh^{1.557})/259.646]^2$ (n = 494)
	LF	$\Delta_{dbh} = [5.073 * 1.595 * dbh^{(1.595 - 1)}] / [5.073 + (dbh^{1.595})/250.827]^2$ (n = 331)
	CF	$\Delta_{dbh} = [6.059 * 1.639 * dbh^{(1.639 - 1)}] / [6.059 + (dbh^{1.639})/248.639]^2$ (n = 509)
Fecundity	SF	Fecundity = 1/(1+Exp(- (0.279*dbh - 7.033))), R^2 (Nagelkerke) = 0.67
	LF	Fecundity = 1/(1+Exp(- (0.091*dbh - 3.426))), R^2 (Nagelkerke) = 0.58
	CF	Fecundity = 1/(1+Exp(- (0.322*dbh - 7.881))), R^2 (Nagelkerke) = 0.61
P. stellata		
Survival	SF	Survival = 1/(1+Exp(- (0.015*dbh + 0.917))), R^2 (Nagelkerke) = 0.09
	LF	Survival = 1/(1+Exp(- (0.020*dbh + 2.908))), R^2 (Nagelkerke) = 0.03
	CF	Survival = 1/(1+Exp(- (0.049*dbh + 3.742))), R^2 (Nagelkerke) = 0.03

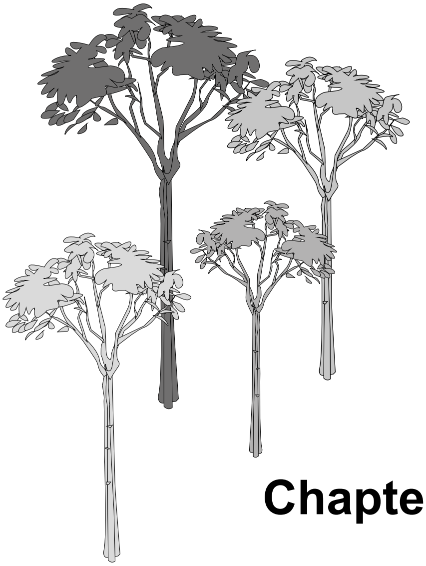
Species	Fragment	Model
dbh growth	SF	$\Delta_{dbh} = [5.749 * 1.504 * dbh^{(1.504 - 1)}] / [5.749 + (dbh^{1.504})/338.909]^2$ (n = 710)
	LF	$\Delta_{dbh} = [2.887 * 1.313 * dbh^{(1.313 - 1)}] / [2.887 + (dbh^{1.313})/652.557]^2$ (n = 458)
	CF	$\Delta_{dbh} = [3.367 * 1.383 * dbh^{(1.383 - 1)}] / [3.367 + (dbh^{1.383})/517.817]^2$ (n = 516)
Fecundity	SF	Fecundity = 1/(1+Exp(- (0.269 *dbh - 5.282))), R^2 (Nagelkerke) = 0.58
	LF	Fecundity = 1/(1+Exp(- (10.620 *dbh - 143.890))), R^2 (Nagelkerke) = 0.46
	CF	Fecundity = 1/(1+Exp(- (0.211*dbh - 3.354))), R^2 (Nagelkerke) = 0.33

Notes: SF = small fragments (< 20 ha), LF = large fragment (> 20 ha and < 151 ha), CF = Continuous forest.

Appendix 3. Observed and predicted (stable) population structures of three large-stature tree species small fragments, large fragments and continuous forest in central Vietnam.



Population structure of three large-stature tree species in small fragments (a), large fragments (b), and continuous forest (c) in central Vietnam. Seedlings are classified into three categories: 0.1- 0.5 m tall (Sl1), 0.51-1.0 m tall (Sl2), and over 1.0 m tall but ≤ 2 cm in dbh (Sl3). For the purpose of showing population structures graphically, trees are classified into five dbh categories: 2.1 - 40; 40.1- 80; 80.1-120;120.1-160; 160.1-180 cm for C.bengalensis or eight dbh categories: 2.1 - 15.9; 16.0 -29.9; 30.0 - 43.9; 44.0 - 57.9; 58.0 - 71.9; 80.0 - 85.9;86.0 - 99.9; 100 - 120 cm for P. annamense and P. stellata. The stable size distribution (dots) obtained from IPM simulations are compared to the observed population structures (bars).



Chapter 4

Forest fragmentation causes genetic erosion and differentiation in spite of high genetic exchange in remnant populations of a threatened tropical tree species in Vietnam

with T.H.Quang, G.A. De Groot, R.G.A. Boot & P.A. Zuidema, submitted

Abstract

Forest fragmentation can decrease the viability of tree populations through changes in genetic mating systems and gene flow. Quantifying these genetic effects is crucial to evaluate the potential contribution of fragmented tree populations in conserving threatened tree species. We used nine microsatellite markers to determine the effects of recent forest fragmentation on genetic diversity in *Parashorea stellata*, a critically endangered tree species, in four forest fragments in central Vietnam. Specifically, we compared the genetic diversity of large, reproductive trees ('adults') of this species which established before fragmentation, with seedlings that germinated after fragmentation. Overall, we observed a strong spatial genetic structure and a relatively low genetic diversity in adults, suggesting a genetic bottleneck due to the decline of the original population. Allele richness was lower in seedlings compared to adults, showing that populations continued to lose genetic variation after fragmentation occurred. In contrast, observed and expected heterozygosity were generally not reduced in seedlings. This may indicate that a new genetic equilibrium has not been reached as yet, but may also be caused by the observed high levels of pollen and seed influx in fragments. In spite of this genetic exchange between remnant populations, pairwise genetic differentiation generally increased after fragmentation. Thus, even though remnant populations appear to be well connected in this agricultural landscape, fragmentation caused genetic erosion and increased genetic differentiation. Our results suggest that multiple remnant populations should be retained in order to conserve genetic variation of tree species in intensive agricultural tropical landscapes.

Key words: Forest fragmentation, genetic consequences, pollen flow, tropical tree, Vietnam.

Introduction

Forest fragmentation is considered to be one of the main causes of tropical biodiversity loss (Heywood 1995, Young et al.2000). It reduces the size and increases the isolation of remnant populations (Young et al.1996, Young et al.2000, Lienert 2004), causing these populations to lose genetic diversity over time (Young et al. 1996, Chen 2000, Van Geert et al. 2008). When fragmentation occurs, it may cause a genetic bottleneck, because a significant portion of individuals is lost from the original population, resulting in a loss of genetic variation (Young et al.2000). The magnitude of this loss depends on the spatial genetic structure in the population. If there is a high level of spatial genetic mixing within the original population, one or a few remnant populations may still contain all genetic variation that was present in the original population. In addition, fragmentation causes populations to be small and less connected (Young et al. 1996). Small populations are more susceptible to a loss of genetic variation due to increased random genetic drift (Lienert 2004). This genetic loss can be aggravated if fragmentation increases mortality of reproductive trees (Laurance et al. 2000) or reduces fecundity rates (Nason and Hamrick 1997, Ghazoul and McLeish 2001, Fuchs et al. 2003). Loss of genetic variation may result in inbreeding depression and a reduced capacity to adapt to environmental changes, leading to reduced viability of trees and tree populations (Lienert 2004, Frankham 2005).

A large share of the remaining area of tropical forests is highly fragmented (Wade et al. 2003, Pimm and Brooks 2013). Therefore, the above explained theoretical framework would imply that species inhabiting these forests - including threatened species - will in many cases experience genetic erosion and differentiation. In reality, however, this genetic isolation is not always observed, a phenomenon known as the ‘paradox of forest fragmentation genetics’ (Kramer et al. 2008). One reason is that fragment boundaries do not necessarily represent boundaries of mating groups (Kramer et al. 2008). Depending on the matrix in which forest fragments are embedded (Wang et al. 2008), remnant populations in such fragments might still be able to exchange genetic information via pollen and seeds (Dick 2001, White et al. 2002, Bacles and Ennos 2008, Dick et al. 2008) or seeds (Bacles et al. 2006), potentially mitigating genetic erosion and its consequences for population viability. Yet, additional case studies from a range of tropical forest systems are required to assess whether the landscape matrix allows such exchange, and whether this indeed effectively prevents genetic erosion. While some examples are available from Amazonia and Europe (Van Geert et al. 2008, Fuchs and Hamrick 2011), studies on the genetic effects of fragmentation for tree species are lacking for tropical Southeast Asia, a region with high rates of recent deforestation and forest fragmentation (Achard et al. 2002).

Here, we study the effects of forest fragmentation on genetic diversity in *Parashorea stellata*, a critically endangered tree species (Oldfield et al. 1998). We studied remnant populations of this species in four small forest fragments in Vietnam, a country where forest cover was reduced from 68% in 1943 to 31% in 2005 (Meyfroidt and Lambin 2008). Forest fragments in the agricultural landscape of our study site in Central Vietnam harbour a large variety of tree species, including ten threatened species (Chapter 3). To quantify the effect of fragmentation (a reduction in population size), we compared large, reproductive trees (‘adults’) which represent the genetic diversity of the original population (possibly affected by the bottleneck effect of population reduction), with the genetic diversity of seedlings that germinated after fragmentation took place. Specially, we ask three questions: (1) Did the adult generation likely experience a genetic bottleneck? (2) Did the small size and isolation of remnant populations cause a loss of genetic diversity in seedlings compared to adults? (3) To what extent are remnant populations genetically connected, and is this through pollen exchange or seed dispersal? This is one of the first studies on the genetic implications of forest fragmentation for tropical dipterocarp species (Finger et al. 2012, Ismail et al. 2014).

Materials and methods

Study species

Parashorea stellata (Dipterocarpaceae) is a large-stature emergent tree species. It is listed as critically endangered in the IUCN Red List (Oldfield et al. 1998). Its trunk is straight and cylindrical, 30 - 35 m high, 80 - 100 cm in diameter. Flowering occurs from April to June and is synchronous among and within populations (own observations). Fruiting takes place from August to October. Fruits are small, 1 cm in diameter, bearing many grey lenticels and stellate hairs, have five wings and are wind dispersed. The seeds germinate immediately after fruits are dispersed (Chinh et al. 2009). The genus Parashorea is known as monoecious, but predominantly out-crossed (Ashton 1982). Trees of this genus are principally insect-pollinated (Ashton 1982) and small wild bees were observed on their flowers (Appanah and Turnbull 1998). *P. stellata* is a light and moisture demanding species and occurs in Cambodia, Myanmar, Laos, Malaysia, and Vietnam on elevations ranging from 300 to 800 m a.s.l. (Chinh et al. 2009).

Study site

We conducted the study in Huong Son commune, Nam Dong district, Thua Thien Hue province, central Vietnam (16°15’N, 107°53’E; Figure 1). The area is hilly with altitude ranging from 40 to 1,700 m. The climate is tropical monsoon with four seasons and two main windy seasons during the year. The northwest wind takes place in summer (dry and hot) from April to July and the southeast wind occurs in winter (wet and cold) from October to January. The total natural forest cover of the commune is 3,996 ha and accounts for 61.4% of the total area (Thang et al. 2010). It was reduced by about 6% from 1975 to 2004 (Thiha et al. 2007). According to local inhabitants, forest fragmentation has taken place since the 1980s when the government started road construction for wood extraction. At that time, certain tree species with a high economic value such as *Hopea pierrei, Erythrophleum fordii, Madhuca pasquieri*, *Peltophorum pterocarpum, Dalbergia cochinchinensis, Dipterocarpus retusus*, *Parashorea stellata*, *Hopea hainanensis, Shorea guiso*, and *Cinnamomum parthenoxylon*, were selectively logged from natural forests. Since 1989, the land cover changed because degraded natural forests were gradually converted into tree and crop plantations for pulp and paper production (Thiha et al. 2007). As a result, the fragments of pristine forest containing *P. stellata* are now embedded in a matrix of plantations of hybrid acacia and rubber, as well as agricultural fields where maize and cassava are grown. Hybrid acacia plantations are the dominant vegetation in the landscape. These trees are known to attract a variety of insects (pollinators) (Sornsathapornkul and Owens 1998).

Sampling strategy

Within the commune area, we selected four small forest fragments (< 25 ha) that contained at least 10 reproductive trees and at least 10 seedlings of the study species. The selected fragments ranged in size from 1.1 to 22.5 ha and had similar environmental conditions (e.g., soil types, topography, altitude and time since fragmentation; Table 1).

