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Effect of topography on the distribution of tree species and radial diameter growth of potential crop trees in a tropical mountain forest in southern Ecuador

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Abstract

Tropical mountain forests (TMF) of the Andes are a biodiversity hot spot with high levels of endemism. At the same time, they provide a wide range of ecosystem services (ESS) to society that are essential for human well-being. Over the last decades, Andean TMF have been threatened by ongoing anthropogenic transformation to other land uses, resulting in a loss of biodiversity and overall ESS provision on the landscape level. As a consequence, global efforts to promote the conservation and sustainable use of TMF have increased. Sustainable forest management (SFM) has been proposed as one tool to contribute towards this objective, as it is considered a balance between full protection and more intensive land uses. However, silvicultural management, an integral part of SFM, is hindered by a lack of location-specific knowledge on ecological aspects as well as on the impact of silvicultural interventions on forest stands in TMF. This thesis therefore aims to expand the current knowledge base on these aspects. Specific objectives were to gain a better understanding on environmental factors shaping the distribution of tree species and to quantify the impacts of silvicultural treatments and environmental factors on tree growth for an upper montane forest in southern Ecuador.

Data for the analyses originated from a silvicultural experiment established in 2003 to study the effects on tree growth and ecological impact of a liberation thinning. Further, topographic predictors were derived from a very high-resolution digital terrain model (DTM), which was generated based on an airborne LiDAR survey. Topographic predictors served as proxies for environmental factors, since topography plays an important role for many ecological processes in TMF, with reported effects on tree growth and the distribution of tree species.

The relationship between the spatial distribution of tree species and topography was analysed employing two presence-only species distribution modelling techniques: The maximum entropy model (Maxent) and the ecological niche factor analysis (ENFA). The locations of all individual trees of the 16 most abundant species within the area of the silvicultural experiment served as occurrence data. Model performance was assessed by the true skill statistic and area under curve (AUC) of the receiver operator characteristic (ROC), using both k-fold data partitions and null-models. Performance varied among species and metrics, but generally Maxent models showed better performance than ENFA models. Furthermore, the ecological plausibility of models was confirmed by comparing them with a previously established forest type classification. Both Maxent and ENFA models identified elevation and the topographic position index (TPI) as the main determinants for the distribution of most of the tree species, whereas a wetness index, aspect and slope only had minor importance. Additionally, prediction maps of habitat suitability were created for each species.

The relative effects of a silvicultural treatment and topography on growth rates at the tree level were analysed using a linear mixed-effect model. The silvicultural treatment consisted of a liberation thinning, i.e. the removal of the strongest crown competitors, which was applied to potential crop trees (PCTs) in 2004. Based on monitoring data from 174 released and 200 reference PCTs of eight timber species, the periodic annual increment (PAI) in the diameter at breast height (DBH) six years after the silvicultural treatment was calculated as the outcome variable. As topographic predictors, elevation and TPI were used. To control for the by-species growth variability, random intercepts for species and random slopes for the effect of treatment on species was included in the model. Results showed that PAI was significantly influenced by the topographic predictors. Over the elevational gradient, growth rates declined on average by 0.73 mm a^{-1} per 100 m increase in elevation. For the topographic position, PCTs in valleys had an average PAI of 2.02 mm a^{-1} compared to 1.04 mm a^{-1} on ridges. The effect of the silvicultural treatment across all species was only marginally significant, but its effect size was nevertheless within the range, but at the lower end of values reported for other tropical forest ecosystems (reference trees: 1.35 mm a^{-1}; released trees: 1.60 mm a^{-1}). Model outcomes suggested that five species responded positively to the silvicultural treatment, whereas three species showed no treatment effect. Overall, tree growth varied substantially as indicated by the large residual variance that remained unaccounted for in the model. Results suggests that silvicultural interventions have potential in the sustainable management of TMF.

The common key takeaway of the analyses is that the spatial distribution of tree species and diameter growth of PCTs were influenced to a large extent by topography in general, and elevation and the topographic position in particular. The fact that fundamental forest characteristics vary considerably within short geographic distances in TMF underlines that instead of “broad-brush” management, multifunctional zoning and management prescriptions should be based on the fine-scale environmental heterogeneity. Promising use cases for topographic predictors in SFM include spatially explicit estimations and mapping of timber stocks and sustainable yield, mapping of ESS, species-specific delineation of areas suited for enrichment planting, and site-species matching in reforestation activities. However, in order to apply these use cases in practice, further research focusing on predictive modelling, improved model transferability and inclusion of nontopographic predictors (e.g. climate variables) is necessary.

Keywords: Silvicultural treatments, Sustainable forest management, Tropical montane forest, Diameter growth, Species Distribution Modelling, Maxent, Biogeography

Zusammenfassung

Tropische Bergwälder (TBW) der Anden weisen eine große Artenvielfalt mit einem hohen Grad an Endemismus auf und bieten der Gesellschaft ein breites Spektrum von Ökosystemdienstleistung (ÖSD), die für das menschliche Wohlbefinden von wesentlicher Bedeutung sind. In den letzten Jahrzehnten wurden TBW durch die fortschreitende anthropogene Umwandlung in andere Landnutzungen bedroht. Dies führte zu einem Verlust der biologischen Vielfalt und vieler ÖSD. Als Folge haben die weltweiten Anstrengungen zur Erhaltung und nachhaltigen Nutzung von TBW zugenommen. Das Instrument der nachhaltigen Waldbewirtschaftung (NWB) kann zu diesem Ziel beizutragen, da sie als Mittelweg zwischen vollständigem Schutz und intensiverer Landnutzung angesehen wird. Waldbauliche Planung, ein wesentlicher Bestandteil von NWB, wird jedoch aufgrund von mangelndem standortspezifischem Wissen über ökologische Aspekte und Auswirkungen von waldbaulichen Maßnahmen auf Waldbestände in TBW behindert. Diese Dissertation zielt deshalb darauf ab, die aktuelle Wissensbasis über diese Aspekte zu erweitern. Konkrete Ziele waren einerseits, ein besseres Verständnis der Umweltfaktoren, die die Verbreitung von Baumarten beeinflussen, zu gewinnen, und andererseits die Auswirkungen waldbaulicher Behandlungen und Umweltfaktoren auf das Wachstum von Bäumen zu quantifizieren.

Die Datenbasis für die durchgeführten Analysen stammt aus einem waldbaulichen Experiment in einem TBW im Süden Ecuadors, das 2003 durchgeführt wurde. Das Ziel des Experiments war es, zu untersuchen, wie sich eine Durchforstung auf den Zuwachs von Z-Bäumen und auf ökologische Aspekte auswirkt. Darüber hinaus wurden topografische Prädiktoren aus einem hochauflösenden digitalen Geländemodell abgeleitet, das basierend auf LiDAR-Daten erstellt wurde. Diese dienten als Proxy-Variablen für Umweltfaktoren, da die Topografie für viele ökologische Prozesse in TBW eine wichtige Rolle spielt und sowohl den Zuwachs von Bäumen als auch die Verteilung von Baumarten beeinflusst.

Der Zusammenhang zwischen der räumlichen Verteilung von den 16 am häufigsten vorkommenden Arten in dem waldbaulichen Experiment und Topografie wurde unter Verwendung von zwei Techniken für die Modellierung von Artenverbreitungen analysiert (Maxent und ENFA). Die Modell-Performance wurde anhand mehrerer Qualitätsmaße bewertet (Fläche unter der ROC-Kurve und „True Skill Statistic“ bezogen auf verschiedene Kreuzvalidierungsverfahren). Die Performance variierte zwischen den Baumarten und Qualitätsmaßen, aber im Allgemeinen schnitten Maxent-Modelle besser ab als ENFA-Modelle. Darüber hinaus wurde die ökologische Plausibilität der Modelle durch einen Vergleich mit einer bereits bestehenden Waldtypklassifikation bestätigt. Die Geländehöhe und die topografische Position stellten sich als wichtigste Prädiktoren für die Verteilung der meisten Baumarten heraus.

Der Einfluss der waldbaulichen Behandlung und Topografie auf den Zuwachs auf Einzelbaumebene wurde unter Verwendung eines linearen gemischten Modells analysiert. Für die waldbauliche Behandlung wurde der stärkste Kronenkonkurrent von potenziellen Z-Bäumen im Jahr 2004 entnommen. Als Zielvariable diente der durchschnittliche jährliche Zuwachs sechs Jahre nach dem waldbaulichen Eingriff. Die Geländehöhe und topografische Position wurden als Prädiktoren verwendet. Des Weiteren wurde die Variabilität des Zuwachses zwischen den verschiedenen Baumarten im Modell berücksichtigt. Die Ergebnisse zeigten, dass der Zuwachs signifikant von den topografischen Prädiktoren beeinflusst wurde. Über den Höhengradienten nahmen die Zuwachsraten im Schnitt um 0.73 mm a^{-1} pro 100 m Höhenzunahme ab. Bei der topographischen Position hatten Z-Bäume in Tälern im Schnitt einen Zuwachs von 2.02 mm a^{-1} im Vergleich zu 1.04 mm a^{-1} auf Graten. Die Auswirkung der waldbaulichen Behandlung über alle Arten hinweg war nicht statistisch signifikant, aber die beobachtete Effektgröße lag dennoch im Rahmen dessen, was in anderen tropischen Waldökosystemen beobachtet wurde (Referenzbäume: 1.35 mm a^{-1}; behandelte Bäume: 1.60 mm a^{-1}). Weiterhin deuteten die Ergebnisse an, dass fünf Baumarten positiv auf die waldbauliche Behandlung reagierten, während drei Arten keinen Behandlungseffekt zeigten. Generell zeigte das Baumwachstum eine erhebliche Variation, was durch das große Residuum angezeigt wird, welches im

Modell nicht berücksichtigt wurde. Die Ergebnisse legen nahe, dass waldbauliche Behandlungen Potenzial für die nachhaltige Bewirtschaftung von TBW haben.

Das übergeordnete Ergebnis der durchgeführten Analysen ist, dass die räumliche Verteilung der Baumarten und der Zuwachs von Z-Bäumen in hohem Maße von der Topographie im Allgemeinen und der Geländehöhe und topografischen Position im Besonderen beeinflusst wurden. Die Tatsache, dass sich grundlegende Waldmerkmale in TBW innerhalb kurzer geografischer Entfernungen erheblich unterscheiden, legt nahe, dass anstelle von verallgemeinernden Bewirtschaftungsrichtlinien multifunktionale Zonierung auf der kleinräumigen Heterogenität der Umweltbedingungen beruhen sollte. Vielversprechende potenzielle Anwendungsfälle für topografische Prädiktoren in der NWB umfassen räumlich explizite Schätzungen von Holzvorräten und nachhaltigen Nutzungspotentialen, Kartierung von ÖSD, artenspezifische Ausweisung von für Anreicherungspflanzungen geeigneten Flächen, und standortsgerechte Aufforstungsmaßnahmen. Um diese Anwendungsfälle in der Praxis anzuwenden, sind jedoch weitere Untersuchungen erforderlich, die sich auf vorhersagende Modellierung, verbesserte Modellübertragbarkeit und die Einbeziehung nicht-topografischer Prädiktoren (z. B. klimatische Variablen) konzentrieren.

Keywords: Waldbauliche Behandlungen, Nachhaltige Waldbewirtschaftung, Tropischer Bergwald, Durchmesserzuwachs, Modellierung von Artenverbreitungen, Maxent, Biogeographie

Scientific publications

This cumulative thesis is based on the following publications:

I. *Kübler, D.*, Hildebrandt, P., Günter, S., Stimm, B., Weber, M., Mosandl, R., Muñoz, J., Cabrera, O., Aguirre, N., Zeilinger, J., Silva, B., 2016. Assessing the importance of topographic variables for the spatial distribution of tree species in a tropical mountain forest. Erdkunde 70, 19–47. https://doi.org/10.3112/erdkunde.2016.01.03.

II. *Kübler, D.*, Hildebrandt, P., Günter, S., Stimm, B., Weber, M., Muñoz, J., Cabrera, O., Zeilinger, J., Silva, B., Mosandl, R., 2020. Effects of silvicultural treatments and topography on individual tree growth in a tropical mountain forest in Ecuador. Forest Ecology and Management 457, 117726. https://doi.org/10.1016/j.foreco.2019.117726.

III. Weber, M., Stimm, B., López, M.F., Gerique, A., Pohle, P., Hildebrandt, P., Knoke, T., Palomeque, X., Calvas, B., Günter, S., Aguirre, N., *Kübler, D.*, 2013. Conservation, Management of Natural Forests and Reforestation of Pastures to Retain and Restore Current Provisioning Services, in: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (Eds.), Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Springer Berlin Heidelberg, Berlin, Heidelberg. Ecological Studies, pp. 171–185. http://dx.doi.org/10.1007/978-3-642-38137-9_13.

The contribution of Daniel Kübler to the publications included in this thesis was as follows:

- Publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020): Conceptualization; data collection and organization; design of methodology; data analysis and interpretation; drafting the article.
- Publication III (Weber et al., 2013): Data analysis; visualization of results; critical revision of the draft.

Contents

1 Introduction

Tropical mountain forests (TMF, see Textbox 1) have an important biological value due to their high floral and faunal species diversity and high levels of endemism at the species level (Kappelle, 2004). This is especially true for Andean TMF, which are one of the "hottest" biodiversity hot spots (Brummitt and Lughadha, 2003; Myers et al., 2000).

Textbox 1: TMF are generally latitudinally restricted to the tropics (i.e. between latitudes of 23.5◦ N and 23.5◦ S). Altitudinal limits of TMF differ between authors. For example, Bruijnzeel et al. (2011b) report that TMF can be found, depending on latitude, between a lower limit of 1,500–2,500 m a.s.l and an upper limit of 2,400–3,300 m a.s.l. In contrast, Kappelle (2004) provide an altitudinal range for TMF between 500 and 4000 m a.s.l. Spracklen and Righelato (2014), on the other hand, define TMF as all forests that occur at altitudes ≥ 1000 m a.s.l between latitudes of 23.5◦ N and 23.5◦ S.

Note that the terms "tropical mountain forests" and "tropical montane forests" are interchangeable, although the latter more specifically refers to the altitudinal vegetation belt (Gradstein et al., 2008). Throughout this thesis, the former term is used.

Forests provide a wide range of ecosystem services (ESS[1]) to society that are essential for human well-being (Brockerhoff et al., 2017). In TMF, hydrological services, such as water supply, hydrological regulation and erosion mitigation, are of particular importance (Bonnesoeur et al., 2019; Martínez et al., 2009). Further, the provision of heterogeneous habitats, a regulating ESS, has been identified as one factor contributing to TMF being a global hotspot of biodiversity (Homeier et al., 2010). Additionally, the role of TMF for carbon storage has been increasingly acknowledged in the last years (Spracklen and Righelato, 2014).

Despite their relevance for ESS provision and as biodiversity hotspots, TMF have long been considered as one of the most threatened tropical ecosystems worldwide (Kappelle, 2004). Major threats to TMF are conversion to pasture for cattle grazing and agricultural land, over-harvesting of timber and fuelwood, alien invasions, roads, and various types of development (Scatena et al., 2011). Anthropogenic transformation of TMF to other land uses can dramatically reduce overall ESS provision on the landscape level, because ESS are strictly related to land use and land cover (Gaglio et al., 2016; Homeier et al., 2013; IPBES, 2019). Further, TMF are highly susceptible to habitat fragmentation and habitat loss due to the high concentration of endemic species. Consequently, conversion of TMF has resulted in a large loss of biodiversity (Peters et al., 2010). Current predictions of climate change suggest that biodiversity loss will be exacerbated during the next century, because many plant and animal species in TMF have a restricted elevation range (Scatena et al., 2011).

Over the past decades, global efforts to promote the conservation and sustainable use of TMF have increased (Bruijnzeel et al., 2011a). Multiple tools, all of which have also been employed in tropical lowland rainforests, have been proposed to reach this objective in TMF. These tools include payment for ecosystem services (PES), networks of protected areas, and sustainable forest management (SFM[2]) (Bruijnzeel et al., 2011a; Günter et al.,

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[1] ESS represent the contributions that ecosystems make to human well-being, i.e. they can be defined according to their specific benefits to society. They can be subdivided into provisioning, regulation and cultural services (Brockerhoff et al., 2017).

[2] SFM can be defined as "the process of managing forest to achieve one or more clearly specified objectives of management with regard to the production of a continuous flow of desired forest products and services without

2008). Here, I focus on the latter, as a large part of the work presented in this thesis has been in the framework of SFM.

It is now widely accepted that conservation of tropical forests cannot be reached by outright protection alone. In that context, forest conservation through SFM has gained worldwide support over past decades (IPBES, 2019; IPCC, 2019). An argument often employed in favour of SFM in tropical forests is of economic nature. Its basic premise is that deforestation will continue as long as conversion to other land uses remains more profitable than standing natural forests. Managing forests for continuous, long-term production under SFM can enhance their economic value and therefore make them more competitive against other land uses (Grulke et al., 2016). While this argument generally holds true in remote areas and on land unsuitable for agricultural production, this is not the case on land suited for agriculture and located in regions with access to markets. In such situations, land uses resulting in forest conversion are normally more profitable than SFM (Grulke et al., 2016). Nevertheless, many stakeholders champion SFM for tropical forests despite its low economic competitivity (IPBES, 2019; IPCC, 2019; Pearce et al., 2003). This can be explained by the fact that SFM is considered a balance between full protection and more intensive land uses; tropical forests under SFM can retain a large part of biodiversity, carbon, and timber stocks, maintain vital forest functions, and continue supplying ESS and various other social and economic benefits (Edwards et al., 2014; Nasi and Frost, 2009; Putz et al., 2012). This balance between multiple objectives makes SFM a promising tool in TMF (Bruijnzeel et al., 2011a). Yet, while there is political will for its implementation, to date only few successful experiences have been reported in TMF.

To achieve SFM in tropical natural forests, seven essential principles have been identified (ITTO, 2015): 1) Forest governance and security of tenure, 2) land-use planning, permanent forest estate and forest management planning, 3) ecological resilience, ecosystem health and climate-change adaptation, 4) multipurpose forest management, 5) silvicultural management, 6) social values, community involvement and forest-worker safety and health, and 7) investment in natural forest management and economic instruments. These principles constitute the crucial foundation for SFM; if any of them is not in place, SFM will not be achieved (ITTO, 2015). This thesis puts emphasis on the fifth principle, i.e. silvicultural management, in the context of TMF.

In its literal meaning, silviculture aims at mitigating and balancing the objectives of conservation of forest ecosystems and functions and anthropogenic uses (Günter, 2011a). A sensible definition is that "silviculture investigates the consequences of decisions about the treatment of forest ecosystems in order to fulfil present and future human needs" (Knoke, 2010). Silvicultural interventions in tropical forests can include 1) enhancement of natural regeneration or enrichment planting to assure forest regeneration, 2) tending of renewals or liberation thinning to regulate competition and therefore optimize the site-given growth potential, and 3) application of reduced-impact logging techniques for the harvest of mature commercial timber species (Grulke et al., 2016). Many principles of silviculture in temperate forests can also be applied to tropical forests. However, a silviculturally relevant difference between these two ecosystems is that tropical forests are generally characterized by high biodiversity. This does not only make silvicultural management more complicated but also puts a higher emphasis on biodiversity conservation (Günter, 2011a).

