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The role of life history traits for coexistence and forest recovery after disturbance – a modelling perspective
Towards a better understanding of species-rich forests

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Abstract

Tropical forests are well known for their exceptional species richness – high diversity of plant species constitute the basis for an equivalently rich fauna. An astonishing variety of plant life strategies has evolved, manifesting itself also in different compositions of life history traits in trees. This thesis investigates the role of tree life history traits (growth, mortality and recruitment) on different processes structuring species-rich forests. Our study system is a montane rainforest located in the Tropical Andes hotspot of biodiversity in southern Ecuador. Here, we find a mosaic of steep ridges and deeply incised valleys, covered with predominantly broadleaf forest. Forest structure and species composition differ considerably depending on altitude and topographic position. The forest cover is frequently interrupted by scars of landslides, which constitute an important type of natural disturbance in this ecosystem.

We utilize ecological models as tools to gain deeper insights into key processes driving the maintenance of tree species richness and affecting forest recovery after landslides. The first part of this thesis concerns the question of species coexistence. We develop a theoretical model to analyze how different trade-offs between life history traits (tree growth, seed dispersal, tree mortality) affect tree species coexistence. We find that the considered trade-offs alone are not sufficient to explain long-term species coexistence. Additional 'stabilizing' mechanisms seem to be indispensable to facilitate coexistence in species-rich forests. Such mechanisms could result from biotic interactions, that alter the relation between inter- and intra-specific competition depending on (local) species abundances (e.g. density-dependent mortality). Other possible coexistence mechanisms likely to be relevant to our particular study system are driven by external, abiotic factors like a complex topography resulting in locally differing habitat types (each supporting a different set of species), or the character of a prevailing disturbance regime (e.g. shallow landslides).

In the second part of the thesis, we investigate the growth dynamics of the ridge forest in our study system. To this end, we utilize the process-based forest growth model FORMIND. We show that after calibration, the model successfully reproduces forest dynamics on different levels of complexity (e.g. basal area and stem size distribution). We then use this forest model to investigate the influence of landslide disturbances on forest dynamics both on the local scale of a single landslide and on the landscape scale. On landslide sites, changes in environmental conditions might lead to changes in different tree life history traits. We analyze scenarios with changes in different traits (tree recruitment, tree growth, tree mortality) and find that while tree biomass can recover within the first hundred years after a landslide, the time until forest structure and species composition is restored is considerably longer (approximately 200 years). Changes in different traits result in differing spatial distributions of tree biomass: reduced tree growth leads to a more homogeneous distribution of biomass, whereas reduced recruitment and increased mortality yield a more heterogeneous biomass distribution ('patchy' vegetation). On the landscape level, overall forest biomass is substantially reduced by landslides (8-

14%), compared to only 2 - 3% of the area marked by visible traces of landslides. Thus this particular type of disturbance considerably influences the total forest carbon balance.

In a complementary investigation we study abiotic and biotic factors that potentially trigger landslide occurrence in our study system. For this, we develop an extension of a standard physically-based model of slope stability. We find that due to the predominantly shallow tree roots, some of the observed landslides might be triggered by the vegetation itself.

This thesis demonstrates that ecological models are useful tools to gain deeper insights into important processes shaping forest communities. They can be applied for theoretical questions such as the question of species coexistence, as well as for more applied, management related questions like predicting forest recovery after disturbances.

Zusammenfassung

Tropische Regenwälder sind bekannt für ihren Artenreichtum – eine hohe Diversität von Pflanzen schafft eine große Vielfalt an Lebensräumen für Tiere. Man findet in den Tropen eine erstaunliche Mannigfaltigkeit verschiedener Lebensstrategien vor, die sich unter anderem in unterschiedlichen Eigenschaften der Lebenszyklen von Bäumen ausdrücken. Die vorliegende Arbeit untersucht, welche Rolle solche 'Lebenszyklus-Charakteristika' (life history traits) für die Strukturierung artenreicher Wälder spielen. Unser Forschungsgebiet ist ein Bergregenwald in Südequador, der zu den tropischen Anden, einem der weltweiten Hotspots der Artenvielfalt gehört. Dieses Gebiet ist gekennzeichnet durch steile Hänge und tief eingeschnittene Täler, die von artenreichem Laubwald bedeckt sind. Baumartenzusammensetzung und Waldstruktur variieren abhängig von der Höhe über dem Meeresspiegel und topographischer Position. Die Waldbedeckung wird häufig durch Erdrutsche unterbrochen, die eine wichtige natürliche Störung in diesem Ökosystem darstellen.

Für die Untersuchung von Schlüsselprozessen, die die Erhaltung der Baumartenvielfalt und die Regeneration von Wäldern nach Erdrutschen beeinflussen, verwenden wir ökologische Simulationsmodelle. Der erste Teil dieser Arbeit konzentriert sich auf die Koexistenz von Baumarten. Es wird ein theoretisches Modell entwickelt, um die Auswirkung verschiedener Zusammensetzungen von Arteigenschaften (Baumwachstum, Samenausbreitung und Mortalität) auf Koexistenz zu analysieren. Ein Hauptresultat dieser Studie ist, dass Unterschiede in den betrachteten Arteigenschaften (trade-offs) alleine nicht ausreichen für eine langfristige Koexistenz der Baumarten. Zusätzliche 'stabilisierende' Mechanismen scheinen notwendig für die Koexistenz von Baumarten auf langen Zeitskalen zu sein. Solche Mechanismen könnten zum Beispiel durch biotische Interaktionen entstehen, die das Verhältnis von inner- und zwischenartlicher Konkurrenz verändern (zum Beispiel dichteabhängige Mortalität). Weitere mögliche Koexistenzmechanismen sind abiotischer Natur, wie zum Beispiel eine komplexe Topographie, die in einer großen

Vielfalt verschiedener Lebensräume für unterschiedliche Arten resultiert, oder spezielle Störungsregime, wie zum Beispiel Erdrutsche in unserem Forschungsgebiet.

Der zweite Teil der vorliegenden Arbeit behandelt die Waldwachstumsdynamik des Gratwaldes in unserem Forschungsgebiet. Hierfür benutzen wir das prozess-basierte Waldwachstumsmodell FORMIND, das nach Kalibrierung die Walddynamik auf verschiedenen Komplexitätsstufen (beispielsweise Stammgrundfläche und Stammzahl-Durchmesserverteilung) reproduziert. Hernach verwenden wir dieses Waldmodell, um den Einfluss von Erdrutschen auf den Wald – sowohl auf der lokalen Ebene einzelner Rutschflächen als auch auf der Landschaftsebene – zu untersuchen. Wir betrachten Szenarien mit verschiedenen Änderungen in Arteigenschaften von Bäumen (Regeneration, Wachstum und Mortalität betreffend) als Reaktion auf veränderte Umweltbedingungen nach Erdrutsch-Störungen. Während die Gesamt-Baumbiomasse innerhalb der ersten 100 Jahre nach einem Rutschereignis regenerieren kann, ist die Zusammensetzung verschiedener Artgruppen deutlich länger verändert (ca. 200 Jahre). Änderungen in den verschiedenen Arteigenschaften führen zu einer unterschiedlichen räumlichen Verteilung der Baumbiomasse auf der Regenerationsfläche: verringertes Baumwachstum führt zu einer homogenen Verteilung der Biomasse, geringere Regeneration und erhöhte Mortalität führen zu einer heterogenen Verteilung der Biomasse. Auf der Landschaftsebene wird die Gesamtbiomasse deutlich stärker durch Erdrutsche reduziert (um 8-14%), als auf Luftbildern erkennbar ist: dort sind nur ca. 2-3% der Fläche von sichtbaren Rutschungsspuren gekennzeichnet. Daher ist die Berücksichtigung dieser speziellen Art von Störung unerlässlich für die Untersuchung der Kohlenstoffbilanz in unserem Forschungsgebiet.

In einer weiteren Studie untersuchen wir potentiell wichtige abiotische und biotische Faktoren für das Auslösen von Erdrutschen in unserem Forschungsgebiet. Hierfür erweitern wir ein etabliertes physikalisch-basiertes Modell für Hangstabilität. Ein wichtiges Ergebnis dieser Untersuchung ist, dass aufgrund sehr flacher Baumwurzeln die Vegetation zum Auslösen von Rutschen betragen könnte.

Diese Arbeit zeigt auf, dass ökologische Modelle nützliche Werkzeuge sind, um wichtige Prozesse in Wäldern zu untersuchen und ihr Zusammenwirken besser zu verstehen – sie können sowohl für eher theoretische Fragestellungen, wie die Koexistenz von Arten, als auch für mehr praxisbezogene Fragen, wie die Waldendwicklung nach Störungen, angewendet werden.

Resumen

Los bosques tropicales son conocidos por su excepcional riqueza de especies – una alta diversidad de especies de plantas constituye la base para una fauna con una diversidad equivalente. Una impresionante variedad de estrategias de vida vegetal ha evolucionado, variedad que se manifiesta también en las diferentes combinaciones de atributos funcionales en los árboles. Esta tesis investiga el papel de atributos funcionales en los

árboles (crecimiento, mortalidad y reclutamiento) en diferentes procesos que estructuran los bosques ricos en especies. Nuestro sistema de estudio es un bosque de lluvia de montaña sito en el hotspot de biodiversidad de los Andes tropicales en el sur de Ecuador. Aquí, encontramos un mosaico de colinas empinadas y valles profundamente excavados, cubiertos principalmente por bosque de frondosas. La estructura del bosque y la composición de especies varían considerablemente en función de la altitud y la posición topográfica. La cubierta forestal es interrumpida con frecuencia por surcos y corrimientos de tierra, que constituyen un importante tipo de alteración en este ecosistema.

En este trabajo utilizamos modelos ecológicos como herramientas para conseguir un conocimiento más profundo de los procesos clave que son responsables del mantenimiento de la riqueza de especies y que afectan a la recuperación del bosque después de los corrimientos de tierra. La primera parte de la tesis se ocupa de la coexistencia de especies. Desarrollamos un modelo teórico para analizar cómo diferentes compromisos (trade-offs) entre de atributos funcionales de los árboles (crecimiento del árbol, dispersión de semilla, mortalidad del árbol) afectan a la coexistencia de especies arbóreas. Como resultados encontramos que, solos, los compromisos considerados no son suficiente para explicar la coexistencia de especies a largo plazo. Mecanismos de estabilización adicionales parecen ser indispensables para facilitar la coexistencia en bosques con alta riqueza de especies. Estos mecanismos podrían resultar de las interacciones bióticas, que alteran la relación entre la competencia inter- e intra-específica, dependiendo de las abundancias (locales) de especies (p. ej. mortalidad dependiente de la densidad). Otros mecanismos de coexistencia probablemente relevantes para nuestro sistema de estudio particular, son conducidos por factores externos y abióticos, como la topografía compleja que deriva en tipos de hábitat localmente diferentes (cada cual manteniendo un conjunto diferente de especies), o el carácter del régimen de una alteración preponderante (p. ej. corrimientos de tierra de poca profundidad).

En la segunda parte de la tesis, se investiga la dinámica de crecimiento del bosque en las zonas de cresta del área de estudio. Para ello, empleamos el modelo de crecimiento forestal basado en procesos FORMIND. Mostramos que, tras la calibración, el modelo es capaz de reproducir la dinámica del bosque bajo diferentes niveles de complejidad (p. ej. área basal y distribución de tamaño del tallo). Posteriormente utilizamos el modelo para investigar la influencia de las alteraciones por corrimientos de tierra en la dinámica del bosque, tanto a la escala local del corrimiento de tierras en particular, como a escala de paisaje. En los terrenos de los corrimientos de tierras, cambios de las condiciones ambientales conducirían a cambios de atributos funcionales de los árboles. Analizamos escenarios con cambios en diferentes características (reclutamiento, crecimiento y mortalidad de árboles) y obtenemos que, mientras la biomasa arbórea puede recuperarse dentro de los primeros cien años después del corrimiento de tierra, el tiempo hasta que la estructura del bosque y la composición de especies son restablecida es considerablemente más largo (aproximadamente de 200 años). Cambios en las diferentes de atributos funcionales en los árboles conducen a diferentes distribuciones espaciales de la biomasa de árboles: un crecimiento arbóreo reducido lleva a una distribución más homogénea de

la biomasa, mientras que un reclutamiento reducido y una mortalidad crecida conducen a una distribución más heterogénea de la biomasa (vegetación "en parches"). A nivel de paisaje, la biomasa total del bosque es reducida sustancialmente por los corrimientos de tierra (8-14%), en comparación con tan solo un 2-3% del área con trazas visibles de corrimientos de tierra. Así, este particular tipo de alteración influencia considerablemente el balance total de carbono del bosque.

En una investigación complementaria, estudiamos factores abióticos y bióticos que pueden provocar corrimientos de tierra en nuestra área de estudio. Para ello, desarrollamos una extensión de un modelo estándar basado en procesos físicos de estabilidad de la pendiente. Encontramos que, debido al predominio de raíces arbóreas de poca profundidad, algunos de los corrimientos de tierra observados podrían ser desencadenados por la propia vegetación.

Esta tesis demuestra que los modelos ecológicos son herramientas útiles para adquirir un conocimiento más profundo sobre procesos importantes que dan forma a las comunidades forestales. Los modelos pueden ser aplicados a cuestiones teóricas tales como la coexistencia de especies, así como a cuestiones más aplicadas y relacionadas con la gestión, como la predicción de la recuperación del bosque después de alteraciones.

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Chapter 1

Introduction

"Wenn der Mensch mit regsamem Sinne die Natur durchforscht, oder in seiner Phantasie die weiten Räume der organischen Schöpfung mißt, so wirkt unter den vielfachen Eindrücken, die er empfängt, keiner so tief und mächtig als der, welchen die allverbreitete Fülle des Lebens erzeugt"

aus: Ansichten der Natur – mit wissentschaftlichen Erläuterungen.
Alexander von Humboldt, 1808, S. 157,
Tübingen, Cotta'sche Buchhandlung

Tropical rainforests belong to the most species rich ecosystems of our planet. They are threatened by deforestation due to timber production, land-use changes and climate change (Malhi et al., 2008; Hansen et al., 2010; Thomson et al., 2010). Over the past decades, research effort in tropical areas has increased, but our knowledge about the processes that maintain their biodiversity and the reaction of these complex systems to natural and anthropogenic disturbances remains incomplete. This thesis is an attempt to further our understanding of key processes in tropical forest systems by utilizing simulation models. The ecosystem that inspired the research presented here and served as study area is a speciose Andean forest in southern Ecuador.

1.1 Tropical Andes: the "global epicenter of biodiversity"[1]

The Tropical Andes are one of the richest and most diverse regions on earth – on less than one percent of the world's terrestrial area we find about a sixth of all plant life (Conservation International). They are home to more than 30,000 plant species, about half of them endemic (Rodríguez-Mahecha et al., 2004), and comprise various vegetation types: tropical wet and moist forest at lower elevations transition into cloud forest at higher elevations to be replaced by shrub- and grasslands (páramo and puna vegetation) above the tree line. Due to past land-use changes, only about one quarter of the original habitat extent of 1,500,000 km^2 remains (Brooks et al.,

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[1]Myers (1988)

Figure 1.1: The "Tropical Andes Hotspot" of biodiversity and a map of Ecuador; the location of the research area is marked with a red square (Source: www.biodiversityhotspots.org & www.lib.utexas.edu/maps).

2002; Mittermeier et al., 2004). These remnants face various threats, including deforestation, mining and oil explorations. The combination of their outstanding biodiversity and the loss of primary vegetation makes the Tropical Andes one of the hotspots of biodiversity of the world (Myers et al., 2000).

The study area for this research is the Reserva Biológica San Francisco (RBSF, 3°59´S, 79°05´W) in Southern Ecuador, part of the biosphere reserve Podocarpus – El Condor, located on the eastern slopes of the Andean Cordillera Real in the valley of the Rio San Francisco (cf. Figure 1.1). The 1000 hectare forest reserve stretches from 1,800 to 3,200 metres above sea level (m asl) and is characterized by steep slopes (up to 70°) and deeply incised valleys. The area has a perhumid climate with an annual average temperature of 15.5 °C and mean annual precipitation of 2050 mm (Bendix et al., 2008.). Major soil types are Histosols, Stagnosols, Cambiosols and Regosols (Liess et al., 2009). The vegetation at the study site can be classified as evergreen lower montane forest (below 2100 m asl), evergreen upper montane forest (2100 - 2700 m asl) and evergreen elfin forest (above 2700 m asl) (Homeier et al., 2008.). So far more than 280 tree species have been identified in this mostly undisturbed forest. The most abundant plant families are Lauraceae, Melastomataceae and Rubiaceae; *Graffenrieda emarginata* (Melastomaceae) is the most common tree species (Homeier and Werner, 2007). Our study area harbours an outstanding diversity not only of vascular plants (1208 spermatophytes and 257 ferns; Homeier and Werner (2007), Lehnert et al. (2007)) – it also contains the highest ever recorded species numbers per unit area of bryophytes (4500 species per 1000 ha; Parolly et al. (2004)) and of geometrid moths (41000 species; Brehm et al. (2005)). This remarkable plant species diversity inspires the

Figure 1.2: Photograph of the research area: forest cover with several visible traces of landslides (with kind permission of E. Beck).

general question: which mechanisms enable the coexistence of such a high number of species?

Another intriguing characteristic of our study area, which is also a feature of montane forests in general, is the natural disturbance by landslides. Due to the steep terrain in the RBSF, shallow landslides are a main source of natural disturbance (Bussmann et al., 2008); approximately 2.6% of the area is covered with visible traces of landslides. Most landslides are shallow translational slides (Stoyan, 2000); in some slide events only the aboveground vegetation is removed (cf. paper 4). Landslide events alter the forest structure in a dramatic way – usually all vegetation on top of the landslide surface is removed. Narrow bands of vegetation slip downwards leaving bare areas of approximately 10 - 30 m width and 20 - 100 m length for primary succession (see Figure 1.2). This conspicuous form of disturbance poses several questions about the role of landslides in this diverse forest ecosystem: how does the forest react on this particular form of disturbance? Do landslides have an effect on (tree species) diversity? And do forest dynamics influence the occurrence of landslides?

1.2 Coexistence and species traits

The high level of biodiversity in our study region is common to many tropical forest ecosystems; tree species richness in tropical forests, for example, can reach more than 300 tree species per hectare (Gentry, 1988; Ashton, 1993; Valencia et al., 1994). At the same time, abiotic conditions are more homogeneous in tropical systems compared to temperate zones: fluctuations in day-length and temperature are small and topography can be uniform over large areas (Dirzo, 2001). How can hundreds of species of one trophic level that seem to depend on few resources (light,

water, nutrients) coexist in a relatively homogeneous environment? This seems to contradict the principle of competitive exclusion (Gause's Law) which states that for every combination of environmental variables, there will be one species which will dominate the community and eventually drive all other species to extinction (e.g. Crawley, 1997a). This apparent contradiction makes it necessary to extend the focus from abiotic to biotic factors and environmental heterogeneity caused by them (Ricklefs, 1977).

The question of how species coexist has inspired ecological research for decades if not centuries – numerous field investigations as well as theoretical research have been undertaken to gain a better understanding of the processes that maintain biodiversity in ecosystems (see 2.1). One focus of biodiversity research is the investigation of differences between species with the purpose of understanding how these differences influence species competition and coexistence. Such differences concern on the one hand directly measurable physiological traits, for instance photosynthesis rate, tree growth rate or leaf level attributes, and on the other hand population level traits like mortality rate. Species attributes that influence the life table of species are studied in life history theory; so called **life history traits** are key characteristics defining the life course of species, for example attributes connected to reproduction, offspring and lifespan, including basic demographic rates like mortality rate, birth rate and also growth patterns (e.g. Stearns, 1992; Crawley, 1997b; Wright et al., 2010). All traits investigated in this thesis are related to tree growth, mortality or regeneration acting on the population level and are hereafter subsumed under the term life history traits. This definition also includes physiological traits that affect the life table of species. Life history theory is based on the idea that available resources are limited and allocation patterns must be a compromise of different competing demands like for example reproductive success and longevity. This leads to **trade-offs**, i.e. negative relationships in trait combinations, when a "benefit realized through a change in one trait is linked to a cost paid out through a change in another" (Stearns, 1992, p. 14). A variety of different trade-offs has been hypothesized to act in forest ecosystems (see e.g. Crawley, 1997b, for an overview).

A prominent example from forest ecology, where differences in species traits – in conjunction with spatial heterogeneity created by disturbance – facilitate species coexistence are pioneer and late successional tree species (Whitmore, 1998). In the low-light conditions of a closed canopy, a light-demanding pioneer tree species may have a competitive disadvantage compared to a shade-tolerant late successional tree species; but by producing a high number of wind-dispersed seeds the pioneer can ensure its survival by establishing its offspring in canopy openings that are created by falling dead trees. In these openings, the pioneers have an advantage over the shade tolerant climax species since they can use the high-light condition more efficiently. In this example different trade-offs are at work: the pioneer species invests into fast population growth (high reproduction rate) at the cost of a high offspring mortality (many seeds end up in unsuitable places). A second typical pioneer trade-off is a high individual growth rate at the cost of a higher mortality rate, i.e. a shorter life span. Typical late successional species in contrast produce a low number of offspring but with a higher offspring surviving probability. Also late successional species tend to grow slow but often have a low mortality rate, i.e. a longer life span (e.g. Crawley, 1997b; Rees and Westoby, 1997). The extent to which such trade-offs contribute to species coexistence is not intuitively clear; we will investigate this question in paper 1.

1.3 Landslides and species traits

"A landslide is the movement of a mass of rock, earth or debris down a slope" (Cruden, 1991). Landslides are a common natural disturbance in tropical montane forest ecosystems (Garwood et al., 1979; Restrepo et al., 2009), resulting from slope destabilization for example due to earthquakes, heavy rains, forest clear cuts, road cuts or volcanic activity. The size of the area affected

by a single landslide ranges from several square meters to many square kilometers (Walker and del Moral, 2003). Environmental conditions on landslide surfaces are considerably altered compared to conditions in undisturbed forest: light is increased (Myster and Fernandez, 1995), soils might be unstable (Walker and Shiels, 2008) and due to the loss of the organic soil layer the soil nutrient content is reduced even many years after the slide event (Zarin and Johnson, 1995; Wilcke et al., 2003). One focus of landslide research is the local scale of single landslides and here mostly the first phase of succession where early landslide colonizers like mosses, lichens, ferns and bamboo dominate the vegetation (e.g. Dalling and Tanner, 1995; Ohl and Bussmann, 2004; Velazquez and Gomez-Sal, 2008). But the changed environmental conditions on landslide sites may also affect life history traits of trees and therefore influence the longer term course of forest recovery. For example, the establishment of trees might be hindered by the harsh environmental conditions and tree growth might be reduced due to nutrient limitation. Changes in different life history traits affect forest structure and productivity on landslide sites and will thus also affect overall forest productivity in forests where landslides occur frequently (Restrepo et al., 2003).