Table 1. Characteristics of the four forest fragments in central Vietnam which contain the studied remnant populations of *Parashorea stellata*. All sampled adult trees were observed to reproduce in 2010 - 2012, and seedlings recruited in 2010 - 2012.

Code of remnant population	Latitude	Longitude	Altitude (m)	Fragment size (ha)	Number of samples	
					Adults	Seedlings
HSC1	107.674	16.161	281	4.8	8	25
HSC2	107.671	16.160	336	10.8	11	25
HSC3	107.648	16.170	323	1.1	25	13
HSC4	107.658	16.158	291	22.5	15	25

The remnant populations were located at 0.5-3.0 km distance from each other (Figure 1).

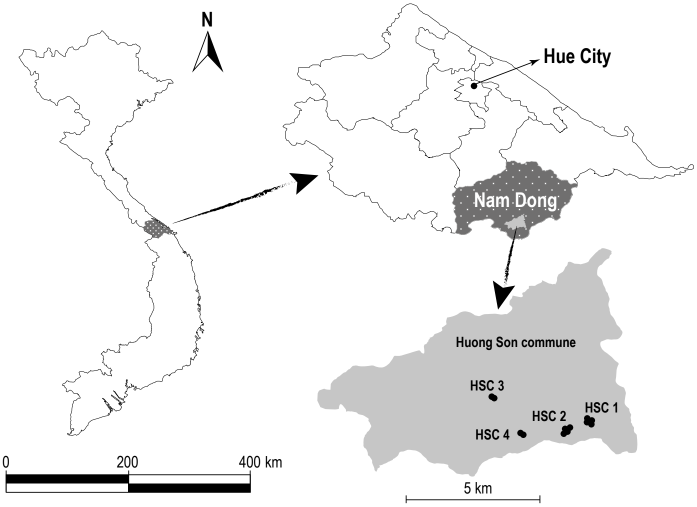


Figure 1. Map of four studied forest fragments in Huong Son commune, central Vietnam, which contain the four remnant populations of Parashorea stellata (see Table 1).

Flowering occurs irregularly in our study species (i.e., some of the large trees do not flower in a given year). Therefore, we observed which individuals had been flowering in June-July of 2010, 2011 and/or 2012, and in July 2012 we took fresh leaf samples in each fragment from all individuals of our study species of >10 cm DBH that had been observed flowering in one of these years. At the same time, we collected leaf samples of a random and representative subset of small seedlings. Per remnant population, 25 seedlings were randomly selected in each of the fragments. We selected seedlings from the entire fragment to maximize the number of adults of the sampled seedlings. The selected seedlings represented 3,8% of the total seedling population in remnant population HSC1, 1,3% in HSC2, and 0,5% in HSC4. In population HSC3, only 13 seedlings were found, and we therefore sampled all of these (see Table 1). We selected seedlings of < 20 cm height, which are either one or two years old because seedling height growth ranges from 7 to 10 cm year^{-1} (Chapter 3). This selection of young seedlings ensures that they have been produced by adult trees that were observed with flowers in 2010-2012, and thus that all potential parents of the sampled seedlings had been identified.

In order to calculate the distances among sampled adults and seedlings, the coordinate of each sample was recorded by a handheld Garmin GPS map-60csx navigation device. Collected leaf samples were immediately dried in the field by transferring them to paper bags containing silica gel. Back in the laboratory, samples were stored in a freezer at -80°C until used. In total, leaf samples were collected from 59 adults and 88 seedlings (Table 1).

DNA extraction

DNA was extracted from leaves using a modified CTAB method (Doyle and Doyle 1990). For each sample, 250 mg of leaves were grinded to fine power in liquid nitrogen with a mortar and pestle. The quality of DNA was checked by agarose gel electrophoresis and visualized UV-vis and quantity of DNA was measured by Nanodrop spectrophotometry.

Microsatellite analysis

Selecting suitable Simple Sequence Repeats (SSR)

In order to select nine SSR for this study, we tested 29 SSR markers which were developed for two congeneric species: *Shorea leprosula* (Lee et al. 2004) and *Shorea curtisii* (Ujino et al. 1998). The goal of the test was to determine the polymorphic levels of these markers for *P. stellata* (Appendix 1). To do so, we randomly selected leaf samples from 12 adult trees of *P. stellata* across the four sampled populations. Among the 29 tested SSR primers, 12 primers showed good amplification while the others did not. The number of alleles in the 12 trees ranged from 2 to 12 (GenAlex calculation). We selected the nine markers with the highest polymorphism for further genetic analyses, leaving out three markers which had a very low number of alleles (Appendix 1). The nine selected primers were fluorescent labelled in forward primers, not reverse primer with HEX, TET and FAM dyes.

Molecular method

PCR was performed in reaction volumes of 20 ml. Each reaction contained 7.5 ml of Dream Taq PCR Master Mix (Thermo Scientific), 8 pmol of each SSR, 4.6 mg of BSA (Thermo Scientific) and 25 ng of DNA. Amplifications were performed in Biorad C1000 thermocycler with cycling profile: initial denaturation step at 95°C for 3 minutes, followed by 40 cycles of 95°C for 1 min, annealing temperature range from 52 to 54°C for 45 seconds and 72°C for 1 min (details in Appendix 1). The final extension step was performed at 72°C for 7 minutes. Purified PCR products were run on an ABI 3130 XL capillary (Applied Biosystems) for genotyping and GENEMAPER 4.0 was used for fragment analysis.

Data analysis

Assessment of genetic diversity and spatial structure

Per forest fragment, the observed and expected heterozygosity (*Ho* and *He*) were calculated in GeneAlex 6.5 (Peakall and Smouse 2006). In addition, the alleles richness (*Ar*), the pairwise levels of differentiation (F_{st}), and Wright's inbreeding coefficient (F_{is}) were calculated in FSTAT 2.9.3.2 (Goudet 2001) using 1,000 permutations. F_{ST} and F_{is} were obtained across loci by the jackknifing procedure. We tested for significant deviations from Hardy-Weinberg equilibrium by evaluating whether F_{is} values within each sample were significantly different from zero. The significant levels were adjusted with sequential Bonferroni correction for multiple tests with $p < 0.05$. To analyse genetic structure, we applied a Bayesian cluster analysis for all individuals using software STRUCTURE (Pritchard et al. 2000) to assign each individual to genetic clusters. Analyses were run for K-values of 1 to 8, the optimal value of K was determined from log likelihood values (Evanno et al. 2005) with five MCMC chains (burn-in: 100,000 interactions; run length: 200,000 interactions; admixture allowed). In order to assess the most likely number of genetic clusters K, we calculated delta K values based on the protocol by Evanno et al. (2005).

The significant differences in genetic diversity parameters between the seedling and adult generations was tested via a two-way ANOVA in IPM-SPSS statistics 21, using generations and fragments as independent variables. Diversity values per microsatellite locus were used as replicates. Although this approach involves pseudoreplication at the level of individual samples, it allows for a check of consistency of the observed patterns among different genetic loci.

Estimating dispersal rates

We used paternity analysis, applying the maximum likelihood-based approach as implemented in CERVUS 3.0 (Marshall et al. 1998), to investigate for each seedling whether one or both of its parents came from the same population, or from one of the other three study populations. A simulation was run using the allele frequencies of all adults and seedlings, with the adults serving as candidate parents. The confidence level for the assignment of the two most likely parents was set at 90%.

Only candidates with < 2 mismatches were considered as potential parents. In case of multiple candidates, we assumed the candidate growing nearest to the seedling to be the most likely mother tree, thereby potentially underestimating seed dispersal rates, which is similar to the procedure used in several previous studies (Tani et al. 2009, Sebbenn et al. 2010, Finger et al. 2012, Ismail et al. 2014). Using this strategy a given seedling could have: (i) no parent within the remnant population, (ii) at least one parent within the remnant population (then assumed to be the mother), or (iii) at least one parent pair within the population. We assumed case (i) to represent seed influx from outside the population, case (ii) to represent pollen influx from outside the population, and case (iii) to represent within-population mating.

Results

Genetic diversity and inbreeding

Genetic diversity was relatively low in both generations (adults and seedlings) in all four remnant populations (Table 2). Estimates of allelic richness (*Ar*) and expected heterozygosity (*He*) were slightly but consistently higher among adults (*Ar* = 3.471 - 4.164; *He* = 0.592 - 0.771) than among seedlings (*Ar* = 3.112 - 4.043; *He* = 0.581- 0.679), although these differences were only significant for *Ar* ($p < 0.05$; Table 3). Both parameters were lowest in remnant population HSC1 and highest in HSC4. In all combinations of generation and remnant populations, except for the seedlings in HSC3, *Ho* was significantly lower than *He*, resulting in relatively high inbreeding coefficients (Table 2).

Table 2. Genetic diversity variation from nine microsatellite loci for adults and seedlings in four remnant populations of *P. stellata*. Shown are the number of genotype samples (*N*), number of alleles (*Na*), allelic richness (*Ar*), observed heterozygosity (*Ho*), expected heterozygosity (*He*), and Wright's inbreeding coefficient (F_{is}).

Code of remnant population	Life stage	*N*	*Na*	*Ar*	*Ho*	*He*	F_{is}
HSC1	Adults	8	3.667	3.471	0.479	0.592	0.257
	Seedlings	25	3.778	3.112	0.432	0.581	0.279
HSC2	Adults	11	3.889	3.515	0.454	0.616	0.314
	Seedlings	25	3.556	3.146	0.446	0.584	0.259
HSC3	Adults	25	4.889	3.881	0.541	0.658	0.218
	Seedlings	13	4.222	3.674	0.632	0.642	0.054
HSC4	Adults	15	4.667	4.164	0.405	0.771	0.456
	Seedlings	25	5.222	4.043	0.390	0.679	0.451

Interestingly, when analysed across all populations, *Ho* and F_{is} were not significantly different between adults and seedlings (Table 3). However, in remnant population HSC3, F_{is} dropped from 0.218 in the adult generation to 0.054 in the seedling generation.

Table 3. Results of a two-way ANOVA test for four genetic diversity parameters (*Ar*, *Ho*, *He* and F_{is}) as a function of generation (adults vs. seedlings), population (four remnant populations) and their interaction. Abbreviations: *Ar* = Alleles richness, *Ho* = observed heterozygosity, *He* = expected heterozygosity, and F_{is} = Wright's inbreeding coefficient. For *Ar*, the effect of population was not tested because of different rarefactions among populations.

Factor	*Ar*		*Ho*		*He*		F_{is}	
	F	Pvalue	F	Pvalue	F	Pvalue	F	Pvalue
Generation	7.161	0.012	0.016	0.901	1.699	0.202	0.148	0.703
Population			1.191	0.329	1.648	0.198	0.797	0.505
Generation × population			0.496	0.688	0.095	0.962	0.841	0.481

Genetic differentiation

Within the adult generation, pairwise F_{ST}-values were relatively low for remnant populations HSC1, HSC2 and HSC3 (Table 4), suggesting relatively low genetic differentiation among these populations.

Table 4. Pairwise genetic differentiation (F_{ST}) across adult (values above the diagonal) and seedling (values below the diagonal) generations of *P. stellata*. HSC1, HSC2, HSC3, and HSC4 are the codes of forest fragments in which the leaf samples of adults and seedlings were collected (more detail see Table 1).

Code of remnant population	HSC1	HSC2	HSC3	HSC4
HSC1		0.03	0.04	0.11
HSC2	0.12		0.06	0.11
HSC3	0.07	0.08		0.13
HSC4	0.09	0.10	0.04	

Remnant population HSC4 showed a much higher differentiation with all three other fragments (Table 4). This strong genetic differentiation of remnant population HSC4 was supported by the results of Bayesian clustering (in the STRUCTURE software), as a division into two clusters (the optimal K value based on Evanno's deltaK-method) separated the adult trees of HSC4 from those of the other fragments (Fig. 2). Interestingly, HSC4 no longer appeared to be most genetically distinct in the seedling generation (for K=2): seedlings of this remnant population were assigned to the same cluster as those of HSC1 and HSC3, while seedlings of HSC2 represented the second cluster. These results are in agreement with those on pairwise F_{st} values. For adults, the pairwise F_{ST} values were particularly high for HSC4, while for seedlings they were higher for HSC2. Thus, genetic differentiation among populations was different for adults and seedlings.