There are only very few reports on silvicultural systems[3] in TMF (see Ashton et al. (2011) for an example for hill mixed dipterocarp forests of southwest Sri Lanka). Developing silvicultural systems, or adapting them from other

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undue reduction of its inherent values and future productivity and without undue undesirable effects on the physical and social environment" (ITTO, 2015).

[3] A silvicultural system can be defined as "the process by which forest trees are tended, removed and replaced by new trees. Silviculture comprises all operations used in manipulating forest stands, including harvesting operations" (ITTO, 2015).

forest ecosystems, requires location-specific knowledge in 1) forest ecology and 2) the impact of silvicultural interventions on forest stands (Hutchinson, 1988; ITTO, 2015; Oliver et al., 1994). However, there is generally a scarcity of research on many ecological aspects in TMF, with major information gaps including the spatial distribution, biological richness, and ecological variation at different spatial scales (Pitman et al., 2011; Scatena et al., 2011). Further, in contrast to tropical lowland forests, where considerable research on silviculture has been conducted over the last decades, there is little knowledge on silvicultural interventions in TMF (Bruijnzeel et al., 2011a; Günter et al., 2008). This lack of scientific information has hampered the development, or adaption, of silvicultural systems and the evaluation of their potential to contribute to SFM. Hence, this thesis aims to expand the current knowledge base about ecological processes and silvicultural interventions in TMF. For this, two specific objectives are addressed for an upper montane forest in southern Ecuador:

1. Gain a better understanding on environmental factors shaping the distribution of tree species.
2. Quantify the impacts of silvicultural treatments and environmental factors on tree growth.

This thesis consists of six chapters. This introduction chapter provides the overall motivation, states the problem, and presents research objectives. The second chapter gives an overview of relevant background information that form the basis of this thesis. To a large extent, the first and second chapter are based on publication III (Weber et al., 2013). The third chapter gives an overview of the overall methodological approach and data sources used in publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020). A special focus in this chapter is on topographic variables, which play an important ecological role in TMF. Chapter 4 presents the main results from Kübler et al. (2016) and Kübler et al. (2020). The fifth chapter discusses the results from the previous chapter in the context of SFM and silviculture in TMF and the information presented in publication III (Weber et al., 2013). The sixth chapter draws overall conclusions.

2 Literature review

This chapter first introduces TMF in Ecuador. Then, the literature on species distribution modelling and silvicultural treatments in the tropics and TMF is reviewed in the second and third section, respectively.

2.1 Tropical mountain forests (TMF) in Ecuador

For the most part, the information presented in this section is based on publication III (Weber et al., 2013), which provides an in-depth overview on the conservation and management of TMF and the reforestation of pastures in Ecuador, with a focus on provisioning ESS. Aspects relevant for this thesis are summarized and complemented with additional references.

TMF in Ecuador are in many aspects exemplary for challenges related to natural resource management in developing countries. On the one hand, TMF deliver important ESS that directly contribute to human well-being. On the other hand, deforestation is an ongoing problem. Efforts for SFM exist, but they often fall short due to weak governance and institutions as well as insufficient enforcement of forest laws. TMF in Ecuador therefore serve as an excellent case study to illustrate the issues and challenges associated with TMF conservation.

In 2015, Ecuador (Figure 1) had a primary forest cover of 12.47 million ha, which corresponds to 46.4% of the Ecuadorian land area (FAO, 2015). Añazco et al. (2010) reported that 7% of the national forest cover occur in mountainous regions. In contrast, around 2.73 million ha, or 21.9% of the primary forest cover, can be classified as TMF (Josse et al., 2009)[4]. For the periods of 1990–2000 and 2000–2010, FAO (2011) reported deforestation rates of 1.5% and 1.8%, respectively. However, more recent estimates of deforestation rates for the same time periods are considerably lower (1990–2000: 0.68%, 2000–2010: 0.58%; FAO, 2015), but still among the highest in South America. One cause for the high rates is that deforestation is not mitigated by reforestation efforts; compared to other South American countries, the area with tree plantations has been growing slowly in Ecuador (Mosandl et al., 2008). Deforestation is an ongoing problem in Ecuador; between 2010 and 2015, a deforestation rate of 0.61% was observed (FAO, 2015).

Figure 1: Ecuador in South America.

2.1.1 Biodiversity and ecosystem services (ESS)

Andean TMF are one of the principal hotspots of global biodiversity and endemism (Brummitt and Lughadha, 2003), and very high diversity and endemism has been reported for Ecuadorian TMF for a number of plant and animal groups. Some of the emblematic species include the spectacled bear (*Tremarctos ornatus*), northern pudú (South American deer, *Pudu mephistophiles*) and mountain tapir (*Tapirus pinchaque*). Factors that have driven the outstanding species diversity range from the global scale (e.g. paleo-ecological factors and the type of seasonal variability) over the landscape and mountain scale (e.g. input of taxa from various directions along mountain chains and orographic heterogeneity) to site-specific factors at the microscale (e.g. micro-relief), which create a

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[4] The following forest types from Josse et al. (2009) were included for this estimation: Bosque Altoandino, Bosque Altimontano and Bosque Montano.

small-scale mosaic of distinct habitat patches with differing environmental conditions (Homeier et al., 2010; Richter, 2008).

In Ecuador, provisioning services of TMF are of high importance, especially to the rural population (Weber et al., 2013). About 75% of the total forest area of Ecuador is used directly or indirectly by indigenous communities and 850,000 people depend directly on forest resources for their livelihoods (Blaser, 2011). While the importance and specific uses of provisioning services of TMF differ between ethnic-cultural affiliations and socio-economic settings, they are generally highly valued across all rural groups (Pohle et al., 2010). As the multifaceted bundle of ESS provided by TMF is predominantly consumed by the local population, non-timber forest products (NTFPs) are of high importance, with at least 589 species being used for NTFPs in Ecuadorian forests (Blaser, 2011).

Further, natural forests have an important provisioning function for the local timber industry in Ecuador, since most of the timber species on the national market come from natural forests (Blaser, 2011). However, since most of these species come from lowland rainforests (Weber et al., 2013), TMF seem to be less relevant for the timber industry. Natural forests also serve as major seed sources for reproductive material of desired tree species (Stimm et al., 2008). This often neglected provisioning ESS is crucial for forest restoration and SFM (Weber et al., 2013).

Additionally, supporting, regulating and provisioning hydrological services as well as erosion prevention are ESS that are of particular importance in Ecuadorian TMF (Breuer et al., 2013; Gaglio et al., 2016).

2.1.2 Land tenure

In Ecuador, forest is either owned by the state, indigenous peoples and local communities, or private landowners. Data on forest tenure is somewhat conflicting, with a significant overlap between different forest ownership categories (REDD desk, 2011). Indigenous and Afro-Ecuadorian communities were reported to be the largest forest owners, holding around 7.5 million ha of native forest (Añazco et al., 2010). According to REDD desk (2011), government-owned forest lands amount to roughly 6.8 million ha, which can be further subdivided into native forests under the National System of Protected Areas ("Sistema Nacional de Áreas Protegidas" (SNAP); ca. 4.8 million ha) and the so-called forest patrimony ("Patrimonio Forestal"; ca. 2 million ha). Private and cooperate forests have a relatively small area (Añazco et al., 2010).

2.1.3 Forest governance

There is a distinction between forests for protection and forests for (potential) production in Ecuador.

2.1.3.1 Forests for protection

The major strategy of the Ecuadorian state for biodiversity and ESS conservation has been the protected area model, which was implemented in 1976 under the SNAP. Nowadays, the system also includes more participative management concepts. Legally, forests within the SNAP cannot be commercially used, but they may be used for subsistence if inhabited by indigenous communities (Añazco et al., 2010).

The SNAP consists of four subsystems: 1) state patrimony of natural areas ("Patrimonio de Áreas Naturales del Estado"; PANE), 2) decentralised areas under administration of subnational governments, mainly municipalities ("Áreas de Gobiernos Autónomos Descentralizados"), 3) communal protected areas ("Áreas Protegidas Comunitarias"), and 4) private protected areas ("Áreas Protegidas Privadas"; Weber et al., 2013). The PANE currently includes 48 protected areas that represent around 20% of Ecuador's total surface (MAE, 2015). The Ministry of Environment of Ecuador has overall responsibility for the protection of these areas, although it is beginning to share management responsibilities with municipalities and private organisations (Weber et al., 2013). In the context of TMF, the conservation of water resources as a main provisioning ESS for civil society is a central goal of the SNAP. In line with that, four of the five national parks that are located in the eastern Cordillera (including the recently created Parque Nacional Río Negro–Sopladora) serve as water reserves for important urban centres or hydropower (MAE, 2018; Weber et al., 2013).

Another important policy related to forest conservation is the incentive-based Socio Bosque program implemented by the Ministry of Environment of Ecuador. It aims to conserve a variety of ecosystems and improve local livelihoods by providing per hectare monetary incentives to landowners for conserving native forests and other ecosystems (Koning et al., 2011). In 2018, over 1.6 million hectares of native ecosystems have been protected under the SocioBosque program (MAE, 2019).

2.1.3.2 Forests for (potential) production

In contrast to many other tropical countries, a forest concession system for production forests does not exist in Ecuador. Instead, the 2 million ha of forest patrimony, which in theory is held by the government, as well as privately-held protection forests ("bosques protectores") can be used as production forests under a management plan (Añazco et al., 2010).

A legal and regulatory framework for forest management exists in Ecuador that includes the "Sustainable Forest Management Programme" (PAFSU) for mechanised logging and the "Simplified Management Programme" (PAFSI) for non-mechanised extraction (Weber et al., 2013). However, Ecuador does not have a large commercial forestry industry. This may be linked to logging permits being short-term in nature as well as difficult access to forest areas (Global Forest Atlas, 2019). Additionally, the normative frameworks in place are rather focused on harvesting forests, and not on managing them (Weber et al., 2013). As a consequence, silviculture aiming to enhance the economic value of natural forests tends to be neither scientifically investigated enough nor applied in practice. Knowledge on the distribution of tree species is one requirement for the development of scientifically sound silvicultural management techniques. For this, recent advances in species distribution modelling are promising.

2.2 Species distribution models (SDM)

The analysis in publication I (Kübler et al., 2016) was based on species distribution modelling, which has gained increased attention in literature over the last decades (Elith and Leathwick, 2009). Here, an overview on theoretical foundations and the importance for ecological research, conservation and sustainable management is provided. Then, I focus on two aspects that are relevant for this thesis: Applying of SDM at the local scale and SDM in TMF.

2.2.1 Theoretical foundations

Modern SDM are the result of the convergence of site-based ecology and advances in GIS and spatial data technologies (Elith and Leathwick, 2009). Their conceptual base originated in the niche concept as defined by Hutchinson (1957). He states that the niche is "the hypervolume defined by the environmental dimensions within which that species can survive and reproduce". The author further differentiated between the fundamental niche and the realized niche. The fundamental potential niche is defined as the response of species to environmental conditions in absence of biotic interactions. The realized niche also includes, besides the environmental conditions in which species can survive and reproduce, the effects of biotic interactions, such as competition or predation (Franklin and Miller, 2009).

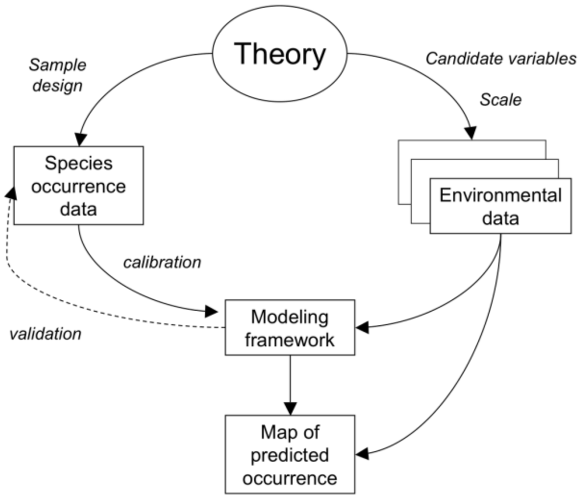

Figure 2: Diagram showing the components of species distribution modelling (Franklin and Miller, 2009).

SDM estimate the niche space occupied by species by linking known species occurrence or abundance with information on environmental conditions in a given study extent (Figure 2; Franklin and Miller, 2009). Based on this, species distributions, i.e. spatially explicit predictions of environmental suitability for species, can be derived. SDM are typically correlative, i.e. they employ a variety of algorithms to estimate statistical relationships between species observations and environmental conditions. It is worth mentioning that mechanical models (also known as process-based models or biophysical models) and expert-based SDM approaches also exist (Guisan et al., 2013).

2.2.2 Importance for ecological research, conservation, and sustainable management

SDM have been used for numerous different research and management applications across terrestrial, freshwater, and marine environments and at widely varying spatial and temporal scales (Elith and Leathwick, 2009). The raise of SDM over the past years has been facilitated by a growing number of well-tested and easy-to-implement modelling algorithms, ever-increasing accessibility of species occurrence information and spatially explicit environmental data as well as more performant software and computational resources (Sofaer et al., 2019). Two broad categories can be distinguished for the uses of SDM: Models for explanation and models for prediction.

2.2.2.1 Models for explanation

When primarily used for explanation, SDM generally have the objective to gain ecological and evolutionary insight or understand ecological relationships (Elith and Leathwick, 2009). Frequently, such models are used to infer which environmental factors define the niche of species and their importance for species distributions (Smith and Santos, 2019). Model outcomes have been used in a number of applications: Understanding evolutionary limitations and modes of speciation (e.g. Quintero and Wiens, 2013), disentangling scale dependencies in species environmental niches (e.g. Mertes and Jetz, 2018), and designing conservation strategies (e.g. Guisan et al., 2013).

2.2.2.2 Models for predictions

The main objective of SDM focusing on prediction is to derive mapped products of species distributions or environmental suitability for species, which can be used for biodiversity management, conservation and land management (Elith and Leathwick, 2009; Guisan et al., 2013; Sofaer et al., 2019). Compared to SDM for explanation, fitting and evaluating these prediction-oriented models have a larger focus on balancing the specific fit to the training data against the generality required for prediction. For this, methods based on holdout data (e.g. cross-validation) from data mining and machine learning are frequently employed for model fitting and evaluating predictive power. Ecological understanding, especially for the selection of predictors and interpretation of results, is still crucial for prediction-oriented SDM (Elith and Leathwick, 2009).

As information on species distributions underlies nearly every aspect of managing biodiversity, SDM for predictions have been used for a variety of applications (Guisan et al., 2013; Sofaer et al., 2019). Potential uses include the identification of biodiversity hotspots, delimitation of valued habitat types and identification of protected areas for the conservation of rare species (Franklin and Miller, 2009; Sofaer et al., 2019). Similarly, sites for habitat restoration and species reintroduction have been identified with prediction-oriented SDM (e.g. Zellmer et al., 2019). Further uses are predicting species responses to changing climate (e.g. Morelli et al., 2016), the anticipation and management of invasive species (e.g. Jones et al., 2010, Petitpierre et al., 2017), mapping the spread of vector-borne diseases (e.g. Kraemer et al., 2015), and designing surveys to find new populations of species (Williams et al., 2009). These examples show that SDM have a large potential to support spatial prioritization of decisions for management actions. Yet, there is still a lack of information on their applicability, relative utility and extent of adoption for a range of contexts in conservation decision making (Guisan et al., 2013).

2.2.3 Species distribution modelling in TMF

2.2.3.1 Potential applications of SDM

While there is a long research history for temperate forests about the relationship between the distribution of tree species and environmental variables (Ellenberg, 2009), the knowledge about this subject is scarce for TMF. Consequently, understanding tree diversity along elevational and latitudinal gradients and the mapping of distributions of key species were included in the research objectives that should be prioritized for the conservation and sustainable governance of forest landscapes in the Andes (Mathez-Stiefel et al., 2017). SDM have been successfully applied in other forest ecosystems to gain knowledge related to these research objectives. Further, SDM also have a great potential to support biodiversity conservation in the tropics, as they can aid in the development of conservation strategies, identify knowledge gaps and examine the potential impacts of environmental change (Cayuela et al., 2009). Additionally, species distribution modelling can be a valuable tool to support SFM (Pecchi et al., 2019).

Despite this potential, there are only few examples for the application of SDM in TMF (e.g. Armenteras and Mulligan, 2010). Yet, examples from other forest types exist, where SDM have been successfully applied for research and management. These examples include predicting the spatial distribution and environmental preferences of 10 economically important forest palms in western South America (Vedel-Sørensen et al., 2013), informing about the potential, realised and future distribution of *Pterocarpus angolensis* DC in southern Africa (Cauwer et al., 2014), assessing the importance of soils in predicting the future of plant habitat suitability in a tropical forest (Zuquim et al., 2019), determining the factors affecting the spatio-temporal dispersion of *Ips typographus* in Bavarian Forest National Park (Lausch et al., 2011), and the construction of species-specific seed transfer zones for ecological restoration (Crow et al., 2018).

2.2.3.2 Considerations of spatial scales

Spatial scale is important for ecological processes in general, and for the distribution of both species and environments in particular (Elith and Leathwick, 2009). For the analysis of species–environment relationships, there is growing evidence that an appropriate selection of two important components of scale is crucial: Extent and grain (Mertes and Jetz, 2018). The extent describes the total area under consideration (e.g. the size of a study area). It depends on the purpose of an analysis; for example, global change studies often have a continental or global extent, whereas studies with a focus on detailed ecological understanding tend to have a local or regional extent. The spatial grain refers to the minimum unit of spatial resolution (e.g. the cell size of raster data). Ideally, it should be consistent with the information content of the data (Elith and Leathwick, 2009). This is especially true for environmental variables with fine spatial structures, because aggregating them to a coarse analysis grain can result in a loss of information on fine-scale heterogeneity (Mertes and Jetz, 2018).

In TMF, where distinct habitat patches with differing environmental conditions tend to occur in a small-scale mosaic (Homeier et al., 2010), an adequately fine spatial grain seems particularly important for SDM. In that context, the application of very high resolution (VHR) digital elevation models (DEMs) has been investigated in mountain areas in recent years in an effort to achieve a more realistic representation of small-scale microenvironments in SDM (Camathias et al., 2013; Lassueur et al., 2006; Pradervand et al., 2014). VHR DEMs, which have emerged due to the development of airborne radar/laser scanning and have seen a rapid expansions in their availability in the last decade, typically have a resolution of 1 m (Lassueur et al., 2006). As a consequence, VHR predictors derived from such VHR DEMs better capture micro-environmental variation. Reports from literature have shown that using VHR predictors in SDM can lead to large improvements in model performance for some species and situations (Camathias et al., 2013; Pradervand et al., 2014). This seems to be especially true for species known to grow in micro-habitats associated with micro-topography (Pradervand et al., 2014).