Apart from the local scale of a single landslide surface, landslides are also an interesting phenomenon to examine on the landscape scale and over long time periods – they create a patchy distribution of different aged sites with differing edaphic conditions and successional stages of vegetation. Therefore, landslides are assumed to be a driver of biodiversity by increasing landscape heterogeneity (e.g. Yamamoto et al., 1995; Geertsema and Pojar, 2007; Elias and Dias, 2009). However, investigating a high number of different aged landslide sites is difficult due to inaccessibility of the terrain, and investigating time periods long enough to observe the 'shaping' character of landslides in a forested landscape exceeds a human life span by far. For this purpose, ecological models can be used.

1.4 Ecological models

The processes and interactions that shape natural communities are often complex and therefore difficult to decipher via observation. Some of the obstacles are the richness of interactions in ecosystems which additionally might occur on different scales, or the slow speed of processes of interest (e.g. forest growth). To gain insights in these processes we need to abstract from reality and reduce complexity. Ecological models should serve this purpose as tools for thinking and learning about interrelationships in ecosystems and analyzing system behaviour under defined conditions. Ecological models can be useful for

- extending our understanding of (general) functional relationships in ecosystems

- testing hypotheses about the functioning of (specific) ecosystems

- predicting the system behaviour under different (e.g. climatic or management) conditions

- investigating scenarios which are impossible to test in the real ecosystem

- inspiring our thinking about the functioning of ecosystems (developing new hypothesis)

- instigating field experiments

The complexity of a model should always be driven by the ecological questions and hypotheses we have in mind (Wissel, 1989). Depending on the set of questions that should be tackled by an ecological model, the model will look differently. One possible categorization for ecological models is to differentiate between more **theoretical models**, that seek general insight into ecological processes and relationships and **applied models**, which aim to describe dynamics of a specific study system and understand interrelationships, often also with the purpose of managing the

system (Bolker, 2008). Yet, those are only the endpoints of a continuous scale with theoretical models on the one end and applied models on the other (Yodzis, 1989). A theoretical model will usually be relatively simple and rather conceptual with a relatively small number of parameters. The coexistence model which was developed to investigate the role of life history traits for species coexistence (paper 1) falls into the category of more theoretical models. Applied models which should reproduce dynamics of a particular system often require a higher level of detail and can thus be more complex than theoretical models. Higher complexity usually involves a higher number of parameters and the parametrization of such models can become a time-consuming task. The forest model that was utilized to simulate forest growth dynamics in our study area and to investigate forest recovery after landslide disturbances (cf. paper 2 and 3) falls in the category of more applied models.

1.5 Structure of the thesis

This thesis comprises four chapters. Following the introduction, the second chapter introduces concepts and methodologies that are important as a broader background of the research presented in this thesis. Chapter three contains four research articles that can be read independently from each other. The **first** article investigates the role of trade-offs between different life history traits (mortality, growth, seed dispersal) for species coexistence. We show that the investigated trade-offs alone do not support long-term coexistence – additional processes that regulate the local competition (e.g. density-dependent mortality) are necessary to enable coexistence. In the **second** article, we study the growth dynamics of the ridge forest within our study region. For that, we utilize a process based forest growth model and develop a parametrization for this model. The article covers a comparison of model output and field measurements as well as a detailed description of the forest model and the parametrization that is also employed in the third article. We demonstrate that our forest model is capable of reproducing the structure and dynamics of mature ridge forest on different levels of complexity. The **third** article analyzes the impact of shallow landslides in tropical montane forests. Different scenarios of forest regrowth with changed life history traits of tree species (mortality, growth, establishment) are compared regarding their effect on forest structure and productivity. We find that on the local scale of the landslide, spatial structure and productivity of the successional forest differs depending on the changes in life history traits. On the landscape scale, landslides reduce forest biomass and considerably modify the spatial distribution of biomass. The **fourth** article investigates a complementary aspect of the interactions between forest and landslides – it addresses the question whether vegetation related biotic factors might be one of the triggering factors for landslides. We present an extension of a classical slope stability model by introducing an independent organic (root) layer atop the mineral soil, which is only loosely connected to the soil. With this modified slope stability model, we can explain the observed shallow landslides in our research area, that almost exclusively involve organic material. The fourth chapter gives a synthesizing discussion of the results of this thesis.

Chapter 2

Concepts and Methodologies

The aim of this chapter is to introduce the concepts and methods applied in this thesis and to embed them in a broader scientific context.

2.1 Species coexistence: concepts and models

The question of biodiversity and its maintenance can be dealt with at different spatial and temporal scales: On the global scale, biogeography and macroecology try to explain plant diversity by climatic factors, habitat heterogeneity and historical/evolutionary processes (Kreft and Jetz, 2007). On the smaller scale of local communities, where climatic conditions are more or less constant in space, species coexistence is thought to be mediated by (intra- and interspecific) competition, predation, diseases, disturbances, spatial and temporal heterogeneity (Ricklefs, 1987; Tilman and Pacala, 1993; Chesson, 2000). The coexistence study presented in paper 1 focuses on species coexistence on the community level.

Competition between species has caught a great deal of attention in ecology for a long time (e.g. Darwin and Wallace, 1858). One reason for this is that in communities, where competition for resources is present, it is likely to have a major effect on species diversity (Huston, 1994) – in this sense the question of species coexistence is closely related to the question of competition between species. Competition can be viewed at the individual scale, where for example one tree shades a neighbouring tree and therefore suppresses its neighbour's growth, and at the population scale, where the composition of all species traits (e.g. species specific growth and mortality rates) and their interactions affect population dynamics and determine whether a species will dominate, coexist with other competitors or go extinct in the long run. Mechanisms for species coexistence can be divided into **stabilizing** and **equalizing** mechanisms: stabilizing mechanisms reduce interspecific competition in relation to intraspecific competition whereas equalizing mechanisms reduce fitness differences between species (Chesson, 2000; Adler et al., 2007). Examples for stabilizing mechanisms are density-dependent processes, e.g. species specific pathogens or herbivores which ensure that locally dominant species experience negative feedbacks (the Janzen-Conell hypothesis: Janzen (1970); Connell (1971)). An example for an equalizing mechanism is the trade-off between growth and survival – slow growing plants have often a larger longevity than fast growing plants (Crawley, 1997b; Kneitel and Chase, 2004).

In general, communities can be in an equilibrium or in a non-equilibrium state: population sizes in a community which is in its equilibrium state are stable (apart from stochastic fluctua-

tions): theoretically the occurring species coexist forever. In communities which are not in an equilibrium state, population sizes change. There can be different reasons for that: maybe time was not sufficient to reach equilibrium or maybe there is no equilibrium state. In the latter case species can nevertheless coexist (e.g. fluctuating system like patch cycles in forest gaps), or species do not coexist over long time periods but species' loss is compensated by speciation or immigration. Chesson distinguishes stable and unstable coexistence: stable coexistence implies that populations can recover from low densities and population densities show no long-term trend. Unstable coexistence implies that populations do not tend to recover from low densities, i.e. in the long run, species can go extinct. While stabilizing mechanisms support stable coexistence, equalizing mechanisms give rise to unstable coexistence.

Field investigations (e.g. Condit et al., 1996, etc.) and experiments (e.g. Tilman, 1994; Hector et al., 1999; Scherer-Lorenzen et al., 2005) have been used to further our understanding of the key processes maintaining biodiversity at the community level. In parallel, different types of theoretical models investigating species interactions and their influence on species coexistence have been developed. As an outcome, two contrasting views on biodiversity have established (Clark et al., 2007; Kraft et al., 2008): the first one assumes that differences in species traits are important for community diversity – it involves physiological trade-offs along a small number of axes in a trait space, including resource competition, 'competition-colonization' and life history traits (for an overview on important trade-offs see e.g. Stearns (1992); Crawley (1997b,a); Tilman (1997)). The second view, neutrality, assumes that species differences are negligible for community diversity; instead, species are assumed to be functionally equivalent, populations follow a random drift and go extinct in the long run (Hubbell, 2001). Thus, neutral theory views nature from the non-equilibrium perspective. In the sense of Chesson (Chesson, 2000), the equalizing mechanism of a neutral model is, that all species have exactly the same fitness (functional equivalence); the model does not bear a stabilizing mechanism, diversity is maintained by immigration (from a species pool) and speciation. In contrast, theories assuming that differences in species traits matter for diversity often use the equilibrium perception and ask how different trade-offs can sustain diversity. Here, both stabilizing and equalizing mechanisms come into play and it is not clear *per se*, whether a specific trade-off acts stabilizing or equalizing. Prominent examples for trade-offs in plant communities are competition-colonization trade-off, survival-reproduction, growth-reproduction and seed-size versus seed-number (e.g. Crawley, 1997b).

Models of coexistence

One of the earliest theoretical model dealing with competition of (two) species and the question under which conditions these species coexist is the Lotka-Volterra competition model (see e.g. Townsend et al., 2003). It consists of two simple differential equations describing a logistic-type population growth of two species depending on growth rates, carrying capacities and competition coefficients of both species. In the Lotka-Volterrra model, all factors affecting competition are subsumed in the competition coefficient. But competition can occur on different axes, i.e. for different resources. Therefore, if we are interested in understanding competition in more detail, an expansion of the simple competition coefficient into ecologically meaningful factors is beneficial. Consequently, the simple and elegant mathematical description of competition in the Lotka-Volterra model has undergone various modifications and extensions and inspires ecological research to date (e.g. Levins and Culver, 1971; Tilman, 1994; Pacala and Rees, 1998; Murrell and Law, 2003). One possible way of categorizing competition models is to differentiate the way they address space. While the original Lotka-Volterra model does not incorporate any spatial

effects, many other models of competition which are based on differential equations treat space implicitly (e.g. Levins, 1969; Slatkin, 1974; Hastings, 1980; Tilman, 1994; Pacala and Rees, 1998). **Spatially implicit** models assume well mixed-populations, i.e. every individual experiences the influence of all other individuals in the system to the same extent. One benefit of spatially implicit models is that they often are analytically tractable. But in many ecosystems, space plays an important role since individuals interact mostly with their local environment; this is particularly relevant for sessile organisms like plants. For example, in a spatially implicit forest model every tree would receive the same (medium) amount of light as a resource. This assumption contradicts the perception of forests as a shifting mosaic of patches of different successional stages (Whitmore, 1998). **Spatially explicit** models of competition, where individuals have an assigned position in the landscape, can account for such local interactions of organisms. Space in these models can be treated continuously or it can be subdivided into discrete units (mostly square lattices). Spatially explicit models are more flexible – they allow incorporating not only local interactions but also factors like spatial heterogeneity or spatially correlated disturbances (e.g. Banitz et al., 2008) – but usually this flexibility entails the loss of analytical solvability (Klausmeier and Tilman, 2002).

Since the ecosystem that is of interest to this thesis is a plant community, and local interactions such as competition for light and space are important, the model developed for investigating species coexistence – presented in paper 1 of the thesis – is spatially explicit. Concerning trade-offs, we focus on the basic demographic traits growth, seed dispersal and mortality. Additionally to trade-offs between these traits, we investigate two processes that modify local competition: density-dependent mortality and light-dependent regeneration. Many existing modelling studies focus on single mechanisms for species coexistence (e.g. Potthoff et al., 2006; Pronk et al., 2007; Clark et al., 2007; Münkemüller et al., 2009; Clark et al., 2010); yet, the question how different mechanisms interact remains open. In addition, recent modelling studies have shown that some trade-offs promote coexistence only in narrow parameter ranges (Lischke and Löffler, 2006; Banitz et al., 2008). We therefore investigate how different trade-offs between life history traits alone and in combination with additional mechanisms that modify local competition affect species coexistence in plant communities.

2.2 Understanding forest dynamics

Eight thousand years ago, prior to the vast expansion of human enterprise across the globe, earth's forests covered an estimated area of 62 million square kilometres (Sizer et al., 1997). Forests have been exploited by humans since ancient times and already Plato noticed the deforestation of the forests of Attica (Thomas, 1956). Today's forests cover approximately 40 million square kilometres ($\sim$ 30% of the world's land cover, FAO (2009)), i.e. about 40% of the original forest cover has disappeared – strongest losses concern temperate and tropical regions (Malhi et al., 1999; Hansen et al., 2010).
Forests fulfil various vital functions: they produce renewable resources such as timber for construction, fuelwood and non-timber products like fruits, medicinal plants etc.; they moderate local climate and water cycles and procure diverse habitats for animals. In recent decades growing attention is given to the role of forests for the global carbon cycle in the context of climate change (Beer et al., 2010) – estimations of carbon stored in the world's forest range from 220 to 540 gigatons (Gt) (Dixon et al., 1994; Houghton et al., 2009), which is a considerable amount compared to circa 750 Gt carbon stored in the atmosphere (Grace, 2004). The rapid rates of ongoing deforestation, accompanied by losses of forest functions and diversity (Fearnside, 2005; van der Werf et al., 2009), brought along the need for a better understanding of forest ecosys-

tems and tools for their management. Forest models are instruments to meet these challenges – accordingly they belong to the pioneers of ecological models. Relevant areas of application for forest models are (Huth, 1999)

- ecological research: understanding forest dynamics

- prediction of forest dynamics under changed conditions (management, climate change)

- planning and guidance of forest management and monitoring

Depending on the purpose of the model, the state variables to describe the forest, as well as the appropriate model design may differ. To date, numerous forest models for different types of forest (boreal/temperate/tropical forests, even-/uneven-aged, single/multiple species) exist. One possible differentiation of forest models is to distinguish between **whole-stand** models, **stand-class** models and **single-tree** models (Vanclay, 1995). Whole-stand models use aggregated variables like stand basal area, wood volume or the age of a stand to describe a forest (e.g. Jeltsch and Wissel, 1994). The traditional type of whole-stand models are yield tables which were first applied in mono-species, even-aged stands. Yield tables predict the harvestable wood volume depending on the planted species, the age of the forest stand, site quality and applied forest management (e.g. Schwappach, 1890). Stand-class models are more detailed than whole stand models: they describe the development of different groups (e.g. diameter size classes, age classes, species groups) of trees. Some stand-class models use differential equations to describe the forest state (e.g. Moser, 1974); another type of stand-class models are so-called Markov models, which describe forest dynamics as stochastic processes: trees have a certain transition probability to move from one diameter size class to the next (Suzuki, 1971; Logofet and Lesnaya, 2000). Single-tree models describe the state and growth of every individual tree (above a certain size) of the stand, and therefore they belong to the class of individual-based models (Grimm and Railsback, 2005). These models incorporate competition between trees for resources, for example competition for space can be accounted for by a factor for crown competition (Ek and Monserud, 1974; Dudek and Ek, 1980; Pretzsch, 2001; Shugart, 2003). Forest gap models belong to the class of single-tree models; they describe the growth of all trees on a small patch of land, the so-called gap (Bugmann, 2001; Shugart, 2002). The underlying idea of gap models is that forests consist of mosaic patches of different successional stages and that each gap passes through the full cycle of succession (cf. Figure 2.1). A derivative of single-tree models are process-oriented models, which explicitly take into account physiological processes like photosynthesis, respiration, water and nutrient-cycling (Bossel and Krieger, 1991; Mohren and Burkhart, 1994; Grote and Erhard, 1999). Such models allow calculating the carbon balance of each tree, and carbon can be allocated to different compounds of the tree (stem, roots, leaves).

The more detailed the forest is described in the model, the more complex the model becomes (e.g. higher number of parameters) and computational demand increases. Also the type of data used for model parametrization changes: whole-stand and stand-class models commonly utilize census data; single-tree models often incorporate additional knowledge on tree allometry and process-based models also incorporate knowledge on physiological processes.

As described in the introduction, we are interested in understanding the dynamics of a tropical montane forest in relation to disturbance (landslides); in particular, we want to investigate how changes in different life history traits of trees affect the regeneration process on landslide sites. This is because various environmental variables change on landslides sites, potentially affecting forest dynamics in the long term and on large spatial scales. For this purpose, a process-based approach that addresses physiological processes explicitly is most suitable. To investigate the
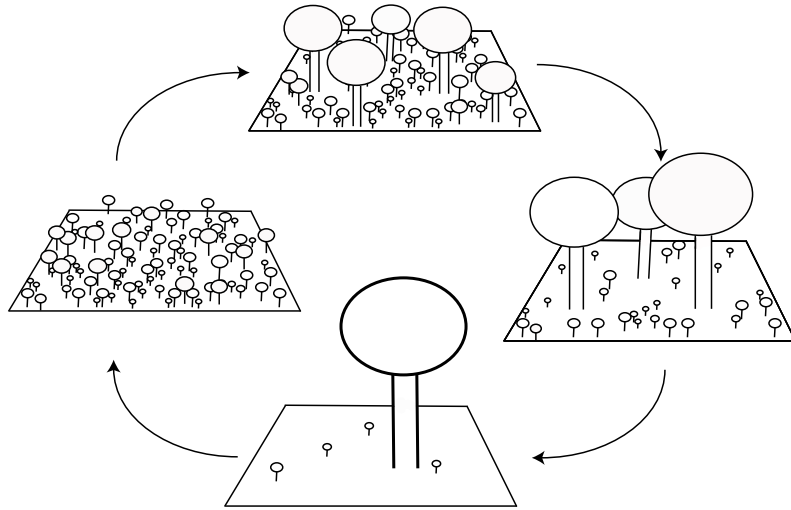
Figure 2.1: Gap-cycle: forest dynamics on a small patch of land, after Shugart (2003). Important processes are mortality (of canopy trees), recruitment, self-thinning, competition.

effect of landslides on the landscape level it is also advantageous to use a spatially explicit approach, where one can simultaneously compare disturbed with undisturbed forest zones. The forest model utilized in paper 2 and 3 of this thesis is the FORMIND model, which combines the gap model approach with the process-oriented philosophy.

The FORMIND model

The FORMIND model and its predecessor model FORMIX are spatially explicit, individual-based forest models. They are designed to analyze the dynamics of uneven-aged, species-rich forest stands with a focus on the impact of natural or anthropogenic disturbances on forest structure and composition (Köhler, 2000). They have been successfully applied to various forests throughout the tropics (Huth et al., 2005; Rüger et al., 2007b; Groeneveld et al., 2009; Gutierrez et al., 2009; Köhler and Huth, 2010). The main processes of the model are tree growth, mortality, establishment of young trees and possibly external disturbances (e.g. landslides, windthrows, fire). On small patches (20 x 20 meter) all trees compete with each other for light and space. The light climate for every patch is calculated and trees grow according to photosynthesis and respiration rates. FORMIND simultaneously simulates a certain number of patches; this way, areas from one hectare up to several hundred square kilometres can be simulated. Patches have explicit positions and interact via two processes: big trees shade trees in neighbouring patches and falling dead trees can damage trees in neighbouring patches.
A common challenge for the parametrization of forest models for tropical forests is the high number of tree species in combination with scarce data. FORMIND uses the plant functional type approach (Smith et al., 1997; Köhler et al., 2000; Jeltsch et al., 2008): species are grouped according to physiological traits like light status or maximal diameter. The parametrization
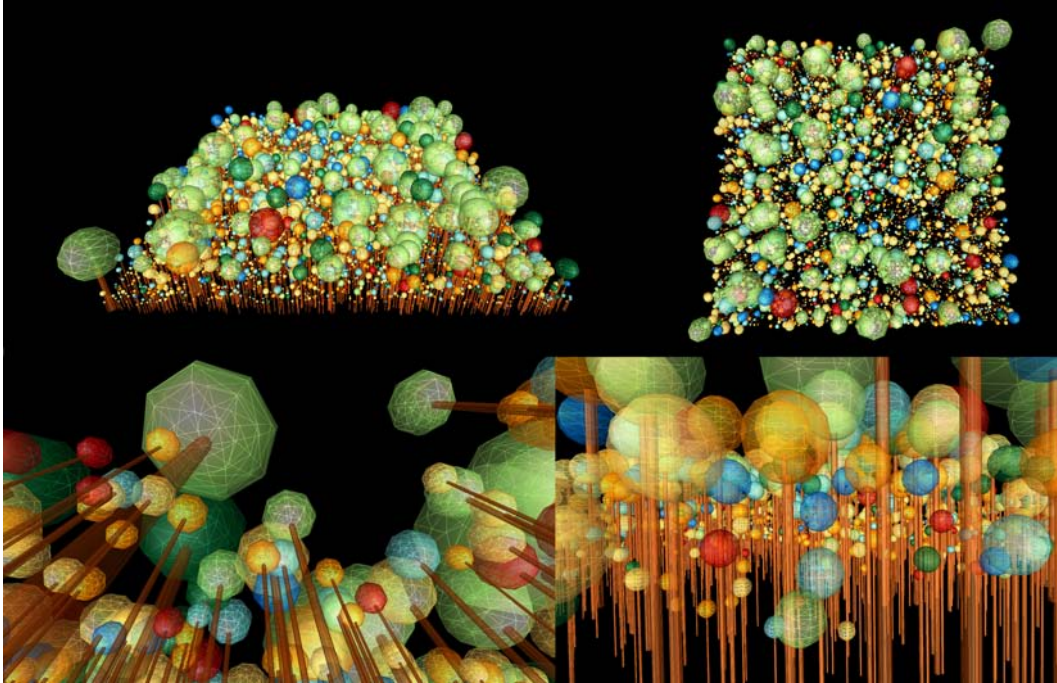
Figure 2.2: Snapshots from the 3D-visualisation of the FORMIND model. Different colours of tree crowns represent different plant functional types.

of such models involves analysis of data from different sources: census data (e.g. diameter and height measurements), physiological measurements (e.g. photosynthesis rate, wood density) and measurements of environmental variables (e.g. radiation above canopy). Where field data is missing, expert knowledge and values from the literature for other forests can help to determine reasonable ranges for parameters which can then possibly be narrowed through model calibration.

In paper 2 we develop a parametrization of FORMIND for the ridge forest, one forest type of our research area. We then utilize the model to investigate the influence of landslides on forest dynamics on the local, as well as on the landscape scale (paper 3). The aim of this investigation is to develop a better understanding of the influence of this special type of disturbance on forest dynamics, particularly on forest structure, biomass and productivity.