The Bayesian clustering analysis resulted in a biologically very relevant pattern for a division into four genetic clusters (K= 4). In this case, the four fragments each formed their own genetically distinct population. A similar genetic differentiation between the four fragments was observed in the seedling generation (Figure 2).

At K=5, however, the seedlings in fragment HSC4 formed two distinct subgroups, suggesting a further genetic substructure within this population. In contrast with the adult generation, various seedlings in population HSC2, HSC3 and especially HSC4 showed indications of an admixed genetic background.

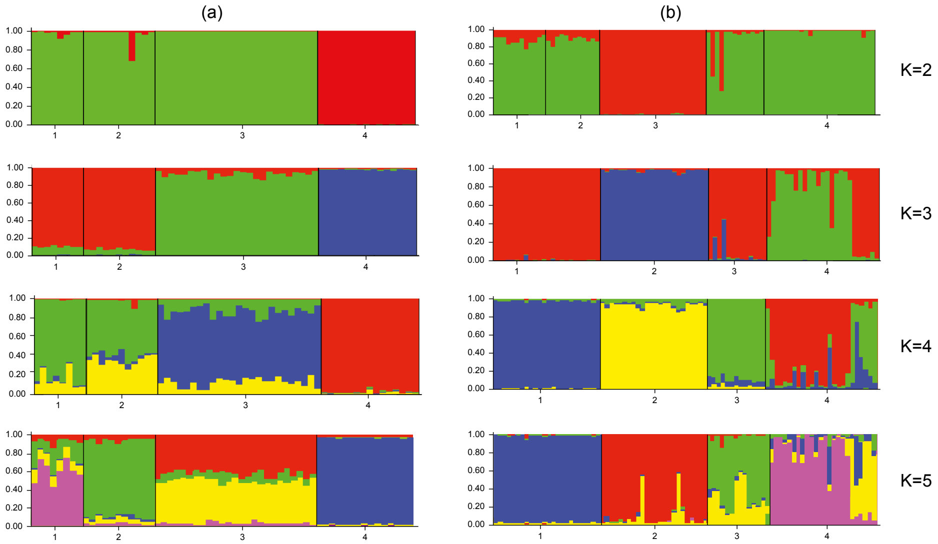


Figure 2. Example results of Bayesian structure analysis using the STRUCTURE software (Pritchard et al. 2000) for adults (a) and seedlings (b) of P. stellata. Each individual in the remnant population is presented by a vertical bar, in which different colours show the proportional membership of each gene pool. The analyses were performed for 2-5 genetic clusters (K). Codes 1- 4 along the x-axis refer to remnant populations HSC1-HSC4.

Reproductive patterns

For 25 of the total 88 seedlings a parent pair could be identified. In the other cases, at least one parent was not present in the studied set of adult trees. Following these results, mating within populations seemed relatively rare in all populations except HSC3 (Figure 3).

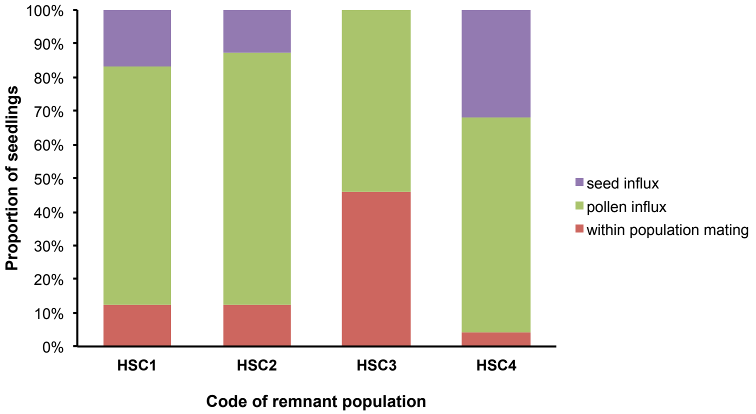


Figure 3. Parental origin of seedlings in four remnant populations of P. stellata. Seed influx means that none of the parents came from the same population as the seedling; pollen influx means that one of the parents came from the same population as the seedling (thereby assuming that this was the mother), and within population mating means that both parents came from the same population as the seedling.

The majority of seedlings in all populations resulted from fertilization by pollen originating from outside the population (Figure 3). In addition, all populations except HSC3 to some extent received seed influx, with the highest proportion being found in HSC4 (Figure 3). We did not observe self-fertilization in any of the populations.

Discussion

Parashorea stellata is an ecologically and economically important large-stature tree species in Southeast Asia (Appanah and Turnbull 1998). In Vietnam, populations of this species are mostly found in forest fragments (Nghia 2000) surrounded by intensive forest plantations (hybrid acacia and rubber). Our study was located in one of these intensive agricultural landscapes and provides insights into the gene flow among small remnant populations and the consequences of fragmentation for genetic diversity of *P. stellata*.

Adult trees: Genetic bottleneck effects through loss of forest area

We found evidence for a clear spatial genetic structure in our study species. This spatial structure probably has contributed to the finding that genetic diversity in adults of *P. stellata* was relatively low in the four remnant populations in terms of mean number of alleles (*Na* = 4.278) and expected heterozygosity (*He* = 0.645). Since fragmentation took place several decades ago, we did not possess information on genetic diversity of adult trees that grew in between the present-day fragments and we could therefore not compare the observed post-fragmentation genetic diversity with pre-fragmentation values. Nevertheless, the values we obtained here fall within the same range as those observed in populations of other dipterocarp species located in forest fragments. For instance, low values were also found for adult populations of the dipterocarp species *Vateriopsis seychellarum* (*Na* = 3.76, *He* = 0.53) (Finger et al. 2012) and *Vateria indica* (*Na* = 5.25, *He* = 0.576) (Ismail et al. 2014). On the other hand, the number of alleles obtained in our study was considerably lower than published values obtained from populations of dipterocarp species in large tracks of forest: *Shorea xanthophylla* (*Na* = 8.83, *He* = 0.66), *Parashorea tomentella* (*Na* = 11.00, *He* = 0.61), *Dipterocarpus grandiflorus* (*Na* = 14.17, *He* = 0.68) (Kettle et al. 2011), and ten other dipterocarp species (*Na* = 5.1 - 28.7, *He* = 0.52 - 0.84) (Harata et al. 2012). The lower number of alleles in remnant populations studied here is probably the result of a genetic bottleneck, which was likely caused by the loss of a significant portion of the original adult population. This has resulted in the loss of some low frequency alleles, thus reducing the size of the gene pool. An alternative explanation for the low genetic diversity in the adults of our studied populations is increased mortality due to deteriorated environmental conditions in fragments (Laurance et al. 2000). We do not have information to quantify the potential magnitude of the latter effect, but population monitoring of the study species revealed that annual mortality of adult trees was markedly higher in small compared to large fragments (5.3% vs 3%; Chapter 3). Thus, increased mortality rates in small fragments will have contributed to the observed loss of genetic diversity in adults.

From adults to seedlings: Loss of genetic diversity in small remnant populations

We found a significant reduction in allelic richness (*Ar*) in the seedlings compared to the adults, but this reduction was relatively small. A similar result has been reported for the dipterocarp Vateriopsis seychellarum: seedlings of this species in remnant populations had significantly lower allelic richness than the adults (Finger et al. 2012). A contrasting result was found by Ismail et al. (2014) for the dipterocarp *Vateria indica*, in which allelic richness did not differ between the adults and the seedlings (Ismail et al. 2014).

Surprisingly, we did not find evidence for the expected reduction in observed and expected heterozygosity as a result of fragmentation (i.e., comparing adults and seedlings). Such a reduction in observed heterozygosity was found for fragmented populations of the dipterocarp *Vateriopsis seychellarum* (Finger et al. 2012). The variability in responses to fragmentation across tree species may be caused by interspecific differences in reproductive biology and dispersal syndromes of pollen and seeds (e.g. Kramer et al. 2008). In some species, the loss of genetic diversity due to fragmentation may be mitigated by elevated rates of gene flow across fragments through pollen (Fuchs and Hamrick 2011, Ismail et al. 2014, Wang et al. 2014). In our study species, we found that remnant populations indeed still received high amounts of pollen and seeds (as shown by parentage analysis), which may lead to high levels of heterozygosity in seedlings. Another explanation for the high heterozygosity in seedlings is that the time since fragmentation has been too short for genetic drift and inbreeding to erode heterozygosity in the seedlings. Our study species is a large-statured and long-lived tree, which requires at least 50 years to become reproductive, which is longer than the period since fragmentation occurred. Finally, selection can also assist in maintaining the high heterozygosity of seedlings. A survival advantage of heterozygotes (Oostermeijer et al. 2003, Stoeckel et al. 2006) may be more pronounced in stressful environmental conditions which may be present in fragments (Lesica and Allendorf 1992), resulting in a higher survival probability of heterozygous seedlings in fragments (Picó 2004). The low number of seedlings present in remnant population HSC3 (Table 1) combined with the high level of heterozygosity (Table 2) in that population is in agreement with this suggested survival advantage of heterozygous individuals. Monitoring of the studied populations revealed that indeed annual seedling survival was lower in small fragments (< 20 ha) compared to larger ones (70.2% vs 82.9%; Chapter 3). Yet, the high heterozygosity in HSC3 could also be partially explained by the combination of a relatively high diversity among the surviving adult trees (Table 2) and a relatively high incidence of within-population mating (Figure 3).

Genetic structure and mating systems

Despite increasing levels of genetic differentiation, we found evidence for high pollen influx in all studied populations (Figure 3). Similar results were found for the dipterocarp *Vateriopsis seychellarum* in fragmented populations (Finger et al. 2012). Following habitat fragmentation, one would expect a reduced pollen flow between remnant populations due to isolation (Lienert 2004). These results could be explained by the abundance of pollinators in tree plantations and agricultural fields surrounding the fragments. Although we did not study the pollinator community, we did observe that small wild bees (*Apis dorsata*), which are known to pollinate dipterocarp species (Momose et al. 1998, Harata et al. 2012, Ismail et al. 2014), were abundant in tree plantations surrounding the fragments. Also, hybrid acacia and rubber trees are known to attract a diverse array of insect pollinators (Sornsathapornkul and Owens 1998, Siregar 2014), some of which may have pollinated our study species. Following population genetic theory, high levels of genetic exchange do not result in genetic differentiation. Nevertheless, we found among most population pairs that the level of genetic differentiation increased from adults to seedlings (higher F_{ST} values, Table 4, and stronger genetic clustering, Figure 2). This seems contrasting at first sight, but can be explained by that for many seedlings that originated from pollen influx (Figure 3), the father was not found in one of the other study populations, but must have come from one of the surrounding non-sampled populations. Thus exchange seemed to take place mostly between the study populations and surrounding (unstudied) populations, instead of among the study populations.

Implications for conservation and restoration

We observed loss of genetic variation within and increasing differentiation among remnant populations of our endangered study species, despite high levels of genetic exchange. The speed at which genetic variation is lost thus exceeded the considerable rate at which new genotypes arrived to the remnant populations.

Our findings have consequences for the conservation of this threatened tree species in forest fragments. First, the strong spatial genetic structure, the reduced genetic variation within remnant populations and the increased genetic differentiation between populations implies that a relatively large number of remnant populations is needed to represent the full genetic diversity of our study species. Thus, conserving the full genetic diversity of this threatened species in forest fragments requires the protection of a large number of fragments. This finding also suggests that the protection of each additional forest fragment (that contains a remnant population) contributes to conserving the genetic diversity and survival of this threatened species. Second, our results show that at this moment, remnant populations are not able to maintain their genetic variation, likely due to enhanced mortality and or reduced reproductive success in small forest fragments (Chapter 3). Mitigation of such effects by enlarging fragment sizes to reduce edge effects (Chapter 3) thus seems necessary in order to conserve variation both at the local and landscape scale. Third, the high gene flow that we observe among remnant populations both assists in maintaining own genetic diversity but may also compensate genetic erosion in other fragments. In this way, remnant populations appear to form a network in which gene flow takes place. Such networks of small forest fragments may connect larger tracks of (protected) forests that contain larger (and more viable) populations and in this way contribute to the conservation of this threatened tree species.