Fine-scale topography having a large impact on tree species composition in TMF in general, and in our study area in particular (see Section 3.1), therefore indicates that the use of VHR predictors is advantageous when analysing how environmental factors shape the distribution of tree species. In Section 3.2.3, it is described in detail how VHR topographic predictors were derived and used in this thesis.

2.3 Silviculture in tropical forests and TMF

Numerous recent studies have suggested that the application of reduced-impact logging is not sufficient to sustain timber yields on the long term in tropical forests under current cutting cycle lengths (Nasi and Frost, 2009; Peña-Claros et al., 2008; Zimmerman and Kormos, 2012). Silvicultural treatments aiming at enhancing the growth and abundance of timber species are therefore a promising approach to contribute to the continued sustainability of forest management in the tropics (Fredericksen and Putz, 2003; Peña-Claros et al., 2008; Ruslandi et al., 2017). In this section, a short overview on silvicultural systems developed for tropical forests is provided first. Then, individual silvicultural treatments, which can be part of silvicultural systems, are presented.

It should be noted that over the last decades, the focus of silviculture has widened, with management goals now increasingly including the production of NTFPs and provision of other ESS (Weber, 2011). Especially in rural economies, NTFPs can be a significant complementary asset to timber production (Ashton and Hall, 2011). However, as the silvicultural treatment investigated in this thesis focuses on timber production, silviculture aiming at NTFP production or ESS protection is not a part of the overview provided in this section.

2.3.1 Silvicultural systems

Silvicultural treatments are usually not applied in isolation, but rather as part of a silvicultural system. To place the silvicultural treatments investigated in this thesis into the broader context of silviculture in the tropics, a short overview on different systems is provided in this section. Following Savill (2004), four types of systems can be distinguished: Selection systems, shelterwood systems, clear-cutting systems and coppice systems.

Selection systems (also called polycyclic systems) rely upon short cutting intervals to promote small gap disturbances that are distributed continuously over the whole area. This results in an opening up of growing spaces, which provide conditions for regeneration establishment (Ashton and Hall, 2011). Selection systems aim to maintain a stable and continuous forest environment with an intimate mixture of trees of all age classes (Savill, 2004). Forest types characterized by shade-tolerant and slower growing canopy trees as well as small and frequent disturbances regimes are well suited for these systems (Ashton and Hall, 2011).

Shelterwood systems (also called monocyclic systems), in contrast, rely on successive regeneration fellings in the overstorey to promote advance regeneration and, once established, removing the remaining overstorey to release the regeneration as a single cohort in a relatively uniform manner (Ashton and Hall, 2011; Savill, 2004). These systems tend to give rise to even-aged stands (Savill, 2004). Shelterwood systems are appropriate for forest types that are characterized by shade-intolerant canopy trees and driven by strong episodic disturbance regimes (Ashton and Hall, 2011).

Clear-cutting and coppice systems are mostly limited to plantation forestry in the tropics. Clear-cutting systems rely almost always on establishment by planting after the mature stand is cleared by a single harvesting operation (Savill, 2004). They are the prevalent silvicultural system in plantations managed for wood production. Coppice systems rely on regeneration of new shoots from the base of harvested stems, i.e. coppice shoots or root suckers. In the tropics, coppicing has been used for the production of pulpwood (e.g. from Eucalyptus) and fuelwood (e.g. from *Leucaena leucocephala*).

2.3.2 Silvicultural treatments for timber production

Following Putz (2004), two broad categories of silvicultural treatments focusing on timber production can be distinguished in the tropics: Treatments to improve stocking and treatments to improve growth.

2.3.2.1 Treatments to improve stocking

The main objective of silvicultural treatments to improve stocking is to secure an adequate regeneration for future harvests. For this purpose, natural regeneration is often preferred over artificial regeneration for a number of reasons. First, seed trees that successfully reproduce in a given environment are probably genetically well-adapted to local biotic and abiotic conditions. In contrast, site-species matching can be challenging in the case of artificial regeneration. Second, operations to promote natural regeneration have generally fewer negative impacts on biodiversity and ecosystem functioning than artificial regeneration. Third, natural regeneration is less expensive than artificial regeneration in most cases (Putz, 2004).

Adequate ecological and silvicultural knowledge is required to ensure that the treatments successfully regenerate commercial species without causing unnecessary harm to the forest ecosystem (Ashton and Hall, 2011). Where possible, treatments should take into consideration whether the understory contains advanced regeneration, i.e. populations of seedlings, saplings, and poles, or advanced residuals, i.e. subcanopy trees, of commercial species. During harvesting, damage to advanced regeneration and advanced residuals should be avoided as much as possible (Putz, 2004). For tree species with few seedlings in the advanced regeneration, it can be necessary to promote seed production and seedling establishment (Ashton and Hall, 2011). This is usually accomplished by retention of sufficient seed-producing individuals during harvesting operations (Putz, 2004).

Enrichment planting, in contrast, uses artificial regeneration to increase the stocking of desired tree species. In the tropics, it is predominantly applied in overexploited and secondary forests where natural regeneration is insufficient (Zimmerman and Kormos, 2012).

2.3.2.2 Treatments to improve growth

Silvicultural treatments to improve the productivity of commercial species typically influence the available growing space using some type of competition control. The underlying assumption is that by increasing the availability of light and soil resources, the growth, quality and health of remaining trees can be improved (Wadsworth and Zweede, 2006). Thinning operations achieve competition control by artificially reducing the number of trees growing in a stand. They can either be applied only in the vicinity of selected future crop trees (FCTs) or to the entire stand. Further, thinning operations can be characterized as commercial, when thinned trees are sold, and precommercial, when no merchantable material is removed from the stand (Putz, 2004).

In the tropics, liberation thinning[5], i.e. the liberation of selected FCTs, is likely to be the most common thinning operation in silviculturally managed forests (Putz, 2004). Several studies have shown that this treatment can

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[5] It is worth noting that similar silvicultural treatments have also been named improvement fellings in other sources (Guariguata, 1999; Günter et al., 2008; Wadsworth and Zweede, 2006). For consistency, I will use the term liberation thinnings throughout this thesis.

significantly increase the growth rate of FCTs (Ashton and Hall, 2011; Peña-Claros et al., 2008; Zimmerman and Kormos, 2012). Liberation thinning increases the access to light and soil resources for FCTs by releasing them from competition from immediate neighbours. As thinning is limited to the vicinity of FCTs, a portion of the stand remains untreated. This not only avoids unnecessary environmental disruption, but is also silviculturally and economically more viable (Putz, 2004). The selection of FCTs for liberation thinning is complex and should be carried out by trained staff. To increase the likelihood of improved volume growth, selected FCTs should not have been heavily suppressed for long periods of time. Crown form is a good indicator for suppression; trees with small and poorly formed crowns may do not respond well to the thinning operation (Putz, 2004). Further, it should be avoided to select trees with heavy vine infestation as FCTs. After selecting FCTs, competitors in the vicinity are removed by cutting, stem girdling or arboricides. The extent of opening depends on species as well as the size of the FCT to be released (Putz, 2004). It is possible that the benefits of a liberation thinning do not persist over time; in that case, it may be necessary to repeat liberation thinnings for maximum stand production (Graaf et al., 1999; Zimmerman and Kormos, 2012).

Thinning operations applied to the entire stand are not very common in tropical managed forests, because they can lead to retention and growth of lower branches, increased stem taper, abrupt changes in wood properties as well as increased susceptibility to windthrow and weed encroachment (Putz, 2004). It should be pointed out that timber harvesting can be comparable to a heavy thinning; its impact on growth of retained trees can be similar to what has been observed in other thinning operations (Avila et al., 2017). In that sense, timber harvesting can be considered the primary thinning treatment in tropical forests (Putz, 2004).

It is important to point out that thinnings are not always guaranteed to result in a positive growth response. For example, previously suppressed FCTs may show no growth increase after thinning, or even a decrease in growth, if they are too rapidly exposed to the post-thinning environment characterized by higher light intensities and higher temperatures (Putz, 2004).

Weed control, i.e. mechanically or chemically removing weeds that interfere with FCTs, is another silvicultural treatment that can lead to improved growth in managed tropical forests. This also applies to pre-felling cutting of woody vines. In stands with vine infestations, often caused by uncontrolled logging in the past, it can be advantageous to carry out this silvicultural treatment before timber harvesting. Its primary objective is generally to reduce post-felling logging damage to the remaining stand, but the treatment can also increase growth rates (Peña-Claros et al., 2008; Putz, 2004; Weber, 2011).

2.3.3 Silvicultural treatments in TMF

Silvicultural systems and treatments for timber production described in this section are currently not components of reduced-impact logging, forest certification under FSC or SFM (Zimmerman and Kormos, 2012). In consequence, they are only employed in a small fraction of tropical forests that are considered to be “managed” (Ashton and Hall, 2011). For TMF, the overall lack of silvicultural research also applies to silvicultural treatments; there is almost no knowledge on the effect of specific silvicultural treatments on forest stands in TMF (Bruijnzeel et al., 2011a; Günter et al., 2008; Weber et al., 2013). Under such conditions, Hutchinson (1988) suggests that silvicultural investigations should start by studying the impact of individual silvicultural treatments. Once the effects of these treatments are reasonably well understood, a tentative silvicultural system combining individual treatments can be developed and tested in different forest stands. In line with that, a silvicultural experiment to investigate the impact of liberation thinning on tree growth was established in southern Ecuador in 2003 (Günter et al., 2008). To my knowledge, this was, and still is up to this date, the first scientific experiment on silvicultural treatments in TMF. It provides the data basis for this thesis and is presented in detail in Section 3.2.1.

3 Material and methods

This chapter gives an overview of the study area as well as data sources and analytical approaches used in publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020). As this thesis was embedded in a wider interdisciplinary research context (see Textbox 2), long-term data on the silvicultural experiment and remote sensing data from project partners were available for my research. For the sake of transparency, throughout this section I will state whether work has been carried out by project partners or me. Further, the main focus of this section is on methods applied in Kübler et al. (2016) and Kübler et al. (2020). Hence, data collection methods used by project partners are only briefly mentioned.

Textbox 2: The research presented in this thesis was carried out in the framework of the DFG-funded interdisciplinary research unit 816 “Biodiversity and Sustainable Management of a Megadiverse Mountain Ecosystem in South Ecuador”. The main focus of the research unit was on the identification of characteristics of science-based sustainable land use management systems that should inform conservation decisions in the biodiversity hotspot of the South Ecuadorian Andes (Bendix et al., 2013). These management systems should preserve biodiversity and ESS, rehabilitate degraded biodiversity and lost land usability, and improve livelihoods for the local population. More specifically, within the research unit my work was embedded in the subproject “Exploration and consolidation of silvicultural knowledge for sustainable management of forest sites in the South Ecuadorian Andes”. The subproject aimed at building-up silvicultural and ecological knowledge needed for the sustainable management of different forest resources in southern Ecuador.

The overall methodological approaches of Kübler et al. (2016) and Kübler et al. (2020) showed some similarities (Figure 3): 1) Analyses were quantitative in nature, 2) the focus was on inference (and not prediction), 3) the relationship between tree-based data (i.e. diameter growth and spatial locations of trees, see Sections 3.2.1 and 3.2.2) and topographic variables (see Section 3.2.3) was statistically described.

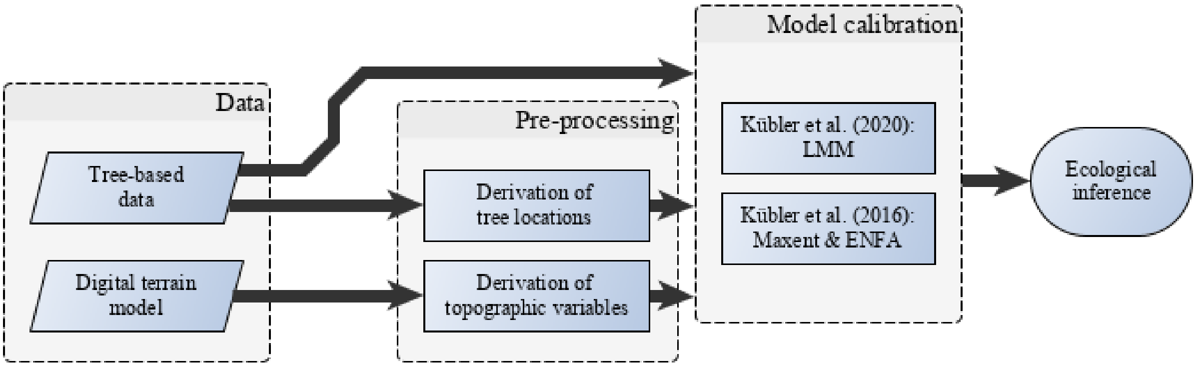

Figure 3: Flowchart of the overall methodological approach of publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020).

3.1 Study area

The research presented in this thesis was carried out in the “Reserva Biológica San Francisco” (RBSF, Figure 4 and Figure 5). It is located in the Cordillera Real in the South Ecuadorian Andes, along the road between the towns Loja and Zamora in the Zamora-Chinchipe Province, bordering on the North of the Podocarpus National Park.

The RBSF has seen more than 15 years of comprehensive interdisciplinary research. The core area of research activities is around the research station “Estación Científica San Francisco” (ECSF). Focal experimental sites in the natural forest of the RBSF range from 1,600 to 3,140 m a.s.l. (Bendix et al., 2013).

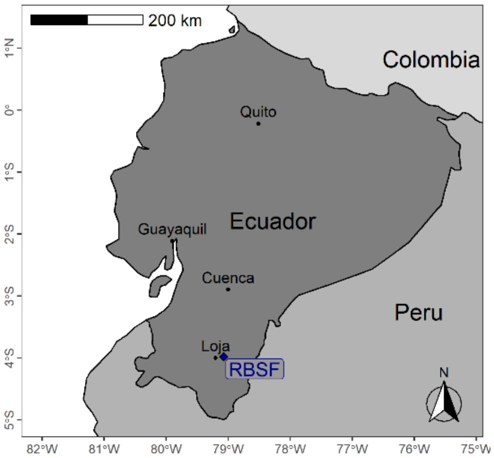

Figure 4: The study area “Reserva Biológica San Francisco” (RBSF) in Ecuador.

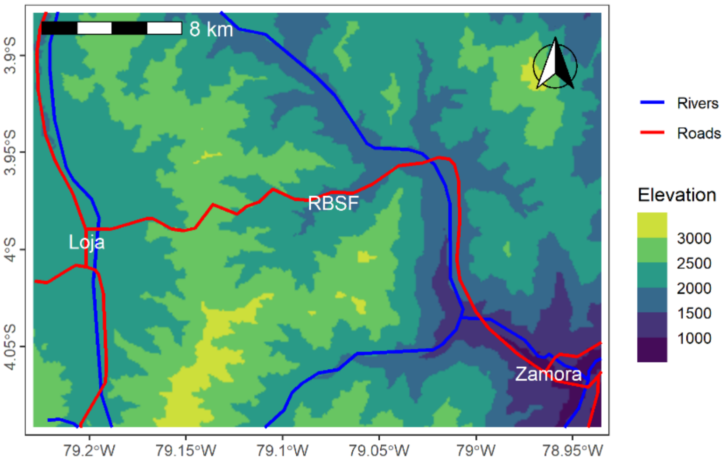

Figure 5: Map of the study region in southern Ecuador.

3.1.1 Climate

Air temperature in the Andes of Ecuador is mostly governed by altitude, with an altitudinal gradient ranging from “tierra caliente” (below 1100 m a.s.l.; annual average temperature between 25 °C and 19 °C) to “tierra templada” (1100–2200 m a.s.l.; 19–13 °C), “tierra fría” (2200–3800 m a.s.l.; 13–6 °C), “tierra helada” (3800–4800 m a.s.l., 6–0 °C) and “tierra nevada ” (> 4800 m a.s.l.). The RBSF lays within the tierra templada and tierra fría (Beck et al., 2008a).

Rainfall in the vicinity of the RBSF shows a marked gradient over a short distance, with the driest point (Catamayo, 383 mm a^{-1}) being only 30 km away from the wettest point (Cordillera Real, 6000 mm a^{-1}). In the RBSF at 1952 m a.s.l., mean annual precipitation is 2100 mm. There is some seasonal variation, with a wet season from April to July and a less humid period from September to December (Bendix et al., 2006).

3.1.2 Natural vegetation

The ecosystem of the RBSF can be classified as “tropical mountain rain forest” (Figure 6; Beck et al., 2008a). However, (mostly) undisturbed natural forest can only be found on the NNW-facing slopes of the San Francisco valley; most of the SSE-facing slopes have been replaced by anthropogenic replacement systems. Further, an altitudinal divide in forest cover has been observed in the region: Above 2,200 m a.s.l. forest cover was 85.4%, whereas below that altitude it was only 45.2%. (Göttlicher et al., 2009). The treeline in the study region, located between 2800 m and 3300 m a.s.l., shows an extraordinary species diversity. This indicates that the ecotone is not affected by temperature or dryness, but rather by strong wind and exceptional high moisture causing water-logging of the soils (Beck et al., 2008a). It is worth noting that the Andes of southern Ecuador are especially high in biodiversity and endemism (Bendix et al., 2013). This can be, in part, explained by high topographic fragmentation, which results in a small-scale mosaic of different habitats with numerous isolated basins and ridges (Homeier et al., 2010).

The natural forest of the RBSF can be classified as lower and upper mountain rain forest, with a limit at around 2150 m a.s.l. between the two forest types. A finer altitudinal zonation of forest types is difficult due to the high climatic and topographic heterogeneity. Instead, it is more sensible to differentiate between the dense ravine forests and more open ridge forests (Beck et al., 2008a).

Homeier et al. (2008) further categorized the ravine and ridge forest formations into five forest types based on floristic composition. Three of these forest types can be found in the elevation range of the silvicultural experiment (1850–2150 m a.s.l.; see Section 3.2.1). Forest type I grows in major ravines and gentle lower slopes on altitudes below 2200 m a.s.l. and is the tallest and most speciose forest. The canopy in this forest type reaches 25–30 m, with some emergents reaching up to 35 m. Common trees of this forest type include *Piptocoma discolor* (Asteraceae), *Handroanthus chrysanthus* (Bignoniaceae), *Hyeronima asperifolia* and *Sapium glandulosum* (Euphorbiaceae), *Nectandra linneatifolia* and *N. membranacea* (Lauraceae), *Meriania* sp., *Miconia punctata* and other *Miconia* spp (Melastomataceae), *Inga* spp (Mimosaceae), *Morus insignis*, *Naucleopsis glabra*, and *Ficus* spp (Moraceae), *Prumnopitys montana* (Podocarpaceae), *Micropholis guyanensis* (Sapotaceae) and *Heliocarpus americanus* (Tiliaceae). After the formation of gaps, distinct succession phases can be observed in Forest type I, with fast-growing pioneer species (e.g. *Piptocoma discolor*, *Cecropia andina*, *Heliocarpus americanus*) being subsequently replaced by late-successional species and long-lived pioneers such as *Handroanthus chrysanthus* and *Cedrela* sp. (Homeier et al., 2008).

Figure 6: Aspects of the TMF in the study area. Top: View on the RBSF from a pasture area. Middle: Tree with dendrometer in Forest type I. Bottom: Example of Forest type II.