2.3 Slope stability models

A common tool for estimating landslide risks in montane regions are physically-based slope stability models. Such models combine topographical, soil and hydrological attributes, as well as vegetation related factors (e.g. root cohesion) in order to predict slope stability (e.g. Montgomery and Dietrich, 1994; Borga et al., 1998; Guzzetti et al., 1999). In combination with GIS-based tools, slope stability models can be used to predict landslide locations and produce landslide risk maps (e.g. Xie et al., 2004). Here, landslide inventories provide tests for model performance by comparing observed landslide locations with model predictions (Borga et al., 1998). A prominent class of slope stability models employ planar infinite slope analysis, assuming that slopes are continuous and long, and that the thickness of the unstable layer is small compared to the slope length (e.g. Sidle, 1992). Based on Mour-Coloumb's failure criterion, the factor of safety

– defined as the ratio of stabilizing and destabilizing forces – describes the stability of a slope. A factor of safety smaller than 1 indicates instable slope conditions. This type of slope stability models have been widely applied to investigate the role of deforestation and the role of roads on slope stability (e.g. Sidle and Wu, 1999; Dhakal and Sidle, 2003; Borga et al., 2005; Imaizumi et al., 2008). In paper 4 we adapt a standard slope stability model to the situation of tropical forests where trees have predominantly shallow roots. For this, we add an aboveground layer, representing the organic layer which potentially might destabilize slopes, to the standard model. This study focusses on the analysis of factors that trigger very shallow translational landslides, involving almost no inorganic material. Thereby, we address not only the question how landslides affect forest dynamics (cf. paper 3) but also how forest vegetation potentially affects landslide occurrence.

Chapter 3

Research Papers

List of papers in this chapter

Summary of the author's contribution

Paper I

Title	What enables coexistence in plant communities? Weak versus strong species traits and the role of local processes
Authors	Claudia Dislich, Karin Johst, Andreas Huth
Status	published 2010 in Ecological Modelling 221, 2227–2236
Contribution	Dislich (70%) Idea, model development, model analysis, conception and writing of manuscript.
	Johst (10%) Discussion of model results, manuscript editing.
	Huth (20%) Idea, feedback/discussion, manuscript editing.

Paper II

Title	Simulating forest dynamics in a tropical montane forest in South Ecuador
Authors	Claudia Dislich, Sven Günter, Jürgen Homeier, Boris Schröder, Andreas Huth
Status	published 2009 in Erdkunde 63, 347–364
Contribution	Dislich (60%) Idea, model development, model analysis, conception and writing of manuscript.
	Günter (10%) Data collection, parametrization development, manuscript editing.
	Homeier (10%) Data collection, parametrization development, manuscript editing.
	Schröder (5%) Discussion of model results, manuscript editing.
	Huth (15%) Idea, feedback/discussion, model development, manuscript editing.

Paper III

Title	Impact of shallow landslides on forest structure in tropical montane forests
Authors	Claudia Dislich, Andreas Huth
Status	in review (Ecological Modelling)
Contribution	Dislich (80%) Idea, model development, model analysis, conception and writing of manuscript.
	Huth (20%) Idea, feedback/discussion, manuscript editing.

Paper IV

Title	Shallow translational landslides in tropical montane forests - a hint towards biotic control?
Authors	Peter Vorpahl, Claudia Dislich, Helmut Elsenbeer, Michael Märker, Boris Schröder
Status	in preparation for resubmission after major revision (Earth Surface Processes and Landforms)
Contribution	Vorpahl (65%) Idea, model development, data acquisition, model analysis, conception and writing of manuscript.
	Dislich (10%) Idea, preliminary model analysis, feedback/discussion, manuscript editing.
	Elsenbeer (5%) Feedback/discussion, manuscript editing.
	Märker (5%) Feedback/discussion, manuscript editing.
	Schröder (15%) Feedback/discussion, manuscript editing.

Claudia Dislich, Karin Johst, Andreas Huth

What enables coexistence in plant communities? Weak versus strong species traits and the role of local processes
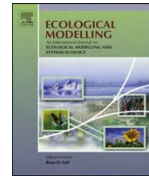
What enables coexistence in plant communities? Weak versus strong species traits and the role of local processes

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ARTICLE INFO

ABSTRACT

Explaining the coexistence of species that basically depend on the same resources has been a brainteaser for generations of ecologists. Different mechanisms have been proposed to facilitate coexistence in plant communities, where space is an important resource. Using a stochastic cellular automaton simulation model we analyze – separately and in combination – the influence of different species traits and processes which alter local competition on the coexistence of plant species over a fixed time horizon. We show that different species traits operate on different time scales in competition. We therefore suggest the concept of weak versus strong traits according to short- or long-term exclusion of species differing in these traits. As a consequence, highly non-linear trade-offs between weak and strong traits can result in communities. Furthermore, we found that trade-offs based on physiological species traits such as plant lifetime, dispersal range and plant growth, did not support broad and long-term coexistence—further processes such as density-dependent mortality and light-dependent colonization were necessary. This suggests that coexistence in plant communities requires (stabilizing) local processes to support the (equalizing) trade-offs in species traits.

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1. Introduction

The question of species coexistence has been challenging ecological research for decades. A bundle of theories has been suggested to explain coexistence between species, prominent examples are niche theory (Hutchinson, 1957), neutral theory (Hubbell, 2001) or the intermediate disturbance hypothesis (Connell, 1978; Roxburgh et al., 2004). Each of these theories has also been discussed in relation to diversity in plant communities. In the framework of niche theory one important factor for species coexistence in plant communities is the existence of interspecific trade-offs in physiological traits (Tilman and Pacala, 1993; Wright, 2002). For example, one species could have an advantage concerning one physiological attribute, but this advantage could be balanced via a disadvantage concerning a second attribute. There is rich literature on different trade-offs, most famous the competition–colonization trade-off (Tilman, 1994; Holmes and Wilson, 1998), where species differ in competitive strength and colonizing ability. This trade-off has been shown to foster coexistence to a certain degree (Klausmeier and Tilman, 2002). Further coexistence mechanisms are related to spatial and/or temporal heterogeneity. Processes that operate on small local/temporal scales can have the potential to enhance species coexistence, for instance local density-dependent processes arising from species specific pests or predation can prevent abundant species to become all-dominant (Chave et al., 2002; Molofsky et al., 1999). Within a theoretical framework Chesson (2000) divides all those different proposed coexistence mechanisms into equalizing mechanisms and stabilizing mechanisms—while equalizing mechanisms reduce fitness differences between species, stabilizing mechanisms reduce interspecific competition in relation to intraspecific competition (see also Adler et al., 2007).

For analyzing and testing coexistence mechanisms, ecological models play an important role (Durrett and Levin, 1994; Kerr et al., 2002; Johst and Huth, 2005). But many model studies focus on only single mechanisms for species coexistence (e.g. Potthoff et al., 2006; Pronk et al., 2007; Esther et al., 2008; Münkemüller et al., 2009); the question how different mechanisms interact remains open. In addition recent model studies have shown that trade-offs alone promote coexistence only in narrow parameter ranges (Lischke and Löffler, 2006; Banitz et al., 2008).

In this study, we therefore investigate competition of plants in a spatial context. We ask, how trade-offs alone and in combination with additional processes that modify local competition (hereafter called local processes) affect coexistence. As sessile organisms plants interact mostly with their local environment; to reflect these local interactions we chose a spatially explicit individual-based approach (Durrett and Levin, 1998). Our model is a stochastic cel-

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lular automaton, inspired by the DivGame Simulator (Alonso and Solé, 2000). The generality of the model allows for applications to different communities with sessile organisms such as grasslands, forests or coral reefs. We focus here on forest communities, therefore our individual entity is a tree. The species traits we examine as trade-off attributes are seed dispersal range, tree growth rate, and mortality rate. We compare conditions for species coexistence in three models: a basic trade-off model and two models where local processes are added to the basic model. These additional local processes are density-dependent mortality (DDM) and light-dependent colonization (LDC). The outcome of competition between two species over a given time horizon is analyzed in two steps: first we investigate the effect of single traits on species coexistence. To do so we look at the competition between two species which are identical in all but one trait. Secondly we introduce all three possible trade-offs between the life-history traits (dispersal-mortality, dispersal-growth, and growth-mortality) and explore the ranges of coexistence with and without local processes. Finally we study the competition between multiple species in a trade-off community and in communities with the additional local processes.

2. Model description

The structure of the model description follows the ODD protocol (Grimm et al., 2006). We seek a model of minimal complexity that captures the essential processes of forest dynamics.

2.1. State variables and scales

Our model is a spatially explicit, individual-based simulation model that includes competition of trees for light and space. Space is divided into patches on a grid. The grid has 20×40 patches (200×400 patches in the multi-species competition); each patch ($10\,m \times 10\,m$) can host a mature tree, thus the simulated forest covers an area of 8 ha. After competition for space among seeds and seedlings, respecitively, a patch accommodates at most one tree at a time. Each tree is characterized by its location, the species it belongs to and its height.

Species differ in the attributes seed dispersal range, mortality rate and growth rate. Maximal tree height is fixed to the same level for all species and all young trees recolonize empty patches with a predefined minimal height. Above a certain threshold height trees are mature and spread seeds within the whole dispersal range.

For the competition of two species we state that a species coexists, if it occupies at least 10% of all patches at the end of the observation period.

2.2. Process overview and scheduling

The dynamics of the community are modelled with an annual time step. Within one time step, N single steps are performed, with N being the number of patches. A single step comprises the processes colonization, mortality and growth completed according to Fig. 1.

2.2.1. Basic (trade-off) model
2.2.1.1. Colonization.
Species may have different dispersal distances. Empty sites can be colonized, if seeds reach that site and if the mean height of neighboring trees (8-patch-neighborhood) is below a threshold h_{tr}. Reoccupation of empty patches after a disturbance is implemented as a lottery competition: the number of seed-producing trees within the dispersal distance of the empty patch is counted and then, weighted according to species abundances, the colonizing species is chosen at random.
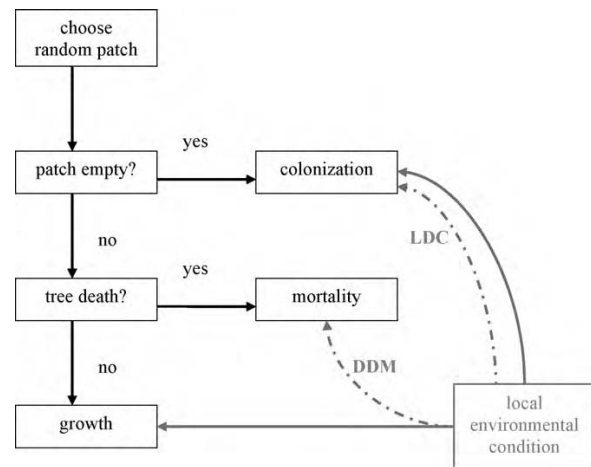

Fig. 1. Order of processes within a single step. This sequence is repeated within one year according to the number of patches. While colonization and growth are always influenced by local environmental conditions, mortality is only influenced by local conditions in the presence of density-dependent mortality (DDM). Light-dependent colonization (LDC) stresses the influence of local environmental conditions on colonization.

2.2.1.2. Mortality.
Each species has a basic mortality rate m, the probability for each tree to die in one year. Dying trees are removed and leave empty patches for recolonization.

2.2.1.3. Growth.
Each species has a growth rate g that represents maximal annual growth in the absence of light competition. Competition for light is asymmetric—in the same environment a big tree receives more light than a smaller tree. Thus growth is reduced if a tree is shaded by neighboring trees. The strength of growth suppression depends on the mean height of the eight neighboring trees (h_m). If this mean height is smaller than the height of the focal tree i, light competition is neglected and the tree grows at its maximal rate:

$$H_i(t + \Delta t) := H_i(t) + g \cdot \Delta t \tag{1}$$

If the mean height of neighbors exceeds the height of the focal tree, growth is reduced by the factor $(H_i(t)/h_m)^{0.5}$, and the new tree height is calculated according to

$$H_i(t + \Delta t) := H_i(t) + g \cdot \left(\frac{H_i(t)}{h_m}\right)^{0.5} \cdot \Delta t. \tag{2}$$

For the reduction of growth under light competition we tested different functions. Preliminary simulations showed that the chosen function results in a reasonable distribution of tree heights where all possible tree heights are represented.

2.2.2. Local processes
2.2.2.1. Intraspecific density-dependent mortality (DDM).
When trees of the same species are locally clumped they might encounter increased mortality due to propagation of pests or species specific herbivores and pathogens (Chave et al., 2002). Density-dependent processes have been detected in forests of different biomes, e.g. in tropical forests (John et al., 2002; Peters, 2003), in boreal forests (Gray and He, 2009) and in temperate forests (Zhang et al., 2009). We introduce an intraspecific density factor $d \in [0,1]$ that increases the basic mortality rate m, if more than half of the neighboring patches are occupied by conspecifics. The new mortality rate m_d of the focal individual increases proportionally with the number of conspecific neighbors. The maximum increment of the basic mortality rate is given by the density factor, e.g. a density factor of 1

leads to a doubling of the mortality rate, when all neighbors are conspecifics. Thus m_d depends on the number of surrounding conspecifics n and the density factor d:

$$m_d = \begin{cases} m & \text{for } n \le 4 \\ m \cdot \left(1 + \dfrac{n-4}{4} \cdot d\right) & \text{for } n > 4 \end{cases} \tag{3}$$

2.2.2.2. Light-dependent colonization (LDC). It is assumed that each species has a preferred light climate at which it is more likely to win the recruitment competition. An index L_i for a certain light requirement, is assigned to each species i, indicating the most favorable light condition for colonization. L is a number between 0 and 1, where 0 represents a light-demanding and 1 a shade-tolerant species. For an empty patch, the light climate index l is calculated via the mean height of the eight neighboring trees ($i = 1..8$):

$$l = \frac{(1/8) \cdot \sum h_i}{h_{tr}} \in [0, 1]. \tag{4}$$

The species i with L_i closer to light climate l is more likely to colonize. We employ the normal distribution with mean L_i and standard deviation σ (here 0.05) to calculate weighting factors w_i for the colonization of each species i:

$$w_i = \frac{1}{\sqrt{2\pi}\sigma} e^{-(l-L_i)^2/2\sigma^2}. \tag{5}$$

According to the weights w_i colonization is then implemented stochastically.

2.3. Design concepts

The model is formulated as a stochastic cellular automaton with periodic boundaries. Colonization and mortality are stochastic processes, growth is deterministic and depends on the height of neighboring trees (Eqs. (1) and (2)). We focus on the observation of species abundances over time. Abundances of species and thus species coexistence and exclusion, respectively, emerge through species traits, spatial distribution of species and initial conditions. Trees interact by suppressing the growth of neighboring trees through shading and via density dependence. Colonization of empty patches depends on species composition around the patch, on light climate and on the light demands of species (Eqs. (4) and (5)).

Within one time step, the patches are chosen at random; updating takes place asynchronously, the grid is updated after each single step. This update procedure adds stochasticity to the (otherwise deterministic) growth process.

2.4. Parameters and initialization

The model parameters (inspired by Alonso and Solé, 2000 and Shugart, 2003) are summarized in Table 1. Each tree has an initial height of 0.1 m and can reach a maximum height of 40 m. Seed dispersal sets in at a tree height of 1 m and the threshold of mean neighbor height for colonization (h_{tr}) is set to 12 m. At the beginning of the simulation, species are randomly distributed at low densities (80 individuals per species), each individual has an initial tree height of 0.1 m. This initialization reflects one possible colonization situation on bare ground. Experiments with different initial conditions concerning the size of initial trees and also the density of trees in the initial state all revealed similar model behavior and results.

We investigate the competition of two species with different traits over a fixed time of 1000 years. The dispersal range varies from 10 m (=length of one patch, only the 4 nearest neighbors) to 100 m with a step width of 5 m. Annual growth rates vary from 0.05 to 1 m/year (m/y) (step width 0.05 m/y) and mortality rates

Table 1
Parameters of the model.

Parameters	Values/ranges
Grid cells	20×40 (200×400^a)
Species number	2 (196^a)
Simulation length [y]	1000 ($15\,000^a$)
Species independent	
Minimal tree height [m]	0.1
Maturing height [m]	1
Maximal tree height [m]	40
Threshold height for colonization [m]	12
Species specific	
Mortality rate [1/y]	[0.005, 0.1]
Dispersal range [m]	[10,100]
Growth rate [m/y]	[0.05, 1]
Density factor d	[0,1]
Light requirement index L	[0,1]

[a] Values for the multi-species competition.

from 0.005 to 0.1 per year (y^{-1}) (step width 0.005 y^{-1}). With these parameter ranges we cover a large variety of ecologically reasonable species traits (e.g. Phillips and Gentry, 1994; Whitmore, 1998; Kohyama et al., 2003; Muller-Landau et al., 2008).

To investigate the role of single traits and trade-offs between two traits we vary only two parameters at a time and fix all remaining traits for both species to medium values within the considered ranges (60 m dispersal range, 0.5 m/y growth rate and 0.05 y^{-1} mortality rate).

3. Results

To get a first idea of the dynamics of the competing populations, Fig. 2 shows the changes in abundances over time and spatial snapshots for three situations. The first example shows competitive exclusion of species 1 after 800 years, triggered by an adverse dispersal-mortality trade-off: the disadvantage of a higher mortality rate for species 1 compared to species 2 is not balanced by the larger dispersal range of species 1. The second example shows neutral coexistence: both species have completely identical traits and we observe a considerable amount of fluctuation in the abundances due to stochasticity. The last example shows coexistence through a combination of a trade-off and a local process: a shade-tolerant species 2 with less dispersal abilities and a higher mortality coexists with a light-demanding species 1.

3.1. Exploration of the basic (trade-off) model

3.1.1. Traits: competing species with differences in only one attribute

We first analyze the effect of single traits on coexistence and examine two species that differ only in one trait (dispersal range, mortality rate or growth rate, Fig. 3). If species differ in dispersal range or mortality rate (Fig. 3a and b), then already after 1000 years competitive exclusion has taken place leading to one dominant species (the species with higher dispersal range or lower mortality rate). We only get coexistence in the neutral case with identical species. In contrast, two species with different growth rates (Fig. 3c) may still coexist after 1000 years. Thus we hypothesize that, compared to growth rate, the attributes dispersal range and mortality rate are 'strong' traits. The 'weak' trait growth rate influences coexistence on a slower timescale; for longer time periods the coexistence range in the diagram for different growth rates also 'shrinks' down to the diagonal (>6000 years, simulated but not shown). (Note that the time span until competitive exclusion takes place also depends on the size of the simulated area—on a bigger grid the dynamics slow down.) Our results show that the
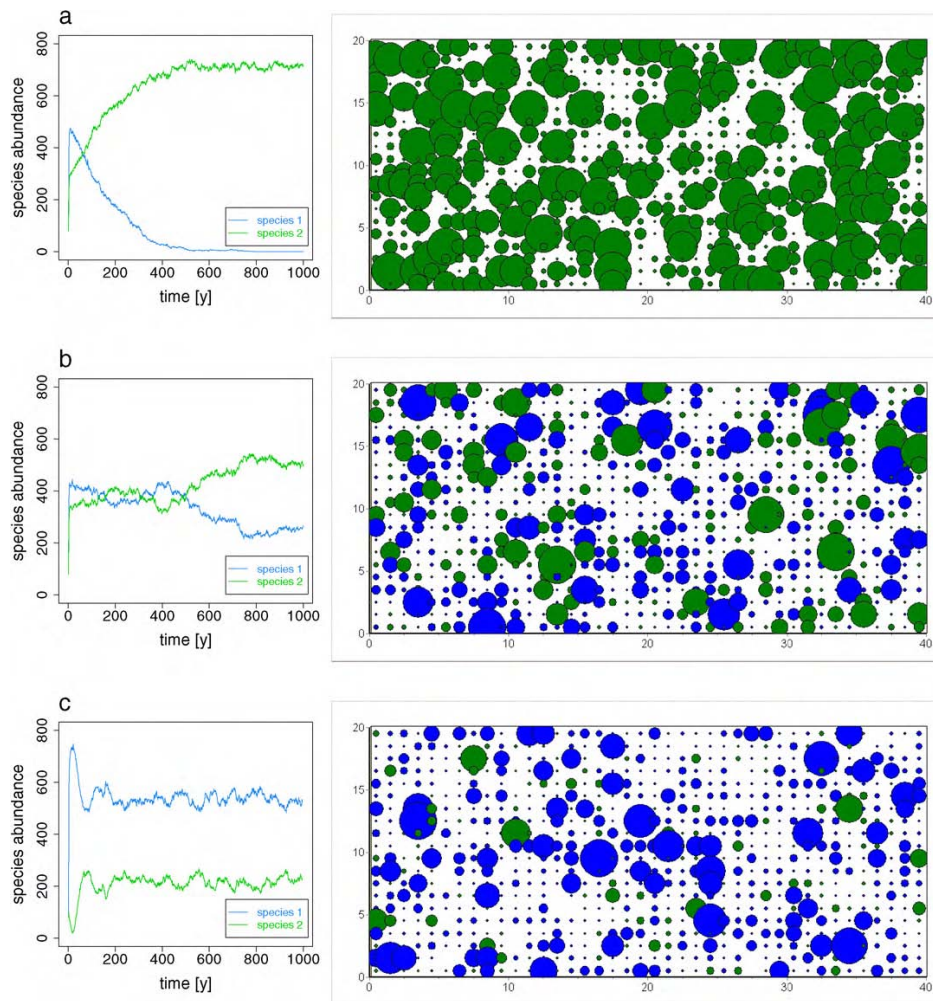
Fig. 2. Species abundance over time and snapshots of the grid after 1000 years of simulation for three parameter combinations. Species 1 is illustrated in blue (grey), species 2 is green (black). Each circle is an individual tree, the circle size indicates tree size. Parameters: (a) respective dispersal ranges of 60 and 50 m, growth rates of 0.5 m/y for both species and respective mortality rates of 0.05 and 0.03 y^{-1}. (b) completely identical species, dispersal ranges of 60 m, growth rates of 0.05 m/y and mortality rates of 0.05 y^{-1}. (c) Model with light-dependent colonization (LDC), species 1 light-demanding ($L_1 = 0$), species 2 shade-tolerant ($L_2 = 1$); respective dispersal ranges of 80 and 60 m, growth rates of 0.5 m/y for both species and respective mortality rates of 0.05 and 0.08 y^{-1}. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

time until competitive exclusion takes place may differ considerably between traits when varied in an ecologically reasonable range; we therefore introduce the concept of weak versus strong traits.

3.1.2. Trade-offs: competing species with differences in two attributes

We now come to trade-offs (Fig. 4), i.e. we consider competing species that differ in two traits. In the following, one species (species 1) is chosen to have medium properties and we are interested in the traits a second species must show to coexist with this 'medium' species.

For all three possible trade-offs, the coexistence ranges are very small for an observation period of 1000 years. In the dispersal-mortality trade-off (Fig. 4a) two species can only coexist, if there is a proper trade-off between the two attributes: if species 2 has a larger dispersal range (e.g. 70 m) than species 1, it must also have a higher mortality rate (0.06 y^{-1}). A slight change of only one attribute (e.g.

species 2 dispersal range 70 m, mortality rate 0.065 y^{-1}) results in the extinction of one species.

For trade-offs involving growth rate (Fig. 4b and c), the parameter combinations which allow coexistence show a non-linear relation within the considered parameter ranges compared to the linear coexistence curve in Fig. 4a. This is again an indicator of the varying strengths of species attributes: the weak trait growth rate cannot balance big differences in strong traits (in particular small dispersal ranges or high mortality rates of species 2). On the other hand, there are levels of dispersal range (respectively, mortality rate) of species 2, where different growth rates of species 2 result in coexistence (for example growth rates between 0.75 and 1 m/y at a dispersal range of 55 m, Fig. 4b).