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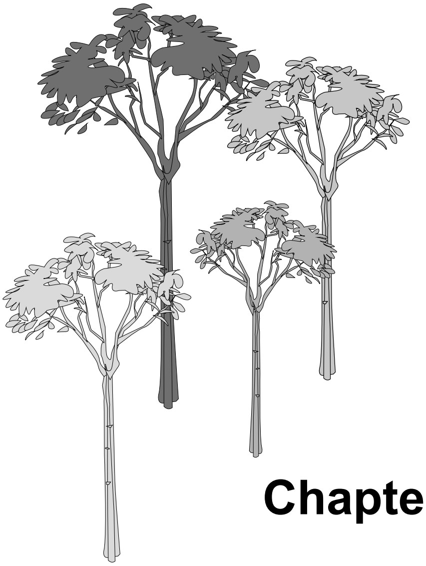
Appendix 1. 29 primers was tested and nine selected primers used for SSR analysis

Order	Primer	Sequence (5'- 3')		Primer chosen	No. of alleles	Annealing temperature (°C)	No. of different alleles
		Forward	Reverse				
1	Sle 074	ATCACCAAGTACCTATCATCA	GCAATGGCACACAGTCTATC				
2	Sle 079	GTTGTCTGTTCTTACCAGGAAG	GCATAAGTATCGTCGCCA				
3	Sle 105	CTGTGTCAAAATCAGTTAGGACTTACGAG	GAGTCGATTGCTTGTCTTCACCC				
4	Sle 111	GGAAACTACTGGAGCAGAGAC	GGTGGGTTATGGAGAATGAG				
5	Sle 118	AAAGCGTACAAATTCATCA	CTATTGGTTGGGTCAGAAGG	Chosen	9	52	5
6	Sle 216	AGAGAACCCAGACCCCAGAC	TTTGAGAAGAACCCAGAACC				
7	Sle 267	CTTAATTGTGATGCCTGTTG	TCTTGTATTTATGCTTCTCC	Chosen	9	52	3
8	Sle 271	CAGGAACCGACTATCTGCC	TCATTCAAATCAAACTAATTTC				
9	Sle 280	GCAACTAAAATGGACCAGA	GAGTAAGGTGGCAGATATAGAG	Chosen	10	52	5
10	Sle 290	TTTTGCTCTTTCTTCTGTTGTCA	ATTTGGCTGTTTGGTCGGAT		3	52	1
11	Sle 291	GTCCCAGATGTAGTTCTCTGTTTGC	TTGCATACTCTCGATTCCATGTTG				
12	Sle294	AACTAAATGTAAAATCTTCC	CTTTTGAGATATAATGTTGA				
13	Sle 303	TCCTTACATGGACTGAGATTCACC	GTTTCAATTATGAGGGGAACTGATTTAC	Chosen	11	52	8
14	Sle 384	CCAAGACAACTCAATCCTCA	AGATGAAGGTGTTGCTGTG				
15	Sle 392	ATGTCCTTGAAGATGTAAAGTGGGTG	AATAATGGAAGTGAGACGAGGCTG	Chosen	10	52	4
16	Sle 465	CAAAGTTGAACCTTGAATCT	ATTTAGAAGCCGTCCAGC				
17	Sle 475	AGCGAAACCCTTGTGGAGA	GAGACTACGGTGGCGACGA				
18	Sle 562	TGATTTGGGTGGTTGTAG	TATTACATTTTTCAAGTCAAGTC		2	52	1
19	Sle 566	TGAGTAACAAGTAATGAGGG	GCAGAGATTGAAACAGAAG				
20	Sle 605	GTGCATTTATTGCCTGAGTAAGGTGG	CAACTAAAATGGACCAGACCGGATG	Chosen	11	52	6
21	Shc01	GCTATTGGCAAGGATGTTCA	CTTATGAGATCAATTTGACAG	Chosen	10	52	6
22	Shc02	CACGCTTTCCCAATCTG	TCAAGAGCAGAATCCAG	Chosen	8	52	6

cont. Appendix 1. 29 primers was tested and nine selected primers used for SSR analysis

Order	Primer	Sequence (5'- 3')		Primer chosen	No. of alleles	Annealing temperature (°C)	No. of different alleles
		Forward	Reverse				
23	Shc03	TTGAAGGGAAGGCTATG	CTTCTCAACTACCTTACC	Chosen	10	52	6
24	Shc04	ATGAGTAACAAGTGATGAG	TATTGACGTGGAATCTG				
25	Shc07	ATGTCCATGTTTGAGTG	CATGGACATAAGTGGAG		3	54	1
26	Shc08	GAGTCTGTGGTTGATATG	TTCTATGCAAGGGCTTTTAG				
27	Shc09	TTTCTGTATCCGTGTGTTG	GCGATTAAGCGGACCTCAG				
28	Shc11	ATCTGTTCTTCTACAAGCC	TTAGAACTTGAGTCAGATAC				
29	Shc17	CTAGAATCCGCCATTTCC	CACAAATACGTCTCCATATC				
	Overall mean				4.1		2.9



Chapter 5

General discussion

In this thesis, we studied three important effects of forest fragmentation on the remaining tree populations in central Vietnam. First, we studied forest structure, tree species diversity, and tree composition (trees with dbh ≥ 10 cm) in 10 permanent 1- ha plots in seven forest fragments and continuous forest in Bach Ma National Park. The studied forest fragments ranged in sizes from 1-150 ha. Fragments are imbedded in a highly fragmented landscape with a matrix of tree plantations (hybrid acacia and rubber) (Chapter 2). Second, we studied the dynamics of three large-stature tree species in the same permanent research plots by using three-year monitoring data to construct Integral Projection Models (IPM) (Chapter 3). Finally, we studied the genetic effects of forest fragmentation on critically endangered populations of *Parashorea stellata* (Dipterocarpaceae) growing in four small remnant forest fragments (Chapter 4).

In this chapter, we summarize and discuss the main findings from the three core chapters. First, we will evaluate the negative effects of forest fragmentation on forest structure, tree species diversity, tree composition, and reduced tree population viability and degraded genetic diversity. Next, we will discuss the implications of these findings for the conservation value of tropical forest fragments in general and Vietnam in particular. Finally, we will provide recommendations for research and methods related to forest fragmentation in Vietnam.

Evaluating the Effects of Forest Fragmentation on Tree Populations

Forest fragmentation may negatively affect tree populations in various ways and through various processes (Figure 1). The processes were already discussed in the introductory chapter of this thesis (Chapter 1). In general, forest fragmentation results in a change of forest structure and tree species composition, loss of tree species diversity, and reduced viability and genetic diversity of tree populations as described in Figure 1.

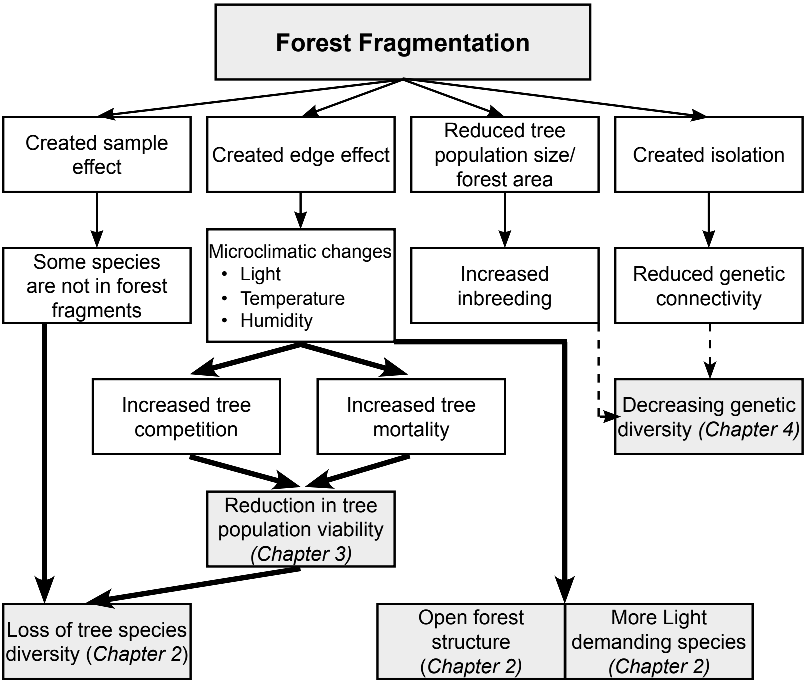


Figure 1. A conceptual representation of the theoretical ways in which four factors (sample effect, edge effects, reduced population sizes, and isolation) may affect remnant tree populations. The bold and dotted line arrows indicate strong and weak relations found in this study respectively. The thin line arrows indicate causal relations not studied in this thesis.

Change in forest structure

Forest fragmentation may lead to a change in forest structure if rates of recruitment, growth and mortality of tree species change after fragmentation (Laurance et al. 2002). In Chapter 2 of this thesis, we evaluated the effects of forest fragment size on forest structure. In line with our expectation, the study showed that a reduction in forest fragment size led to a reduction in tree density, in density of large trees (dbh > 20cm), in total basal area (Chapter 2, Figure 1a, 1b, and Figure 2a, 2b), and in recruitment (Chapter 3). These findings suggest that there was a change in the size structure of the population towards more small individuals in the small fragments. Such a shift in population structure was found for a late-successional tropical tree species (*Poulsenia armata*) in Mexican forest fragments (Zambrano and Salguero-Gómez 2014). Several studies in tropical forest fragments showed that tree density (Tripathi et al. 2010), the number of large trees (Arroyo-Rodríguez and Mandujano 2006, Tripathi and Reynald 2010), and the basal area (Tripathi et al. 2010) reduced with decreasing forest fragment size. The increased mortality and the more open forest structure is likely caused by edge effects (Laurance et al. 1998, Laurance et al. 2002, Laurance et al. 2011, Magnago et al. 2014). Tree mortality rates increase sharply close to forest edges and in small forest fragments (Laurance et al. 1998, Laurance et al. 2000, Laurance et al. 2014a). In addition, stochastic events such as droughts (Laurance et al. 2001) and wind turbulence (Laurance et al. 2000) may elevate tree mortality in forest edges or small fragments, further reducing tree density and basal areas in small forest fragments (Echeverría et al. 2007, Tripathi et al. 2010). In summary, fragmentation causes shifts in forest structure, which may reduce tree recruitment and increase tree mortality.

Loss of tree species diversity

Forest fragmentation may lead to a reduction in tree species diversity through sample and edge effects (Figure 1). In Chapter 2 of this thesis, we evaluated the effects that forest fragmentation has on tree species diversity. We demonstrated that tree species diversity was significantly decreased in small forest fragments compared to those in large forest fragments and the continuous forest (Chapter 2, Figure 3a, 3b, and 3c). In forest fragments of >100 ha, tree species diversity was similar to that of the continuous forest. In a similar way several studies (Hill and Curran 2001, Hill and Curran 2003, Zhu et al. 2004, Tripathi et al. 2010, Magnago et al. 2014) found that the size of forest fragments affect tree species diversity, with higher diversity as fragment size increases (Zhu et al. 2004, Tripathi and Reynald 2010, Magnago et al. 2014). In general, larger forest fragments are expected to contain more tree species than smaller fragments (Turner 1996, Hill and Curran 2001).

As we discussed in the General introduction (Chapter 1), one possible explanation for a reduction in tree species diversity due to fragmentation is the sample effect. Some species may be absent in the small forest fragments at the time of forest fragmentation (Laurance et al. 2011). Another reason may be the high rate of mortality that occurs in small fragments (Chapter 3) due to edge effects (Laurance et al. 1998) resulting in a reduction in tree species diversity in small fragments. It is possible that the present tree diversity in forest fragments is an overestimate of the diversity that can be conserved in these fragments. High tree mortality and lack of recruitment can lead to population declines of tree species and lead to their local extinction. The phenomenon that current species richness is higher than future species richness is called “extinction debt” (Kuussaari et al. 2009). There is ample debate about the magnitude of extinction debt in forest fragments and its relation to fragment size. Some hold the opinion that the extinction debt does not depend on the size of the fragment (Wearn et al. 2012, 2013), whereas others hold the opposite opinion (Halley et al. 2013). So far, some studies have found that tree species in fragments continue to be present in the forest for some time (Vellend et al. 2006, Kuussaari et al. 2009). This was also found in 25-year old Malaysian forest fragments (Thomas 2004), 30 -year old fragments in Vietnam (this study), in 32- year old Amazonian forest fragments (Laurance et al. 2011), and in forest fragments in Europe that are older than a century (Vellend et al. 2006). These examples demonstrate that substantial tree diversity can be retained in (small) forest fragments.