Forest type II can be found on upper slopes and ridges between 1900–2100 m a.s.l., with a canopy height of 15 m. This forest type, characterized by a thick humus layer, is dominated by the tree species *Alzatea verticillata* (Alzateaceae), *Dictyocaryum lamarckianum* and *Wettinia aequatorialis* (Arecaceae), *Weinmannia pinnata*, *W. sorbifolia* and *W. spruceana* (Cunoniaceae), *Abarema killipii* (Fabaceae), *Hyeronima moritzinana* (Euphorbiaceae), *Ocotea aciphylla* (Lauraceae), *Graffenrieda emarginata* and *Miconia calophylla* (Melastomataceae), *Podocarpus oleifolius* (Podocarpaceae) and *Matayba inelegans* (Sapindaceae). In contrast to Forest type I, early and late successional phases show a similar species composition in Forest type II (Homeier et al., 2008).

In Forest type III, found between 2100 and 2250 m a.s.l., the trees usually do not surpass 12 m. Characteristic tree species include *Hedyosmum translucidum* (Chloranthaceae), *Clusia* cf *ducuoides*, *Clusia* spp and *Tovomita weddeliana* (Clusiaceae), *Weinmannia haenkeana* and *W. ovata* (Cunoniaceae), *Purdiaea nutans* (Clethraceae), *Alchornea grandiflora* (Euphorbiaceae), *Endlicheria oreocola*, *Licaria subsessilis*, *Ocotea benthamiana* and *Persea subcordata* (Lauraceae), *Eschweilera sessilis* (Lecythidaceae), *Graffenrieda emarginata* (Melastomataceae), *Calyptranthes pulchella* and *Myrcia* sp. (both Myrtaceae) and *Podocarpus oleifolius* (Podocarpaceae).

3.1.3 Land use

Land use in the larger vicinity of the RBSF is varying and depends mainly on local climatic conditions. A field rotation system with two harvests per years is possible in arable lands in the valley bottoms to the east of the Cordillera Real. The drier western part of the Cordillera Real, in contrast, allows for only one harvest of field crops per year, followed by a longer fallow. In that drier part, sugar cane is grown on irrigated fields on alluvial soils. In the humid Zamora valley, orchards with coffee, bananas and other fruits can be found. Throughout the humid parts of the region, pasture systems provide fodder for cattle herds (Beck et al., 2008a).

In the close vicinity of the RBSF, the native TMF has been cleared mainly for pasture land (Bendix et al., 2013; Tapia-Armijos et al., 2015), with principal drivers being colonisation laws and land reforms, population pressure, the existence of state-owned land and unclear property regimes as well as improved accessibility to forest areas (Bendix et al., 2013). It should be noted that this mode of land use is not sustainable; fire is used to clear the forest and maintain pastures, which results in the invasion of fire-resistant weeds. Subsequently, pastures frequently have to be abandoned after 10 years or less (Beck et al., 2008a; Bendix et al., 2013). Weber et al. (2013) argue that this substantial and growing reservoir of unproductive land in the study region should be reintegrated into the production area. Attempts to reforest abandoned pasture areas with *Pinus patula* or various species of Eucalyptus seem successful in early stages, but plantations frequently suffer from mineral deficiency in later stages (Beck et al., 2008a). Reforestation attempts with *Alnus acuminata* and other indigenous tree species proved promising (Aguirre, 2007; Knoke et al., 2014; Palomeque, 2012).

3.2 Data sources and pre-processing

Publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020) relied on data from a long-term silvicultural experiment in the RBSF in general and tree locations within the experiment and high-resolution topographic data in particular. In this section, these data sets are presented in detail.

3.2.1 Silvicultural experiment

The silvicultural experiment was established in 2003 in visibly undisturbed natural forest of the RBSF to study the effect on tree growth and ecological impact of a moderate liberation thinning (Günter et al., 2008). At the start of the experiment, 52 permanent sample plots with an area of 0.25 ha each were installed. The total sample area was 13 ha on the ground, which corresponds to 11.1 ha in projected map view[6]. Plots were distributed over three adjacent microcatchments named MC2, MC3 and MC5, with sample areas of 5, 4 and 4 ha on the ground, respectively (Figure 7). The elevation of the permanent sample plots was 1850–2150 m a.s.l. and the maximal distance between farthest points 870 m (east–west direction, projected map view).

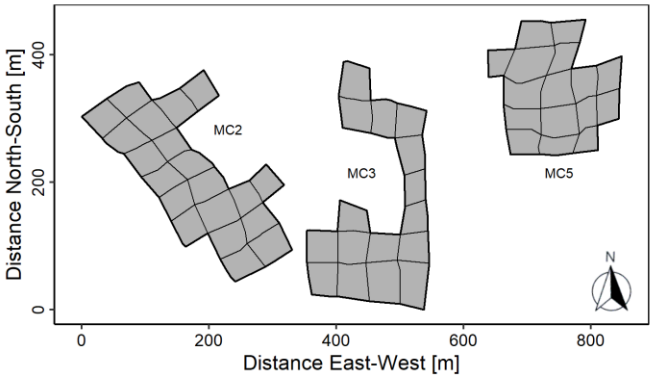

Figure 7: Location of the 52 permanent sample plots of the silvicultural experiment in microcatchments MC2, MC3 and MC5.

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[6] The difference between "on the ground" and "map view" area is due to actual ground distances being used as the metric for the establishment of the permanent sample plots. As maps represent plane distances, these actual distances on the ground exceed map distances according to the steepness of the terrain.

All trees with a diameter at breast height (DBH) ≥ 20 cm were measured for DBH, mapped (see Section 3.2.2), individually labelled, and identified to species level. Trees with DBH < 20 were not assessed on the whole sample plot area, but on smaller subplots; however, these data were not used in Kübler et al. (2016) nor Kübler et al. (2020).

In 2004, a total of 449 potential crop trees (PCTs, similar to FCTs presented in Section 2.3.2.2) from a pool of nine different species were selected. These species were *Cedrela montana*, *Clusia ducuoides*, *Ficus citrifolia*, *Handroanthus chrysanthus*, *Hyeronima asperifolia*, *Hyeronima moritziana*, *Inga acreana*, *Nectandra membranacea* and *Podocarpus oleifolius*. They were selected based on their (potential) commercial value and, where possible, additional ecological and/or medicinal importance. Criteria for the selection of individual trees as PCTs were a straight butt log, single leading stem, small branches and no defects.

A liberation thinning was applied to 205 PCTs in a campaign between April and May 2004 (Günter et al., 2008). For this, the strongest competitor in the upper canopy of each selected PCT was determined based on tree form, crown diameter and social position within the forest stand (Figure 8). These competitors were then removed using directional felling to minimize damage to the residual stand. A total of 244 PCTs in MC2, MC3 and MC5 remained as reference trees without silvicultural treatment (Table 1). Different treatment intensities were applied in the micro-catchments to study the influence on water fluxes at the catchment level (Wilcke et al., 2009). MC2 served as reference area without any treatment and MC3 and MC5 as areas of moderate and intense liberation thinning, respectively.

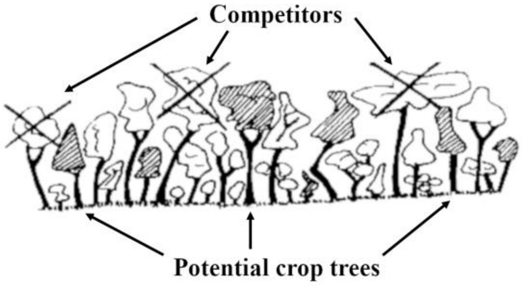

Figure 8: Scheme of the liberation thinning applied in the silvicultural experiment. Adapted from Cabrera et al. (2019).

Table 1: Overview of treatment intensity and removed basal area (adapted from Günter et al., 2008). Basal area (BA) values represent all trees and palms with DBH ≥ 20 cm).

	MC2	MC3	MC5
Size (ha)	5	4	4
PCTs	136	133	180
Released PCTs	-	76	129
Reference PCTs	136	57	51
Pre-treatment BA (m²/ha)	17.4 (±1.7)	10.3 (±0.8)	24.3 (±1.8)
Removed trees/ha	-	18	32
Removed BA/ha (m²/ha)	-	0.62 (±0.16)	2.5 (±0.64)
Ratio of removed BA/ha to pre-treatment BA/ha (in %)	-	6.0	10.3

Home-made steel band dendrometer were installed on each PCT at breast height (1.30 m above ground) or above buttresses or other irregularities, if present. The dendrometer were fitted six months prior to the silvicultural interventions, because newly installed dendrometers often underestimate radial growth (Pélissier and Pascal, 2000). Subsequently, growth has been measured once per month.

3.2.2 Tree locations

In publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020), tree-based data from the silvicultural experiment were spatially linked to high-resolution topographic variables (see Section 3.2.3). It was therefore crucial to obtain data on tree locations that were accurate and precise. This was challenging due to the steepness and high topographic fragmentation of the terrain. Common methods for tree mapping in permanent sample plots, such as the installation of regular grids and sub-grids as a reference system, were not feasible under such conditions. Instead, the method of traversing, which is better suited in undulating and steep terrain (Basak, 2014), was used to determine tree locations.

For traversing, multiple trees in close proximity were spatially linked through a single "traverse network", i.e. a series of connected lines forming a closed circuit. The length, azimuth and inclination of these connected lines were measured using a Vertex III and a survey compass. This form of traversing, where the finishing point coincides with the starting point, is called a closed traverse (Basak, 2014). Additionally, reference points within the permanent sample plots were registered with a differential GNSS (Trimble GPS Pathfinder Pro) in 2009. Each tree and reference point in the permanent sample plots was included in at least one traverse network. In total, 53 reference points and around 2000 traverse networks consisting of around 7500 single observations of length, azimuth and inclination from three field campaigns (2004, 2008 and 2009) were used for computation.

To compute tree coordinates, I applied an angle adjustment method. For this, the sum of the measured interior angles was first calculated for each traverse network. This sum was then compared to the geometrically correct total sum of interior angles for the network, i.e. $(n - 2) \times 180°$, where n is the number of sides of the network. The difference between the two sums describes the angular misclosure. Each measured angle within a traverse network was adjusted by the result of the division of the angular misclosure by the number of interior angles (Basak, 2014).

Subsequently, I computed tree coordinates iteratively using the angle-adjusted traverse networks and reference points. In the first iteration, only traverse networks containing reference points were included. For a given traverse network, the geographic latitude and longitude of each tree in the network was calculated with respect to the coordinate of the reference point using trigonometric functions. The next iteration included all traverse networks with at least one known tree coordinate, as computed during the previous iteration. Coordinates for all trees in these networks were calculated and the next iteration started. This process was repeated until coordinates for all trees in the data sets were available.

The computation method required as few iterations as possible, which in turn minimized the accumulation of errors throughout the process. For error estimation, it proved useful that the position of some trees could be calculated starting from two different reference points in the same number of iterations. Such trees therefore had two associated coordinates. The Euclidean distance between these pairs of coordinates were used as a proxy for precision. Distances between pairs of coordinates were in the range of 2 to 10 m, which proved satisfactory for the analyses carried out in Kübler et al. (2016) and Kübler et al. (2020).

3.2.3 Topographic variables

For the statistical analyses in Kübler et al. (2016) and Kübler et al. (2020), it was crucial to select environmental predictors that are relevant to the ecological processes being investigated (Elith and Leathwick, 2009). Topography plays an important role for many ecological processes in TMF in general (e.g. Baldeck et al., 2013; Takyu et al., 2002), and in the RBSF in particular (e.g. Ließ et al., 2011; Oesker et al., 2008). For the research questions raised in this thesis, it is of special interest that in TMF, topography has an reported effect on tree growth (Bellingham and Tanner, 2000; Bräuning et al., 2008) and the distribution of tree species (Homeier et al., 2010; Lassueur et al., 2006; Lippok et al., 2014). Therefore, topographic variables were used as proxies for environmental factors in Kübler et al. (2016) and Kübler et al. (2020).

The importance of appropriate spatial scales for SDM was illustrated in Section 2.2.3.2. This is especially true for the area of the silvicultural experiment in the RBSF, which 1) does have an extraordinarily small spatial extent compared to common study area sizes in SDM, and 2) is characterized by high topographic fragmentation resulting in a small-scale mosaic of different habitats. Under such conditions, the use of very high resolution (VHR) predictors seemed appropriate (Lassueur et al., 2006). In this section, the underlying data source as well as methods for the derivation of VHR topographic variables are presented.

3.2.3.1 Data source

I derived all topographic variables from a Digital Terrain Model (DTM), which is a digital description of the terrain surface using a set of heights over 2D points residing on a reference surface (Hirt, 2014). To create the DTM, Silva et al. (2015) applied linear interpolation to point cloud data from a helicopter-based LiDAR survey in the RBSF from 2012. As airborne LiDAR can penetrate forest cover, the resulting DTM represents the bare ground surface without vegetation. The quality of the DTM was assured by visual inspection, correction of classification and ghost reflections as well as removal of artefacts due to misclassification, resulting in a horizontal accuracy within 5 cm. The final DTM is a rectangular raster grid with a spatial resolution of 1 m, i.e. it can be described as VHR (Lassueur et al., 2006).

3.2.3.2 Derivation of variables

The following topographic variables were derived: Elevation, Topographic Position Index (TPI), aspect, SAGA Wetness Index (WI) and slope (Figure 9). Kübler et al. (2016) included all five variables in the statistical analysis, whereas Kübler et al. (2020) only included elevation and TPI. Variable selection was based on assumed ecological relevance (see Table 2). The area modelled in Kübler et al. (2016) and Kübler et al. (2020) corresponds to the area of the permanent sample plots of the silvicultural experiment. However, some of the topographic variables use a moving window for their calculation and are therefore sensitive to edge effects. To prevent this, a buffer of 1 km around the permanent sample plots was used for spatial processing. Subsequently, the resulting topographic variables were clipped to the modelled area.

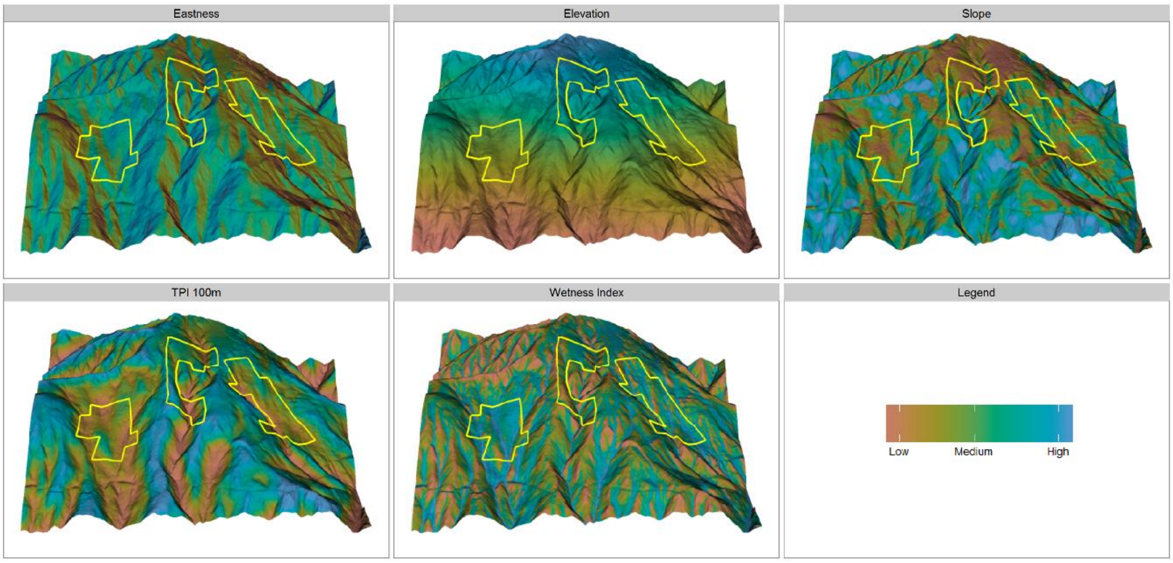

Figure 9: Maps of the topographic variables used for the analyses in publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020). Yellow lines show the permanent sample plots of the silvicultural experiment. For better visualization, the 3D maps show a view on the NNW-facing slopes of the RBSF, i.e. the orientation is reversed compared to the 2D maps in this thesis.

Topographic variables were calculated using the open source software SAGA GIS (SAGA Development Team, 2008) and the R-package "RSAGA" (Brenning, 2008). More detailed information on calculation methods for each variable is presented in Table 2.

Table 2: Overview of topographic variables, their calculation methods and ecological relevance in the RBSF.

Variable	Calculation method	Ecological relevance
Aspect (Eastness)	A 2nd degree polynomial fit was used to calculate aspect. Subsequently, the circular variable aspect was converted into northness and eastness by using the sine and cosine transformations, respectively. These two variables quantify the degree to which the aspect is north and east.	Eastness has an ecological importance as prevalent wind direction and climate influence is usually in an east-west gradient in the RBSF (Rollenbeck, 2006). In contrast, values for northness show little variation between permanent sample plots because they are located on a northern flank. Northness was therefore not included in the analysis.
Elevation	The pixel values of the DTM correspond to elevation.	In the RBSF, elevation impacts tree growth (Bräuning et al., 2008; Homeier et al., 2010) and the spatial distribution of tree species (Homeier et al., 2010).
SAGA Wetness Index	The SAGA Wetness Index is calculated similarly to the more commonly used Topographic Wetness Index, but is based on a modified catchment area calculation (Böhner et al., 2002).	Soil moisture is an important factor structuring local pattern of species distributions (Pélissier et al., 2002). The SAGA Wetness Index represents relative local soil moisture availability.
Slope	For the calculation of slope, a 2nd degree polynomial fit was used.	Slope is an indicator of the intensity of gravitational and disturbance processes acting upon vegetation, which play an important role in the RBSF (Muenchow et al., 2012; Vorpahl et al., 2012).
TPI	The TPI expresses whether a given pixel is in a valley/lower slope (negative values of TPI), midslope (values around zero of TPI) or ridge/upper slope (positive values of TPI) compared to surrounding pixels (Guisan et al., 1999). The TPI is scale-dependent; for its calculation, a moving circular window is used, whose size can be varied. In a pre-analysis, I assessed different sizes ranging from 50 to 400 m for plausibility and retained a TPI with a moving window of 100 m radius.	The topographic position has a strong influence on numerous biotic and abiotic factors in the RBSF (Vorpahl et al., 2012; Werner et al., 2012; Wilcke et al., 2011), including tree growth and species distribution (Homeier et al., 2010; Svenning et al., 2009).

Cross-correlation between topographic variables was relatively low (Table 3). This is important, because the modelling approaches employed in this thesis are susceptible to multicollinearity in predictors (Elith et al., 2011; Zuur, 2009).

Table 3: Pearson correlation coefficients of the topographic variables. All correlations are significant.