The general result of this investigation for the basic model is that coexistence is only possible for certain fine-tuned combinations of species traits. While even small changes in strong traits (here dispersal range and mortality rate) lead to the extinction of one species, changes in weak traits (growth rate) can preserve coexistence.
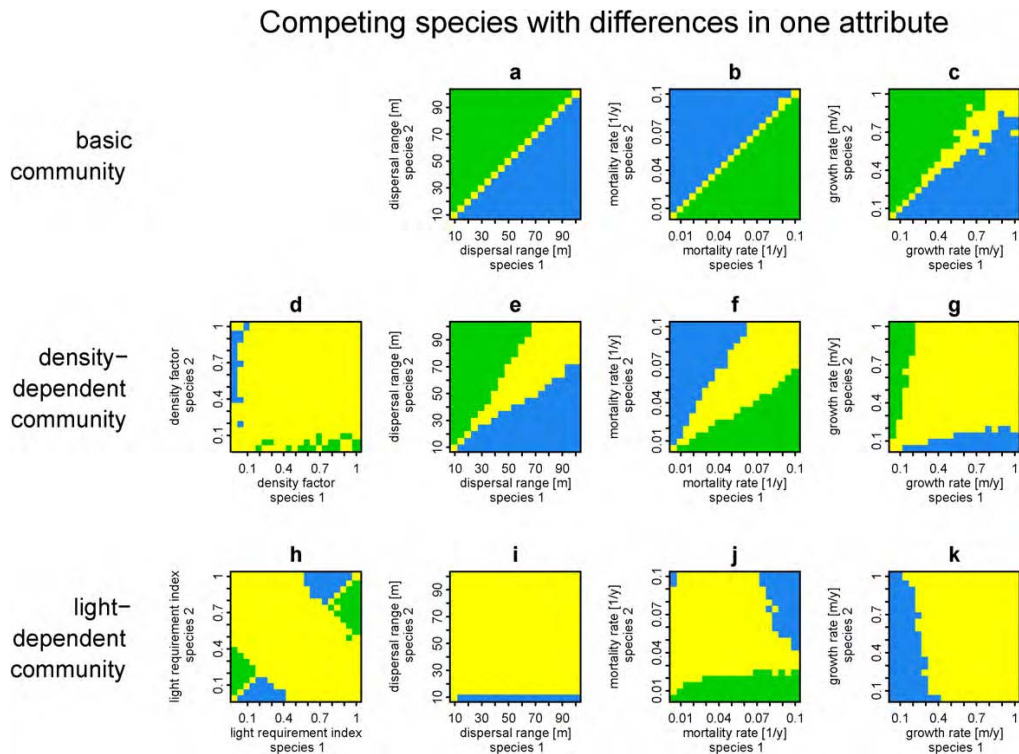
Competing species with differences in one attribute

Fig. 3. Variation of single attributes in a two-species community. Each point is the outcome of a single simulation run after 1000 years; a yellow (white) point represents coexistence, while blue (grey) stands for dominance of species 1 and green (black) for dominance of species 2. First row: basic community without local process. Second row: community with local density-dependent mortality (DDM); in e, f and g both species have density factor $d = 1$. Third row: community with light-dependent colonization (LDC); in i, j and k species 1 is light-demanding (light requirement index $L_1 = 0$) and species 2 shade-tolerant ($L_2 = 1$). Column 0: variation of the local processes (d) density factor and (h) light requirement index. Column 1: variation of dispersal ranges. Column 2: variation of mortality rates. Column 3: variation of growth rates. The remaining parameters are fixed to: 60 m dispersal range, 0.5 m/y growth rate and 0.05 y^{-1} mortality rate. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

3.2. Exploration of the local processes

3.2.1. Traits: competing species with differences in only one attribute

We investigate two different processes which modify local competition: density-dependent mortality and light-dependent colonization. Two species that have completely identical traits and only differ in the strength of density-dependent mortality nearly always coexist (Fig. 3d). Only if one species experiences strong density dependence while the other species does not show density dependence, can the latter be a superior competitor. The addition of local density-dependent mortality for both species increases the coexistence range (Fig. 3e–g). It modifies the competitive strength of species traits: the strong traits (dispersal range and mortality rate) become weaker and the weak trait (growth rate) becomes almost irrelevant for coexistence.

With light-dependent colonization (Fig. 3, light-dependent community), two otherwise identical species coexist for a broad range of trait combinations with various light requirements (Fig. 3h). In this way this additional species attribute acts in a different manner to the previously considered traits (Fig. 3a–c).

The competition of a light-demanding species 1 and a shade-tolerant species 2 results in much larger coexistence ranges for all three single attributes (Fig. 3i–k) than in the basic community. Dispersal ranges (Fig. 3i) become almost irrelevant to coexistence. If both species experience high mortality (Fig. 3j), the light-demanding species dominates the forest, while the shade-tolerant species dominates if it has a low mortality rate. We observe the

most notable change in the coexistence pattern compared to the basic community in relation to growth rates (Fig. 3c and k). In the investigated range there is no combination of growth rates where the shade-tolerant species 2 dominates the competition, and for some combinations, where in the basic model species 1 was excluded, it now wins the competition.

3.2.2. Trade-offs: competing species with differences in two attributes

Concerning species that differ in two traits (Fig. 4) we observe much larger coexistence ranges for both local processes compared to the basic trade-off community. The coexistence ranges show a clear and even widening if mortality depends on the local density of conspecifics (Fig. 4d–f).

For the model with light-dependent colonization we analyze two cases where species 1 has a medium light requirement index ($L_1 = 0.5$) and species 2 is shade-tolerant ($L_2 = 1$, Fig. 4, light-dependent community I) or light-demanding ($L_2 = 0$, Fig. 3, light-dependent community II). The borders of dominance versus coexistence areas are not as sharp as for the other models. The coexistence ranges mainly expand in sectors where in the basic model species 2 was dominant. Thus the species with medium traits profits from the introduction of light-dependent colonization, because it can now coexist, where previously it was excluded.

A shade-tolerant species (here species 2) will only dominate the competition if it has a low mortality rate (Fig. 4g and i) and a light-demanding species will almost never exclude the intermediate species (here species 1, Fig. 4j–l).

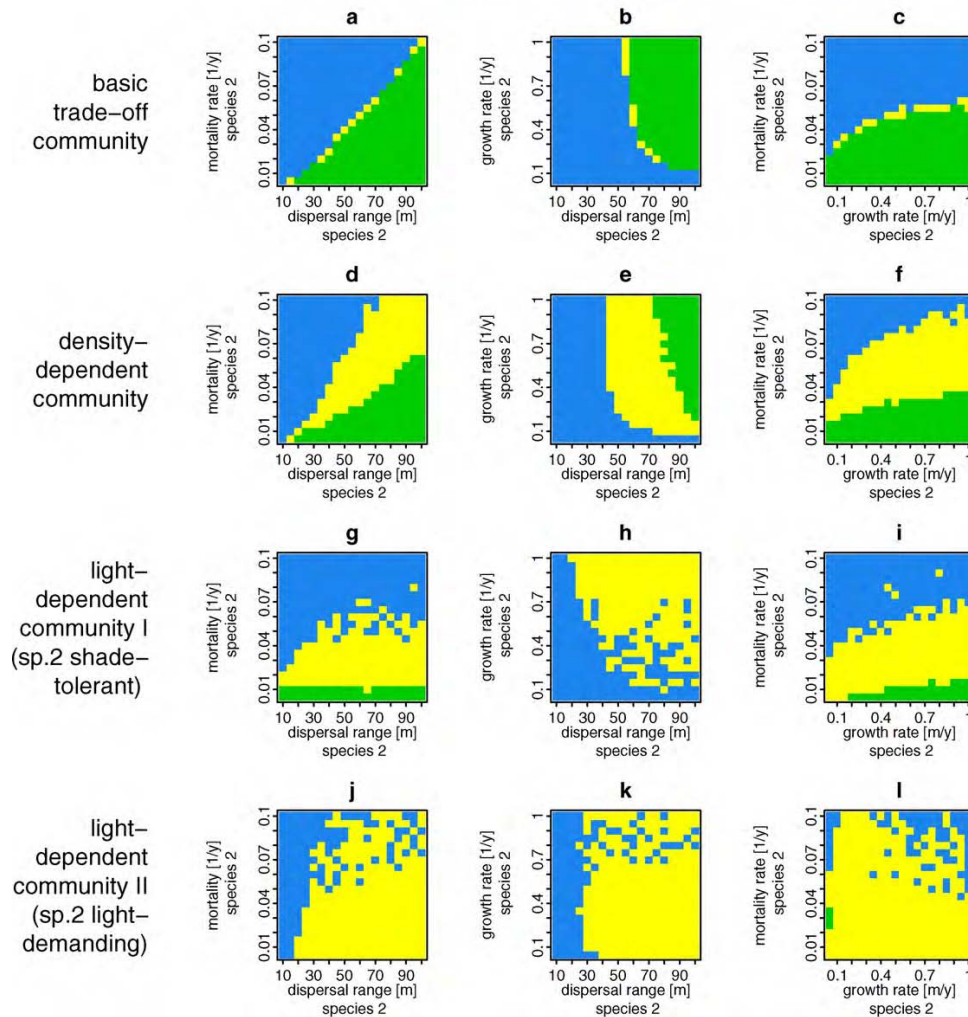## Competing species with differences in two attributes

Fig. 4. Variation of two attributes in a two-species community. Species 1 has medium properties: dispersal range 60 m, mortality rate 0.05 y^{-1} and growth rate 0.5 m/y. First row: basic trade-off community without local process. Second row: community with density-dependent mortality (DDM) of both species ($d = 1$). Third and fourth row: community with light-dependent colonization (LDC): species 1 is medium light-demanding (light requirement index $L_1 = 0.5$). In light-dependent community I species 2 is shade-tolerant ($L_2 = 1$) and in light-dependent community II species 2 is light-demanding ($L_2 = 0$). Column 1: dispersal-mortality trade-off, growth rate (species 2) = 0.5 m/y. Column 2: dispersal-growth trade-off, mortality rate (species 2) = 0.05 y^{-1}. Column 3: growth-mortality trade-off, dispersal range (species 2) = 60 m.

A substantial effect of both local processes, DDM and LDC, compared to the basic model is that coexistence is mostly stable over long periods of time. Without such local processes, the coexistence ranges are already narrow for 1000 years and disappear in long-term simulations (15 000 years, see Appendix Fig. 7). Note that even identical species do not coexist in the long run due to stochasticity in colonization and mortality.

4. Discussion

4.1. Traits act differently: weak versus strong traits

Our results show that physiological traits of plants may 'act' on different temporal scales, since the patterns of coexistence for growth rates differ from those for dispersal ranges and mortality rates (Fig. 3). To understand this we need to look at how these processes affect reproduction. Having a large dispersal range is a clear advantage of one species over another since it directly results in a higher probability of colonizing an empty patch. Having a low mortality rate is also a strong advantage: the number of dying trees is reduced and the number of seed-producing trees is increased. On the other hand, high mortality rates allow more space for colonization resulting in a higher turnover in the community while at the same time changing the hight structure of the forest; there are more small trees and the number of seed-producing trees is reduced.

Compared to these 'strong' traits, growth rates act more indirectly on colonization: for reproduction it is only important that a tree reaches its mature height. Secondly, the actual growth of a tree is not directly determined by the growth rate, since growth is also influenced by the height of the surrounding trees (Eq. (2)). A high growth rate leads to an increased number of large trees and thus also to increased suppression of small trees due to shading. Hence a high growth rate is an advantage for a species, but one that works indirectly and thus more slowly than the advantage of a strong trait

such as a large dispersal range or a low mortality rate. The traits 'act' on different time scales; this also leads to non-linear coexistence relations in the trade-offs involving growth rates (Fig. 4b and c). Thus there might be thresholds above or below which we cannot expect functioning trade-offs between strong and weak traits.

Note that the dispersal-growth trade-off is one we would not anticipate for forests, where generally pioneer species have large dispersal ranges and are at the same time rather fast growing while late successional species have smaller dispersal ranges and slower growth. A dispersal-mortality or growth-mortality trade-off is more likely to match forest ecosystems.

Even over relatively short timescales (1000 years) coexistence is only possible for certain combinations of species traits; even small changes in strong traits result in species extinction. This suggests that the basic trade-off model is insufficient to explain species coexistence.

4.2. Functioning of local processes

We explored the functioning of two local processes, that could potentially facilitate coexistence—density-dependent mortality and light-dependent colonization. Both mechanisms have a similar strong effect of increasing coexistence by softening the strength of single species attributes. Density-dependent mortality directly promotes coexistence by reducing the locally abundant species. We find a similar effect if locally rare species experience a reduced mortality rate (not shown). Both phenomena have been discussed for forests (Janzen, 1970; Wills et al., 2006). Density-dependent mortality increases the intraspecific competition whenever a species becomes locally abundant—this weakens the strength of species attributes (Fig. 3, density-dependent community). Most combinations of growth rates lead to coexistence, i.e. the (weak) trait growth rate becomes almost irrelevant for coexistence.

The second local process investigated assumes different light requirements for colonization; this process is directly related to the heterogeneous height-structure within a forest, which is highly dynamic over time. Without light-dependent colonization (LDC) the local height-structure only influences tree growth, but not the regeneration. With LDC, empty patches become more amenable to colonization by one or the other species and spatio-temporal niches are thus created. Therefore two species with different light requirements compete to a lesser extent for the same patches and this enhances coexistence. Seen in terms of the classical Lotka–Volterra competition model, interspecific competition is reduced by introducing LDC.

The dispersal range trait becomes almost irrelevant for coexistence (Fig. 3e), since the recruitment lottery, which previously depended solely on the number of potential parental trees within the neighborhood, is replaced—now the seedling that is best adapted to the light climate in the empty patch has the best recruitment chances.

While density-dependent mortality expands coexistence ranges symmetrically (Fig. 3e–g), adding different light requirement results in asymmetric changes in coexistence ranges for mortality and growth rates (Fig. 3j and k).

High mortality rates (Fig. 3j) of both species result in many empty patches and small trees. This results in high light availability and the light-demanding species 1 dominates the competition. Both species can coexist if the light-demanding species 1 experiences low mortality and the shade-tolerant species 2 experiences medium to low mortality, because the shade-tolerant species profits from the high abundance of big trees.

A similar argument explains the somewhat counterintuitive result (Fig. 3k) that the light-demanding species 1 dominates competition, if it has low growth rates: the shade-tolerant species

2 simply does not find enough suitable patches for colonization, because of the low tree heights of species 1.

As in the case of the single traits (Fig. 3), coexistence ranges become considerably larger for all three considered trade-offs (Fig. 4), when a local process is added to the basic trade-off model. While the coexistence range expands evenly for density-dependent mortality (Fig. 4d–f), the majority of new coexistence space caused by light-dependent colonization (LDC) is in areas where species 2 had previously dominated the competition. This suggests that the medium species 1 generally does better than light-demanding or shade-tolerant species, because it is not as highly specialized for certain light conditions. The discontinuity of the coexistence patterns (Fig. 4, light-dependent community I and II) stems from the fact that the equilibrium abundances of species can differ so much (see Fig. 2c), that one species constantly "scratches" on the border of coexistence. Rare species also have a higher probability of going extinct due to stochasticity.

The only case where one, in terms of light demands, more specialized species dominates the medium species is a shade-tolerant species with low mortality rates (Fig. 4g and i). Such a species benefits twofold from low mortality—by a low number of dying individuals as well as by creating suitable colonization conditions for itself.

4.3. Equalizing versus stabilizing mechanisms

In the terminology of Chesson (2000), we found that the trade-offs investigated here in the basic trade-off model are equalizing mechanisms that balance differences between species, but do not promote stable, i.e. long-term coexistence. Our results show that coexistence is only possible if the species attributes show a fixed relation; any deviation from this relation leads to extinction.

In contrast, the local processes (density-dependent mortality and light-dependent colonization) produce broader coexistence ranges (Fig. 3d–k, Fig. 4d–l) that remain stable over long time periods (Fig. 7). Therefore they can be assigned to stabilizing mechanisms. With these local processes, trade-offs need not be fine-tuned; in this sense, the local mechanisms considered contribute to stable coexistence. On the other hand, local mechanisms alone do not guarantee coexistence when fitness differences between species are large. For example, the addition of density-dependent mortality cannot balance a substantial difference in dispersal ranges (Fig. 3e). The adjustment of a second attribute, such as mortality rates, is necessary to obtain coexistence (Fig. 4d). According to the theoretical findings of Chesson (2000) we conclude that equalizing trade-offs and stabilizing local mechanisms are both crucial key processes for facilitating species coexistence in plant communities.

Compared to the analytically tractable, spatially implicit population models investigated in Klausmeier and Tilman (2002) our spatially explicit model resembles the local founder control model in the essential point that the colonization only takes place in empty patches. Similar to our basic trade-off model the coexistence ranges in the local founder control model are marginal; only the (theoretical) case of identical colonization–mortality ratios of species leads to coexistence.

The majority of simple models dealing with the role of trade-offs for coexistence investigate trade-offs, where one trait is the competitive ability of species (e.g. Adler and Mosquera, 2000; Yu and Wilson, 2001; Kisdi and Geritz, 2003). In these models it is assumed, that there is a fixed hierarchical order of competition between species—a better competitor can always invade patches that are occupied by an inferior competitor. Coexistence is enabled because 'colonization niches' are created: some patches can only be colonized by one of the competitors. In this way trade-offs with a fixed competitive hierarchy involve a stabiliz-

ing facet and facilitate coexistence to a certain degree. In contrast to the competition–colonization trade-off (Tilman, 1994; Muller-Landau et al., 2008), where stable coexistence of a potentially unlimited number of species can be observed, the trade-offs in physiological traits considered in our study do not bear a stabilizing component. We do not anticipate an a priori hierarchy of local competition; instead fitness differences evolve directly from physiological species traits. Only few studies examining trade-offs mention the insufficiency of such trade-offs alone to support coexistence (Chesson, 2000; Lischke and Löffler, 2006; Banitz et al., 2008).

4.4. Outlook: competition of multiple species

Up to now, we have limited our investigation to the competition between two species. Intuitively one might ask how our results translate if we expand the model from a two-species to a multi-species competition. For a first test of the effect of the local processes on species diversity we simulated a community with 196 species, choosing all trait combinations that lead to coexistence in a two-species competition with the medium species. We preserved the initial conditions (population size and density) of the two-species experiments by enlarging the simulated area. While we observe a rapid decline of species number for the basic trade-off community (leading to a community with only one dominant species), both local processes, density-dependent mortality and light-dependent regeneration, clearly enhance diversity in the community (Fig. 5). This preliminary result underpins the relevance of processes that modify local competition for species diversity.

4.5. Limitations

In the study presented here the dispersal of seeds is modelled in a simplified way (similar to Alonso and Solé, 2000): seed dispersal distances are entangled with seed number, since a tree disperses seeds in each patch within its dispersal range. In real forests one often finds that far-dispersing species produce many seeds and have a higher fecundity compared to species with short dispersal distances (Westoby et al., 2002; Muller-Landau, 2010). To simplify the model structure, we connected dispersal distance to fecundity, which is the reason why dispersal distance plays such an important role for coexistence. Generally, the particular strength of species traits also depends on the specific implementation of processes.
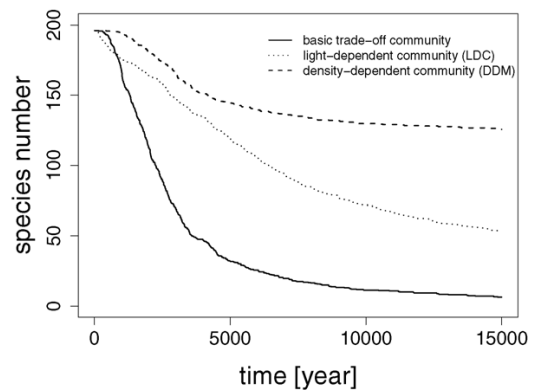

Fig. 5. Multi-species competition: all trait combinations (of dispersal ranges, mortality and growth rates), that coexist with the species with medium traits after 1000 years, are selected. This community of 196 species is simulated for the basic trade-off model, the model with light-dependent colonization (LDC) and with density-dependent mortality (DDM). For LDC, a random light requirement index between 0 and 1 is assigned to each species; for DDM, all species have density factor 1. Each graph shows the average species number of three simulation runs.

In plant communities species often differ in more than two or three physiological characteristics and a trade-off between multiple attributes may give rise to a higher coexistence potential. However, we did not find increased coexistence ranges for a three-way trade-off between the considered traits (see Appendix Fig. 6). The dominance of a species is governed by the trade-off in the strong traits dispersal range and mortality rate; incorporating an additional difference in growth rates only shifts the dominance between species but does not enlarge coexistence areas. We would only expect enhanced coexistence in a trade-off between two or more weak traits.

The considered time frame and coexistence criterion are chosen in a way, which allows observing the way and direction, in which the additional mechanisms alter coexistence ranges. For the basic model, it is not crucial, which limit is chosen for the coexistence criterion, since for most parameter combinations, already after the considered simulation length of 1000 years, one of the two species is gone extinct. Thus our results would look very similar with a chosen coexistence criterion of 1% patch occupancy (instead of 10%). When the local processes density-dependent mortality or light-dependent regeneration are added, the coexistence
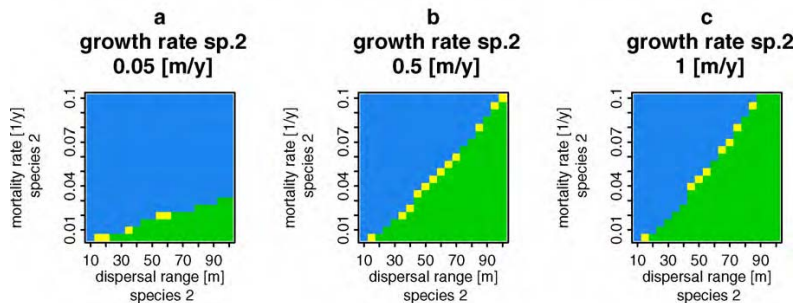
Fig. 6. Variation of two attributes in a two-species community. Each point is the outcome of a single simulation run after 15 000 years. Species 1 has medium properties: dispersal range 60 m, mortality rate 0.05 y^{-1}, growth rate 0.5 m/y. First row: basic trade-off community without local process. Second row: community with density-dependent mortality (DDM) of both species (d = 1). Third and fourth row: community with light-dependent colonization (LDC): species 1 is medium light-demanding (light requirement index L_1 = 0.5). In light-dependent community I species 2 is shade-tolerant (L_2 = 1) and in light-dependent community II species 2 is light-demanding (L_2 = 0). Column 1: dispersal-mortality trade-off, growth rate (species 2) = 0.5 m/y. Column 2: dispersal-growth trade-off, mortality rate (species 2) = 0.05 y^{-1}. Column 3: growth-mortality trade-off, dispersal range (species 2) = 60 m.