Change of tree species composition

Forest fragmentation may lead to changes in tree species composition (Figure 1). In Chapter 2 of this thesis, we evaluated the effects of forest fragment size on tree species composition. We showed that the tree species composition in small forest fragments strongly changed with a higher proportion of fast growing tree species at the expense of slow growing tree species (Chapter 2, Figure 4). Similarly several studies (Hill and Curran 2001, Hill and Curran 2003, Zhu et al. 2004, Tripathi et al. 2010, Magnago et al. 2014) reported that the tree species composition changed as a function of forest fragment size, with a higher proportion of pioneer species than shade-tolerant species in small fragments compared to large fragments (Popma et al. 1988, Zhu et al. 2004, Echeverría et al. 2007). A possible reason for changing tree species composition is the high level of competition between seedlings of slow growing and fast growing species.

In small forest fragments, forest canopy gaps that are created by dead trees may create favourable conditions for seedlings of fast growing species (Popma et al. 1988). Seedlings of slow growing species are outcompeted by those of fast growing species leading to a reduction in the proportion of slow growing tree species. Consequently, in small fragments, species composition will be dominated by fast growing tree species (Chapter 2).

Reduced viability of tree populations

Forest fragmentation may lead to a reduction in the viability of tree populations (Figure 1). In Chapter 3 of this thesis, we studied the effects of the size of forest fragments (1-150 ha) on the dynamics of three large-stature tree populations. We collected three-year demographic data (dbh growth, mortality, and recruitment), and used these data to construct Integral Projection Models to quantify the tree population growth rate. We showed that the studied populations were naturally regenerating, even in very small forest fragments (1 - 20 ha). Nevertheless, the rate of seedling recruitment was lower in small compared to large fragments (> 20 ha) and the continuous forest. The tree population growth rate was slightly decreased in the small fragments (< 20 ha, $\lambda < 1$, Chapter 3, Table 1) and stable in large fragments (> 20 ha, $\lambda > 1$) and the continuous forest ($\lambda > 1$, Chapter 3, Table 1). These results are consistent with those obtained in a study on the growth rate of tree population in Mexican forest fragments that showed that the tree population growth rate (λ) did not decrease ($\lambda > 1$) in forest fragments that had the size of our 'large fragment' category (> 20 ha) (Zambrano and Salguero-Gómez 2014). In this study, we indicated that the demographic mechanisms behind the decline of tree populations in small forest fragments were a low recruitment rate and a high tree mortality rate (Chapter 3). Our results are in agreement with some previous studies that showed a reduction in seedling recruitment (Benitez-Malvido 1998, Benitez-Malvido and Martínez-Ramos 2003, Núñez-Ávila et al. 2013), and a high rate of tree mortality (Laurance et al. 1998, Laurance et al. 2011), that especially reduced tree survival of potential reproductive trees (Alvarez-Buylla and Garcia-Barrios 1991, Alvarez-Buylla et al. 1996) in small fragments.

A large share of the remaining tropical forests in the world are highly fragmented (Wade et al. 2003, Pimm and Brooks 2013), implying that tree populations inhabiting these remnant forest fragments will be affected by forest fragmentation. Therefore, it is crucial to understand the future prospects of tree populations in fragments and the demographic mechanisms leading to changes in tree populations in forest fragments. Important first insights in this viability can be obtained using studies on demography of fragmented tree populations. However, from our knowledge, there is only one such study conducted in Mexican forest fragments (Zambrano and Salguero-Gómez 2014). Therefore, more demographic studies are needed to get a better insight into the demographic mechanisms that lead to the reduction of tree population viability in forest fragments. In addition, most studies in recently fragmented tree populations could not determine how long tree populations will persist in small forest fragments. Naturally, the negative demographic consequences of forest fragmentation on the dynamics of fragmented tree populations may take years to become apparent, especially for long-lived tree species as our studied tree species. Since our results are based on an assessment of tree populations in 30-year old forest fragments, we may not completely assess the effects of the size of forest fragment on the viability of these tree populations in the long run. Therefore, these forest fragments should be continuously monitored to fully understand the change in tree population viability over time.

Reduced genetic diversity

Forest fragmentation may result in a reduction of genetic diversity in tree populations through reduced population size and increased isolation (Figure 1). The reduction of population size will increase inbreeding, and the increased spatial isolation will limit genetic exchange among fragments (Young et al.2000). Theoretically, these effects may lead to a reduction in genetic diversity of fragmented tree populations (Young et al.1996, Young et al.2000), but the empirical studies have yielded contradictory results (Kramer et al. 2008, Bacles and Jump 2011). This contradiction has been called the 'paradox of forest fragmentation genetics' (Kramer et al. 2008). That is to say, some studies have found the negative effects of forest fragmentation on the genetic diversity of tree populations (Ortego et al. 2010, Finger et al. 2012), whereas others did not find such negative effects (White et al. 2002, Ismail et al. 2014, Wang et al. 2014) (Table 1). In Chapter 4, we investigated the genetic effects of forest fragmentation on a threatened tree species (*Parashorea stellata*) by comparing the genetic diversity of adult trees with that of seedlings. We found that forest fragmentation has not affected the genetic diversity of the seedling generation compared to the adult generation in terms of observed heterogygosity and expected heterogygosity, but the allelic richness was significantly reduced in the seedlings compared to the adults. In addition, forest fragmentation has probably affected the genetic diversity of the adult trees in forest fragments negatively when compared to that of adult trees of other dipterocarp species in continuous forests (Chapter 4, Table 2). Our results may also be considered an example of the paradox of forest fragmentation genetics.

Table 1. The change of genetic diversity parameters in the seedlings with respect to the adults in fragmented populations of three dipterocarp species. Number of alleles (*Na*), Allelic richness (*Ar*), Observed heterogygosity (*Ho*), Expected heterogygosity (*He*). 0 = no significant reduction, - = significant reduction.

Dipterocarp species	*Na*	*Ar*	*Ho*	*He*
Vateriopsis seychellarum (Finger et al. 2012)	0	-	-	0
Vateria indica (Ismail et al. 2014)	0	0	-	0
Parashorea stellata (this study)	0	-	0	0

Are the results obtained in this study comparable to those of other studies? Table 1 shows the effects of fragmentation of three Dipterocarp species presented in different studies. One possible reason for the differences among species is that the fragment boundaries do not represent boundaries for genetic exchange among fragments (Kramer et al. 2008). Trees in multiple isolated fragments may still be able to exchange genetic information via pollen (Dick 2001, White et al. 2002, Bacles and Ennos 2008, Dick et al. 2008) or seeds (Bacles et al. 2006). Only in this way, the remnant populations may mitigate genetic erosion, but whether such genetic exchange is possible among fragments depends strongly on the distance and vegetation surrounding fragments (Wang et al. 2008) and the life history trait of tree species (Young et al. 1996, Aparicio et al. 2012)B. Our analysis of reproductive patterns disclosed that the majority of seedlings in all studied populations have resulted from fertilization by pollen originating from outside the population. It means that the pollen dispersal is the main mode of genetic exchange among fragments (Chapter 4, Figure 3). Pollen dispersal contributed significantly to maintain high levels of observed and expected heterogygosity in the seedlings.

For many tropical tree species, including a large number of threatened species, forest fragments offer crucial habitat today and in the future. To conserve tropical tree diversity, it is therefore important to understand the genetic consequences of forest fragmentation for tree populations. These effects can be obtained by studying the genetic diversity of tree populations before and after fragmentation. More studies are needed to advance our understanding of the mechanism behind genetic degradation of tropical tree populations. Such studies will provide scientific information to improve management and restoration of tree populations and forest fragments.

Implications for Forest Biodiversity Conservation

The conservation values of tropical forest fragments

There seems to be a general reluctance among conservation organizations to actively support the conservation of (small) tropical forest fragments. Most conservation organizations focus on large tracks of forest and large protected areas (IUCN 1993, UN 2003, UNEP 2003). This reluctance may be influenced - among others - by three scientific debates: (i) the discussion on whether to conserve one single large or several small areas (SLOSS), (ii) the debate on land - sharing versus land -sparing, and (iii) the notion that extinction debt may be substantial in small fragments.

First, in the 1970s and 1980s, there was the SLOSS debate about whether a single large reserve area conserves more species than several small reserve areas do. Until now, this debate has never been fully resolved (Tjørve 2010), but the dominant idea among conservation organizations and governments is that conservation areas should be large in order to be effective. As a result, the conservation value of small forest fragments embedded in agricultural landscape is often not considered in national conservation policies, as is the case in Vietnam (MARD 2009). Over the last decades, several studies have shown that (small) forest fragments can contribute to the conservation of tropical biodiversity. For instance, several studies showed that small forest fragments that are located in highly fragmented tropical landscapes can maintain high levels of the original biodiversity (Arroyo-Rodríguez et al. 2009, Arroyo-Rodríguez et al. 2012, Hernández-Ruedas et al. 2014). Fragments accommodate about 14 - 32 tree species (fragments < 25 ha, dbh > 10 cm, this study), 228 tree species (fragments < 100 ha, dbh > 2.5 cm) (Hernández-Ruedas et al. 2014), and 221 plant species (fragments < 5 ha) (Arroyo-Rodríguez et al. 2009). In addition, in this study (Chapter 3), we found that there was no clear sign of extinction debt of three tree species in small forest fragments (> 20 ha), suggesting that tree populations may persist for a substantial amount of time after fragmentation. These results also demonstrate that relatively small forest fragments (> 20 ha) can be valuable for the maintenance of tree populations (Arroyo-Rodríguez et al. 2009, Hernández-Ruedas et al. 2014).

The second debate is on the land-sharing versus the land-sparing strategy for agricultural production and biodiversity conservation (Fischer et al. 2014, Laurance et al. 2014b). The land-sharing strategy integrates two objectives of biodiversity conservation and food production on the same land. The land-sparing strategy argues that some areas are used for high-yield farming while other areas are set aside for biodiversity conservation (Phalan et al. 2011). Until now, this debate is still on-going. One study argues that land-sharing and land-sparing are equally important in tropical regions because biodiversity conservation and rural livelihood should be balanced (Scariot 2013). Whether land-sharing or land-sparing is the best option for biodiversity conservation depends on scale (Fischer et al. 2014). For instance, at the scale of a landscape our study site can be considered an example of the land-sharing strategy in which our studied fragments conserve diversity but are located in the same area with agricultural lands. In contrast, if we consider forests fragments as a particular form of land use our study sites can be seen as an example of the land-sparing strategy where the studied fragments with clear boundaries are used for intensive biodiversity conservation. Independent of that view, small forest fragments studied here contribute to conserving forest biodiversity at our study site.

Finally, there is the extinction debt debate (Wearn et al. 2012, Halley et al. 2013, Wearn et al. 2013). In general, tree species are expected to become extinct from small isolated fragments (Kuussaari et al. 2009). In contrast, one study argues that the extinction debt of tree species does not seem to depend on the area of forest fragments (Wearn et al. 2012). This debate presents the challenge for biodiversity conservation in fragmented landscape. The biodiversity conservation policy in fragmented landscapes should focus on improving habitat quality in forest fragments in order to increase viability of species (Kuussaari et al. 2009). In short, all three debates may have resulted in the reluctance of conservation organizations and governments to actively support the conservation of small tropical forest fragments.

Forest fragment conservation in Vietnam

Although forest fragments likely provide a significant contribution to conserving forest biodiversity in Vietnam, they have not received recognition so far in conservation policies. This is probably due to the strongly different views among biologists and the government. From a conservation point of view, the challenge is to develop a sustainable land use management system that satisfies both the needs of local livelihoods and biodiversity conservation. Implementing such a land use management system is likely to be difficult for developing countries such as Vietnam, a country where most local inhabitants still strongly depend on agricultural production for their livelihoods. In order to improve the livelihood of local inhabitants, the government legally allows the conversion of forest fragments into rubber plantations (MARD 2009). This policy does not pay attention to the values of forest fragments for conserving forest biodiversity and has created a debate in Vietnam. Conservationists have raised their voice to protect natural forests from expanding rubber plantation areas (Quang 2011), but so far, this has not had a decisive influence on government policies. This study, for the first time, assessed the values of forest fragments for conserving forest biodiversity in Vietnam. The findings showed that forest fragments not only retained 87% (Table 3, Chapter 2) of total tree species recorded in the research plots, including threatened tree species (Table 3, Chapter 2), but also played a role as stepping stones (Chapter 4) for bridging genetic exchange among the forest fragments and between the forest fragments and large forest reserves. This study thus shows the high values of forest fragments for conserving forest biodiversity. We therefore call for the development of forest and land use policies in Vietnam that recognize the biodiversity and conservation values of forest fragments.