	Eastness	Elevation	Slope	TPI 100m
Elevation	-0.03			
Slope	0.07	-0.17		
TPI 100m	-0.03	0.45	-0.21	
Wetness Index	-0.05	-0.33	-0.26	-0.39

Within the research unit, multiple spatially explicit numerical models on environmental conditions, such as precipitation (Fries et al., 2014), soil properties (Ließ et al., 2011) and landslide risk (Vorpahl et al., 2012) have been developed. However, these models proved to be not viable for the analyses in this thesis for two reasons. First, the spatial resolution was too coarse (i.e. 10x10 m or 20x20 m). Second, the environmental conditions in these models were estimated using some type of topographic variables as predictors, and in consequence they are very highly correlated with the topographic variables used in Kübler et al. (2016) and Kübler et al. (2020).

3.3 Statistical analysis

A detailed description of the analyses is available in the individual papers in the appendix. Here, a short overview is provided.

3.3.1 Spatial distribution of tree species

In publication I (Kübler et al., 2016), the spatial distribution of the 16 most abundant tree species in the RBSF and its relationship with topographic variables was evaluated at a fine-scale ecological level using two presence-only species distribution modelling techniques: The maximum entropy model (Maxent) and the ecological niche factor analysis (ENFA). The analysis consisted of three steps: 1) Compilation of species occurrence data and environmental predictor variables, 2) fitting of SDM, and 3) model evaluation and inference.

3.3.1.1 Compilation of species occurrence data and environmental predictor variables

The locations in the permanent sample plots of all individual trees with DBH ≥ 20 cm of the 16 tree species were used as the occurrence data for the SDM (Figure 10). Total occurrence of each species ranges from 55–196 trees, corresponding to 4.95–17.66 trees / ha. The 16 tree species represent 49% of abundance and 52% of basal area of all trees with DBH ≥ 20 cm in the permanent sample plots.

All five topographic variables (elevation, TPI, aspect, SAGA Wetness Index and slope; see Section 3.2.3) were used as environmental predictor variables.

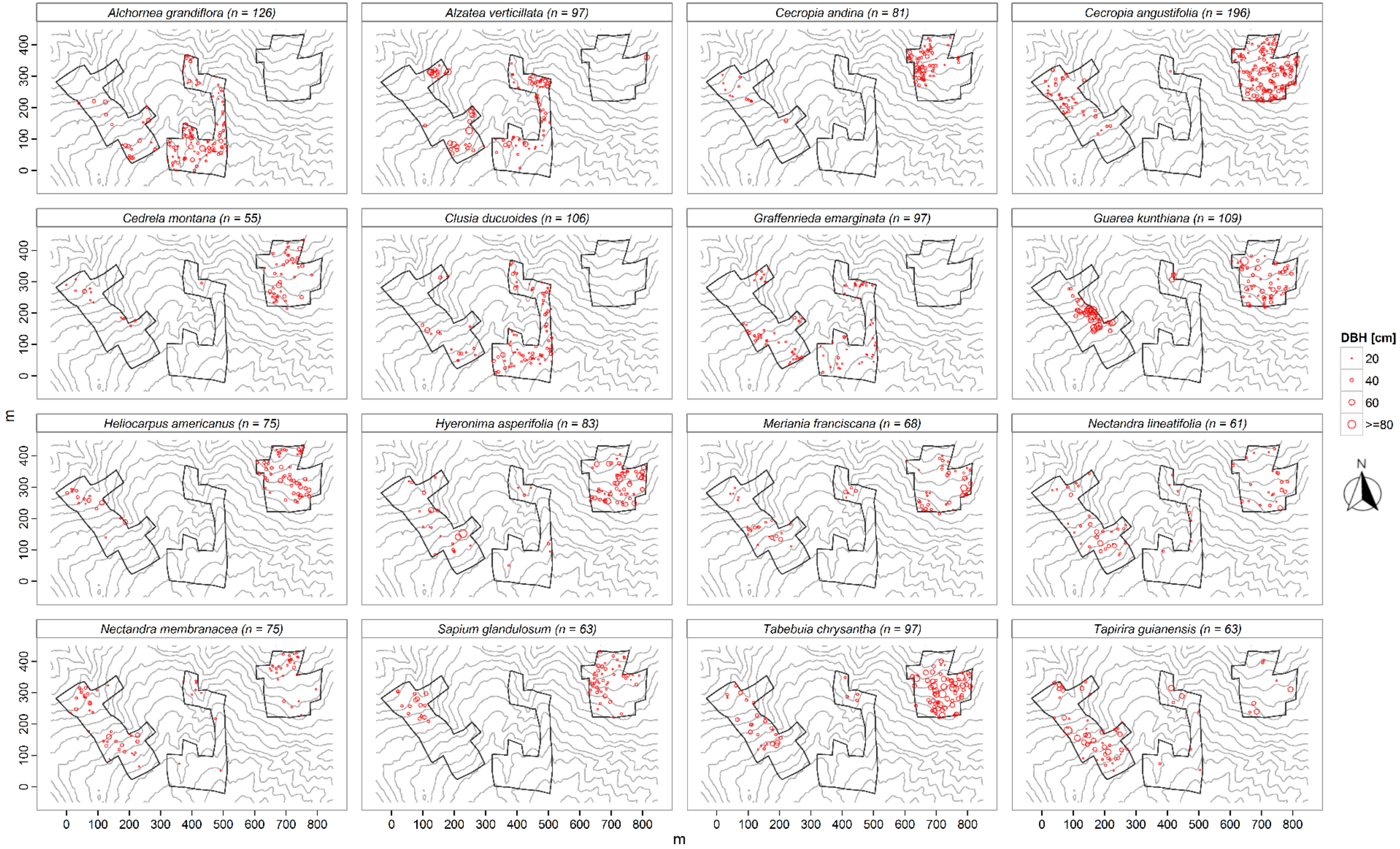

Figure 10: Stem distributions of all trees with DBH ≥ 20 cm on the permanent sample plot in the RBSF for the 16 most abundant tree species. Each red circle represents one tree; the size of the circle shows the DBH of trees. Grey lines are elevation contour lines at 20-m intervals. Black lines are limits of the permanent sample plots.

3.3.1.2 Model fitting

Models were fitted using Maxent software (version 3.3.3k; Phillips et al., 2006) and R-packages “adehabitat” (Calenge, 2006) and “dismo” (Hijmans et al., 2013).

Maxent is a machine-learning technique that fits a probability distribution of species occurrence with environmental layers over the entire study area (Peterson, 2006). It does not only perform well in comparison to other presence-only SDM algorithms (Elith et al., 2006; Hernandez et al., 2008; Pearson et al., 2007; Wisz et al., 2008), but also allows to infer the importance of environmental variables for species distribution (Elith et al., 2011). The following configuration was used for the analysis:

- Maxent allows for different “feature types” (linear, product, quadratic, hinge, threshold and categorical) to describe the relationship between the probability of occurrence and an environmental variable. Models with simple features only (linear, product and quadratic) had a similar performance as models with more complex features (hinge, threshold and categorical), but seemed ecologically more sensible and much less prone to overfitting. Therefore, only models fitted with simple feature types were reported.
- Maxent uses random background samples for the model fitting process (Elith et al., 2011). I created 10,000 random samples within the modelled area with the R-package “dismo” (Hijmans et al., 2013), which were also used during the evaluation of model performance (see below).
- All other settings were left on default: Convergence threshold (0.00001), maximum iterations (1,000), and regularization multiplier ($r = 1$).

The ENFA compares the ecological conditions of sites where a species occurs with conditions of the entire study area (Hirzel et al., 2002). It is well suited for determining the importance of environmental variables for the characterization of the ecological niche of a given species (Basille et al., 2008). For the ENFA, all settings were left on default.

3.3.1.3 Model evaluation and inference

To evaluate different aspects of predictive performance, multiple approaches were used (Elith and Graham, 2009). The true skill statistic (Allouche et al., 2006) and area under curve (AUC) of the receiver operator characteristic (ROC, Fielding and Bell, 1997) were used as evaluation metrics. These were calculated for 1) final models (created with the complete available dataset), 2) different permutations of null-models to test if the final models differ significantly from what would be expected by chance alone (Raes and ter Steege, 2007), 3) randomly split k-fold cross validation data partitions (Fielding and Bell, 1997) and 4) spatially separated data partitions to examine the effect of spatial autocorrelation on model performance (Veloz, 2009).

Additionally, the ecological realism of models was evaluated by comparing our models with results previously obtained by Homeier et al. (2008) and Homeier et al. (2010). Those authors described three different forest types in the elevation range of our permanent sample plots (1850–2150 m a.s.l.; see Section 3.1.2) and assigned each species to one or multiple forest types. To translate SDM outcomes into distinct groups of tree species, we performed a hierarchical cluster analysis based on values of the ENFA marginality factor of each species and topographic variable. We then assessed if these cluster groups agreed with the previously defined forest types (Homeier et al., 2008). Further, we explored for each species to what extent the grouping based on ENFA models concurred with the classification of Homeier et al. (2010).

For inference, the importance of each topographic variable was assessed for each species for both SDM algorithms. For Maxent, this was achieved using a jackknife test that builds several models using the same occurrence data, but a different set of predictor variables. At first, models for each species were created excluding one variable each run and then, models were run with only one variable at a time. Finally, the regularized training gain of those different models and models created with all predictor variables were compared for each species. For the ENFA, the absolute value of the "marginality" was reported as a proxy for the ecological importance of a topographic variable for a given species (Hirzel et al., 2002). For its calculation, the environmental variables are reduced to a small number of orthogonal factors. The marginality is the first factor that contains most of the information. Negative and positive coefficients of marginality indicate that a species prefers lower and higher values of an environmental variable, respectively (Basille et al., 2008).

3.3.2 Growth of potential crop trees (PCTs)

In publication II (Kübler et al., 2020), the relative effects of silvicultural treatments and topography on growth rates at the tree level in the RBSF were studied. In this section, 1) the compilation of tree growth data, 2) selection of predictors, 3) the applied linear mixed-effect model (LMM) and 4) model evaluation and inference are described.

3.3.2.1 Compilation of tree growth data

Tree growth data consisted of monthly registrations of dendrometers between June 2004 (i.e. when silvicultural treatments were applied) and April 2010 for all PCTs in the silvicultural experiments (see Section 3.2.1). The outcome variable of the LMM was the periodic annual increment (PAI) in DBH over the total time period for each individual tree, which were the independent sampling units of observation in the statistical analysis.

The following PCTs were removed from the analysis: 1) Reference trees with a distance of less than 20 m from an improvement felling (n = 13), 2) all trees of *Ficus citrifolia* (n = 20), because only four PCTs had been released for this species, and 3) all PCTs that have died over the monitoring period ($n_{reference}$ = 9; $n_{released}$ = 8). This resulted in a total of 399 PCTs from eight species included in our study. For trees with DBH ≥ 20 cm, the PCTs in Kübler et al. (2020) comprised 18.8% of the total number of trees and 19.6% of the total basal area per hectare of the initial forest stand. For all PCTs in this study, the location, species and applied silvicultural treatment are shown in Figure 11 and Table 4.

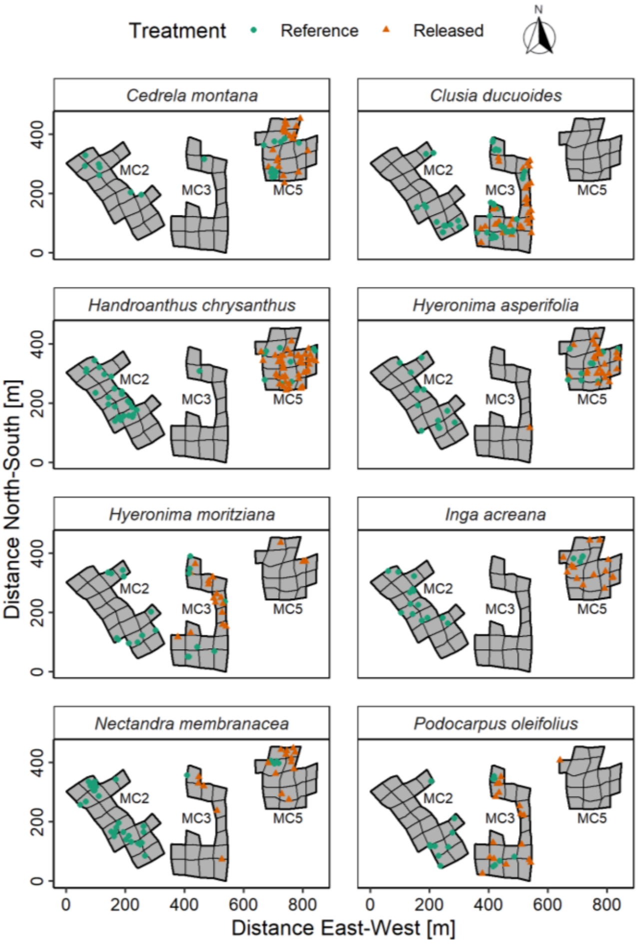

Figure 11: Location of PCTs in the 52 experimental plots and applied silvicultural treatment.

Species	Reference	Released	Total
Cedrela montana	20	21	41
Clusia ducuoides	40	34	74
Handroanthus chrysanthus	35	44	79
Hyeronima asperifolia	24	27	51
Hyeronima moritziana	19	19	38
Inga acreana	18	14	32
Nectandra membranacea	34	17	51
Podocarpus oleifolius	16	17	33
Total	206	193	399

Table 4: Number of released and reference PCTs included in the study.

3.3.2.2 Selection of predictors

Four predictors at the tree level with a strong a priori justification based on their theoretical ecological relevance and reported effects on PAI were selected (e.g. Clark et al., 2015; Le Bec et al., 2015; Rapp et al., 2012; Ruslandi et al., 2017): 1) Silvicultural treatment, 2) initial DBH, as measured before the application of the silvicultural treatment, 3) elevation, and 4) TPI.

Different intensities of the silvicultural treatment were applied in the three microcatchments (MC2 = reference area without any treatment, MC3 = moderate liberation thinning, MC5 = intense liberation thinning). For individual PCTs, however, the liberation effect was comparable between MC3 and MC5 since the strongest competitor was removed for each PCT. Therefore, we did not differentiate between treatment intensities and only use “reference” and “released” as factor levels.

Only elevation and TPI were used as topographic predictors (see Section 3.2.3). The respective values for the spatial locations of each PCT was extracted from the elevation and TPI rasters. The other three topographic variables (aspect, SAGA Wetness Index and slope) were not included, because 1) they were not significant in (non-published) preliminary analyses, 2) they were the least important variables in Kübler et al. (2016), and 3) the sample size for some tree species was relatively small, which required a limitation in the number of predictors.

3.3.2.3 Model fitting

All data were fitted in a single LMM in an iterative model building process to determine which model best describes the empirical data (Zuur, 2009). For model building, alternative models were compared based on the Akaike information criterion (AIC) and likelihood ratio tests. It is worth noting that no systematic stepwise model selection method was employed, because all predictors have a theoretical justification for their inclusion. Instead, only models including all predictors were considered (Whittingham et al., 2006). Models were fitted using package lme4 (Bates et al., 2015) in the R statistical environment (R Core Team, 2018).

The final LMM with the optimal fixed effects structure and random effects structure was:

$$\begin{aligned}\ln(\mathrm{PAI}_{isp}+1) = \; & \beta_0 + \beta_1 \times \mathrm{Treatment}_{isp} + \beta_2 \times \mathrm{Elevation}_{isp} + \beta_3 \times \mathrm{TPI}_{isp} + \beta_4 \times \mathrm{DBH}_{isp} \\ & + \mu_{0s} + \mu_{1s} \times \mathrm{Treatment}_{isp} + \mu_{2p} \\ & + \varepsilon_{isp}\end{aligned}$$

where

- PAI_{isp} is the response variable indicating the value of DBH growth per year. It was transformed using the natural logarithm of (PAI + 1) to reduce non-normality of residuals and heteroscedasticity.
- $\mathrm{Treatment}_{isp}$ indicates the silvicultural treatment with dummy coding (reference level = 0, released level = 1).
- $\mathrm{Elevation}_{isp}$, TPI_{isp} and $\mathrm{initialDBH}_{isp}$ are the respective values of the continuous predictors. Two-way interactions between predictors did not lead to a better model performance and were therefore not included. The continuous predictors were scaled by centring them on 0 and dividing them by two times their standard deviation (SD).
- μ_{0s} denotes a random intercept for species s to account for interspecific difference in growth rates (Bräuning et al., 2008).
- $\mu_{1s} \times \mathrm{Treatment}_{isp}$ denotes random slopes for the effect of treatment on species s to account for interspecific differences of responses to the silvicultural treatment (Günter et al., 2008).
- μ_{2p} denotes a random intercept for each experimental plot p to account for heterogeneity across plots within the RBSF.

3.3.2.4 Model evaluation and inference

The LMM was evaluated based on standard model validation plots (fitted values vs. residuals for the entire model, a normal Q-Q plot, model residuals vs. all predictors, and fitted values vs. residuals for each species; Zuur, 2009).

The significance of fixed effects was estimated based on 50% and 95% likelihood profile confidence intervals on variance-covariance and fixed effects parameters (Bates et al., 2015). If the confidence limits of a fixed effect coefficient did not contain zero at the 95% confidence level, we considered this effect as significant. If the 95% confidence interval included zero but the 50% confidence interval did not, we described such an effect as marginally significant (Shenkin et al., 2015). Likelihood ratio tests statistics were used to test whether random intercepts and random slopes improved model performance (Zuur, 2009).

We computed predicted PAI responses for each fixed effect while leaving all other fixed effects constant at their respective observed mean value to visualize effect sizes at the population level. For these predictions, 95% confidence intervals were estimated using parametric bootstrapping (number of simulations = 2000; Bates et al., 2015). For visualization, predicted PAI and confidence intervals were back-transformed from the ln(1+x)-scale to their original scale using a “ratio estimator” correction factor to avoid bias (Snowdon, 1991). The continuous TPI values were classified into five discrete slope position classes (valley, lower slope, middle slope, upper slope and ridge; Weiss, 2001) to improve the interpretability of the TPI plot.

Further, species-specific best linear unbiased predictions (BLUPs) were computed to inform about the PAI of reference PCTs (random intercepts) and the effect of treatment on PAI (random slopes). We estimated prediction intervals at the 95%-level for BLUPs based on conditional variance-covariance matrices of the random effects (Pinheiro and Bates, 2000). BLUPs and their predictions intervals were back-transformed to their original scale using the “ratio estimator” from above.

4 Results

This chapter presents results from publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020).

4.1 Spatial distribution of tree species

The main results from publication I (Kübler et al., 2016) include 1) quantitative evaluation metrics for Maxent and ENFA models, 2) information on the most important variables for the characterization of habitat suitability, 3) a comparison of model outcomes with a previous forest type classification, and 4) prediction maps of habitat suitability.

4.1.1 Quantitative evaluation metrics

Figure 12 provides an overview of the model performance for all 16 species. Figure 13 shows detailed outcomes for the different quantitative evaluation metrics for the average across all species and for each of the 16 species. Key results for model evaluation were:

1. Model performance varied among species and metrics, but generally Maxent models showed better performance than ENFA models.
2. For the final models, area under curve (AUC) scores were higher than the 95% confidence interval of the respective null-models in 15 of the 16 species for Maxent and in all 16 species for ENFA.
3. For cross validation (CV) with random data partitioning, average scores across all species of Maxent models were higher than scores of ENFA models for both area under curve (AUC) and true skill statistic (TSS).
4. For cross validation with spatially separated data partitions, scores for nearly all species were lower than scores from cross validation with random data partitioning.