Competing species with differences in two attributes (longterm)

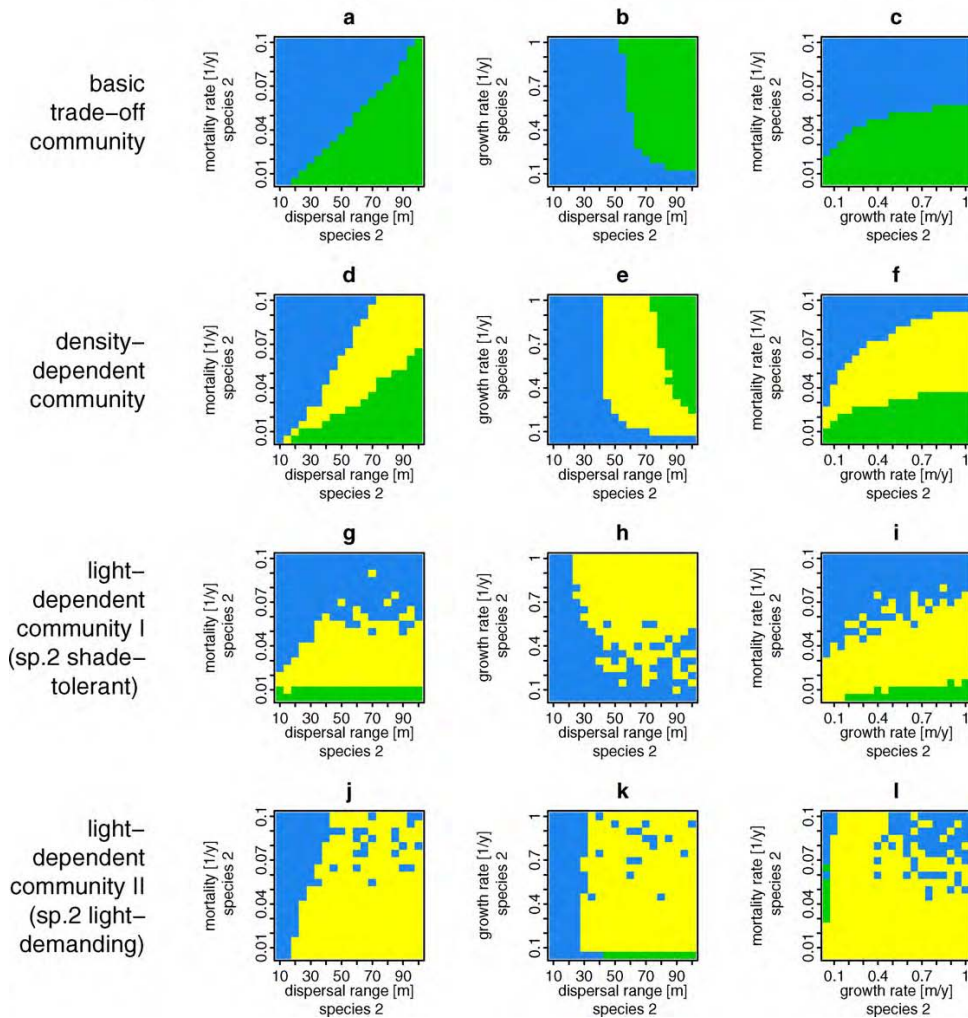**Fig. 7.** Dispersal-mortality trade-off for different height growth rates of species 2 (0.05, 0.5 and 1 m/y). Species 1 has medium properties: dispersal range 60 m, mortality rate 0.05 y^{-1} and growth rate 0.5 m/y.

ranges in general become larger with a more rigorous coexistence criterion.

4.6. Synthesis

Investigating the performance of different plant species traits in trade-offs to facilitate coexistence and the role of local processes, we provide insights on how species diversity is maintained in plant communities. Our three major findings are:

- The considered trade-offs between physiological attributes alone cannot support long-term coexistence. The attributes have no stabilizing effect, thus trade-offs act only equalizing.
- The timescale on which different species attributes operate in competition can differ; we therefore suggest the concept of weak and strong traits. As a consequence, highly non-linear coexistence curves in the trait space result when a strong and a weak trait are involved.
- The narrow coexistence ranges of trade-off communities are considerably broadened by the inclusion of the local processes density-dependent mortality and light-dependent colonization.

Thus we have shown that these local processes can make an important contribution to coexistence in forest communities.

Appendix A.

A.1. Long-term coexistence

Observing longer timescales (15 000 years, Fig. 7) for the two-species competition further emphasizes the stabilizing strength of

the selected local processes: while there is no coexistence in the basic trade-off model, the coexistence ranges with additional local mechanisms remain almost unchanged compared to the shorter simulation time of 1000 years (Fig. 4).

A.2. Three-way trade-off

In the main text we investigated species that differ only in one or two of the three traits considered. Does a three-way trade-off produce larger coexistence ranges? Starting from the dispersal-mortality trade-off, do we gain larger coexistence ranges if additionally the growth rate of the second species differs from that of the other species? Fig. 6 shows the outcome of competition for the dispersal-mortality trade-off with different growth rates for species 2. For high as well as for low growth rates of species 2 the coexistence ranges do not increase. As in the two-way trade-offs these points of coexistence are still sensitive to minor changes in strong traits. Most notably, a low growth rate of species 2 changes the position of the coexistence range (Fig. 6a). Here, a balancing trade-off between mortality and dispersal is only possible if species 2 has a relatively low mortality rate ($<0.03\,\mathrm{y}^{-1}$).

References

Adler, F., Mosquera, J., 2000. Is space necessary? interference competition and limits to biodiversity. Ecology 81, 3226–3232.

Adler, P.B., HilleRisLambers, J., Levine, J.M., 2007. A niche for neutrality. Ecol. Lett. 10, 95–104.

Alonso, D., Solé, R.V., 2000. The divgame simulator: a stochastic cellular automata model of rainforest dynamics. Ecol. Model. 133, 131–141, http://www.sciencedirect.com/science/article/B6VBS-415R3W4-F/2/f1a5c8250da5960f1802c33aa46d8e22.

Banitz, T., Huth, A., Grimm, V., Johst, K., 2008. Clumped versus scattered: how does the spatial correlation of disturbance events affect biodiversity? Theor. Ecol. 1, 231–240.

Chave, J., Muller-Landau, H.C., Levin, S.A., 2002. Comparing classical community models: theoretical consequences for patterns of diversity. Am. Nat. 159, 1–23.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31, 343–366.

Connell, J., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Durrett, R., Levin, S., 1994. Stochastic spatial models: a user's guide to ecological applications. Phil. Trans. R. Soc. Lond. B 343, 329–350.

Durrett, R., Levin, S., 1998. Spatial aspects of interspecific competition. Theor. Popul. Biol. 53, 30–43.

Esther, A., Groeneveld, J., Enright, N., Miller, B., Lamont, B., Perry, G., Schurr, F., Jeltsch, F., 2008. Assessing the importance of seed immigration on coexistence of plant functional types in a species-rich ecosystem. Ecol. Model. 213, 402–416.

Gray, L., He, F., 2009. Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of alberta. For. Ecol. Manage. 259, 98–106.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., J(rgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vab(, R., Visser, U., DeAngelis, D., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198, 115–126, http://www.sciencedirect.com/science/article/B6VBS-4K606T7-3/2/1dad6192bec683f32fce6dee9d665b51.

Holmes, E.E., Wilson, H.B., 1998. Running from trouble: long-distance dispersal and the competitive coexistence of inferior species. Am. Nat. 151, 578–586.

Hubbell, S., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Monographs in Population Biology. Princeton University Press.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22, 415–427.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528.

John, R., Dattaraja, H., Suresh, H., Sukumar, R., 2002. Density-dependence in common tree species in a tropical dry forest in mudumalai, southern india. J. Veg. Sci. 13, 45–56.

Johst, K., Huth, A., 2005. Testing the intermediate disturbance hypothesis: when will there be two peaks of diversity? Divers. Distrib. 11, 11–20.

Kerr, B., Riley, M.A., Feldman, M.W., Bohannan, B.J.M., 2002. Local dispersal promotes biodiversity in a real-life game of rock–paper–scissors. Nature 418, 171–174.

Kisdi, E., Geritz, S., 2003. On the coexistence of perennial plants by the competition–colonization trade-off. Am. Nat. 161, 350–354.

Klausmeier, C.A., Tilman, D., 2002. Spatial models of competition. In: Sommer, U., Worm, B. (Eds.), Competition and Coexistence. Springer, Berlin, pp. 43–78.

Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T., Kubo, T., 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a bornean mixed dipterocarp forest. J. Ecol. 91, 797–806.

Lischke, H., Löffler, T., 2006. Intra-specific density dependence is required to maintain species diversity in spatio-temporal forest simulations with reproduction. Ecol. Model. 198, 341–361.

Molofsky, J., Durrett, R., Dushoff, J., Griffeathand, D., Levin, S., 1999. Local frequency dependence and global coexistence. Theor. Popul. Biol. 55, 270–282.

Muller-Landau, H., 2010. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. PNAS 107, 4242–4247.

Muller-Landau, H.C., Wright, S.J., Calderon, O., Condit, R., Hubbell, S.P., 2008. Inter-specific variation in primary seed dispersal in a tropical forest. J. Ecol. 96, 653–667.

Münkemüller, T., Bugmann, H., Johst, K., 2009. Hutchinson revisited: patterns of density regulation and the coexistence of strong competitors. J. Theor. Biol. 259, 109–117.

Peters, H., 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. Ecol. Lett. 6, 757–765.

Phillips, O.L., Gentry, A.H., 1994. Increasing turnover through time in tropical forests. Science 263, 954–958.

Potthoff, M., Johst, K., Gutt, J., Wissel, C., 2006. Clumped dispersal and species coexistence. Ecol. Model. 198, 247–254.

Pronk, T.E., Duringa, H.J., Schievinga, F., 2007. Coexistence by temporal partitioning of the available light in plants with different height and leaf investments. Ecol. Model. 204, 349–358.

Roxburgh, S.H., Shea, K., Wilson, J.B., 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85, 359–371.

Shugart, H., 2003. A Theory of Forest Dynamics—The Ecological Implications of Forest Succession Models. The Blackburn Press.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2–16.

Tilman, D., Pacala, S., 1993. The maintenance of species richness in plant communities. In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities. University of Chicago Press, pp. 13–25 (Ch. 2 The Maintenance of Species Richness in Plant Communities).

Westoby, M., Falster, D., Moles, A., Vesk, P., Wright, I., 2002. Plant ecological strategies: some leading dimensions of variation between species. Annu. Rev. Ecol. Syst. 33, 125–159.

Whitmore, T.C., 1998. An Introduction to Tropical Rain Forests. Oxford University Press.

Wills, C., Harms, K.E., Condit, R., King, D., Thompson, J., He, F.L., Muller-Landau, H.C., Ashton, P., Losos, E., Comita, L., Hubbell, S., LaFrankie, J., Bunyavejchewin, S., Dattaraja, H.S., Davies, S., Esufali, S., Foster, R., Gunatilleke, N., Gunatilleke, S., Hall, P., Itoh, A., John, R., Kiratiprayoon, S., de Lao, S.L., Massa, M., Nath, C., Noor, M.N.S., Kassim, A.R., Sukumar, R., Suresh, H.S., Sun, I.F., Tan, S., Yamakura, T., Zimmerman, E., 2006. Nonrandom processes maintain diversity in tropical forests. Science 311, 527–531.

Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130, 1–14.

Yu, D., Wilson, H., 2001. The competition–colonization trade-off is dead; long live the competition–colonization trade-off. Am. Nat. 158, 49–63.

Zhang, J., Hao, Z., Sun, I.-F., Song, B., Ye, J., Li, B.W.X., 2009. Density dependence on tree survival in an old-growth temperate forest in northeastern china. Ann. For. Sci. 66, 204–213.

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Simulating forest dynamics in a tropical montane forest in South Ecuador

SIMULATING FOREST DYNAMICS OF A TROPICAL MONTANE FOREST IN SOUTH ECUADOR

Cʟᴀᴜᴅɪᴀ Dɪsʟɪᴄʜ, Sᴠᴇɴ Güɴᴛᴇʀ, Jüʀɢᴇɴ Hᴏᴍᴇɪᴇʀ, Bᴏʀɪs Sᴄʜʀöᴅᴇʀ and Aɴᴅʀᴇᴀs Hᴜᴛʜ

Summary: The montane forests of Ecuador are part of one of the world's hotspots of biodiversity and they also suffer the highest deforestation rate amongst South American countries. The processes that drive the dynamics of these highly diverse ecosystems are poorly understood. This is particularly true for transient dynamics, which are crucial for the protection and sustainable management of such forests. Dynamic simulation models can be used to analyse the growth of forests, but so far they have been applied mostly to temperate forests and to some few tropical lowland forests. In this study we investigate whether a process-based, individual-oriented simulation model like FORMIND is capable of reproducing the dynamics of tropical montane forests. For this purpose we develop a parameterisation for the model and validate the model against field observations of different (structural) patterns. We then analyse the predicted succession dynamics. The model is capable of reproducing the structure and dynamics of mature ridge forest on different levels of complexity. The main results indicate that, in terms of relative abundances of different species groups and stem size distribution in the tree community, our model predicts the observed patterns in the field. Additional field studies and model modifications are required to simulate the succession processes that follow different types of disturbances. FORMIND is a promising tool for the extrapolation of local measurements and for simulating the dynamics of tropical montane forests. Parameterisations of the model for further forest types within the research area are intended. The model has a number of potential applications, ranging from investigating the impact of (different) natural disturbances on forest structure and tree species diversity to analysing different potential management strategies.

Zusammenfassung: Die tropischen Bergregenwälder Ecuadors sind Teil eines der weltweiten Hotspots der Biodiversität und erfahren gleichzeitig die höchste Entwaldungsrate Südamerikas. Das Verständnis der Prozesse, die diese hochdiversen Ökosysteme strukturieren, ist noch lückenhaft. Dies betrifft insbesondere transiente Dynamiken, die entscheidend für den Schutz und ein nachhaltiges Management dieser Wälder sind. Waldwachstumsmodelle untersuchen die Dynamik von Wäldern. Sie wurden allerdings bisher hauptsächlich in temperierten Wäldern und vereinzelt in tropischen Tieflandregenwäldern angewandt. In dieser Studie untersuchen wir die Dynamik eines tropischen Bergregenwaldes mit dem prozess-basierten, individuen-orientierten Simulationsmodell FORMIND. Wir entwickeln eine Parametrisierung des Models und vergleichen unterschiedlich komplexe Muster des simulierten Waldes mit Felddaten. Des Weiteren analysieren wir die Sukzessionsdynamik des Waldes. FORMIND reproduziert die Struktur und Dynamik des ausgewachsenen Gratwalds auf verschiedenen Komplexitätsebenen. Unsere Resultate zeigen eine gute Übereinstimmung von im Feld beobachteten Mustern und Modellergebnissen, insbesondere von relativen Häufigkeiten funktioneller Baumartengruppen und Stammzahl-Durchmesserverteilungen. Die Modellierung der Sukzession nach verschiedenartigen Störungen erfordert weitere Feldstudien sowie zusätzliche Modellanpassungen. Das Waldwachstumsmodell FORMIND ist ein vielversprechendes Werkzeug zur Untersuchung der Dynamik tropischer Bergregenwälder. Parametrisierungen des Modells für weitere Waldtypen innerhalb des Untersuchungsgebiets sind geplant. Anwendungen des Modells reichen von der Untersuchung des Einflusses verschiedener natürlicher Störungen auf die Waldstruktur und Baumartenreichtum bis hin zur Analyse verschiedener Managementstrategien.

Keywords: forest growth model, FORMIND, simulation, plant functional types, tropical montane forest

1 Introduction

Tropical montane rain forests have received less scientific attention compared to tropical lowland forests, but they are considered to be just as highly endangered, due mainly to conversion of forests into pastures or the exploitation of high timber value species (Mᴏsᴀɴᴅʟ et al. 2008) and climate change (Cᴏʟᴡᴇʟʟ et al. 2008). Ecuadorian forests suffer the highest deforestation rate in South America (1.7%, FAO 2009). Nonetheless, as part of the Tropical Andes, the Andean forests of Ecuador belong to one of the world's hotspots of biodiversity (Bʀᴜᴍᴍɪᴛᴛ and Lᴜɢʜᴀᴅʜᴀ 2003).

The processes that drive the dynamics of these highly diverse forest ecosystems are poorly understood. This is particularly true for transient dynamics such as forest regrowth after disturbances. To ensure the protection and sustainable management of timber, water and other ecological services of these forests, we need to broaden our knowledge of these ecosystems and their dynamics.

Forest simulation models can play an important role in incorporating available (local) data and process understanding for extrapolation to larger temporal and spatial scales (Pacala and Kinzig 2002). Process-based spatially explicit forest growth models such as FORMIND (Köhler 2000) simulate ecological processes like recruitment, mortality and growth explicitly and allow for the simulation of spatiotemporal forest dynamics over several hectares and centuries (Pacala et al. 1996). There is a rich literature describing quantitative and qualitative fundamental ecological processes in forests and a long tradition of different forest modelling approaches (Shugart 1998, 2002). The high number of tree species found in the tropics poses a challenge for any study. The concept of plant functional types (PFT), where species are grouped according to selected functional attributes, has proven to be a useful approach for analysing such diverse ecosystems (Jeltsch et al. 2008; Köhler et al. 2000; Smith and Shugart 1997). Commonly used traits for the categorisation of plant functional types (PFT) in tropical forests are shade tolerance and maximum potential height (e.g. Poorter et al. 2006). Most applications of process-based forest models in montane regions have so far concentrated on temperate forests (e.g. Goreaud et al. 2006; Rammig et al. 2006).

In this study, we investigate whether the dynamics of a montane rain forest in South Ecuador can be described using the individual-oriented, process-based forest model FORMIND. We reformulate parts of the model to achieve a unified model structure which allows for more time-efficient simulations (see Appendix). We develop a parameterisation of the model and validate the model against field observations of different structural patterns and then analyse the predicted succession dynamics. The exploration of undisturbed forest dynamics is an indispensable prerequisite for the investigation and comparison of the effect of different natural and human-induced disturbances on the forest. Within our research area, disturbances caused by landslides are a main source of natural disturbance and are therefore of special interest (Bussmann et al. 2008; Restrepo et al. 2009, Richter et al. 2009).

2 Study area

Study site is the evergreen montane forest of the Reserva Biológica San Francisco (3°58'S, 79°04'W), located on the eastern slopes of the Andes in southern Ecuador. The reserve stretches from 1800 up to 3200 metres above sea level (a.s.l.). With an average slope of 40° the terrain is very steep. Shallow landslides are a common disturbance; approximately 3.5% of the area is covered with visible traces of landslides (Stoyan 2000). To date, more than 280 tree species have been identified in the 1000 ha area (Homeier and Werner 2007). The forest can be divided into four forest types which differ strongly in structure and species composition (Homeier et al. 2008.). At the level between 1900 and 2100 m a.s.l. we distinguish between ridge and ravine forest. The ridge forest has a higher stem density, lower basal area and also a lower canopy height (15−20 m) compared to the more species-rich ravine forest. The remaining two forest types are located at higher elevations; canopy height, stem density and species richness decrease on these sites (Homeier et al. 2002). Our study focuses on the analysis of the ridge forest (1900–2100 m a.s.l.). We utilize data from repeated inventories (2004, 2005, and 2007) of 4.88 ha, in which all trees with a breast height diameter (dbh) > 20 cm where surveyed. In addition, we utilize data from 1200 m² with all trees above dbh=5 cm measured (and extrapolate this data to 1 ha).

3 Model description

In the following we give a detailed description of the forest model FORMIND. The model description follows the ODD protocol (**O**verview, **D**esign concepts, **D**etails (Grimm et al. 2006)) and updates previous descriptions (see Appendix in Grimm et al. 2006, Köhler 2000). Here we present the first two parts of the protocol (i.e. overview and design concepts), the submodels are described in detail in the Appendix.

3.1 Overview

Purpose − FORMIND is designed to analyse the dynamics of uneven-aged species-rich forest stands with a focus on the impact of natural or anthropogenic disturbances on forest structure and composition.

State variables and scales – The FORMIND model is a spatially explicit, individual-based forest model. Forest stands from one hectare up to several square kilometres can be simulated. Each hectare is divided into patches of 20 × 20 square metres. Within a patch trees do not have a spatial explicit position. To enable an individual-based simulation of species-rich forest communities, tree species are grouped into plant functional types (PFT) according to the physiological attributes maximum attainable diameter at breast height (dbh) and maximum annual diameter growth. Figure 1 shows snapshots of a visualisation of FORMIND.

The smallest entity of the model is a single tree. Trees of the same size and PFT within one patch are assumed to have the same physiological attributes. The shape of a tree is simplified and described by assuming a cylindrical crown and a conic stem. Each tree is described by its aboveground biomass; the tree geometric attributes, e.g. dbh, tree height and crown diameter are derived from biomass using allometric

relationships (see Appendix). Each patch is characterized by the list of its trees and its location within the simulation area. We use periodic boundary conditions at the border of the simulation area. FORMIND works with an annual time step and usually several hundreds of years are simulated.

Process overview and scheduling – The model comprises four submodels characterizing establishment, mortality, recalculation of light climate and growth, which are applied in this order. While establishment and light climate are calculated on the patch level, mortality and growth are applied on the level of individual trees. Trees can establish if light climate on the forest floor is adequate and if space in lower height layers is sufficient.