Recommendations for Fragmentation Research in Vietnam

This study has been conducted on just one location in Vietnam. This obviously limits possibilities to generalize its results to other regions in Vietnam. We therefore recommend that similar studies are conducted in other regions and also that studies on related topics are conducted in Vietnam. Further research on forest fragmentation in Vietnam is recommended as follows:

1. A detailed inventory of the magnitude and extent of forest fragmentation should be made at national and regional levels. This should include measurements of basic characteristics of forest fragments such as the number of fragments, the type of forest fragments, the size of fragments, the ownership of fragments, the surrounding land use, and the diversity of animals and plants in forest fragments. Such an inventory will provide an important overview and baseline of information on forest fragmentation in Vietnam that is directly relevant to conservation and land-use policies.
2. An evaluation of the conservation values of forest fragments, again at regional and national level. It is important that knowledge is obtained about the presence and abundance of threatened animal and plant species in Vietnamese forest fragments. Such an evaluation will provide important information on the degree to which the conservation of these species depends on forest fragments. This may support the development of conservation policies for threatened species in Vietnam.
3. Evaluation of the dependence of local livelihoods on products from forest fragments. Local people are known to gather non-timber forest

products (including medicinal plants) and hunt in forest fragments. It is important to quantify the contribution of forest fragments to livelihoods in rural areas in Vietnam. A first inventory of fragment use is necessary to later set up guidelines for sustainable harvesting and management of forest resources from fragments.

4. Finally, the viability of plant and animal populations in forest fragments should be studied. Such research will provide ecological viability of plant and animal populations. There are two relatively new methods that are only sporadically used, which can help to understand the consequences of fragmentation on viability of remnant populations. These are studies on population dynamics and on population genetics, both of which have been applied in this thesis. Both types of studies help to determine the long-term viability of species in forest fragments. We recommend using these methods to study the effects of forest fragmentation on viability of plant and animal populations. The establishment of molecular labs in Vietnam and the development of skills of Vietnamese researchers to conduct this type of research allow such studies to be conducted.

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Summary

Millions of square kilometers of the Earth's surface is covered by forest fragments, and a quarter of remaining tropical forest has been fragmented. In Southeast Asia, about 650,000 ha of natural forests are fragmented per year. Fragmentation of old growth forests is considered to be the greatest threat to tropical forest biodiversity.

Forest fragmentation has many negative effects on tree species. It causes edge effects, reduces population sizes and increases isolation between populations. This has potentially large implications for tree species and forest dynamics. In this thesis, the effects of forest fragmentation on tree diversity, population dynamics, and genetic diversity in Vietnam are analyzed. The objectives of the study were (1) to evaluate the effects of forest fragment size on forest structure, tree diversity, and tree composition; (2) to evaluate the effects of fragment size on the dynamics of tree species; and (3) to assess the effects of forest fragmentation on genetic diversity of tree species.

Forest fragmentation affects tree populations in various ways. First, sample effect may lead to the local loss of tree species because forest fragments are samples of the original forests and some of the tree species may not have been present in the patches of forests that remain. Second, edge effects may lead to changes in the forest structure, tree species richness, tree composition, and seedling recruitments because microclimatic conditions in fragment edges are very different from those in the core of the fragment. These change in environmental conditions may increase seedling and tree mortality in forest fragments, especially in small fragments. Third, reduced population sizes in fragments may result in elevated extinction risk of tree species due to stochastic events, but extinctions may take quite some time to occur because of the long lifespan of trees. Finally, isolation of tree populations in forest fragments may limit gene flow between populations, possibly leading to increased inbreeding and reduced fitness of offspring. Over time, these effects can reduce genetic diversity and viability of remnant populations.

In this PhD study, we studied three important effects of forest fragmentation in central Vietnam. First, we studied effects of fragment size on forest structure, tree species diversity, and tree composition in seven forest fragments and continuous forest. Second, we studied the dynamics of three large-stature tree species in relation to forest fragment size. Finally, we studied the effects of forest fragmentation on genetic diversity of a critically endangered tree species in four small forest fragments.

Effects of forest fragment size on forest structure and tree diversity

We investigated forest structure and tree diversity in seven forest fragments (1-150 ha in size) and continuous forest (Bach Ma National Park). The studied forest fragments were located in a highly fragmented landscape with a matrix of tree plantations (hybrid acacia and rubber). A sample plot of 1 ha was established in the centre of each fragment. In each sample plot, we measured diameter at breast height (dbh) above buttresses for all trees ≥10 cm dbh. As a reference, we established three similar sample plots in a continuous forest. We recorded a total of 3,475 individuals pertaining to 63 species, including 10 IUCN Red-listed species. Tree density, basal area and the density of large tree were substantially lower in fragments <100 ha compared to larger fragments or continuous forest. Tree species richness positively increased with fragment size and tree species composition was shifted towards a higher proportion of fast-growing species in small fragments. Our results suggested that small forest fragments (1-10 ha) still retain a significant amount of tree species richness, and that large forest fragments (≥ 100 ha) are similar to continuous forest in terms of forest structure, species richness and species composition. We conclude that forest fragments, including very small fragments, may play an important role in conserving biodiversity in intensive tropical agricultural landscapes.

Effects of forest fragment size on tree population dynamics

We investigated the demographic effects of forest fragmentation for three large-stature tree species: *Canarium bengalensis* (Burseraceae), *Palaquium annamense* (Sapotaceae), and *Parashorea stellata* (Dipterocarpaceae). We conducted a 3-year monitoring study to quantify recruitment, growth and survival of the study species in 10 permanent sample plots of 1 ha each in small fragments (< 20 ha), large fragments (20-150 ha) and in a continuous forest (3 plots) in Central Vietnam. We found that growth in diameter at breast height (dbh) was not significantly different among fragments and continuous forest, but mortality rate was higher in small fragments than in large fragments and continuous forest. Using integral projection models (IPMs), we then compared tree population dynamics between small fragments, large fragments and continuous forest. For all three species, the asymptotic population growth rate (λ) was slightly below 1 (0.98 - 0.99) in small fragments and not significantly different from 1 in large fragments and continuous forest. These results indicate that populations are projected to slightly decline in small fragments, while remaining stable in large fragments and continuous forest. Life Table Response Experiments (LTRE) analysis showed that differences in λ between forest types were mainly attributed to differences in survival, followed by seedling dynamics and fecundity. Our results suggest that small fragment size limits the viability of our study species, but that these species have rather good prospects to survive in fragments of >20 ha. We call for more attention to the contribution of forest fragments to conserving tropical tree species.

Effects of fragmentation on genetic diversity of a threatened tree species

We used nine microsatellite markers to evaluate the effects of recent forest fragmentation on genetic diversity in *Parashorea stellata*, a critically endangered tree species. Specifically, we compared the genetic diversity of large, reproductive trees ('adults') of this species which established before fragmentation, with seedlings that germinated after fragmentation. Overall, we observed strong spatial genetic structure and a relatively low genetic diversity in adults, suggesting a genetic bottleneck due to the decline of the original population. Allele richness was lower in seedlings compared to adults, showing that populations continued to lose genetic variation after the fragmentation event. In contrast, observed and expected heterozygosity were generally not reduced in seedlings. This may indicate that a new genetic equilibrium has not been reached yet in remnant populations, but may also be caused by the observed high levels of pollen and seed influx in fragments. In spite of this genetic exchange between remnant populations, pairwise genetic differentiation generally increased after fragmentation. Thus, even though remnant populations appear to be well connected in this agricultural landscape, fragmentation caused genetic erosion and increased genetic differentiation. Our results suggest that multiple remnant populations should be retained in order to conserve genetic variation of tree species in intensive agricultural tropical landscapes.

Recommendations for forest fragmentation research in Vietnam

This is the first study on effects of forest fragmentation in Vietnam. As our study was conducted in just one location and included effects on tree species only, results cannot be extrapolated to other areas, species or species groups in Vietnam. We therefore recommend that similar studies are conducted in other regions and for other species (groups). Specifically, we recommend the following studies on forest fragmentation in Vietnam.

1. A detailed inventory of the magnitude and extent of forest fragmentation should be made at national and regional levels. This should include measurements of basic characteristics of forest fragments such as the number of fragments, the type of forest fragments, the size of fragments, the ownership of fragments, the surrounding land use, and the diversity of animals and plants in forest fragments. Such an inventory will provide an important overview and baseline of information on forest fragmentation in Vietnam that is directly relevant to conservation and land-use policies.

2. An evaluation of the conservation values of forest fragments, again at regional and national level. It is important that knowledge is obtained about the presence and abundance of threatened animal and plant species in Vietnamese forest fragments. Such an evaluation will provide important information on the degree to which the conservation of these species depends on forest fragments. This may support the development of conservation policies for threatened species in Vietnam.

3. Evaluation of the dependence of local livelihoods on products from forest fragments. Local people are known to gather non-timber forest products (including medicinal plants) and hunt in forest fragments. It is important to quantify the contribution of forest fragments to livelihoods in rural areas in Vietnam. A first inventory of fragment use is necessary to later set up guidelines for sustainable harvesting and management of forest resources from fragments.

4. Finally, the viability of plant and animal populations in forest fragments should be studied. Two relatively new and sporadically used methods can help to understand the consequences of fragmentation on viability of remnant populations: studies on population dynamics and on population genetics. Both types of studies have been applied in this PhD research. We recommend using these methods to study the effects of forest fragmentation on viability of other plant and animal populations, in several regions in Vietnam. The establishment of molecular labs in Vietnam and the development of skills of Vietnamese researchers to conduct this type of research allow such studies to be conducted.

Samenvatting

Vele miljoenen vierkante kilometers van het wereldoppervlak zijn bedekt met bosfragmenten -- kleine stukken bos die vaak zijn ontstaan door ontbossing. In de tropen is een kwart van het bosareaal gefragmenteerd. En in Zuidoost Azië raakt jaarlijks 650 duizend hectare bos gefragmenteerd. De versnippering van oude bossen wordt beschouwd als een van de grootste bedreigingen van de biodiversiteit in de tropen.

Bosfragmentatie heeft veel negatieve effecten voor boomsoorten. Het veroorzaakt veranderingen in microklimaat en bosstructuur aan de randen van bosfragmenten, verkleint boompopulaties en vergroot de isolatie tussen boompopulaties. De mogelijke gevolgen voor boomsoorten en bosdynamiek zijn groot. In dit proefschrift onderzoeken wij de effecten van bosfragmentatie in Vietnam op soortendiversiteit, populatiedynamiek en genetische diversiteit van boomsoorten. De doelen van de studie waren: (1) het evalueren van de effecten van de grootte van bosfragmenten op de bosstructuur en op de soortendiversiteit en genetische diversiteit van boomsoorten; (2) het bepalen van de effecten van fragmentgrootte op de populatiedynamiek van boomsoorten; en (3) het bepalen van de effecten van bosfragmentatie op de genetische diversiteit van boomsoorten.

Bosfragmentatie beïnvloedt boomsoorten op verschillende manieren. Ten eerste zorgt het zogenaamde steekproefeffect ervoor dat sommige boomsoorten niet vertegenwoordigd zijn in bosfragmenten omdat ze niet aanwezig waren in die delen van het oorspronkelijke bos die zijn overgebleven. Ten tweede kunnen de sterke veranderingen in microklimaat aan de randen van bosfragmenten zorgen voor een gewijzigde bosstructuur, een lagere soortendiversiteit en een vermindering van de natuurlijke verjonging van boompopulaties. Deze effecten treden met name op in kleine bosfragmenten. Ten derde hebben de kleinere populaties in bosfragmenten een hogere kans om lokaal te verdwijnen als gevolg van toevalsprocessen, maar dat kan voor boomsoorten lang duren vanwege hun lange levensduur. En als laatste kan de isolatie van boompopulaties in bosfragmenten de genetische uitwisseling tussen populaties verminderen, waardoor inteelt kan toenemen en de *fitness* van nakomelingen kan afnemen. In de loop van de tijd kunnen deze effecten leiden tot een lagere genetische diversiteit en een verminderde overlevingskans van boompopulaties.