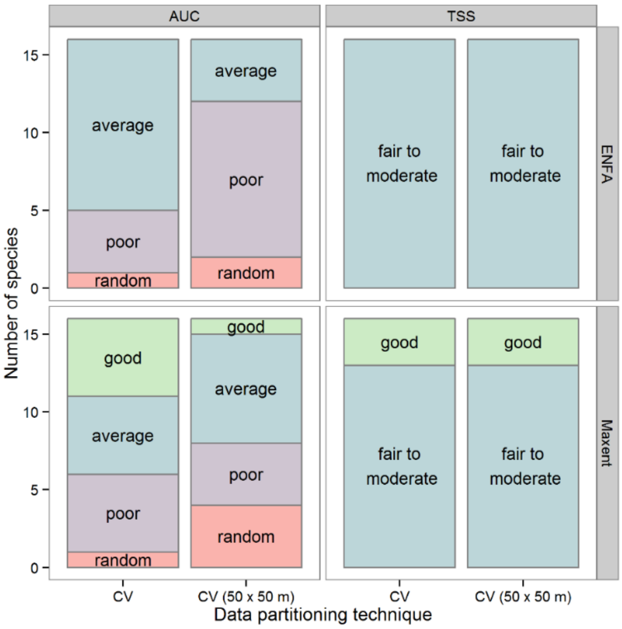

Figure 12: Summary of the model performance for all 16 species. AUC scores (left) were classified into quality classes (<0.6 random, 0.6–0.7 poor, 0.7–0.8 average, 0.8–0.9 good, 0.9–1 excellent, Merckx et al., 2011). The classification scale of Landis and Koch (1977) was used for true skill statistic scores (right, <0.2 poor, 0.2–0.6 fair to moderate, >0.6 good). Results are shown for SDM algorithms (Maxent and ENFA) and data partitioning techniques (cross-validation with random partitions (CV) and cross-validation with spatially separated partitions (CV 50 x 50 m)).

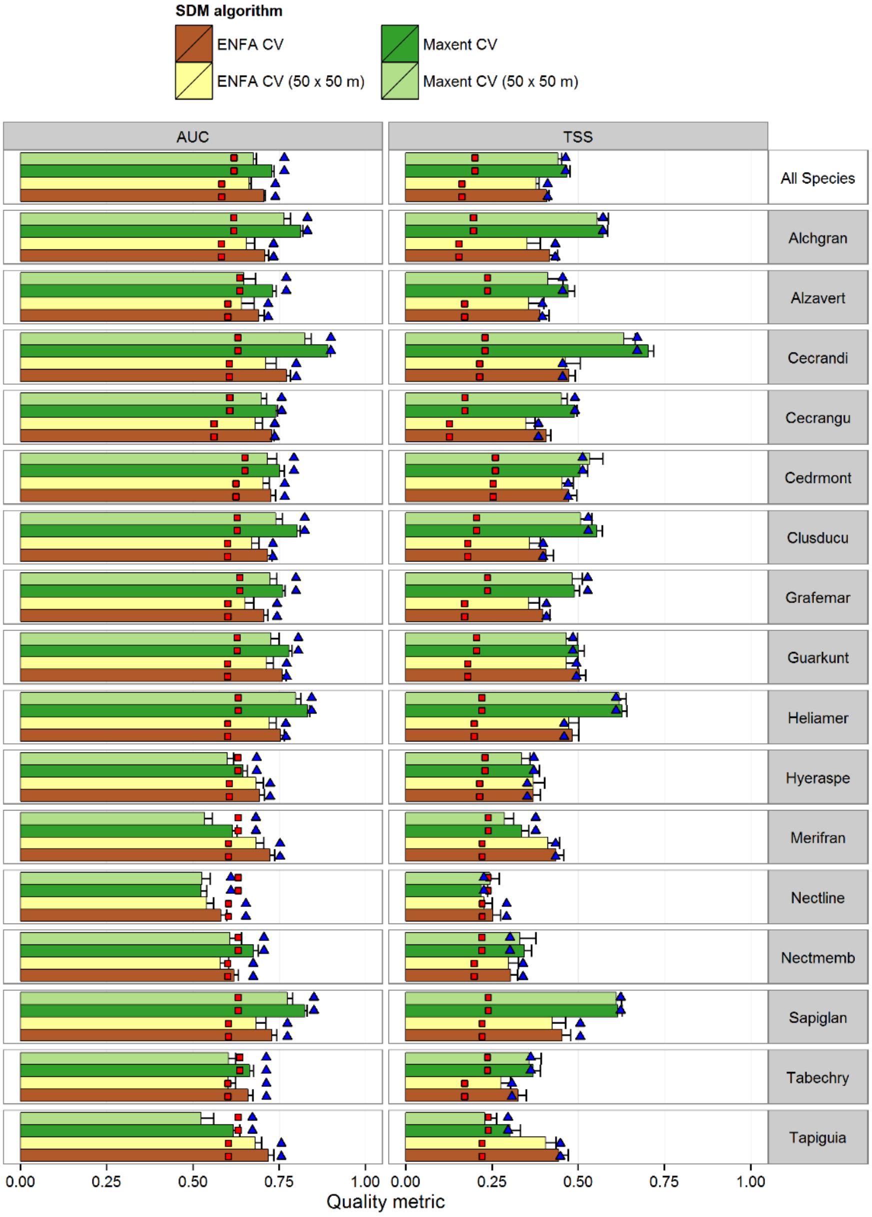

Figure 13: Model evaluation for the mean across all species (top row) and for each species (remaining rows). Results for the area under curve (AUC) and true skill statistic (TSS) are on the left and right side, respectively. ENFA models are indicated by brown bars and Maxent models by green bars. Dark green/brown colours show random data partitioning for cross-validation (CV), while light green/brown colours show cross-validation with spatially separated data partitions (CV 50 x 50 m). Error bars indicate the 0.95 confidence interval. Red squares symbolize the upper 0.95 quantile of the quality metrics for the null-models. Blue triangles show the quality metrics of the final models for each species.

4.1.2 Most important variables for characterization of suitable habitat for tree species

Overall, the mean importance of each topographic variable was similar for ENFA and Maxent models (Table 5). The Maxent jackknife test where models were created with only one variable in isolation (named “gain with only variable”) and the absolute marginality of the ENFA indicated that elevation and Topographic Position Index (TPI) were the main determinants for the distribution of most of the tree species. In contrast, the SAGA Wetness Index, eastness and slope only had minor importance. The Maxent jackknife test where each variable is excluded in turn and a model created with the remaining variables (named “gain without variable”) identified elevation as the variable that mostly decreased training gain when excluded.

Table 5: The mean importance of topographic variables across all species according to ENFA and Maxent. The absolute value of marginality of the ENFA describes how far species depart from the mean available conditions in the study area. For Maxent, the jackknife test named “gain with only variable” shows the regularized training gain of models created individually with only one ecological variable compared with models created with all variables. The jackknife test named “gain without variable” compared the regularized training gain of models with one variable excluded compared with models created with all variables. Values in parenthesis indicate the 0.95 confidence interval.

Variable	ENFA: Absolute marginality	Maxent: Gain with only variable	Maxent: Gain without variable
Eastness	0.26 (0.15–0.37)	0.09 (0.05–0.13)	0.45 (0.31–0.59)
Elevation	0.70 (0.59–0.81)	0.34 (0.22–0.46)	0.34 (0.22–0.46)
Slope	0.17 (0.11–0.23)	0.03 (0.02–0.04)	0.48 (0.34–0.62)
TPI	0.41 (0.33–0.50)	0.17 (0.10–0.25)	0.46 (0.32–0.59)
Wetness Index	0.31 (0.26–0.37)	0.08 (0.03–0.13)	0.48 (0.34–0.62)

Outcomes for the importance of topographic variables for the distribution of each individual species can be found in Kübler et al. (2016).

4.1.3 Comparison with previous forest type classification

Tree species groups were determined using a hierarchical cluster analysis based on the ENFA marginality factor of each species and topographic variable. For this, a dissimilarity matrix was calculated using Euclidean distance and subsequently, three species groups (Group A, B and C) were identified with the complete linkage method.

Group B was the largest group, consisting of 10 species. It showed a clear preference for lower elevations and valleys (i.e. lower coefficients of TPI and higher coefficients of Wetness Index) compared to the mean of the available conditions in the study area. Hence, this group seems to reflect Forest type I from the previous forest type classification of Homeier et al. (2008; see Section 3.1.2). Group C, composed of four species, on the other hand, preferred higher elevation and ridges (i.e. higher coefficients of TPI and lower coefficients of Wetness Index). This group therefore reflects Forest types II and III as defined Homeier et al. (2008). Group A consisted of only the species *Tapirira guianensis* and showed no similarities to any of the previously identified forest types.

Further, the assumption that Group B and Group C correspond to Forest type I and Forest types II/III, respectively, is generally in line with Homeier et al. (2010). These authors assigned individual species to forest types, which is well reflected in the groups resulting from the cluster analysis. Only three species were not congruent with the previous assignment; no information was provided for *Cedrela montana* by Homeier et al. (2010), *Graffenrieda emarginata* was assigned to all three forest types, and *Tapirira guianensis* was assigned to Forest type I.

4.1.4 Prediction maps of habitat suitability

Maps of habitat suitability for each species were created based on the results for ENFA and Maxent models. As examples, Figure 14 presents these maps for three species. It is noteworthy that the maps visually emphasize the cluster groups identified in the previous section: Species of Group B generally had higher scores for habitat suitability on lower elevations and in valleys, whereas species of Group C preferred higher elevations and ridges.

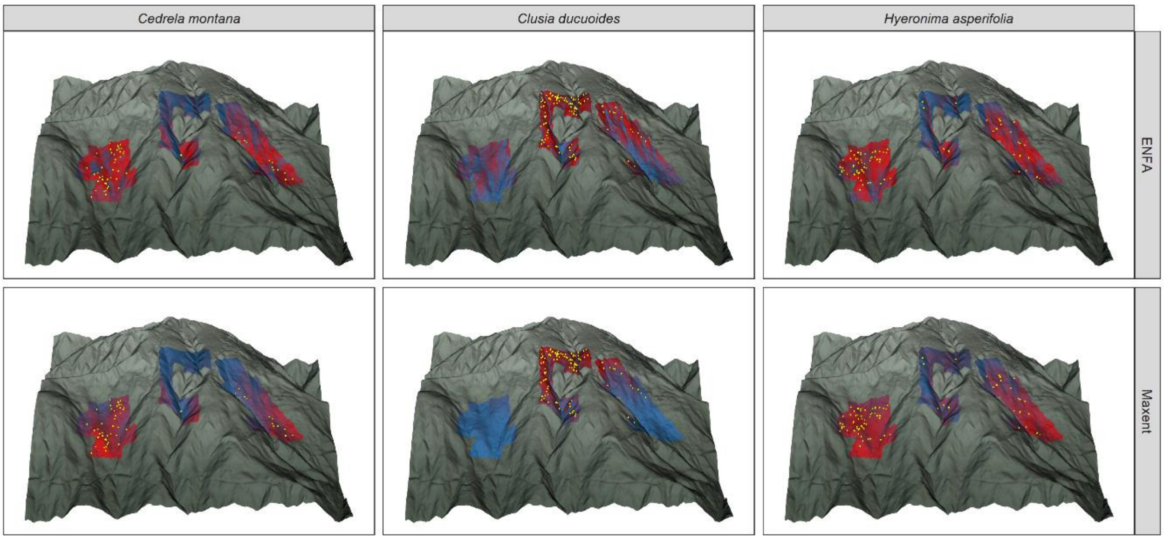

Figure 14: Habitat suitability maps of three trees species from final ENFA and Maxent models. Blue colours indicate unsuitable conditions and red colours suitable conditions. Yellow points show the registered occurrences which were used for model creation. *Cedrela montana* and *Hyeronima asperifolia* (Group B) tend to have areas predicted as suitable in valleys and lower altitudes, whereas areas with high predicted suitability for *Clusia ducuoides* (Group C) are located on ridges and higher altitudes. For better visualization, the 3D maps show a view on the NNW-facing slopes of the RBSF, i.e. the orientation is reversed compared to the 2D maps in this thesis.

4.2 Growth of PCTs

For publication II (Kübler et al., 2020), main results include 1) the model evaluation as well as outcomes for the 2) fixed effect structure and 3) random effect structure.

4.2.1 Model evaluation

Model validation graphs for the final LMM revealed no violations of model assumptions (Figure 15). Model residuals appeared to be normally and homogeneously distributed and no trends in residuals vs. predictor variables could be observed. Multicollinearity was not an issue, as correlation between fixed effects was low.

4.2.2 Fixed effect structure

The main outcomes for the fixed effect structure of the LMM, as presented in Figure 16 and Figure 17, were:

- Growth rates of PCTs was significantly influenced by elevation and TPI, whereas the silvicultural treatment was only marginally significant and the initial DBH was not a significant predictor.
- Growth rates decreased with increasing elevation, with an average decline of 0.73 mm a^{-1} per 100 m increase in elevation
- Growth rates increased over the topographic gradient, with PCTs in valleys having an average PAI of 2.02 mm a^{-1} compared to 1.04 mm a^{-1} on ridges
- The overall response to the silvicultural treatment was moderate, with reference trees growing 1.35 mm a^{-1} and released trees 1.60 mm a^{-1}.
- The intercept of fixed effects, i.e. the estimated value of PAI when all fixed effects were set to 0, was 1.35 mm a^{-1}.

It should be noted that the estimates presented here were predicted at the population-level, i.e. across all species.

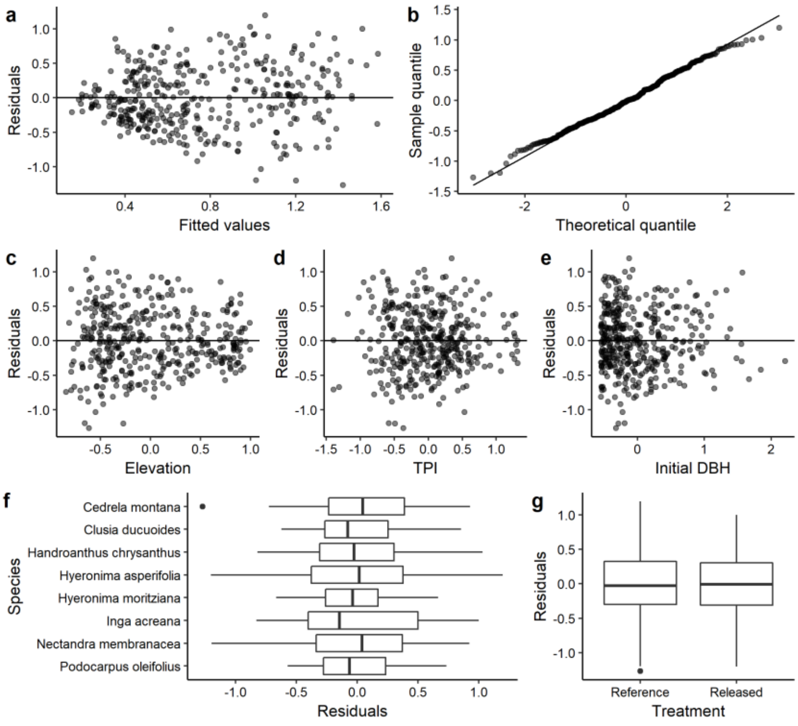

Figure 15: Model validation graphs for the final LMM. The plots show Pearson residuals vs. fitted values (a), normal Q-Q plot (b) as well as Pearson residuals vs. elevation (c), TPI (d), initial DBH (e), species (f) and silvicultural treatment (g).

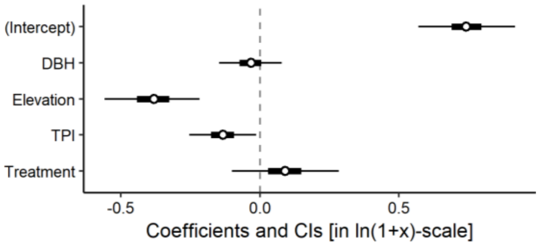

Figure 16: Parameter estimates for the fixed effect structure of the final LMM. The centre dots show coefficients for the effect of predictors on PAI (in the ln(1+x)-transformed scale). The 50% and 95% confidence intervals of coefficients are indicated by thick horizontal lines and thinner, wider horizontal lines, respectively. The vertical dashed grey line marks the null value.

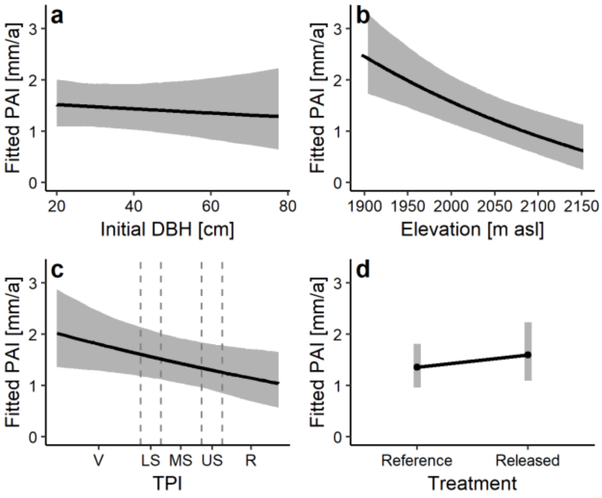

Figure 17: Prediction of PAI responses over the observed range of each fixed effect while leaving all other fixed effects constant at their mean value. Random effects were set to zero. Grey areas around the black line show 95% confidence intervals based on parametric bootstrapping. PAI and fixed effects were back-transformed to their original scales after computation of predictions. TPI values (c) were classified into V (valley), LS (lower slope), MS (middle slope), US (upper slope) and R (ridge) according to Weiss (2001).

4.2.3 Random effect structure

Likelihood ratio tests indicated that the final model with random intercepts for experimental plots and species as well as random slopes for the effect of treatment on species performed better than any model with a reduced random effect structure.

Figure 18 presents best linear unbiased predictions (BLUPs) and prediction intervals for species-specific intercepts, i.e. baseline growth rates, and slopes for treatment, i.e. the effect of the silvicultural treatment. *Cedrela montana* had by far the highest PAI when all fixed effects were zero, while *Handroanthus chrysanthus*, *Hyeronima moritziana* and *Podocarpus oleifolius* showed the lowest PAI. The highest positive treatment effects were predicted for *Hyeronima asperifolia* and *Inga acreana*, followed by lower positive effects for *Clusia ducuoides, Podocarpus oleifolius* and *Nectandra membranacea*. Three species (*Cedrela montana*, *Handroanthus chrysanthus* and *Hyeronima moritziana*) had a slightly negative predicted treatment effect. Overall, uncertainties of the species-specific treatment effect were high, with the prediction interval of only two species not crossing the zero line.