There are different sources of mortality: normal mortality due to ageing, increased mortality for small trees, mortality due to high tree density (self-thinning) and mortality due to gap creation when large trees fall and damage other trees.
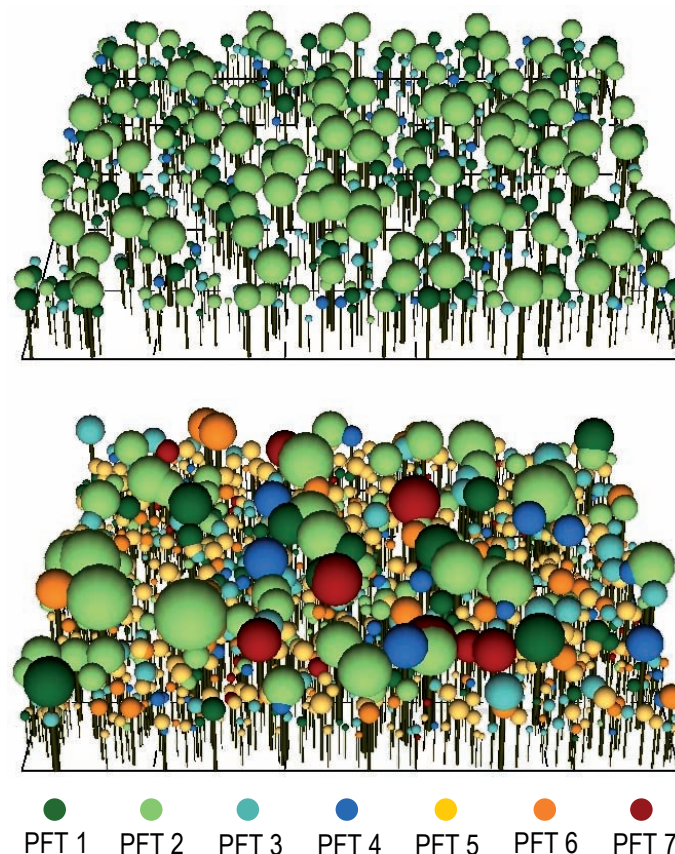

Fig. 1: Visualisation of FORMIND, showing all trees above a threshold dbh of 5 cm on an area of 1 ha. Each colour represents one PFT. (a) Snapshot after 20 years of simulation. The dominant canopy group comprises the fastest growing species (PFT 2) that reach a potential dbh of 70 cm, see table 1. (b) Snapshot after 400 years.

It is assumed that light availability is the main driving force for individual tree growth and forest succession. Within each patch all trees compete for light and space. Light climate is calculated via a light extinction law according to the distribution of leaves in a patch (Mᴏɴsɪ and Sᴀᴇᴋɪ 1953). Tree growth is calculated on the basis of carbon balance according to light availability and the main physiological processes photosynthesis and respiration. The process of calculating respiration rates has been revised for this study (see Appendix).

3.2 Design concepts

FORMIND is built in the tradition of forest gap models (Sʜᴜɢᴀʀᴛ 1998; Bᴜɢᴍᴀɴɴ 2001). Competition for light and space are assumed to be the dominant driving factor of forest dynamics; competition for nutrients is included indirectly. Light climate strongly influences the process of growth and also establishment; the competition for space is realized by implementing a crowding mortality.

Emergence – All facets of forest structure, for instance PFT abundances and tree size distributions emerge through the characteristics of trees and interactions among trees. Realized annual diameter growth rates and recruitment rates are not directly built into the model but result from the light climate in patches.

Sensing/Interaction – Trees react on the light climate they are exposed to, which is mainly influenced by surrounding trees, i.e. they "sense" other trees indirectly. Large tree crowns can grow into neighbouring patches. Direct interaction between trees of different patches occurs when dying large trees fall over and destroy a proportion of trees in the patch where their crown hits the ground.

Stochasticity – All sources of mortality are modelled as stochastic processes. Mortality due to space competition affects randomly chosen trees. A "tree fall probability" determines, if a dying tree will fall.

Collectives – Tree species are grouped into different plant functional types (PFT). All trees of the same PFT that establish at the same time are grouped into one cohort.

Observation – The individual-based approach allows us to compare model outcomes with field observations on the individual tree level, on the population level as well as on the level of the entire tree community. The main output variables we analyse are: basal area, stem number and tree size distribution on hectare level over all PFTs as well as PFT-specific.

Initialisation – We start from a treeless area which is assumed to be suitable for regeneration of all PFTs. Simulation area is normally 4 hectares.

Input – Site conditions are assumed to be homogeneous and there is no inter-annual variability of environmental conditions. Table 1 gives an overview of the parameters of FORMIND.

Parameterisation – On the basis of field observations and expert knowledge we grouped 71 tree species of the ridge forest into seven PFTs according to the characteristic maximum attainable diameter and maximum annual growth (see Tab. 2). To estimate the growth capacity of species in the Reserva Biológica San Francisco, we referred to expert knowledge on the maximal annual growth rates for each PFT (Tab. 2). Assuming that nutrient limitation is correlated to tree growth, the competition for nutrients is implicitly included by using the diameter growth rates. Parameters for mortality, recruitment and the potential maximum growth curve (see Tab. 1) were then calibrated by iterated simulations so that the model output fits the observed stem size distribution. We developed diameter-height relationships for each PFT according to the maximal height reached by trees of the respective PFT (see *Tree geometry* in the Appendix and Tab. 1).

4 Results

As a first step we calibrated the model (see Parameterisation). The full parameterisation is presented in table 1. After calibration, we found a good agreement of predicted and observed stem size distributions (Fig. 2). The model accurately reproduces abundances for trees in different size classes, but the frequency of larger trees is slightly overestimated. On the level of single PFTs we also find a reasonably good agreement of simulated and observed stem size distributions.

The model accurately predicts basal area on different levels, for trees with dbh above 5 cm, and 20 cm respectively (Fig. 3a, b). Simulated basal area matches very well to the observed basal area for overall as well as PFT-specific basal area on both levels. The rank of PFTs differs significantly between the two levels: while PFT 5 contributes the second highest share to basal area of trees with dbh above 5 cm, it contributes only marginal to the basal area of trees with dbh above 20 cm. The PFT 5 comprises those species that grow in the understorey and reach a maximum dbh of 25 cm (see Tab. 2). The overall stem numbers of trees
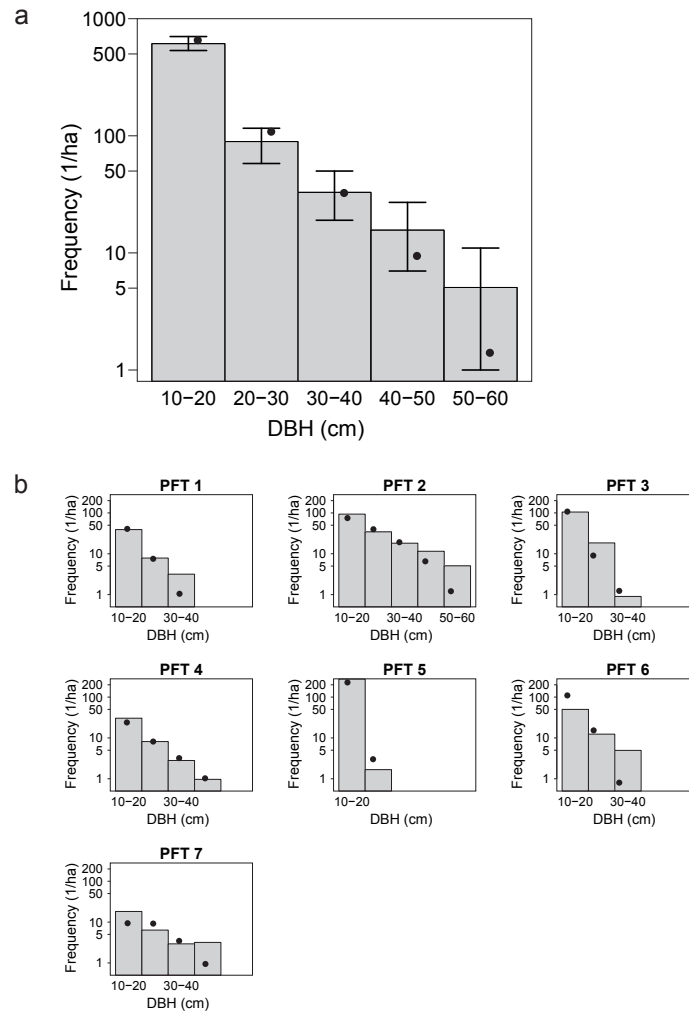
Fig. 2: Stem size distribution of the whole stand and for each individual PFT. Red dots show observed frequencies; bars show the averages of the model taken from different points in time of one run, error bars show minimum and maximum frequencies occurring over time. Note the logarithmic scale, which is used to better display abundances of large trees.

with dbh above 5 cm are slightly underestimated by the model (Fig. 3c); this is mainly due to the underestimation in stems of PFT 5. Stem numbers of the remaining PFTs are predicted fairly well. Also for trees with dbh above 20 cm we observe a good fit between model and data (Fig. 3d).

To examine model variation we reduce the simulated area to one hectare and depict several single model runs (Fig. 4). There is a notable temporal variation of overall basal area within single model runs (and within short time) that generally fits to the variation we find between plots. The mean overall basal area is slightly overestimated by the model compared to the basal area of the whole inventory plot (cf. Fig. 3b again). This is due to a slight overestimation of the fast-growing species (Fig. 4b). The overall temporal variation is mainly caused by the variation of these species.

The succession of overall basal area shows a rapid increase within the first 40 years and a slight overshoot before basal area reaches a stable level, where stems with dbh above 5 cm comprise a ba-
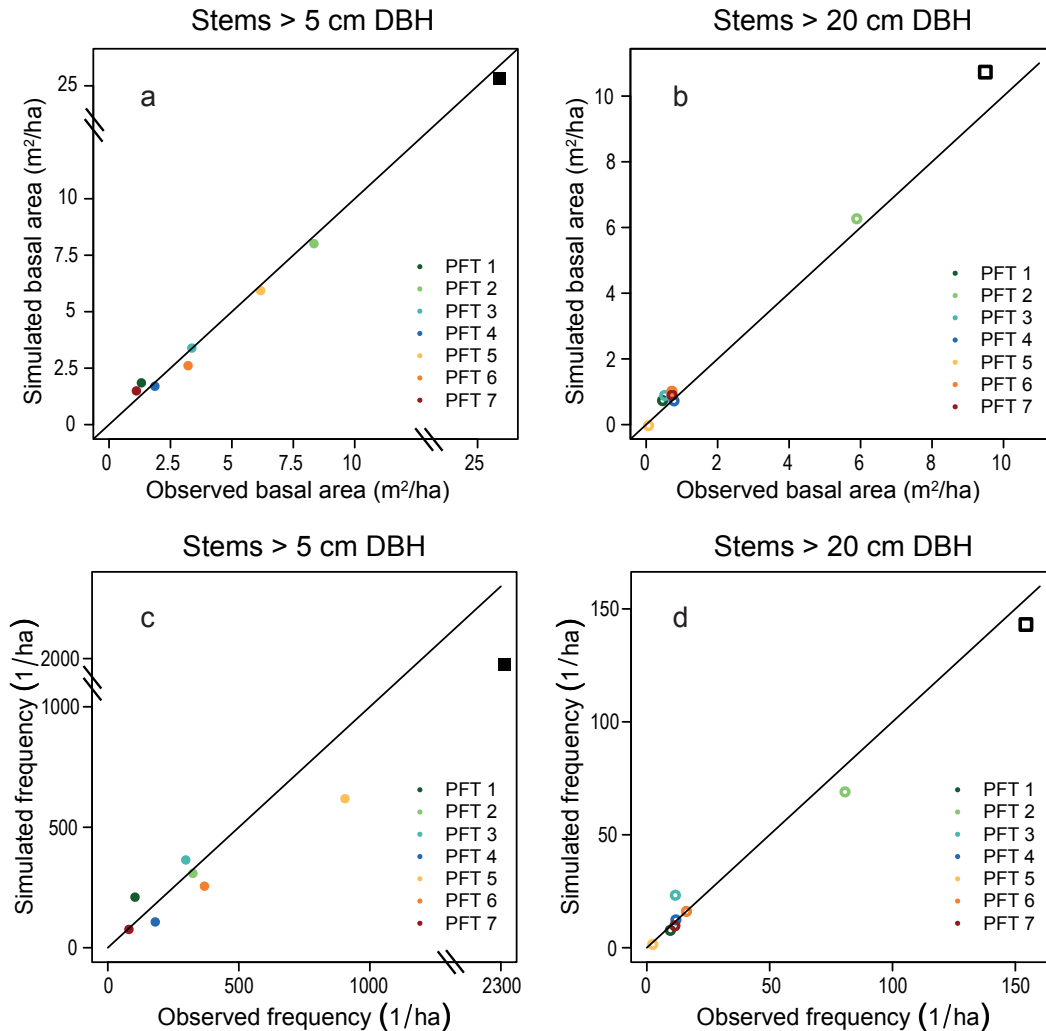
Fig. 3: Simulated versus observed basal area (a, b) and stem number per hectare (c, d). Trees above 5 cm dbh are shown with filled symbols, trees above 20 cm dbh with open symbols.

sal area around 25 m² per hectare (Fig. 5a). On the level of single PFTs (Fig. 5b) it takes much more time for basal area to reach a stable level than for the overall basal area. The overshoot in overall basal area in the beginning of simulation is caused by the overshoot in basal area of PFT 2. Only the fast-growing species groups (PFT 1 and 2) display an excess in basal area in the early phase of succession, the other groups approach their stable basal area with different paces. It takes around 500 years for all species groups to reach a stable basal area.

5 Discussion

In this study we applied the forest model FORMIND to simulate the dynamics of the ridge forest of the Reserva Biológica San Francisco in southern Ecuador. The strength of the individual-based model approach is that it allows us to distinguish patterns on different spatial and temporal levels, ranging from individuals to entire landscapes. These different patterns have been intensively investigated and compared with available field data from various tropical sites (cf. e.g. HUTH and DITZER 2000;

Fig. 4: Succession of basal area of trees with dbh > 20 cm dbh. Ten model runs of a 1 ha area (nine of them in paler shades) show variation between model runs and fluctuation within single runs. The filled points show data of the whole inventory area (4.88 ha), open circles show data from 1 ha subplots of the inventory area. For convenience of illustration we aggregated PFT into fast-growing species (PFT 1 and 2), species with intermediate growth rates (PFT 3 and 4) and slow-growing species (PFT 5, 6 and 7).

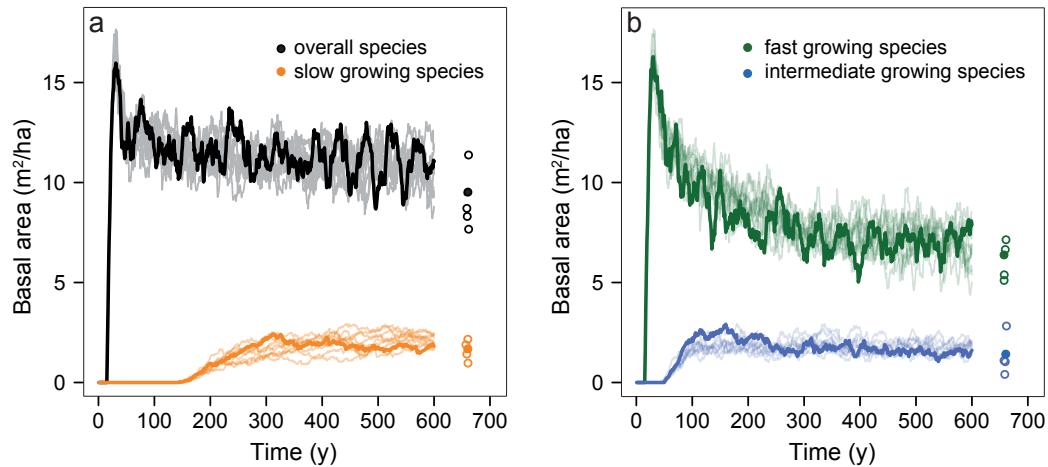KÖHLER et al. 2003; RÜGER et al. 2008). These studies have shown that in those cases FORMIND accurately reproduces patterns on different levels of complexity.

Our main results indicate that the model predicts the main structural patterns of the ridge forest observed in the field i.e. the relative abundance of different PFTs (Fig. 3), variation of model runs (Fig. 4) and stem size distribution in the tree community (Fig. 2). In addition, we used the model to investigate the course of succession (Fig. 5); this comprises the opportunity for further investigation of the different characteristics of succession in relation to the type of disturbance. As stated in the introduction, shallow landslides form one major source of natural disturbance in our research area (VORPAHL et al., submitted). The version of FORMIND presented here did not explicitly include landslides as a disturbance, since the inventory data used were derived from plots in which the disturbance of landslides is expected to be of minor importance.

Two interesting insights gained from the model are (i) that we did not observe a species group that displayed typical "pioneer" behaviour and (ii) that there is a high temporal variability in the overall basal area, which occurs within short time ranges and does not subside with time (cf. Fig. 4). These two patterns are further discussed in detail below.

As evident from figure 5, we observe two main successional responses concerning basal area in time: (1) species exhibiting rapid growth overshoot

their stable state of basal area at the beginning of succession and reduce with time (fast-growing PFT 1 and 2), and (2) species reaching their stable basal area at different speeds without overshooting (medium and slow-growing PFT 3–7). The fast-growing groups, however, do not display the behaviour of typical "pioneers", which show high abundances in early stages of succession and are later replaced by other "climax" groups (SHUGART 1998). Instead, the fastest growing PFT 2, which dominates the first phase of succession, retains the major share of basal area throughout the succession. Species of Podocarpaceae, (*Podocarpus oleifolius* is the most abundant species in PFT 4) are considered to form the climax stage of many natural stands around the Podocarpus National Park (LOZANO 2002). They can reach diameters of up to 100 cm (GÜNTER, HOMEIER pers. observ.; MARÍN VELEZ 1998). However, in our study area the maximum diameter observed is only approximately 50 cm. There are two possible explanations for this: either edaphic conditions prevent the development of *Podocarpus oleifolius* (and hence PFT 4) so that it does not become as dominant as in other primary forests of the region, or that the forest has not yet reached the climax stage. However, the dominance of PFT 2 might also relate to the heterogeneous nature of the ridge forest, where trees stay small in height and disturbances due to natural landslides are frequent. Thus, even in a mature ridge forest, there exist abundant locations with suitable condi-
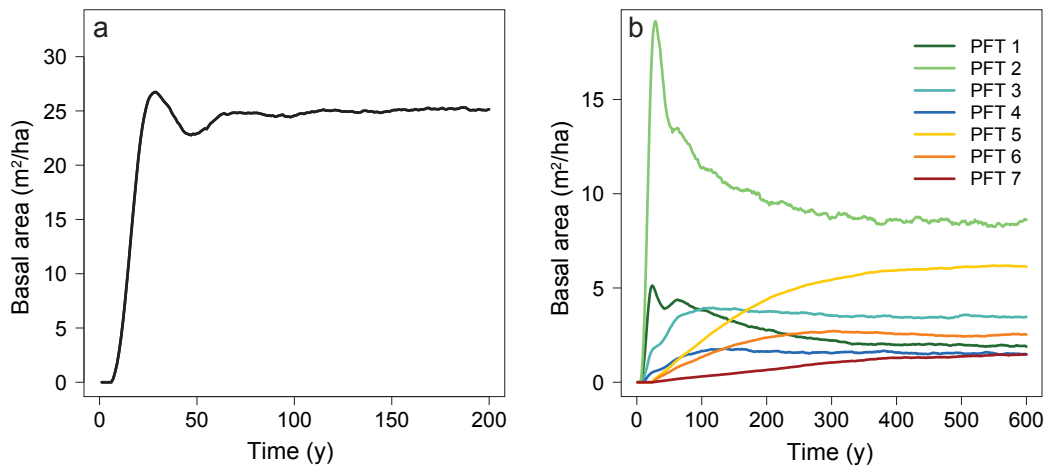
Fig. 5: Succession of basal area. Lines show the average of 10 single model runs with simulated area of 4 ha. (a) Overall basal area for all trees above 5 cm dbh. (b) Basal area above 5 cm dbh for each PFT. Please note the different time scales.

tions for these rather fast-growing species. Apart from this, it might also be the case that in our list of species (Tab. 2) some species with typical pioneer behaviour are missing, since the data we utilize was collected primarily on trees greater then 20 cm in diameter.

As evident from figure 4, the model produces a high variability of basal area in time. Figure 4b shows that in fact most of this variability originates from the fast-growing trees, due to their high abundance and rapid response; the slower growing species groups do not compensate these fluctuations. A comparison of model variation with temporal variability within sites would require long-term field measurements across several decades. At present such measurements are not available for our study site. But the extent of variability between sited fits to the model variation. This means that the variability between sites can in fact represent temporal and not only spatial heterogeneity.

The structural reality of the forest model used corresponds with its relatively high number of parameters. Unfortunately, as is the case for most applications of rather detailed models, not all parameters can be estimated with empirical data from the specific study site. Parameters for mortality, recruitment and growth are particularly difficult to obtain. To gather reliable information on these parameters, one needs to collect data over long periods and over large areas (WHITMORE 1998). We used a combination of data from the literature, expert knowledge and calibration processes to determine these parameters (see Tab. 1). The ap-

plied parameter values lie within occurring ranges for tropical forests (PHILLIPS and GENTRY 1994). One would also expect higher mortality rates for fast-growing species compared to slow growing species since they exhibit more "pioneer characteristics" (e.g. lower wood density). However, we noted that the realized simulated growth is slightly faster than the majority of observed growth. As a consequence, the calibrated mortality and recruitment rates should be considered as preliminary, in particular for the fast-growing species and species with intermediate growth rates (see Tab. 1). In the mature forest, only few individuals come close to reaching their estimated growth potential. This calls for more empirical data from disturbed localities or from experimental data, where competition is removed to assess reliable values for potential diameter growth.

The predicted speed of accumulation of the overall basal area is based on the assumption that the unforested site in the initialisation is equally suitable for regeneration of all PFTs and also recruitment rates are not limited, e.g. due to environmental constraints. As a consequence, the time until the forest reaches its mature state in the model should be considered as a lower limit. Depending on different initial environmental conditions, one can expect succession to proceed differently, most probably more slowly; also seed dispersal limitation might influence recruitment success on larger unforested areas. In the study area, empty sites might occur as a result of landslides, fire, logging or pasture abandonment; each of these events

probably result in very different conditions for regeneration concerning e.g. the size of the disturbed area or nutrient and mycorrhiza limitations of the ground. Following a landslide for example, it takes several years before trees start recolonising a site (Bussmann et al. 2008).

Another caveat originates from the fact that all empirical data that was used for this study was taken from "mature" forest sites. Results of a study on a 38-year-old secondary forest (Günter et al. 2007) and observations on a 15-year-old site (Homeier, pers. comm.) confirm that most species in early successional stages belong to the fast-growing group PFT 2 (particularly *Alchornea grandiflora*, *Alzatea verticillata*, *Hieronyma moritziana*). However, on the 38-year-old site, also slow-growing species as *Graffenrieda emarginata* (PFT 6) and *Purdiaea nutans* (PFT 7) where found. Thus slow- and fast-growing species can simultaneously be members of the same successional stage. To investigate transient dynamics of these forests, additional data from disturbed sites would be useful in order to analyse early-stage succession in more detail.

Our study demonstrates that FORMIND is a promising tool for the simulation of tropical montane forests dynamics. This model will help to further our understanding of certain aspects of the complex dynamics of these highly diverse and vulnerable ecosystems.