In dit promotieonderzoek werden drie belangrijke effecten van bosfragmentatie in centraal Vietnam onderzocht. Ten eerste onderzochten we de effecten van fragmentgrootte op de bosstructuur en de diversiteit en samenstelling van boomsoorten in zeven bosfragmenten en aaneengesloten bos. Ten tweede bestudeerden we de populatiedynamiek van drie boomsoorten in relatie tot fragmentgrootte. En als laatste onderzochten we de effecten van bosfragmentatie op de genetische diversiteit van een bedreigde boomsoort in vier kleine bosfragmenten.

Effecten van fragmentgrootte op bosstructuur en diversiteit van boomsoorten

We onderzochten de bosstructuur en diversiteit van boomsoorten in zeven bosfragmenten (1-150 ha in oppervlakte) en in een aaneengesloten bos (nationaal park Bach Ma) in centraal Vietnam. De bestudeerde bosfragmenten bevinden zich in een sterk versnipperd landschap waarin vooral plantages van snelgroeiende boomsoorten staan (acacia en rubber). In het midden van elk bosfragment werd een onderzoeksparceel van 1 ha uitgezet. In elk van deze parcelen maten wij de diameter op borsthoogte (dbh) van alle bomen met een dbh van 10 cm of meer. Ter referentie hebben we ook drie vergelijkbare onderzoeksparcelen uitgezet in een aaneengesloten stuk bos. In de parcelen maten we in totaal 3.475 individuen, behorende tot 63 soorten. Tien van deze soorten staan op de Rode Lijst van IUCN. De dichtheid aan bomen, het grondoppervlak van bomen en de dichtheid van grote bomen waren substantieel lager in bosfragmenten kleiner dan 100 ha vergeleken met grotere fragmenten of aaneengesloten bos. De rijkdom aan boomsoorten was positief gecorreleerd met het oppervlak van bosfragmenten en de samenstelling van boomsoorten verschoof naar meer lichtminnende soorten in kleine bosfragmenten. Onze resultaten suggereren dat kleine bosfragmenten (1-10 ha) ook een aanzienlijk deel van de rijkdom aan boomsoorten kunnen herbergen, en dat grote bosfragmenten (≥100 ha) een vergelijkbare bosstructuur, soortenrijkdom en soortensamenstelling hebben als aaneengesloten bos. Onze conclusie is dat zowel grote als kleine bosfragmenten een belangrijke rol kunnen vervullen in het beschermen van biodiversiteit in tropische landschappen waar intensieve landbouw wordt bedreven.

Effecten van fragmentgrootte op populatiedynamiek van boomsoorten.

Wij onderzochten de demografische effecten van bosfragmentatie aan drie boomsoorten die het kronendak van het bos bereiken: *Canarium* *bengalensis* (Burseraceae), *Palaquium annamense* (Sapotaceae), and *Parashorea stellata* (Dipterocarpaceae). We voerden een driejarige veldstudie uit waarin de natuurlijke verjonging, groei en overleving van de onderzochte soorten werd gevolgd in 10 permanente onderzoeksparcelen van elk 1 ha, in enkele kleine bosfragmenten (<20 ha), grote bosfragmenten (20-150 ha) en in een aaneengesloten bos (3 parcelen). We vonden geen significante verschillen in diametergroei tussen bomen in bosfragmenten en in aaneengesloten bos, maar de kans op boomsterfte was hoger in kleine bosfragmenten dan in grote fragmenten of aaneengesloten bos. Daarna maakten we gebruik van integral projection models (IPMs) om de populatiednamiek van boomsoorten te vergelijken tussen kleine bosfragmenten, grote bosfragmenten en aaneengesloten bos. Alle drie onderzochte soorten hadden populatiegroeisnelheden (λ) kleiner dan 1 (0.98 - 0.99) in kleine bosfragmenten. In grote bosfragmenten en aaneengesloten bos was de populatiegroeisnelheid niet significant anders dan 1. De verwachting is dus dat boompopulaties in kleine bosfragmenten in de loop van de tijd zullen afnemen, terwijl populaties in grotere fragmenten en in aaneengesloten bos gelijk zullen blijven in grootte. Analyses met Life Table Response Experiments (LTRE) lieten vervolgens zien dat de verschillen in populatiegroeisnelheid vooral worden veroorzaakt door de lagere boomoverleving in kleine fragmenten, en in mindere mate door de verschillen in de dynamiek van kiemplanten en reproductie van bomen. Onze resultaten suggereren dat de levensvatbaarheid van de onderzochte boomsoorten in kleine bosfragmenten relatief laag is, maar dat deze soorten redelijk goede overlevingskansen hebben in bosfragmenten van meer dan 20 ha. We vragen om meer aandacht voor de bijdrage die bosfragmenten kunnen leveren aan de bescherming van tropische boomsoorten.

Effecten van bosfragmentatie op de genetische diversiteit van een bedreigde boomsoort

We hebben negen microsatellietmerkers gebruikt om de effecten van recente bosfragmentatie op de genetische diversiteit van de ernstig bedreigde boomsoort *Parashorea stellata* te onderzoeken. We vergeleken de genetische diversiteit van grote reproductieve individuen van deze boomsoort – die zich vestigden voordat bosfragmentatie plaatsvond – met die van zaailingen die ontkiemden na bosfragmentatie. We vonden een sterke ruimtelijke genetische structuur in de populatie en een relatief lage genetische diversiteit in grote bomen. Dit resultaat suggereert dat de boompopulatie door een genetische flessenhals is gegaan als gevolg van de decimering van de oorspronkelijke populatie. De lagere allelenrijkdom in zaailingen dan in grote bomen laat zien dat genetische variatie van de populaties bleef afnemen. Echter, de geobserveerde en verwachte heterozygositeit waren over het algemeen niet lager in zaailingen. Dit laatste resultaat kan erop duiden dat zich nog geen nieuw genetische evenwicht heeft ingesteld in de gefragmenteerde populaties, maar het kan ook het gevolg zijn van de grote mate van uitwisseling van stuifmeel en zaden tussen populaties in bosfragmenten. Ondanks de grote mate van genetische uitwisseling tussen overblijvende populaties, was de paarsgewijze genetische differentiatie tussen populaties aanzienlijk hoger na bosfragmentatie. Dus, hoewel er veel genetische uitwisseling plaatsvond tussen gefragmenteerde boompopulaties van de onderzochte soort, heeft bosfragmentatie geleid tot genetische erosie en verhoogde genetische differentiatie tussen populaties. Onze resultaten suggereren dat voor de bescherming van genetische variatie van boomsoorten in gefragmenteerde landschappen een redelijk groot aantal boompopulaties behouden dient te blijven.

Aanbevelingen voor onderzoek naar bosfragmentatie in Vietnam

Dit is de eerste wetenschappelijke studie naar de effecten van bosfragmentatie in Vietnam. Onze studie is uitgevoerd op slechts één locatie en beschouwt alleen de effecten op boomsoorten. Onze resultaten kunnen dan ook niet worden toegepast op andere gebieden, soorten of soortengroepen in Vietnam. We raden daarom aan om vergelijkbare studies uit te voeren in andere regio's en andere soortgroepen. We raden met name de volgende studies naar bosfragmentatie aan in Vietnam:

1. Een gedetailleerde inventarisatie op regionaal en nationaal niveau van de mate waarin Vietnamese bossen gefragmenteerd zijn. In deze studie zou basale informatie over bosfragmenten moeten worden verzameld, zoals het aantal, type en oppervlak van bosfragmenten, het eigendom van bosfragmenten, het landgebruik rondom bosfragmenten en de diversiteit aan dieren en planten in bosfragmenten. Een dergelijke inventarisatie zal een belangrijk overzicht kunnen geven van bosfragmentatie in Vietnam en is daarmee relevant voor natuurbescherming en de planning van landgebruik.

2. Een evaluatie van de natuurwaarden van bosfragmenten op regionaal en nationaal niveau. Het is belangrijk dat kennis wordt vergaard over het voorkomen en de dichtheden aan (beschermde) plant- en diersoorten in Vietnamese bosfragmenten. Een dergelijke evaluatie levert belangrijke informatie op over de mate waarin de

bescherming van deze soorten afhankelijk is van bosfragmenten. Deze studie kan een ondersteuning geven voor de ontwikkeling van natuurbeschermingsmaatregelen voor bedreigde soorten in Vietnam.

3. Een analyse van de mate waarin de lokale bevolking afhankelijk is van bosfragmenten. Het is bekend dat de lokale bevolking niet-houtige bosproducten (onder meer medicinale planten) verzamelt in bosfragmenten en daar ook jaagt. Het is belangrijk om de bijdrage van bosfragmenten aan inkomsten en welzijn van lokale bevolking te becijferen. Een eerste inventarisatie van het gebruik van bosfragmenten is noodzakelijk om in een later stadium te komen tot richtlijnen voor duurzame exploitatie van producten uit bosfragmenten.

4. En als laatste dient de levensvatbaarheid van plant- en diersoorten in bosfragmenten te worden onderzocht. Er bestaan twee relatief nieuwe en weinig gebruikte methodes die de consequenties van bosfragmentatie op overblijvende populaties kunnen bepalen: studies aan populatiedynamiek en aan populatiegenetica. Beide typen studies zijn toegepast in dit promotieonderzoek. Wij raden het gebruik van deze methodes aan om de levensvatbaarheid van andere plant- en diersoorten te onderzoeken en dat uit te voeren in meerdere regio’s in Vietnam. De oprichting van laboratoria voor genetisch onderzoek in Vietnam en het aanleren van onderzoekvaardigheden door Vietnamese onderzoekers zorgt ervoor dat deze methodes kunnen worden toegepast in Vietnam.

Tóm tắt luận văn

Hàng triệu km2 bề mặt trái đất được bảo phủ bởi các mảnh rừng, và ¼ diện tích rừng nhiệt đới còn lại đã bị phân mảnh. Khoảng 650.000 ha rừng tự nhiên bị phân mảnh mỗi năm tại khu vực đông nam châu á. Sự phân mảnh của rừng già được cho là mối đe dọa lớn nhất đến đa dạng sinh học rừng nhiệt đới.

Rừng phân mảnh có nhiều ảnh hưởng xấu đến các loài cây rừng, đó là ảnh hưởng viền, giảm kích cỡ quần thể, và gia tăng sự cô lập giữa các quần thể. Trong luận văn này, chúng tôi phân tích các ảnh hưởng của rừng phân mảnh đến đa dạng loài cây, động thái quần thể và đa dạng nguồn gien cây rừng tại Việt Nam. Các mục tiêu nghiên cứu cụ thể là (1) đánh giá các ảnh hưởng của diện tích mảnh rừng đến cấu trúc rừng, đa dạng và thành phần loài cây; (2) đánh giá các ảnh hưởng của diện tích mảnh rừng đến động thái loài cây rừng;(3) đánh giá các ảnh hưởng của rừng phân mảnh đến đa dạng nguồn gien cây rừng.

Rừng phân mảnh có nhiều ảnh hưởng đến quần thể cây rừng. Đầu tiên, ảnh hưởng của mẫu không đại diện có thể dẫn đến mất loài cây bản địa, bởi các mảnh rừng là nguyên mẫu của rừng nguyên sinh, nhưng một số loài cây có thể không phân bố ở các mảnh rừng này và chúng đã bị mất đi. Thứ hai, ảnh hưởng viền có thể làm thay đổi cấu trúc rừng, số lượng loài cây, tổ thành loài và số lượng cây con, bởi môi trường tiểu khí hậu tại các vùng viền xung quanh mảnh rừng thay đổi so với bên trong lõi của mảnh rừng. Những thay đổi về tiểu điều kiện môi trường khí hậu này có thể làm gia tăng cây chết trong các mảnh rừng, đặc biệt là các mảnh rừng nhỏ. Thứ ba, giảm kích thước quần thể trong các mảnh rừng có thể dẫn đến gia tăng nguy cơ tiệt chủng của loài, bởi các sự kiện bất lợi không lường trước, nhưng sự tiệt chủng có thể phải mất một thời gian dài mới xảy ra bởi đặc điểm đời sống lâu dài của cây. Cuối cùng, sự cô lập của các quần thể cây rừng trong các mảnh rừng có thể hạn chế trao đổi nguồn gien giữa các quần thể, điều này dẫn đến gia tăng lai cận huyết và giảm sức sống của cây con. Qua thời gian, các ảnh hưởng này có thể giảm đa dạng nguồn gien và sức sống của các quần thể còn tồn tại trong các mảnh rừng.