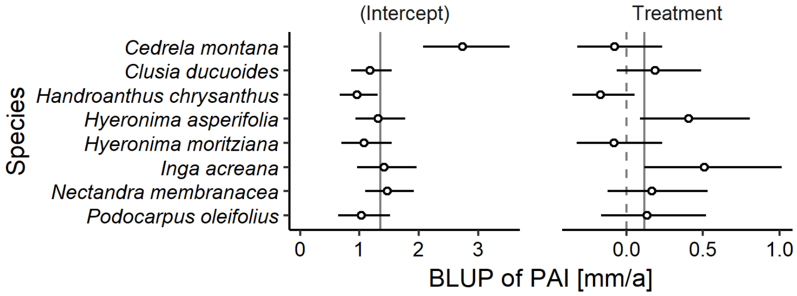

Figure 18: Back-transformed BLUPs of species-specific intercepts (left) and slopes of treatment (right). Horizontal lines show the 95% prediction interval. Solid vertical grey lines show the estimated fixed coefficients across all species, i.e. the estimated PAI when all fixed effects as well as the treatment effect were zero (left) and the estimated change in PAI due to the silvicultural treatment (right). The vertical dashed grey line (right) marks a zero treatment effect.

5 Discussion

This chapter addresses how the individual papers answer research objectives of this thesis. For this, results specific to the individual papers are first discussed, followed by a discussion of results that overlap between publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020). Throughout this chapter, the contributions and limitations of these findings for SFM and silviculture in TMF are assessed, with a focus on aspects raised in publication III (Weber et al., 2013).

5.1 Spatial distribution of tree species

Publication I (Kübler et al., 2016) showed that SDM is an adequate tool to analyse the ecological relationships between species and the environment at local scales in tropical forests. All topographic predictors were derived from a VHR DTM, which will be increasingly available in the future. This will allow applying SDM-based methods in a wider range of situations and regions. Here, the following three aspects of the research paper are discussed: 1) model evaluation, 2) the effect of spatial autocorrelation on model performance, and 3) predictions of habitat suitability. A discussion on the importance of topographic predictors and their contribution to SFM can be found in Section 5.3.

5.1.1 Model evaluation

The area under curve (AUC) is currently considered to be one of the standard methods to assess the accuracy of SDM, but its use for this purpose has been challenged (Lobo et al., 2008). In Kübler et al. (2016), AUC values were low for many species, indicating that six Maxent models and five ENFA models could be considered as poor or random. In contrast, all models performed at least fairly to moderately according to true skill statistic values and all final ENFA and 15 out of 16 final Maxent models performed significantly better than the null-models. Additionally, the ecological interpretation of models was in line with pre-existing knowledge about forest types and the membership of different tree species to these forest types. This suggests that AUC underestimated the performance of the models. Results from Kübler et al. (2016) therefore support the notion that the AUC should not be the sole evaluation metric and that more than one performance criterion should be used to evaluate SDM.

5.1.2 Effect of spatial autocorrelation on model performance

Evaluation metrics were lower for cross validation with spatially separated data partitions compared to randomly separated data partitions. A possible interpretation of this is that spatial autocorrelation in the tree occurrence data may have falsely inflated metrics that are based on randomly separated data partitions (Merckx et al., 2011; Veloz, 2009). However, Kübler et al. (2016) argue that it should be differentiated between spurious and real spatial autocorrelation. The former can be caused, for example, by biased sampling and should be removed from the data, whereas the latter should not be discarded for SDM as it corresponds to the actual spatial structure of species distribution (Fortin et al., 2002; Kamino et al., 2012). I assume that existing spatial autocorrelation in the occurrence data of Kübler et al. (2016) is real, because the origin of the data is a complete tree census without spatial sampling bias. Further, real spatial autocorrelation can either be caused by endogenous and exogenous processes. The former are directly associated with the biological occurrence data through processes such as dispersal or competition. The latter are independent from the occurrence data and caused by, for example, spatially structured environmental gradients (Franklin and Miller, 2009). There is ample evidence that the distribution of tree species in the RBSF is largely influenced by environmental gradients, i.e. by exogenous processes (e.g. Homeier et al., 2008; Oesker et al., 2008). Under such circumstances, reducing spatial autocorrelation by spatially separating training and test data can result in a loss of information and, in consequence, less accurate models with lower evaluation metrics (Franklin and Miller, 2009; Lennon, 2000; Segurado et al., 2006).

5.1.3 Maps of habitat suitability

Kübler et al. (2016) created prediction maps of habitat suitability for each species. It should be emphasised that this study focused on gaining a better understanding on how environmental factors shape the distribution of tree species. In consequence, models were primarily developed for explanation, and not for prediction (see Section 2.2.2). In line with that, the maps of habitat suitability can rather be considered as an additional evaluation tool to visually assess the ecological plausibility of models. The maps emphasize the identified cluster groups (see Section 4.1.3): Species of group B, which was associated with Forest type I, generally had higher scores for habitat suitability on lower elevations and in valleys, whereas species of group C, associated with Forest type II and III, preferred higher elevations and ridges. Nevertheless, the question rises whether models and prediction maps from Kübler et al. (2016) can be used for management purposes. This is discussed in Section 5.3.3.

5.2 Growth of PCTs

Publication II (Kübler et al., 2020) investigated the relative effects of a liberation thinning and topography on growth rates at the tree level. A main finding of the study was that topographic variables were more relevant for tree growth than the silvicultural treatment. Growth rates of PCTs strongly decreased with increasing elevation and over the topographic gradient from valleys to ridges. In contrast, the overall response to silvicultural treatment was moderate but only marginally significant. This section focuses on a discussion of growth rates across all species as well as on the effect of the silvicultural treatment on growth rates.

5.2.1 Growth rates across all species

Predicted diameter growth of PCTs across all species differed considerably between topographic conditions, ranging from approximately 2.0−2.5 mm a^{-1} in valleys and at lower elevations to 0.6−1.0 mm a^{-1} on ridges and at higher elevations. These large differences indicate that management prescriptions should take the fine-scale environmental heterogeneity into account; this is discussed in Section 5.3.3.1.

It is generally considered that tree growth in TMF, and in consequence preconditions for sustainable management for timber, is unfavourable compared to tropical lowland forests (Günter, 2011b). To assess whether results from Kübler et al. (2020) support this, Table 6 lists a sample of diameter growth rates from neotropical lowland forests that were reported in literature. While this does not constitute an exhaustive or systematic literature review, it nevertheless allows for a rough comparison between forest types. Growth rates on ridges and at higher elevations in the study area seem to be lower than the lowest reported values in Table 6. In contrast, growth rates in valleys and at lower elevations appear to be within the range of growth rates from neotropical lowland forests. This assessment is supported by Bräuning et al. (2008), who studied diameter growth rates in the RBSF.

For SFM in TMF it seems promising at first glance that diameter growth rates in valleys and at lower elevations are comparable to tropical lowland forest ecosystems that have been managed for timber. However, information on wood volume growth and standing timber volume is more relevant for an estimation of sustainable timber yields than information on diameter growth. Wood volume growth is not only determined by diameter growth, but also by tree height, which generally decreases with increasing altitude (Günter, 2011b). This is also the case in the RBSF: The canopy in Forest type I reaches 25–30 m, with few emergents reaching up to 35 m, whereas Forest types II and III have canopy heights of 12–15 m (Homeier et al., 2008). In contrast, tropical lowland evergreen rainforests can be 45 m or more tall (Saw, 2004). This indicates that, despite comparable diameter growth rates, wood volume growth is likely higher in lowland forests than in TMF.

For standing timber volume, aboveground biomass (AGB) can be used as a rough proxy (Sasaki et al., 2016). Spracklen and Righelato (2014) reported that AGB declines moderately with elevation, and that mean AGB is significantly lower in neotropical mountain forests (247 t ha^{-1}) than in neotropical lowland forests (~300 t ha^{-1}).

For the study area in the RBSF, the mean AGB was 106 t ha^{-1} (González-Jaramillo et al., 2018). However, this value was estimated across valleys and ridges; valleys showed considerably larger AGB, with a maximum of 664 t ha^{-1} found at the lower ravines in undisturbed and dense forest stands. This high variability of AGB indicates that further studies are necessary for a robust comparison of sustainable timber yields in TMF and tropical lowland forests.

Table 6: Sample of reported diameter growth rates in neotropical lowland forests.

Authors	Mean or median diameter growth rates [mm a^{-1}]	Silvicultural treatment	Previous logging	Ecoregion	Population
Dauber et al., 2005	2.2−4.1	No	No	Four principal forest ecoregions of Bolivia	FCTs of commercial species
Finegan and Camacho, 1999	5.0	No	Yes	Tropical wet forest in Costa Rica	PCTs of commercial species
	5.0-7.0	Yes	Yes		
Worbes and Schöngart, 2019	2.0−2.9	No	No	Terra firme rain forest in Brazil	Trees of three important commercial species
Pereira de Carvalho et al., 2004	~2.6	No	No	Terra firme rain forest in Brazil	Trees of commercial species
	~4.0	No	Yes		
Korning and Balslev, 1994	2.7	No	No	Rain forest in the Ecuadorian Amazon	Trees of 22 common species
Vieira et al., 2005	1.0−2.0	No	No	Three different locations in the Brazilian Amazon	Randomly selected trees across all species

5.2.2 Effect of the silvicultural treatment on growth rates

Findings from Kübler et al. (2020) may appear contradictory at first: There was only weak evidence to reject the null hypothesis of a zero effect of the silvicultural treatment, but the point estimate for the effect of the silvicultural treatment on growth rates seemed nevertheless non-negligible. Both these findings are discussed in the following. A discussion on the importance of topographic predictors can be found in Section 5.3.

5.2.2.1 Treatment only marginally significant

The silvicultural treatment was only marginally significant. What are the causes for the silvicultural treatment not reaching the conventional threshold level of statistical significance? One possible explanation is that there was indeed a true zero treatment effect. However, the aphorism "absence of evidence is not evidence of absence" applies here (Alderson, 2004); multiple alternative explanations are plausible. First, species-specific BLUPs predicted a slightly negative effect for three of the eight analysed species. It is therefore conceivable that the treatment effect on tree growth, which was estimated across all species, was "averaged out" during computation. Second, the large effects of the topographic predictors might have obfuscated potential (smaller) effects of the silvicultural treatment in our statistical analysis. Third, a large part of the variability in growth rates unexplained by the fixed effects was due to between-tree differences. It is likely that this caused a large overlap in growth responses, which in turn lowered the statistical power of the analysis. Consequently, the probability of detecting statistical significance of a potential effect of the silvicultural treatment might have been low.

5.2.2.2 Effect of silvicultural treatments on tree growth

Despite its marginal significance, the liberation thinning showed a moderate positive effect on tree growth across all species: The PAI of reference trees and released trees was 1.35 mm a^{-1} and 1.60 mm a^{-1}, respectively. This corresponds to a treatment effect of 0.25 mm a^{-1} or a percentage increase of 18.5%. In tropical lowland forests, percentage increases in growth rates after silvicultural treatments were, for example, 22–27% (Villegas et al., 2009), 50–60% (Peña-Claros et al., 2008), 13–28% (Souza et al., 2015) and 19–24% (Vatraz et al., 2016). These reports suggest that the percentage increase of PAI due to the silvicultural treatment in Kübler et al. (2020) is within the range, but at the lower end of reported values from tropical forests.

The focus of Kübler et al. (2020) was not on species-level inference, but rather on inference across species; in-depth analyses and discussions of species-level responses to the silvicultural treatments in our study area can be found in Günter et al. (2008) and Cabrera et al. (2019). Nevertheless, it is worth discussing two aspects of species-level responses in this section. First, a slightly negative response to the silvicultural treatment was predicted for *Cedrela montana*, *Handroanthus chrysanthus* and *Hyeronima moritziana*. According to Putz (2004), one possible cause for this is that PCTs might have been suppressed for long time periods before they were released, and therefore do not respond well to the liberation thinning. Similarly, PCTs might have been heavily infested by vines. Additionally, repeated liberation treatments might have been required for some species because the benefits of release may not persist over time.

Second, for *Cedrela montana*, long-term growth data from tree ring analyses is available for 38 of the total of 41 PCTs in the silvicultural experiment (Spannl et al., 2012). Between 1976 and 2003, i.e. before the application of the silvicultural treatment, the mean growth rate for the reference group was considerably higher than for the released group ($PAI_{reference}$ = 2.31 mm a^{-1}, $PAI_{released}$ = 1.43 mm a^{-1}). These pre-treatment differences in growth rates between the reference and released group existed by chance, probably due to the large between-tree growth variability and environmental heterogeneity in our study area. As tree growth in tropical forests tends to be autocorrelated in time (Brienen et al., 2006; Dionisio et al., 2018), the differences likely persisted after the application of the silvicultural treatment. In view of these pre-treatment differences, findings from three studies which analysed tree growth data from the silvicultural experiment in the RBSF can be compared. Günter et al. (2008) and Cabrera et al. (2019) reported considerably lower growth rates for released trees compared to reference trees of *Cedrela montana*, whereas the statistical model of Kübler et al. (2020) suggests that there is only a minor difference between reference and released trees. This indicates that by controlling for environmental heterogeneity, some of the pre-treatment growth differences between the reference and released groups were accounted for in Kübler et al. (2020).

5.2.2.3 Implications for SFM

Due to uncertainties of outcomes, Kübler et al. (2020) cannot conclusively answer whether liberation thinnings are a silviculturally viable management option in Ecuadorian TMF or not. Nevertheless, even partial answers are valuable, because knowledge on the effect of specific silvicultural treatments on forest stands in TMF is scarce (Weber et al., 2013) and the implementation and monitoring of large silvicultural experiments in the tropics are costly and operationally difficult.

It can be considered promising that the magnitude of the overall impact of liberation thinnings on PCTs was within the range of values reported from other tropical forest ecosystems. This, in conjunction with results from an earlier study that showed that the silvicultural treatment had only minor ecological impacts on the remaining stand in the study area (Günter et al., 2008), suggests that silvicultural interventions have potential in the sustainable management of TMF. However, liberation thinnings are only one (not mandatory) part of a silvicultural system. Future studies in TMF should therefore focus on the development of a tentative silvicultural system for the production of timber, and where applicable, NTFPs (Hutchinson, 1988). Which type of silvicultural system is best suited for TMF? Generally, Andean TMF do not only have an irregular structure and shade-tolerant species, but also occur on steep slopes. Under such conditions, selection systems are appropriate (Savill, 2004). However, the choice and adaption of a silvicultural system for a specific TMF area ultimately depends on management objectives as well as multiple silvicultural, ecological, and socioeconomic factors, and is therefore beyond the scope of this thesis.

It seems silviculturally relevant that the effect of the liberation thinning on tree growth showed large variability between species, with some species having a negative reaction. This suggests that the silvicultural treatment should not be applied indiscriminately across the whole stand, but only to species that responded positively. However, species-specific outcomes in Kübler et al. (2020) are associated with large uncertainties, and should therefore not be considered as robust information for management decisions. Hence, subsequent research is required for reliable recommendations on the species level. Further, in hyper-diverse forest ecosystems, it can be challenging to liberate PCTs of species that react positively while assuring that PCTs of species that react negatively are not affected by the liberation.

For the study region in southern Ecuador, Knoke et al. (2013) demonstrated that sustainable use and conservation of forests and their ESS can be achieved by a combination of conservation payments to protect the existing natural forest, re-establishment of pastures, reforestation on abandoned lands, and sustainable low-impact management in part of the natural forest area. This raises the question if such a diversified land-use system could be improved by the application of liberation thinnings in natural forests. For this, further research should perform an economic evaluation of the silvicultural treatments, because farmers, who are the ones that take decisions on land management, have to be convinced mainly by economic arguments (Knoke et al., 2009). In that context, there are two limitations that may prevent the widespread adaptation of liberation thinnings. First, forest operations are more expensive and complex in TMF than in lowland forests due to the remoteness and steepness of mountainous terrain (Günter, 2011b). This, combined with the effect of the silvicultural treatment being on the lower end of reported values from other forest ecosystems, calls the economic viability of liberation thinnings in TMF into question. Second, smallholder farmers in developing countries tend to be risk-averse (Knoke et al., 2013). The effect of liberation thinnings on tree growth was only marginally significant in Kübler et al. (2020), and economic returns from an investment in this silvicultural treatment are therefore uncertain. Hence, landowners' willingness to invest in liberation thinnings may be limited.

5.3 Overlapping results: Importance of topography

Publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020) had two different outcome variables (the spatial distribution of tree species and diameter growth of PCTs) and, in consequence, different methodological approaches. Nevertheless, these two papers had a common key takeaway: The outcome variables were influenced to a large extent by topography in general, and elevation and topographic position in particular. First, potential causes for the importance of elevation and TPI are discussed in this section. A discussion of the importance of aspect, SAGA Wetness Index and slope, which played a less important role, can be found in Kübler et al. (2016). Second, potential contributions of topographic predictors for the SFM of TMF are addressed.

5.3.1 Importance of elevation

Elevation was the most important predictor in both Kübler et al. (2016) and Kübler et al. (2020). In TMF, it is well established that elevation influences species distribution (Gentry, 1988; Humboldt and Bonpland, 1805) and forest growth (Clark et al., 2015; Grubb, 1977; Sherman et al., 2012) on large and intermediate scales. Most of the studies on the influence of elevation investigated altitudinal gradients ranging over large vertical differences of 2000 m or more. In contrast, the vertical difference between the lowest and highest point of the silvicultural experiment in the RBSF was only 250 m. In TMF, only few studies reported an impact of elevation on species distribution (Ledo et al., 2013) and tree growth (Bräuning et al., 2008; Homeier et al., 2010) on such a small scale.

What are the causes for the high importance of elevation in the RBSF? An important reason is that vegetation shifts from Forest type I to Forest type II and III over the altitudinal range of the silvicultural experiment (Homeier et al., 2010; see Section 3.1.2). Compared to Forest type II and III, Forest type I occurs at lower elevations, has a different species composition and shows higher diameter growth rates of trees (Bräuning et al., 2008). It seems therefore likely that this transition of forest types, which occurs concomitantly with increasing elevation, contributed to the high importance of this topographic variable. This is partially supported by results from Kübler et al. (2020): Species had a substantial effect on tree growth, and species characteristic of Forest type I tended to have higher growth rates than species found in Forest type II and III. However, species-specific model outcomes were uncertain and differences in growth rates between species were generally small. Additionally, (unpublished) models without species effects, which were explored during the iterative model building process, had considerably larger effect sizes for elevation than the final model in Kübler et al. (2020). This indicates that the high importance of elevation is not only caused by shifting species composition due to forest type transitions, but also other factors.