6   Perspectives

Currently, efforts are being made to link the model to landslide disturbances, which are one main cause of natural disturbance in our research area (Bussmann et al. 2008). In the future, we intend to develop parameterisations for the remaining forest types: the ravine forest, which differs substantially from the ridge forest in terms of structure, growth dynamics and species richness, and the forest types at higher elevations. Covering all main forest types of the Reserva Biológica will allow developing a model that simulates forest dynamics on a regional scale. Such an integration of models for different forest types over large altitudinal gradients is a unique exercise which has not been attempted before. The model has a number of potential applications ranging from investigating the impact of different natural disturbances on forest structure and tree species diversity, to analysing different potential management strategies. The latter aspect is of great importance due to the

high pressure on Andean montane forests and the need to develop ecologically sustainable, economically attractive strategies as an alternative to livestock farming.

Table 1: Parameters of FORMIND for the ridge forest of the tropical montane rain forest of the Reserva Biológica San Francisco, South Ecuador.

Parameter	Description	Unit	PFT 1
	Environmental Parameters		
k	Light extinction coefficient	m²ground m⁻²leaf	
I_0	Average irradiance above canopy	μmol(photons) m⁻²s⁻¹	
s_d	Length of daily photosynthetic active period	h	
	Recruitment Parameters		
d_s	Diameter of ingrowing trees	m	
I_m	Minimum light intensity for establishment	% of I_0	10
N	Maximum recruitment rates of small trees	ha⁻¹y⁻¹	160
	Mortality Parameters		
m_b	Basic mortality	y⁻¹	0.05
m_u	Maximum mortality of small trees	y⁻¹	
d_s	Diameter up to which mortality is increased	m	
d_f	Minimum diameter of falling trees	m	
p_f	Falling probability of dying trees	%	
	Tree Geometry Parameters		
H_1	Diameter-height relationship		
H_2			0.56
F_1			
F_2	Form factor		
C_0			
C_1	Crown diameter as function of diameter-curves		
C_2			
g_m	Maximum diameter growth	mm y⁻¹	10
d_m	Maximum diameter	cm	40
h_m	Maximum height	m	20
c_1	Crown length factor as function of height-curves		
L_1	Leaf area index per tree		
L_2			
σ	Fraction of stem wood biomass to total biomass		
	Biomass Production Parameters		
p_m	Maximum photoproducitvity for different lgrp	μmol(CO₂)m⁻²s⁻¹	7
α	Slope of light response curve for different lgrp	μmol(CO₂) μmol(photons)⁻¹	0.2
ϱ	Wood density for different lgrp	t m⁻³	0.40
r_g	Parameter of growth respiration		
G_3			-0.02344
G_2	Parameter of maximum diameter growth curve		-0.12500
G_1			0.03458
G_0			0.00767
m	Transmission coefficient of leaves		
φ	Parameter of conversion in organic dry matter	t μmol(CO₂)⁻¹	
	Technical Parameters		
a	Patch size	m²	
Δh	Step width of vertical discretization	m	

PFT 2	PFT 3	PFT 4	PFT 5	PFT 6	PFT 7	Reference
		0.6				estimated
		700				BENDIX et al. 2008
		12				RÜGER 2007
		0.01				technical parameter
10	5	5	1	1	1	RÜGER 2006
300	150	50	200	280	50	calibrated
0.09	0.05	0.05	0.006	0.016	0.008	calibrated
		0.1				RÜGER 2007
		0.1				RÜGER 2007
		0.1				estimated
		20				estimated
		2.5				derived from inventory data
0.54	0.56	0.59	0.55	0.56	0.53	
		0.77				calibrated
		-0.18				
		0.2				estimated
		0.1				
		0.5				
20	6	6	2	2	2	S. GÜNTER and J. HOMEIER pers. Comm.
70	40	50	25	40	50	derived from inventory data
25	20	25	15	20	20	derived from inventory data
		0.25				RÜGER 2007
		2.2				estimated
		0.1				
		0.6				estimated (NENNINGER 2006)
7	5	5	3	3	3	estimated
0.2	0.25	0.25	0.4	0.4	0.4	RÜGER 2006
0.40	0.57	0.57	0.60	0.60	0.60	estimated (NENNINGER 2006)
		0.2				RYAN 1991
0.36581	0.27328	-0.03537	0.42989	-0.07212	-0.03673	
-0.48239	-0.21630	-0.02452	-0.18816	0.01995	0.01261	calibrated
0.14906	0.03076	0.01112	0.01260	-0.00147	-0.00114	
0.00656	0.00481	0.00499	0.00189	0.00201	0.00201	
		0.1				LARCHER 2001
		0.63 *44e(-12)				LARCHER 2001
		400				technical parameter
		0.5				technical parameter

Table 2: Grouping of tree species into plant functional types. Common species are printed in bold type.

Group	Maximum diameter at breast height (cm)	Maximum annual diameter growth (mm/year)	Species
PFT 1	40	10	*Hieronyma asperifolia* Pax & K. Hoffm.
			Hieronyma duquei Cuatrec.
			Myrcia sp. nov.
			Ocotea aciphylla (Nees) Mez
			Vismia cf. *tomentosa* Ruiz & Pav.
PFT 2	70	20	**Alchornea grandiflora Müll. Arg.**
			Alzatea verticillata Ruiz & Pav.
			Clethra revoluta (Ruiz & Pav.) Spreng.
			Clusia cf. *ducuoides* Engl.
			Hieronyma moritziana (Müll. Arg.) Pax & K. Hoffm.
			Nectandra lineatifolia (Ruiz & Pav.) Mez
			Persea ferruginea Kunth
			Persea sp.4
			Persea sp.5
			Tapirira guianensis Aubl.
PFT 3	40	6	*Abarema killipii* (Britton & Rose ex Britton & Killip) Barneby & J.W. Grimes
			Aniba muca (Ruiz & Pav.) Mez
			Calyptranthes cf. *pulchella* DC.
			Elaeagia pastoense L.E. Mora
			Elaeagia utilis (Goudot) Wedd.
			Endlicheria griseo-sericea Chanderbali
			Eugenia sp.
			Hedyosmum goudotianum Solms
			Ilex hippocrateoides Kunth
			Inga striata Benth.
			Ladenbergia stenocarpa (Lamb.) Klotzsch
			Lauraceae sp.
			Matayba inelegans Spruce ex Radlk.
			Nectandra membranaceae (Sw.) Griseb.
			Ruagea glabra Triana & Planch
PFT 4	50	6	*Ficus cuatrecasana* Dugand
			Meliosma sp.
			Micropholis guyanensis (A. DC.) Pierre
			Myrsine coriaceae (Sw.) R. Br. ex Roem. & Schult.
			Naucleopsis francisci Berg & Homeier (ined.)
			Podocarpus oleifolius D. Don ex Lamb.
PFT 5	25	2	*Alchornea triplinervia* (Spreng.) Müll. Arg.
			Aniba sp.
			Clusia sp. 1
			Eschweilera sessilis A.C. Sm.
			Faramea coerulescens K. Schum. & K. Krause
			Guatteria sp. 1
			Hedyosmum anisodorum Todzia
			Miconia cf. *calophylla* Triana

			Miconia tinifolia Naudin
			Miconia theaezans (Bonpl.) Cogn.
			Ocotea sp.1
			Persea areolatocostae (Allen) van der Werff
			Persea subcordata (Ruiz & Pav.) Nees
			Persea weberbaueri Mez
			Schefflera sp.
			Siphoneugena sp. 1
			Sloanea sp. 1
			Weinmannia cf. sp.1
			Weinmannia elliptica Kunth
			Weinmannia haenkeana Engl.
			Weinmannia sorbifolia Kunth
PFT 6	40	2	*Chrysophyllum lanatum* T.D. Penn.
			***Graffenrieda emarginata* (Ruiz & Pav.) Triana**
			Ilex cf. *amboroica* Loes.
			Licaria subsessilis van der Werff
			Meriania franciscana Ulloa & Homeier
			***Miconia punctata* (Desr.) D. Don ex DC.**
			Ocotea benthamiana Mez
			Ocotea sp.2
			Ocotea sp.4
			Roupala montana Aubl.
PFT 7	50	2	*Endlicheria oreocola* Chanderbali
			Nectandra subbullata Rohwer
			***Purdiaea nutans* Planch.**
			Stilpnophyllum oellgaardii L. Andersson

Appendix

We reformulated parts of the model structure compared to previous applications of FORMIND (e.g. Appendix in GRIMM et al. 2006; KÖHLER 2000). We use power laws for the diameter-height relations as well as for the form factor; as a result of these modifications, the biomass is also a power law of the diameter. Hence we can directly recalculate the maintenance respiration from the maximal growth curve and the biomass (see below). Previously, these calculations where performed using look-up tables, which is more time-consuming than a direct calculation.

Tree geometry

Tree height h is calculated as a power law from the diameter at breast height d

$$h(d) = H_1 \cdot d^{H_2}.$$

Crown length c_l is a constant fraction of tree height

$$c_l(h) = C \cdot h.$$

Crown diameter c_d is calculated as

$$c_d(d) = C_0 \cdot d + C_1 \cdot exp(-C_2 \cdot d).$$

Crown area c_a is calculated as

$$c_a(c_d) = \frac{\pi}{4} \cdot c_d^2.$$

The form factor f is the correction factor for the deviation of stem form from a cylindrical shape. It is calculated as a power law

$$f(d) = F_1 \cdot d^{F_2}.$$

(For this study, we calibrated F_1 and F_2, such that the resulting tree biomass suits observed diameter-biomass relationships (NENNINGER 2006; CHAVE et al. 2005))

Aboveground tree biomass b is a central variable of the model; it is connected to d, the diameter at breast height, via the equation

$$b(d) = \underbrace{\frac{\pi}{4} \cdot d^2 \cdot h(d) \cdot f}_{\text{stem volume}} \cdot \frac{\varrho}{\sigma} \, ,$$

where f is the form factor, ϱ is the wood density and σ the fraction of stem wood biomass to total aboveground tree biomass. Using the above stated relations we arrive at

$$b(d) = \left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma} \right) \cdot d^{2+H_2+F_2}. \quad (1)$$

Submodels of FORMIND

Within one year the four submodels – establishment, mortality, recalculation of light climate and tree growth – are applied in the following order.

Establishment

If the irradiance on the forest floor in a patch exceeds the minimum light I_m for establishment of a PFT, a new cohort of small trees with dbh=1 cm establishes. The number of recruits per hectare is calculated as the maximum number of recruits per hectare N_m divided by the number of patches per hectare (25). Additionally, it is checked that the layer of seedling crowns is not completely crowded prior to establishment.

Mortality

There are different sources of mortality:

1. Normal mortality: each species group (PFT) has a specific basic mortality rate m_b

2. Mortality of small trees: trees with diameter $d < d_s$ are affected by an additional size dependent mortality m_s

$$m_s = \begin{cases} m_u \cdot \left(1 - \dfrac{d}{d_s} \right), & \text{if } d < d_s \\ \\ 0 & , \text{else} \end{cases}$$

where m_u is the maximum size-dependent mortality of small trees. (For cohorts with less than 100 individuals or diameter $d \geq 10$ cm, mortality is stochastically determined for each tree of the cohort. Otherwise, the number of dying trees is calculated deterministically.)

3. Self-thinning: if height layers in a patch are overcrowded with tree crowns, i.e. crown area exceeds patch area, mortality of trees with crowns in these layers is increased due to competition for space. Trees are randomly removed until tree crowns fit into the patch (crown area ≤ patch area).

4. Gap building: Large falling trees kill a proportion of the trees in the patch where their crown hits the ground. When a tree with diameter $d > d_f$ dies, it falls with probability p_f. The falling direction is determined randomly and the probability that a tree in the target patch is killed is proportional to the ratio between the crown projection

area c_a of the falling tree and the patch size a. (Again, for tree cohorts with <100 individuals and diameter $d \geq 10$ cm, the number of killed trees is determined stochastically for each tree, otherwise it is calculated deterministically.) Only trees, which do not overtop the falling tree by more than 1 metre, can be killed.

Light climate
The vertical distribution of leaf area determines the light climate in a patch. Each tree has a leaf area index L_T that is calculated as

$$L_T(d) = L_1 \cdot d^{L_2}.$$

The forest canopy is divided into height layers of size Δh in each patch. A tree contributes leaf area to the height layers that contain a part of the tree crown. The leaf area index L_i of height layer i is calculated as

$$L_i = \frac{1}{a} \cdot \sum_{\text{trees in layer } i} c_a \cdot L_T \cdot \frac{\Delta h}{c_l},$$

where c_a is the crown area, c_l the crown length, L_T the leaf area index of the tree and a the area of a patch. The cumulative leaf area index $\widetilde{L}_i$ of a layer i is the summed up leaf area index of all height layers above layer i

$$\widetilde{L}_i = \sum_{j>i} L_j.$$

For a tree, the amount of light that reaches the top of its crown I_{T_i} in layer i is then calculated via an extinction law

$$I_{T_i} = I_0 \cdot e^{-k \cdot \widetilde{L}_i},$$

where I_0 is the average irradiance above the canopy, and k the light extinction coefficient of the forest.

Tree growth and light competition
We calculate light extinction within the forest canopy and leaf-level rates of photosynthesis following the classical approach of THORNLEY and JOHNSON (1990). For calculation of tree growth, incident irradiance and photosynthesis rate are considered on the level of a single leaf (per unit leaf area) and on tree-crown level (per unit crown projection area). Accounting for self shading of leaves, a single leaf at height i within the canopy receives the irradiance of

$$I_L = \frac{k}{1-m} \cdot I_{T_i},$$

where k is the light extinction coefficient and m the transmission coefficient of leaves. The rate of photosynthesis for a single leaf P_L (per unit leaf area) is then calculated as a saturation function

$$P_L(I_L) = \frac{\alpha \cdot I_L \cdot p_m}{\alpha \cdot I_L + p_m},$$

where α is the initial slope of the light response curve and p_m the maximum rate of photosynthesis. For the calculation of the instantaneous rate of photosynthesis of a tree P_T (per unit crown projection area), P_L is integrated over the leaf area index of the tree

$$P_T = \int_0^{L_T} P_L(\widetilde{L}) d\widetilde{L},$$

where $\widetilde{L}$ is the cumulative leaf area index of the tree. Solving this integral leads to

$$P_T(I_T) = \frac{p_m}{k} \ln \frac{\alpha \cdot k \cdot I_T + p_m \cdot (1-m)}{\alpha \cdot k \cdot I_T \cdot e^{-k \cdot L_T} + p_m \cdot (1-m)}$$

(THORNLEY and JOHNSON 1990).

For the calculation of annual gross biomass production of the tree P_B, the photosynthesis rate has to be multiplied by the duration of the photosynthetic active period over the year s, the crown area of the tree c_a and the conversion coefficient (φ) from absorbed CO_2 to organic dry mass:

$$P_B = P_T(I_T) \cdot s \cdot c_a \cdot \varphi.$$

One way to calculate s in seconds is $s = 365 \cdot s_d \cdot 60 \cdot 60$ where s_d is the average daily photosynthetic active period in hours. The model utilizes a maximal diameter growth curve $g(d)$ reflecting the maximal diameter increments under full light condition

$$g(d) = G_3 \cdot d^3 + G_2 \cdot d^2 + G_1 \cdot d + G_0. \qquad (2)$$

Respiration processes consist of growth and maintenance respiration. Growth respiration is assumed to be a constant fraction of net biomass production; maintenance respiration depends on the biomass of the tree. The increment in biomass b_i is calculated as

$$b_i = (1 - r_g) \cdot \underbrace{\left(P_B - r_m \cdot b\right)}_{\text{net biomass production}}, \qquad (3)$$

where r_g is the parameter for growth respiration, b the biomass and r_m the fraction of biomass that is lost due

to maintenance respiration. Maintenance respiration is calculated such that under full light the maximal diameter growth is realized. That means, under full light conditions we assume (for clarity, the diameter is now denoted with D)

$$b_i = \frac{db}{dt} = \frac{db}{dD} \cdot \frac{dD}{dt}$$

$$= \frac{d\left(\left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma}\right) \cdot D^{2+H_2+F_2}\right)}{dD} \cdot g\,(D) \quad \text{(Eq. (1) and (2))}$$

$$= \left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma}\right) \cdot \left(2 + H_2 + F_2\right) \cdot D^{1+H_2+F_2} \cdot g\,(D).$$

Inserting this expression in equation (3) and using the diameter-biomass relation (1), we arrive at

$$r_m(D) = \frac{P_B}{b(D)} - \frac{2 + H_2 + F_2}{(1 - r_g) \cdot D} \cdot g(D)$$

$$= \frac{P_B}{\left(\frac{\pi}{4} \cdot H_1 \cdot F_1 \cdot \frac{\varrho}{\sigma}\right) \cdot D^{2+H_2+F_2}} - \frac{2 + H_2 + F_2}{(1 - r_g) \cdot D} \cdot (G_3 \cdot D^3 + G_2 \cdot D^2 + G_1 \cdot D + G_0).$$

References

BENDIX, J.; ROLLENBECK, R.; RICHTER, M.; FABIAN, P. and EMCK, P. (2008): Climate. In: BECK, E.; BENDIX, J.; KOTTKE, I.; MAKESCHIN, F. and MOSANDL, R. (eds.): Gradients in a tropical mountain ecosystem of Ecuador. Ecological Studies 198. Berlin, Heidelberg, 63–73.

BRUMMITT, N. and LUGHADHA, E. (2003): Biodiversity. Where's hot and where's not. In: Conservation Biology 17, 1442–1448. Doi:10.1046/j.1523-1739.2003.02344.x

BUGMANN, H. (2001): A review of forest gap models. In: Climatic Change 51, 259–305. Doi:10.1023/A:1012525626267

BUSSMANN, R.; WILCKE, W. and RICHTER, M. (2008): Landslides as important disturbance regimes – causes and regeneration. In: BECK, E.; BENDIX, J.; KOTTKE, I.; MAKESCHIN, F. and MOSANDL, R. (eds.): Gradients in a tropical mountain ecosystem of Ecuador. Ecological Studies 198. Berlin, Heidelberg, 319–330.

CHAVE, J.; ANDALO, C.; BROWN, S.; CAIRNS, M.; CHAMBERS, J.; EAMUS, D.; FÖLSTER, H.; FROMARD, F.; HIGUCHI, N.; KIRA, T.; LESCURE, J.; NELSON, B.; OGAWA, H.; PUIG, H.; RIÉRA, B. and YAMAKURA, T. (2005): Tree allometry and improved estimation of carbon stocks and balance in tropical forests. In: Oecologia 1451, 87–99.

COLWELL, R. K.; BREHM, G.; CARDELÚS, C. L.; GILMAN, A. C. and LONGINO, J. T. (2008): Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. In: Science 322, 258–261. Doi:10.1126/science.1162547

FAO (2009): State of the world's forests 2009. Rome.

GÜNTER, S.; WEBER, M.; ERREIS, R. and AGUIRRE, N. (2007): Influence of distance to forest edges on natural regeneration of abandoned pastures: a case study in the tropical mountain rain forest of southern Ecuador. In: European Journal of Forest Research 126, 67–75.

GOREAUD, F.; ALVAREZ, I.; COURBAUD, B. and DE COLIGNY, F. (2006): Long-term influence of the spatial structure of an initial state on the dynamics of a forest growth model: a simulation study using the Capsis Platform. In: Simulation 82, 475–495. Doi:10.1177/0037549706070397

GRIMM, V.; BERGER, U.; BASTIANSEN, F.; ELIASSEN, S.; GINOT, V.; GISKE, J.; GOSS-CUSTARD, J.; GRAND, T.; HEINZ, S. K.; HUSE, G.; HUTH, A.; JEPSEN, J. U.; JØRGENSEN, C.; MOOIJ, W. M.; MÜLLER, B.; PE'ER, G.; PIOU, C.; RAILSBACK, S. F.; ROBBINS, A. M.; ROBBINS, M. M.; ROSSMANITH, E.; RÜGER, N.; STRAND, E.; SOUISSI, S.; STILLMAN, R. A.; VABØ, R.; VISSER, U. and DEANGELIS, D. (2006): A standard protocol for describing individual-based and agent-based models. In: Ecological Modelling 198, 115–126. Doi:10.1016/j.ecolmodel.2006.04.023

HOMEIER, J. and WERNER, F. (2007): Spermatophyta checklist. In: LIEDE-SCHUMANN, S. and BRECKLE, S.-W. (eds.): Provisional checklists of flora and fauna of the San Francisco valley and its surroundings (Reserva Biológica San Francisco/Prov. Zamora-Chinchipe, southern Ecuador). Ecotropical Monographs 4. Bonn, 15–58.

HOMEIER, J.; DALITZ, H. and BRECKLE, S.-W. (2002): Waldstruktur und Baumartendiversität im montanen Regenwald der Estatión Científica San Francisco in Südecuador. In: Ber. d. Reinh. Tüxen-Ges. 14, 109–118.

HOMEIER, J.; WERNER, F. A.; GRADSTEIN, S.; BRECKLE, S.-W. and RICHTER, M. (2008): Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: BECK, E.; BENDIX, J.; KOTTKE, I.; MAKESCHIN, F. and MOSANDL, R. (eds.): Gradients in a tropical mountain ecosystem of Ecuador. Ecological Studies 198. Berlin, Heidelberg, 87–100.

HUTH, A. and DITZER, T. (2000): Simulation of the growth of a lowland Dipterocarp rain forest with FORMIX3. In: Ecological Modelling 134, 1-25. Doi:10.1016/S0304-3800(00)00328-8

JELTSCH, F.; MOLONEY, K.; SCHURR, F. M.; KOCHY, M. and SCHWAGER, M. (2008): The state of plant population modelling in light of environmental change. In: Perspectives in Plant Ecology Evolution and Systematics 9, 171–189. Doi:10.1016/j.ppees.2007.11.004

KÖHLER, P. (2000): Modelling anthropogenic impacts on the growth of tropical rain forests. Ph.D. thesis. Kassel.

KÖHLER, P.; DITZER, T. and HUTH, A. (2000): Concepts for the aggregation of tropical tree species into functional types and the application to Sabah's lowland rain forests. In: Journal of Tropical Ecology 16, 591–602. Doi:10.1017/S0266467400001590

KÖHLER, P.; CHAVE, J.; RIÉRA, B. and HUTH, A. (2003): Simulating the long-term response of tropical wet forests to fragmentation. In: Ecosystems 6, 114–128. Doi:10.1007/s10021-002-0121-9

LARCHER, W. (2001⁶): Ökophysiologie der Pflanzen. Stuttgart.

LOZANO, P. (2002): Botánica Austroecuatoriana. In: Los tipos de bosque en el sur de Ecuador, Abya Yala. Quito. 29–50.

MARÍN VELEZ, A. (1998): Ecología y silvicultura de las Podocarpáceas andinas de Colombia. In: Smurfit Carton de Colombia. Colombia.

MONSI, M. and SAEKI, T. (1953): Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. In: Journal of Botany 14, 22–52.

MOSANDL, R.; GÜNTER, S.; STIMM, B. and WEBER, M. (2008): Ecuador suffers the highest deforestation rate in South America. In: BECK, E.; BENDIX, J.; KOTTKE, I.; MAKESCHIN, F. and MOSANDL, R. (eds.): Gradients in a tropical mountain ecosystem of Ecuador. Ecological Studies 198. Berlin, Heidelberg, 37–40.