Trong luận văn tiến sỹ này, chúng tôi đã nghiên cứu 3 ảnh hưởng quan trọng của rừng phân mảnh tại miền trung Việt Nam. Đầu tiên, chúng tôi đã nghiên cứu ảnh hưởng của diện tích mảnh rừng đến cấu trúc rừng, đa dạng và tổ thành loài cây trong 7 mảnh rừng và rừng liên tục. Thứ hai, chúng tôi đã nghiên cứu mối quan hệ giữa động thái của 3 loài cây gỗ lớn với diện tích mảnh rừng. Cuối cùng, chúng tôi đã nghiên cứu các ảnh hưởng của rừng phân mảnh đến đa dạng nguồn gien của một loài cây nguy cấp tiệt chủng phân bố tại 4 mảnh rừng nhỏ.

Ảnh hưởng diện tích mảnh rừng đến cấu trúc rừng và đa dạng loài cây

Chúng tôi nghiên cứu cấu trúc rừng và đa dạng loài cây trong 7 mảnh rừng (diện tích từ 1 - 150 ha) và rừng liên tục (vườn quốc gia Bạch Mã). Các mảnh rừng nghiên cứu nằm trong vùng sinh cảnh bị phân mảnh mạnh với một ma trận cây trồng (keo lai và cao su). Một ô tiêu chuẩn 1 ha được thiết lập tại trung tâm mỗi mảnh rừng. Trong ô tiêu chuẩn, chúng tôi đo đường kính ngang ngực của tất cả các loài cây có đường kính ≥ 10cm. Đối với rừng đối chứng tại Bạch Mã, chúng tôi cũng lập 3 ô tiêu chuẩn tương tự. Chúng tôi xác định được 3,475 cây thuộc 63 họ, gồm cả 10 loài cây trong danh sách bảo tồn của quỹ bảo tồn thiên nhiên thế giới (IUCN). Mật độ cây đứng, thiết diện ngang và mật độ cây lớn đường kính ≥ 20cm ở các mảnh rừng < 100 ha thấp hơn ở các mảnh rừng diện tích lớn hơn và rừng liên tục. Số lượng loài cây tăng khi diện tích mảnh rừng tăng, tổ thành loài cây thay đổi theo hướng nhiều tỷ lệ cây mọc nhanh hơn tại các mảnh rừng nhỏ. Kết quả nghiên cứu của chúng tôi chỉ ra rằng các mảnh rừng nhỏ (1-10ha) vẫn chứa đựng sự đa dạng loài nhất định, và các mảnh rừng có diện tích lớn (≥ 100 ha) có cấu trúc rừng, số lượng loài cây và tổ thành loài tương tự như rừng liên tục không phân mảnh. Chúng tôi kết luận rằng mặc dù diện tích nhỏ, nhưng các mảnh rừng vẫn đang đóng một vai trò quan trọng trong bảo tồn đa dạng sinh học trong những vùng sinh cảnh thâm canh nông lâm nghiệp nhiệt đới.

Ảnh hưởng diện tích mảnh rừng đến động thái quần thể loài cây

Chúng tôi nghiên cứu ảnh hưởng của rừng phân mảnh đến động thái quần thể của ba loài cây gỗ lớn, Trám chũa (*Canarium bengalensis*), Chay trung bộ (*Palaquium annamense*), và Chò đen (*Parashorea stellata*). Chúng tôi đã tiến hành theo dõi quần thể 3 năm để tính toán số lượng cây con sinh ra, sinh trưởng, phát triển, và sự sống của các loài cây nghiên cứu trong 10 ô tiêu chuẩn cố định, mỗi ô 1ha tại các mảnh rừng nhỏ (≤ 20 ha), các mảnh rừng lớn diện tích (20 -150 ha) và rừng liên tục không phân mảnh (3 ô tiêu chuẩn) tại miền trung Việt Nam. Chúng tôi tìm ra rằng sinh trưởng đường kính ngang ngực (dbh) của các loài cây nghiên cứu không có sự khác biệt giữa các mảnh rừng và rừng liên tục, nhưng tỷ lệ cây chết ở các mảnh rừng nhỏ cao hơn so với mảnh rừng lớn và rừng liên tục. Sau đó, chúng tôi sử dụng mô hình ma trận tổng hợp (IPMs) để so sánh động thái quần thể của ba loài giữa mảnh rừng nhỏ, mảnh rừng lớn và rừng liên tục. Chúng tôi sử dụng chỉ số tốc độ tăng trưởng quần thể (λ) thu được từ mô hình ma trận tổng hợp, quần thể đang sinh trưởng và phát triển tốt khi chỉ số λ > 1 và quần thể bị suy thoái khi λ < 1. Đối với cả ba loài, chỉ số λ nhỏ hơn 1 (0,98 - 0,99) tại mảnh rừng nhỏ, và chỉ số λ lớn hơn 1 (1,02 - 1,04) tại mảnh rừng lớn và rừng liên tục. Những kết quả này chỉ ra rằng quần thể của ba loài cây nghiên cứu có chiều hướng bị suy giảm trong các mảnh rừng diện tích nhỏ và chúng có chiều hướng ổn sinh trưởng và phát triển trong các mảnh rừng lớn và rừng liên tục. Sự khác biệt về chỉ số λ giữa các mảnh rừng phần lớn là do sự khác nhau về tỷ lệ sống, sau đó là động thái cây con và sự ra hoa quả của loài cây nghiên cứu. Những kết quả nghiên cứu của chúng tôi chỉ ra rằng diện tích mảnh rừng nhỏ có ảnh hưởng đến sức sống của quần thể các loài cây nghiên cứu, nhưng chúng có triển vọng sống sót tốt tại các mảnh rừng có diện tích ≥ 20 ha. Chúng tôi kêu gọi sự quan tâm nhiều hơn nữa đến sự đóng góp của các mảnh rừng cho bảo tồn loài cây nhiệt đới.

Ảnh hưởng rừng phân mảnh đến đa dạng nguồn gien của loài cây bị đe dọa tiệt chủng

Chúng tôi sử dụng 9 chỉ thị vi vệ tinh (microsatellite) để đánh giá ảnh hưởng của rừng phân mảnh đến đa dạng nguồn gien cây Chò đen (*Parashorea stellata*), một loài cây nguy cấp tiệt chủng. Cụ thể, chúng tôi so sánh đa dạng nguồn gien của thế hệ cây bố mẹ (thể hiện và lưu giữ đa dạng nguồn gien trước khi rừng phân mảnh) với đa dạng nguồn gien của thế hệ cây con vừa mới được sinh ra (thể hiện và lưu giữ nguồn gien sau khi rừng bị phân mảnh). Nhìn chung, chúng tôi quan sát thấy cấu trúc khoảng cách di truyền lớn và đa dạng nguồn gien của thế hệ cây bố mẹ đã bị suy giảm. Điều này chứng tỏ rừng phân mảnh cũng đã ảnh hưởng đến cấu trúc và đa dạng nguồn gien của thế hệ cây bố mẹ, thông qua hiệu ứng cổ chai (genetic bottleneck) bởi nhiều cá thể cây bố mẹ trong tự nhiên đã bị mất đi và chúng mang theo sự đa dạng nguồn gien mà các cây bố mẹ còn lại không có. Khi so sánh thế hệ cây bố mẹ và cây con, cho thấy tổng số alen thấp hơn ở thế hệ cây con, điều này chứng tỏ rằng quần thể vẫn bị tiếp tục suy giảm đa dạng nguồn gien sau khi rừng bị phân mảnh. Ngược lại, mức độ dị hợp tử quan sát và dị hợp tử mong muốn không suy giảm ở thế hệ cây con so với thế hệ cây bố mẹ. Điều này có thể do quần thể chưa đạt được sự cân bằng nguồn gien trong tự nhiên, và cũng có thể do sự gia tăng về phát tán trao đổi phấn hay hạt giữa các mảnh rừng. Mặc dù có sự trao đổi nguồn gien giữa các mảnh rừng, nhưng sự khác biệt về đa dạng nguồn gien giữa hai thế hệ vẫn gia tăng sau khi rừng phân mảnh. Vì vậy, dù các quần thể vẫn có mối liên hệ với nhau trong một sinh cảnh canh tác nông lâm nghiệp, nhưng rừng phân mảnh vẫn làm suy thoái và gia tăng sự khác biệt nguồn gien của cây rừng. Những kết quả nghiên của chúng tôi chỉ ra rằng cần giữ lại đa dạng các quần thể còn sót lại để bảo tồn đa dạng nguồn gien loài cây trong những khu sinh cảnh thâm canh nông nghiệp nhiệt đới.

Đề xuất nghiên cứu về rừng phân mảnh tại Việt Nam

Đây là một nghiên cứu đầu tiên về rừng phân mảnh tại Việt Nam và mới chỉ triển khai một điểm nghiên cứu tại Việt Nam, do vậy kết quả nghiên cứu không thể áp dụng ở những nơi khác, loài khác hay nhóm loài khác tại Việt Nam. Cụ thể chúng tôi đề xuất các nghiên cứu về rừng phân mảnh tại Việt Nam như sau:

1. Tiến hành điều tra chi tiết về quy mô và sự mở rộng rừng phân mảnh ở cấp quốc gia và khu vực. Điều tra này giúp thu thập các số liệu cơ bản về số lượng, loại rừng, kích thước, sở hữu, hiện trạng sử dụng đất, sự đa dạng các loài cây và con trong các mảnh rừng. Qua đó có một tổng quan về rừng phân mảnh và nó liên quan trực tiếp đến bảo tồn và chính sách sử dụng đất tại Việt Nam.

2. Đánh giá các giá trị bảo tồn của các mảnh rừng ở cấp quốc gia và khu vực. Việc làm này sẽ cung cấp thông tin về các loài cây, loài con đang bị đe dọa tiệt chủng phân bố trong các mảnh rừng của Việt Nam, qua đó giúp chúng ta cân nhắc mức độ bảo tồn các mảnh rừng và cũng làm cơ sở cho phát triển chính sách bảo tồn các loài bị đe dọa tại Việt Nam.

3. Đánh giá sự phụ thuộc cuộc sống của người dân vào khai thác các sản phẩm từ các mảnh rừng. Người dân địa phương được biết đến là người thu hái các lâm sản ngoài gỗ (gồm cả cây thuốc) và săn bắn trong các mảnh rừng. Điều này, giúp lượng hóa giá trị đóng góp của các mảnh rừng đến cuộc sống của người dân nông thôn và giúp xây dựng các hướng dẫn quản lý, khai thác bền vững nguồn tài nguyên rừng trong các mảnh rừng.

4. Cuối cùng, sức sống của các quần thể thực, động vật trong các mảnh rừng nên được nghiên cứu. Có hai phương pháp mới nghiên cứu và được sử dụng không thường xuyên có thể giúp hiểu ảnh hưởng của rừng phân mảnh đến sức sống của các quần thể đang tồn tại

đó là nghiên cứu động thái và đa dạng nguồn gien quần thể. Cả hai phương pháp đã được sử dụng trong luận văn nghiên cứu tiến sỹ này. Chúng tôi khuyến cáo sử dụng hai phương pháp này để nghiên cứu ảnh hưởng của rừng phân mảnh đến sinh trưởng và phát triển của quần thể thực, động vật ở nhiều khu vực tại Việt Nam. Sự thành lập các phòng thí nghiệm tế bào và phát triển kỹ năng của các nhà nghiên cứu Việt Nam cho phép những nghiên cứu tương tự sẽ được triển khai.

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Curriculum vitae

Ha Van Tiep was born on 10 October, 1972 in Kien Xuong district, Thai Binh province, Vietnam. He entered Vietnam Forest University in Xuan Mai, Hanoi in 1991 and got his bachelor degree in 1996. After that he worked in the Forest Science Centre of North West Vietnam in Son La province. This Centre belongs to the Vietnamese Academy of Forest Science.

He carried out several research projects related to ecology and agroforestry in Son La province and in other areas within Vietnam. The next step of his study progress was a master degree in 2005 at the Asian Institute of Technology (AIT) in Thailand, for which he received financial support from the Ford Foundation. In 2009, he was selected to conduct his Ph.D study at Plant Ecology and Biodiversity Group, Utrecht University, the Netherlands with financial support from Tropenbos International. His research focused on the effects of forest fragmentation on the diversity, population dynamics and genetic variation of tree species in Vietnam

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