It should be noted that topography can either influence ecological processes directly or indirectly, i.e. by affecting other factors which in turn affect ecological processes. In TMF, increasing elevation can result in changes in many direct factors, such as temperature, rainfall, cloud cover, incoming solar radiation, wind speed, nutrient inputs and soil type (Spracklen and Righelato, 2014). In the RBSF, numerous studies have shown a correlation between direct factors and the indirect factor elevation. In terms of climatic direct factors, Fries et al. (2009) reported an annual average lapse rate of -0.52 K / 100 m in the study area for the altitudinal range of the silvicultural experiment (1850–2150 m a.s.l.), which translates to a difference of annual average temperatures of 1.56 K between the lowest and highest point in the permanent sample plots. Similarly, average annual precipitation increases by 250 mm / 100 m (corresponding to a difference of 750 mm between lowest and highest point) and fog input augments by 40 mm / 100 m (corresponding to a difference of 120 mm between lowest and highest point; Rollenbeck, 2006). With regards to soil properties, the general trend in tropical mountains that increasing elevation results in decreasing soil fertility and decreased N availability (Tanner et al., 1998) was confirmed for the RBSF (Wilcke et al., 2008; Wolf et al., 2011). Further, in our study area the mineral soil depth decreases, the thickness of the organic layer and pH increase and soil texture becomes coarser in the A horizon with increasing elevation (Ließ et al., 2011; Wilcke et al., 2008; Wolf et al., 2011). These strong gradients of direct factors help to understand why elevation is the most important variable for species distribution and growth rates of trees, even at small scales.

5.3.2 Importance of the Topographic Position Index (TPI)

TPI was the second most important predictor for the distribution of tree species (Kübler et al., 2016) and tree growth (Kübler et al., 2020). For the interpretation of these outcomes, the meaning of TPI should be recalled: It expresses the position on a topographical gradient ranging from valleys to mid-slopes to ridges (Guisan et al., 1999). It can therefore be considered as a quantitative expression of the horizontal gradient formed by the topographical structure. It is worth mentioning that in the RBSF, elevation is only weakly correlated to TPI, i.e. ridge positions can be found at lower elevations and valley positions at higher elevations.

Findings from previous studies at similar spatial scales agree on the influence of topography on forest composition and species distribution in tropical forests in general (Chuyong et al., 2011; Lan et al., 2009; Liu et al., 2014; Queenborough et al., 2007; Valencia et al., 2004; Wang et al., 2009; Webb et al., 1999) and in TMF in particular (Aiba et al., 2004; Homeier et al., 2010; Takyu et al., 2002). For growth rates of trees, previous studies are only partially in line with results from Kübler et al. (2020). A decline of growth rates over the gradient from valleys to ridges has been reported by Homeier et al. (2010) and Liu et al. (2014), whereas other studies found no significant difference in growth rates between valleys and lower slopes (Bellingham and Tanner, 2000), or higher growth rates on ridges compared to lower slopes (Herwitz and Young, 1994).

The interpretation of the importance of TPI and elevation shows some similarities. A shift in species composition from Forest type I in valleys to Forest type II and III on ridges (as defined by Homeier et al., 2010) occurs in the area of the silvicultural experiment. This partially explains the large influence of TPI on growth rates, as tree species of Forest type I tend to grow faster than species of Forest type II and III (Homeier et al., 2010). However, as interspecific differences in growth rates were accounted for in the statistical analysis of Kübler et al. (2020), it is likely that other factors than shifting species composition contribute to the importance of TPI.

In the RBSF, the topographic position has a strong impact on numerous direct factors by creating a variety of microhabitats along a topographic gradient, with many parameters changing from valleys to ridges (Beck et al., 2008b). Compared to valleys and lower slopes, ridges and upper slopes are characterized by higher humus concentrations, lower pH and less nutrients (Wilcke et al., 2011; Wolf et al., 2011). Further, throughfall in valleys is more abundant and nutrient-richer than on ridges (Oesker et al., 2008) and herbivory and leaf litter decomposition is considerably lower on ridges than on valleys (Werner and Homeier, 2015). These differences between topographic positions can be partly explained by lateral transport of water and matter from ridges to valleys, frequent landslides and the resulting removal of mineral soil on ridges (Vorpahl et al., 2012), and a plant-mediated, nutrient-driven feedback cycle (Werner and Homeier, 2015). This feedback cycle is maintained by slow-growing tree species adapted to belowground competition in nutrient-poor soils being more competitive on ridges. These slow-growing species are generally characterized by large investments in long-living foliage with antiherbivore defences (Coley et al., 1985), which, in combination with mechanically resistant leaves due to increased wind and drought exposure, result in poor litter decomposability. This causes an accumulation of litter and mor humus, which in turn immobilizes basic cations, contributes to soil acidification, and further enhances soil nutrient limitations on upper slopes and ridges. Moreover, ridges are more prone to drought due to higher solar radiation compared to valleys (Bussmann, 2003), although this might be mitigated by the fact that ridges receive more scavenged cloud water than valleys (Homeier et al., 2010). It is likely that these changes in environmental conditions explain the ecological importance of TPI in the RBSF.

5.3.3 Contribution to sustainable forest management (SFM)

This section discusses management-relevant use cases for topographic variables. It focuses on the importance of topography for two aspects raised in publication III (Weber et al., 2013): The management of natural forests and reforestation. Weber et al. (2013) argue that agricultural and forestry activities should be integrated by combining agriculture, plantations and selective management of natural forests in the study region in southern Ecuador. This would not only lead to a more sustainable land use and reduced deforestation, but also higher income for smallholders (Knoke et al., 2009).

Two distinct but related discussion levels are used in this section. First, promising use cases for topographic predictors in the context of SFM are identified in Section 5.3.3.1 and 5.3.3.2. Second, the potential and limitations of the numerical models developed and calibrated in Kübler et al. (2016) and Kübler et al. (2020) for these use cases are discussed Section 5.3.3.3.

5.3.3.1 Management of natural forests

Forests in the study region face multiple demands. On the one hand, there is political will to conserve the unique biodiversity hotspot and to secure the delivery of regulating and cultural ESS. On the other hand, forests should provide an ongoing supply of timber and NTFPs to fulfil the need for forest products of the local population. Additionally, reproductive material from forests is required for reforestation activities in the study region (Weber et al., 2013). Under such conditions, silviculture has to carefully integrate the different social and political dimensions (Günter, 2011a). One option to incorporate these different management goals in forest management planning is multifunctional zoning, which is a process for identifying areas where timber and NTFPs may be harvested sustainably and areas for which other objectives, such as the protection of regulating or cultural ESS, may be prioritized (ITTO, 2015). In the process of multifunctional zoning, different priority forest functions are grouped and mapped according to whether they are compatible with low-impact logging or not.

How could multifunctional zoning be implemented in TMF? For hill mixed dipterocarp forest of southwest Sri Lanka, Ashton et al. (2011) presented protocols for sustainable management. Similar to the study region in Ecuador, these forests are characterized by ridge-valley topography. In order to explicitly take the environmental heterogeneity into account, the authors argue that stand-level delineation and prescription should consider the floristic association, topographic relief, soils and hydrology, and that silvicultural treatments should be stand-specific. They further argue for an integration of spatial and temporal planning that allows for allocation of stands within the forest landscape for different use values, such as protection or production. The implementation of stand level delineation and planning could considerably improve forest management, watershed protection, and biodiversity conservation in tropical forest landscapes (Ashton and Hall, 2011).

Findings from Kübler et al. (2016) and Kübler et al. (2020) show that microtopography and related ecological processes have a strong impact on the spatial distribution of tree species and on diameter growth of PCTs. Additionally, microtopography heavily influences biomass stocks in the study area (González-Jaramillo et al., 2018). This has two consequences. First, the fact that fundamental forest characteristics vary considerably within short geographic distances in TMF underlines that instead of “broad-brush” management, multifunctional zoning and management prescriptions should be based on the fine-scale environmental heterogeneity. Second, topographic variables seem to be good proxies for the floristic composition and fine-scale environmental heterogeneity in TMF. These variables were derived from a high-resolution DTM, which will be increasingly available in the future. This indicates that topographic variables could be used for multifunctional zoning in future SFM of TMF.

Using field measurements and topographic variables, the floristic composition (Kübler et al., 2016), growth rates (Kübler et al., 2020) and above-ground biomass (González-Jaramillo et al., 2018) can be predicted on a spatially explicit fine-scale level. To increase the relevance for SFM, further studies could focus on combining these predictions into models with multiple response variables. Such models could have multiple use cases in the context of SFM, such as spatially explicit estimations of timber stocks and sustainable yield, guidance for field inventories (e.g. pre-harvest inventories could focus on areas where high timber stocks are likely to occur), mapping of ESS (e.g. carbon stocks for climate regulation), creation of adequate small-scale management units for multifunctional zoning according to their priority use, and species-specific delineation of areas suited for enrichment planting, which is an important option for SFM in TMF (Weber et al., 2013).

5.3.3.2 Reforestation

In Ecuador, a national forest and reforestation programme aiming to restore a higher forest cover and to increase forest production was adapted in 2006. It envisages the establishment of 750,000 ha of industrial forest plantations, 150,000 ha of agroforestry practices and 100,000 ha of protective plantations within 20 years (Weber et al., 2013). Further, Ecuador joined the Initiative 20x20 in 2014 with a pledge to restore 500,000 ha of degraded land by 2017 (Initiative 20x20, 2014). For the study region in southern Ecuador, 32.3% of the land resource consists of abandoned areas that neither contribute to the livelihoods of the local people nor to the conservation of biodiversity (Göttlicher et al., 2009). Weber et al. (2013) argue that the reintegration of this increasing amount of unproductive and degraded land into the production area is an important element of the efforts to reduce the pressure on natural forests and to rehabilitate the provisioning of forest ESS. The authors show that plantations either with native or exotic species are an adequate tool for this. Two use cases of topographic variables for reforestation with native species are identified in the following.

First, an important challenge of plantation silviculture in the tropics is to achieve the best match between the site requirements of a species and the conditions at the planting site (Günter et al., 2011). This is especially true for reforestation with native species in the heterogeneous biophysical environment of degraded landscapes, where site edaphic factors can vary within tens of metres due to topographic relief, and species can respond differently to these conditions (Cheesman et al., 2018). Developing decision support systems for reforestation activities is a major challenge for silvicultural science and practice due to a lack of knowledge on proper site classification and site requirements of native tree species (Günter et al., 2011). Kübler et al. (2016) and Kübler et al. (2020) showed that topographic predictors allow for fine-scale species-specific estimations of natural habitat conditions that are optimal in terms of habitat suitability and growth rates. This information on environmental conditions at the natural habitat of a given tree species could provide guidance for reforestation site requirements of this species (Onyekwelu et al., 2011). Further, predictions of numerical models of habitat suitability and growth rates could be extended to potential reforestation sites, provided that topographic predictors for that area are available. Such models could therefore be an integral part of decision support systems for site-species matching in reforestation activities in TMF. However, similarity in terms of topographic conditions between a species' native habitat and a potential reforestation site does not ensure reforestation process. Hence, environmental similarity should only be considered as a first guideline; field trials are still necessary for precise site-species matching (Onyekwelu et al., 2011).

Second, the appropriate management of a network of seed stands for the sustainable production of seed and seedlings is a prerequisite to meet the reforestation goals of Ecuador (Weber et al., 2013). Discovering new populations of focal species as potential seed stands can be challenging in the study region, because accessibility of forest stands is often difficult due to the steep and rugged topography. To increase the efficiency of field surveys, SDM approaches can be used to sample areas with a high habitat suitability for focal species (see Williams et al. (2009) for an application in a different forest ecosystem). Further, intraspecific variation and local adaptations should be taken into account for seed-sourcing decisions to minimize the risk of maladaptation (Baughman et al., 2019). In that context, the outcomes of SDM have been successfully used to define provenance zones for seed collection (e.g. Crow et al., 2018; Ramalho et al., 2017).

5.3.3.3 Potential and limitations of calibrated models

The potential use cases identified above raise the question whether the statistical models developed and calibrated in Kübler et al. (2016) and Kübler et al. (2020) could have any direct use potential for SFM. There exist three important limitations for such an application.

First, models in Kübler et al. (2016) and Kübler et al. (2020) were developed for scientific purposes, as their aim was to gain knowledge on the underlying relationships between predictors and outcome variables. Hence, the statistical analyses in these studies focused on explanatory modelling (*sensu* Shmueli, 2010; see Section 2.2.2 for the difference between models for explanation and models for prediction). This limits the application potential for most of the potential use cases because they rely mostly on spatial predictions of outcome variables.

Second, in order to contribute to natural resource management, ecological models need to have appropriate temporal and spatial scales to address a given management situation (Schuwirth et al., 2019). Models from Kübler et al. (2016) and Kübler et al. (2020) were calibrated using data from the rather confined area of the silvicultural experiment. In contrast, the potential SFM use cases mentioned above would be applied in considerably larger areas. This raises the question of transferability, i.e. whether it is appropriate to project the models beyond the spatial bounds of their underlying data. Transferable models may have a huge potential for natural resource management in TMF, where the development of site-specific models is often hindered by data scarcity, lack of silvicultural knowledge, and limited research funding. On the other hand, models with low transferability may misguide management decisions (Yates et al., 2018). The transferability of ecological models depends to a large extend on the environmental similarity between the reference area of calibration and the target area. It should be noted that geographic distance between areas is frequently a poor predictor of environmental similarity (Yates et al., 2018). The fact that the study region in southern Ecuador is characterized by large environmental heterogeneity over short distances (Beck et al., 2008b) therefore indicates that models from Kübler et al. (2016) and Kübler et al. (2020) only have a limited transferability. For the case of SDM, the transferability and predictive power is further limited if the study area does not represent the complete species distribution range (El-Gabbas and Dormann, 2018). This applies for Kübler et al. (2016), where the used occurrence data only represent a very small subset of the full range of environmental conditions of the investigated species.

Third, models from Kübler et al. (2016) and Kübler et al. (2020) exclusively used VHR topographic predictors as proxies for environmental conditions. This was a sensible approach for the area of the silvicultural experiment where topography is strongly correlated to multiple environmental variables (see Section 5.3.1 and 5.3.2). However, these correlations are much weaker on larger scales. For example, the study region in southern Ecuador is characterized by considerable climatic variability (Rollenbeck, 2006); over a distance of 30 km in east-west direction, Beck et al. (2008b) reported a gradient of mean annual precipitation ranging from 3103 to 1068 mm on equal elevations (1950 m a.s.l.). In line with that, Günter et al. (2004) delineated a very high number of 134 potential genecological zones for the Province of Loja based on nontopographic ecological parameters. These examples indicate that additional environmental predictors should be used when modelling over wider, management-relevant areas.

These limitations suggest that it is inappropriate to directly apply models from Kübler et al. (2016) and Kübler et al. (2020) for SFM use cases. Nevertheless, outcomes from the two studies show a clear potential for management-relevant applications that could be improved upon in the future. For this, there are some recommendations for subsequent studies. First, the modelling process should be aligned to specific management objectives (Guisan et al., 2013; Schuwirth et al., 2019). Second, these studies would need a methodical shift towards predictive modelling. For this, a large toolbox of methods exists (e.g. Zuur et al., 2007), with algorithms from machine learning likely resulting in a higher predictive accuracy (Shmueli, 2010). Third, models developed with the aim of decision support in SFM will have to be calibrated for a larger spatial extent, and hence a wider range of environmental conditions. Forth, including climate predictors would allow for models to support forest management strategies under climate change (Pecchi et al., 2019). This is especially relevant for TMF, which may be more susceptible to changing climate than lowland forests (Günter, 2011b; Mathez-Stiefel et al., 2017; Vuille et al., 2015). Potential uses in the context of SFM include, for example, climate-adjusted provenancing for seed collection (Doherty et al., 2017; Prober et al., 2015) and analysing potential climate change impacts on areas suitable for particular tree species (Booth, 2018). For this, the combination of coarse-scale climatic variables with fine-scale topographic variables may improve the predictive capabilities of models (Pradervand et al., 2014).

Availability and quality of calibration data is an important prerequisite for the development of management-relevant models. Due to long-standing interdisciplinary research activities, these data were available for the area of the RBSF. In contrast, data are frequently scarce in many TMF areas (Scatena et al., 2011) and in the study region in southern Ecuador. There is a growing number of satellite missions that provide VHR stereo-images, which can be used to create VHR DEMs that can compete with traditional aerial photogrammetric products (Barbarella et al., 2017). The production of VHR topographic predictors, which are based on VHR DEMs (see Section 2.2.3.2), will therefore be increasingly available and affordable for larger spatial extents in the future. However, the availability of field data from forest inventories will likely remain a limiting factor.

6 Conclusions

This thesis set out to expand the current knowledge base about ecological processes and silvicultural interventions in TMF. For this, field data from a silvicultural experiment in the Andes of southern Ecuador and topographic variables obtained from a VHR digital terrain model were combined. Publication I (Kübler et al., 2016) showed that SDM techniques are an adequate tool to model the distribution of tree species at a very fine scale in a TMF and that it is important to use more than one performance criterion for the evaluation of SDM. The study further predicted habitat suitability and provided insight into the ecological relationships between tree species and topography. Publication II (Kübler et al., 2020) quantified how diameter growth rates of PCTs were impacted by liberation thinnings and topography across all species as well as on the species-level. Findings indicate that positive effects of silvicultural treatments in TMF are likely to exist, but that they are possibly obfuscated by strong topographical gradients and large between-tree growth variability. As an overarching result, elevation and the topographic position were the predictors that most influenced the distribution of tree species and diameter growth rates.

An important contribution of this thesis is the application of a novel methodological approach, i.e. the combination of ground-based tree data from a silvicultural experiment with high-resolution remote sensing data, which, to my knowledge, has rarely been carried out in TMF research. Further, results from the studies build on the existing evidence that topography is important for many ecological processes by providing quantitative and robust estimations on the effect of specific topographic variables at a local scale. Additionally, only very few studies have analysed the effect of silvicultural treatments on tree growth in TMF.

Publication III (Weber et al., 2013) showed that forests have an important provisioning function for the local population in the study region in southern Ecuador. The modelling approaches from publication I (Kübler et al., 2016) and publication II (Kübler et al., 2020) open the door for potential new applications that may contribute to the sustainable management of natural forests and reintegration of unproductive and degraded land into the production area. In order to draw on this potential, there is need for additional research that 1) facilitates the development of fine-scale and spatially explicit management prescriptions taking elevation and microtopographic variation into account, and 2) investigates the ecological and economic impacts of these prescriptions. Further, it is crucial that field methods and management prescriptions are adapted to enable smallholders and foresters in developing countries to make suitable management decisions under difficult field conditions.

These opportunities related to technical innovations cannot and should not be considered in isolation, but instead embedded in the broader context of approaches to protect biodiversity and ESS, sustain livelihoods, tackle food security challenges, and adapt to the impacts of climate change in TMF. In the tropics, such approaches include community engagement, the creation of clear legal frameworks, policies that secure tenure rights and remove incentives for clearing forests, financial measures such as payments for ESS and REDD+, and landscape approaches that integrate agricultural and forestry activities to come to more sustainable land use.

7 References

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8 Appendices

Appendix A Further publications of the author (not part of thesis)

Falk, T., Spangenberg, J.H., Siegmund-Schultze, M., Kobbe, S., Feike, T., **Kuebler, D.**, Vorlaufer, T., Settele, J., 2018. Identifying Governance Challenges in Ecosystem Services Management – Conceptual Considerations and Comparison of Global Forest Cases. Ecosystem Services 32, 193–203. https://doi.org/10.1016/j.ecoser.2018.07.012.

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