NENNINGER, A. (2006): Biomasseuntersuchungen an ausgewählten Baumarten des tropischen Bergregenwaldes Südecuadors. Master's thesis. München.

PACALA, S. and KINZIG, A. (2002): Introduction to Theory and the Common Ecosystem Model. In: KINZIG, A. P.; PACALA, S. W. and TILMAN, D. A. (eds.): The functional consequences of biodiversity: empirical progress and theoretical extensions. Princeton, 169–174.

PACALA, S.; CANHAM, C.; SAPONARA, J.; SILANDER, J.; KOBE, R. and RIBBENS, E. (1996): Forest models defined by field measurements: estimation, analysis and dynamics. In: Ecological Monographs 66, 1–43. Doi:10.2307/2963479

PHILLIPS, O. and GENTRY, A. (1994): Increasing turnover through time in tropical forests. In: Science 263, 954–958. Doi:10.1126/science.263.5149.954

POORTER, L.; BONGERS, L. and BONGERS, F. (2006): Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. In: Ecology 87, 1289–1301. Doi:10.1890/0012-9658(2006)87[1289:AOMTST]2.0.CO;2

RAMMIG, A.; FAHSE, L.; BUGMANN, H. and BEBI, P. (2006): Forest regeneration after disturbance: a modelling study for the Swiss Alps. In: Forest Ecology and Management 222, 123–136. Doi:10.1016/j.foreco.2005.10.042

RESTREPO, C.; WALKER, L. R.; SHIELS, A. B.; BUSSMANN, R.; CLAESSENS, L.; FISCH, S.; LOZANO, P.; NEGI, G.; PAOLINI, L.; POVEDA, G.; RAMOS-SCHARRÓN, C.; RICHTER, M. and VALZQUEZ, E. (2009): Landsliding and its multi-scale influence on mountainscapes. In: BioScience 59, 685–698. Doi:10.1525/bio.2009.59.8.10

RICHTER, M.; DIERTL, K.-H.; EMCK, P.; PETERS, T. and BECK E. (2009): Reasons for an outstanding plant diversity in the tropical Andes of Southern Ecuador. In: Landscape Online 12, 1–35. Doi:10.3097/LO.200912

RÜGER, N. (2006): Dynamics and sustainable use of species-rich moist forests. A process-based modelling approach. Ph.D. thesis. Osnabrück.

RÜGER, N.; GUTIÉRREZ, A. G.; KISSLING, W.; ARMESTO, J. and HUTH, A. (2007): Ecological impacts of different harvesting scenarios for temperate evergreen rain forest in southern Chile. A simulation experiment. In: Forest Ecology and Management 252, 52–66. Doi:10.1016/j.foreco.2007.06.020

RÜGER, N.; WILLIAMS-LINERA, G.; KISSLING, W. and HUTH, A. (2008): Long-term impacts of fuelwood extraction on a tropical montane cloud forest. In: Ecosystems 11, 868–881. Doi:10.1007/s10021-008-9166-8

RYAN, M. (1991): Effects of climate change on plant respiration. In: Ecological Applications 1, 157–167. Doi:10.2307/1941808

SHUGART, H. H. (1998): Terrestrial ecosystems in changing environments. Cambridge, UK.

– (2002): Forest gap models. In: MOONEY, H. A. and CANADELL, J. G. (eds.): Encyclopedia of global environmental change 2: The Earth system: biological and ecological dimensions of global environmental change. Chichester, 316–323. http://www.uvacres.org/uploads/docs/encyclopedia%20article.pdf

SMITH, T. and SHUGART, H. H.(1997): Plant functional types – their relevance to ecosystem properties and global change. Cambridge, UK.

STOYAN, R. (2000): Aktivität, Ursachen und Klassifikation der Rutschungen in San Francisco/Südecuador. Master's thesis. Erlangen.

THORNLEY, J. and JOHNSON, I. (1990): Plant and crop modelling – a mathematical approach to plant and crop physiology. Oxford, UK.

VORPAHL, P.; ELSENBEER, H.; MÄRKER, M. and SCHRÖDER, B.: What causes landslides in undisturbed tropical mountain rain forests? Submitted.

WHITMORE, T. (1998): An introduction to tropical rain forests. Oxford, UK.

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Impact of shallow landslides on forest structure in tropical montane forests

Impact of shallow landslides on forest structure in tropical montane forests

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Abstract

Shallow landslides are a main cause of natural ecosystem disturbance in tropical montane forests. Due to landslides, vegetation and often also the upper soil layer are removed, leaving space for a primary succession under altered environmental conditions. We utilize a process-based forest simulation model and develop possible scenarios to investigate, how changes in different life history traits of trees influence forest recovery on landslide sites. We then apply the model to an evergreen tropical montane forest in Southern Ecuador. For all regrowth scenarios, it takes at least 200 years until the post-landslide forest reaches its mature structure. On the local scale of landslides forest productivity is reduced considerably for most regrowth scenarios. Landslides produce distinct spatio-temporal variation in tree biomass within the first decades of recovery, which could possibly be compared to remotely sensed data. On the landscape level overall tree biomass is reduced by 13% due to landslide disturbances, forest productivity is only slightly reduced ($\sim 5\%$). The effect of landslides on landscape heterogeneity is pronounced: they create a mosaic of forest patches of different ages, similar to the well-studied gap-building process but on a larger spatial scale. Landslides produce hotspots of biomass loss and potentially also of forest productivity.

Keywords: forest model, landslide, forest dynamics, tropical montane forest, FORMIND

1. Introduction

Landslides are a major cause of natural ecosystem disturbance in tropical montane forests (Restrepo et al., 2009). Vegetation and often the upper soil layers are removed from the slide surface, leaving space for a primary succession (cf. Figure 1). Landslides alter environmental conditions on the slide surface considerably: photoactive radiation is increased (Myster and Fernandez, 1995), soils might be unstable (Walker and Shiels, 2008) and due to the loss of the organic soil layer the soil nutrient content is reduced even many years after the slide event (e.g. Zarin and Johnson, 1995; Wilcke et al., 2003). These changed conditions can affect different life history traits of trees and therefore influence forest recovery on landslide sites (cf. Figure 2).

Several observational studies of vegetation recovery on landslides sites have focused on the first years of succession (e.g. Ohl and Bussmann, 2004; Velazquez and Gomez-Sal, 2008; Shiels et al., 2008). These studies found a high variability in species assemblage and spatio-temporal pathways of regeneration, that are likely influenced by small scale erosion and scattered substrates and are thus hard to predict. Studies investigating long term effects of landslides often utilize chronosequences of landslides, assuming space-for-time substitution (Pickett, 1989). Investigated ecosystem attributes are for example temporal changes in biomass (Reddy and Singh, 1993; Restrepo et al., 2003), species and structural diversity (Dalling, 1994; Elias and Dias, 2009) and soil nutrients (Zarin and Johnson, 1995; Frizano et al., 2002; Wilcke et al., 2003). Estimated recovery time of different attributes varies considerably - while soil nutrients are assumed to recover within several decades (Restrepo et al., 2009), restoration of biomass can take more than 100 years (Dalling, 1994; Restrepo et al., 2003). Different general mechanisms are suggested to influence the pathways of regeneration, including facilitation and inhibition (Stern, 1995; Kessler, 1999; Walker and del Moral, 2003; Walker et al., 2009), as well as feedbacks of vegetation both on on abiotic factors and on vegetation development itself. Nutrition experiments support the hypothesis, that nutrient limitation (mostly N limitation) is a key limiting factor of plant growth on landslide sites, but they mostly focus on few study species and short term effects

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Figure 1: Mountain ridge with several traces of shallow landslides (left) and trace of a recent landslide (middle). Both pictures are taken in our study site, the Reserva Biológica San Francisco in Southern Ecuador. Right: Visualization of the FORMIND model with a recent landslide; different colors represent different species groups.

(e.g. Dalling and Tanner, 1995; Fetcher et al., 1996). Most empirical studies focus on a local scale, i.e. the scale of single landslides, and investigate different zones within landslides (e.g. Wilcke et al., 2003; Velazquez and Gomez-Sal, 2008). But landslides are also an important phenomenon to examine on the landscape scale where they pose a reoccurring disturbance that influences forest dynamics and produces a patchy distribution of different aged sites. However, investigating a high number of different aged landslide sites is difficult since old landslides are undetectable on aerial photographs and hard to find and access within closed forests in complex terrains. Remote sensing techniques offer new possibilities to investigate high numbers of landslides and provide tools to address questions about landslide effects on the landscape level (Davis et al., 2004; Lin et al., 2004).

However, our knowledge about recovery processes of forest on older landslide sites still remains limited and involves uncertain, possibly interacting, parameters. In this study, we therefore propose a modelling framework to investigate dynamics of landslide-affected forests. Process-based forest models are suitable tools to investigate changes of forest dynamics after natural or anthropogenic disturbances (Shugart, 1998). Particularly individual based spatially explicit models have the advantage, that one can observe dynamics on small spatial scales, such as the surface of a single landslide, as well as on the larger spatial scales of the landscape level. We utilize the individual based, spatially explicit simulation model FORMIND to investigate the influence of landslides on forest structure, succession and aboveground carbon cycle. The model simulates forest growth and has been used to analyze different types of disturbances in various tropical forests sites (e.g. Köhler et al., 2003; Rüger et al., 2008; Groeneveld et al., 2009). The process-based design of FORMIND allows to change single life history traits and analyze their impact on post-landslide succession.

In this study we investigate the effects of landslides on forest dynamics in an evergreen montane forest in southern
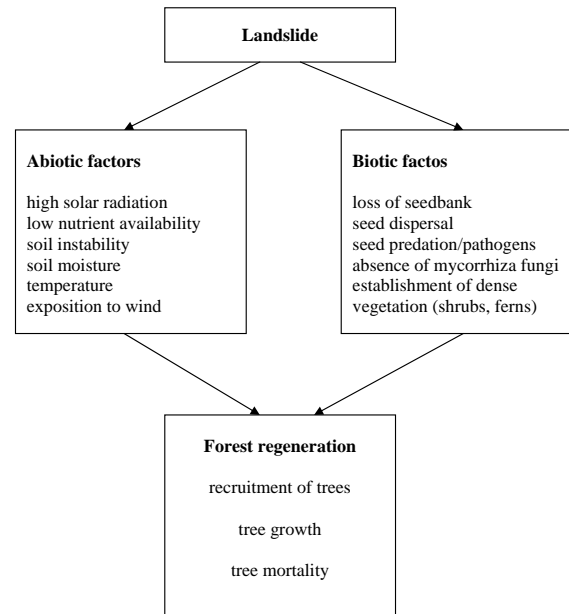

Figure 2: Overview of abiotic and biotic factors that are influenced by landslides and potentially affect forest regeneration.

Ecuador. Since empirical knowledge on forest regeneration in our study region is scarce, we develop different scenarios of forest regrowth with changed life history traits of trees. This study is divided into two parts: first we concentrate on the local scale of the landslide surface and processes that influence forest recovery and forest structure during succession: we analyze the spatio-temporal forest recovery process at the landslide site and compare the carbon balances for different scenarios. In the second part we upscale to the landscape level - here we investigate the impact of landslides on spatial heterogeneity and carbon budget of the forest and compare the disturbance regime of landslides with the more frequent but less severe disturbance regime of gap-building (due to falling trees).

2. Methods

2.1. Study site

Our study area is the Reserva Biológica San Francisco (RBSF), part of the biosphere reserve Podocarpus - El Condor, located on the eastern slopes of the Andes in southern Ecuador within one of the worldwide hotspots of biodiversity (Brummitt and Lughadha, 2003). The forest reserve stretches from 1800 up to 3200 meter above sea level (asl) and is characterized by steep slopes (on average 40°) and deeply incised valleys. The RBSF is very rich in tree species, with more than 280 species identified so far in the 1000 ha area (Homeier and Werner, 2007). The forest can be classified as evergreen montane forest and divided into four forest types with distinct structure and species composition (Homeier et al., 2008). Between 1900 and 2100 m asl we distinguish ridge and ravine forest. The ridge forest has lower basal area and also a lower canopy height ($15 - 20\ m$) but higher tree density compared to the ravine forest, where the canopy reaches up to 35 meter. With approximately 70 tree species, the ridge forest is not as species-rich as the ravine forest. The two other forest types are located at higher elevations; in these sites canopy height and species richness decrease (Homeier et al., 2008; Moser et al., 2008). In this study we focus on the ridge forest (1900-2100 m asl).

Within the RBSF, shallow landslides are a main source of natural disturbance (Bussmann et al., 2008); approximately 2.6% of the area is covered with visible traces of landslides. Most slides are shallow translational slides (Stoyan, 2000); in some slide events only the aboveground vegetation is removed - these slides can be termed vegetation slides (Vorpahl et al., submitted). Landslide events alter the forest structure in a dramatic way - usually all vegetation on top of the landslide surface is removed (see Figure 1). Narrow bands of vegetation slip downwards and leave bare areas of approximately 10-30 m width and 20-100 m length.

2.2. The FORMIND model

To study the influence of landslides on forest dynamics we utilize the individual based, spatially explicit forest growth model FORMIND (cf. Figure 1 right). In order to handle the high diversity of tree species in tropical forests (many of them extremely rare), tree species within the model are grouped into plant functional types (PFT) according to physiological attributes like maximum attainable diameter. All trees within small patches, hereafter called plots (we use a plot size of 20 x 20 meter), compete for light and space; tree growth is realized on the basis of carbon balance according to photosynthesis and respiration rates. The main processes included in the model are the establishment of young trees, tree mortality and tree growth. Dying trees can fall over and damage other trees; we refer to this process as gap-building. A detailed description of the current model version used for this study can be found in Dislich et al. (2009).

As a first step towards this study, FORMIND has been parameterized for the ridge forest of the RBSF. In this detailed parametrization, 70 tree species of the ridge forest were grouped into seven plant functional types (for details see Dislich et al., 2009). For this study, we subsumed these seven groups into three: pioneer (fast growing species: 10-20 mm maximal annual diameter growth), mid-successional (6 mm maximal growth) and climax (slow growing: 2 mm maximal growth) species. We slightly adapted the previous version of the model and included landslides as a special type of disturbance into the model (see section 2.5 and Appendix A).

2.3. Different pathways of regeneration after landslides

Accounting for scarcity of data on processes and parameters affecting forest dynamics following landslides in our study area, we compiled results from other studies to develop different possible scenarios of forest regrowth accounting for changed environmental conditions which are described in more detail below.

The first scenario serves as a reference scenario, where the only effect of landslides is the removal of trees with no additional effect on life history traits. In the remaining scenarios the new establishing trees experience changes in life history traits due to landslides (reduced growth, reduced recruitment, increased mortality). We implemented changes in life history traits of trees with a feedback mechanism, which controls the magnitude of changes in life history traits depending on the amount of already established vegetation. This feedback mechanism is inspired by the general idea of indirect facilitation on the community level (Walker and del Moral, 2003): the more the already established community resembles the pre-disturbance community, the more adequate are the conditions for forest recovery, i.e. trees experience less disadvantages. Empirical confirmation for such feedback mechanisms exists for nutrient accumulation: Reddy and Singh (1993) found that the accumulation of soil nutrients on landslides sites in the Himalaya proceeds in a non-linear way and is interdependent with the recovery process of vegetation. The spatial level at which we consider changes in life history traits are plots of 20 x 20 m size. We aim at a simple and comparable formulation of the scenarios.

Scenario 1: undisturbed regrowth
In this first scenario we assume that after a landslide all life history traits of trees are as in the undisturbed forest. Consequently, the only environmental change due to landslides that is sensed by the trees is the increase in light levels.

Scenario 2: reduced growth (due to nutrient limitation)
It is a well established fact in landslide research that nutrient limitation causes slow forest regrowth on landslides sites (e.g. Dalling and Tanner, 1995; Zarin and Johnson, 1995; Singh et al., 2001; Shiels et al., 2008). Experiments in a Puerto Rican forest found an increase in biomass of

tree seedlings after nutrient addition in the order of magnitudes (Fetcher et al., 1996), and Chaudhry et al. (1996) report up to 90% growth reduction of planted tree seedlings on a young landslide compared to growth in undisturbed himalayan forest. On the other hand, vegetation is likely to feed-back on the course of nutrient accumulation on slide surfaces via decomposition of litter and dead wood, and impeding further leaching of soils by reducing erosion.

We therefore develop a scenario of reduced tree growth where the amount of growth reduction depends on the so far accumulated dead biomass on the slide surface.

Tree growth is expressed in biomass increment per year. We assume a 90 % reduction of growth in the beginning of succession and reduced growth until the accumulated dead biomass (b_{dead}) on the plot equals the minimum standing biomass in a mature plot (b_{mat}). Therefore, the reduced biomass increment ($binc_{red}$) is calculated from the biomass increment under undisturbed growth ($binc$) as

$$binc_{red} = \underbrace{\left(\frac{0.9 \cdot b_{dead}}{b_{mat}} + 0.1 \right)}_{reduction factor} \cdot binc.$$

Scenario 3: reduced recruitment (due to thicket forming vegetation)

The first vegetation that establishes on landslide surfaces are mosses, lichens and grasses. It has been observed that subsequently a cover of a thicket-like vegetation of ferns can establish on landslides (Guariguata, 1990; Walker, 1994; Russell et al., 1998). Such dense vegetation might inhibit the establishment of trees. The first trees establishing within this thicket produce shade, that slowly results in a dieback of ferns and little by little generates more suitable conditions for tree recruitment.

We therefore develop a scenario with reduced recruitment of trees where the amount of reduction depends on the biomass of already established trees on the slide.

The model uses fixed recruitment rates of tree seedlings ($ingrowth$) per hectare and year and plant functional type. For consistency between scenarios, we assume a 90% reduction of recruitment rates in the beginning of succession and reduced recruitment until the standing biomass b on the plot equals the minimum standing biomass in a mature plot. Therefore the reduced recruitment rate $ingrowth_{red}$ is calculated as

$$ingrowth_{red} = \underbrace{\left(\frac{0.9 \cdot b}{b_{mat}} + 0.1 \right)}_{reduction factor} \cdot ingrowth.$$

Scenario 4: increased mortality (due to instable physical conditions)

Different factors might account for an increased mortality on young landslides: instability of soil, amplified changes in soil moisture and temperature, exposition to wind, predation and pathogens. We assume that these threats diminish with regrowing tree biomass.

We therefore develop a scenario with increased mortality rates of trees where the amount of mortality increment depends on the biomass already established on the slide.

In the forest model there are different sources of mortality (size-, density- and PFT-specific), which sum up to the overall mortality rate $mort$. We assume a 90% increment of this overall mortality in the beginning of succession and increased mortality until the standing biomass b on the plot equals the minimum standing biomass in a mature plot.

Therefore the increased mortality rate $mort_{inc}$ is calculated as

$$
\begin{aligned}
mort_{inc} &= \left[1 + \underbrace{\left(1 - \left(\frac{0.9 \cdot b}{b_{mat}} + 0.1 \right) \right)}_{increment factor} \right] \cdot mort \\
&= \left(1.9 - \frac{0.9 \cdot b}{b_{mat}} \right) \cdot mort.
\end{aligned}
$$

Combination of Scenario 2 and Scenario 3

In addition to the above described scenarios, where only one life history trait is changed at a time, we test a combination of reduced growth and reduced recruitment of trees; both traits are reduced by 90 % in the beginning of succession.

2.4. Time lag for regeneration after landslides

The forest model considers trees with stem diameter > 1 cm at breast height. Since after a landslide trees are removed from the surface, there is a time lag between slide occurrence and the time until the first trees reach the size of 1 cm diameter at breast height. Based on the potential growth of trees in the undisturbed forest (S. Günter, pers. comm.), we estimate these time lags as 3 years for the fast growing species, 5 years for intermediate growing species and 12 years for the slow growing species. This is only a rough estimation, since variation in growth dynamics of seedlings is high, but moderate changes in these time lags do not have a strong effect on our results. The same time lags are applied for all scenarios.

2.5. Implementation of landslides into FORMIND

For the first part of this study, we assume that the whole simulation area (1 hectare) is affected by a landslide. In the second part we investigate dynamics on the landscape scale, where landslides are a reoccurring disturbance that affects only small parts of the simulated area (cf. Figure 1 right). To estimate landslide frequency and sizes, we utilize aerial photographs of our study area, which have been processed and evaluated by Stoyan (2000). In the period between 1989 and 1998, 183 landslides have been observed; this results in a disturbance rate of approximately 0.02 slides per hectare and year. The size distribution of landslides was derived from the 1998 aerial photograph using

ArcGIS; slide sizes range from 80 to 8317 m^2, with an average slide size of 1120 m^2.

We implement landslides on the landscape level into FORMIND in the following way: every year a randomly drawn number determines, if a landslide occurs. The landslide size is drawn from the size distribution of landslides, rounded for the model plot size of 20 x 20 meter. The direction of landslides is always the same, the starting location of the landslide is arbitrary. Neighboring plots are affected until the slide reaches the predetermined size. To avoid edge effects the landscape is modelled as a torus. Forest recovery then proceeds according to one of the scenarios described above.

3. Results

3.1. Landslide level

At first we focus on the succession of trees on the slide surface and compare different scenarios of forest regrowth. Figure 3 (left column) depicts the buildup of biomass divided into pioneer, mid-successional and climax tree species. The landslide removes the complete tree biomass from the slide surface and for all scenarios the subsequent accumulation of new tree biomass is at first dominated by the fast growing pioneer species before mid-successional species and eventually also climax species increase in biomass. The course of biomass recovery differs between the scenarios; in the first scenario, where trees do not suffer any drawback due to changed environmental conditions, we observe a rapid regrowth of tree biomass within the first 30 years of succession. In all remaining scenarios, succession is slowed down. If tree growth is reduced (scenario 2), tree biomass is very low within the first 40 years after the landslide, followed by a similar steep increase in biomass as in the undisturbed regrowth scenario. For scenario 3 and 4 (reduced establishment and increased mortality) the increment in the buildup phase is less steep. In all scenarios, a tree biomass of approximately 100 tons per hectare has established after 100 years. For the combination of scenario 2 and 3 the recovery of tree biomass is strongly delayed and sets in only around 180 years after the landslide event.

All scenarios produce a distinct pattern of spatial variation in biomass within the first decades of succession (Figure 3, second column). While in the first scenario spatial variation is almost the same as in mature forest, the spatial variation is lower than in the mature forest, if growth rates of trees are reduced (scenario 2). Spatial variation in biomass increases strongly if recruitment on the slide surface is reduced (scenario 3), i.e. vegetation is more patchy; also for increased mortality (scenario 4), spatial variation in biomass increases, but to a lesser extent and in a humped-shaped form. A much stronger increase in spatial heterogeneity of biomass is produced in the combined scenario of reduced growth and reduced recruitment; here it takes more than 300 years until variation returns to
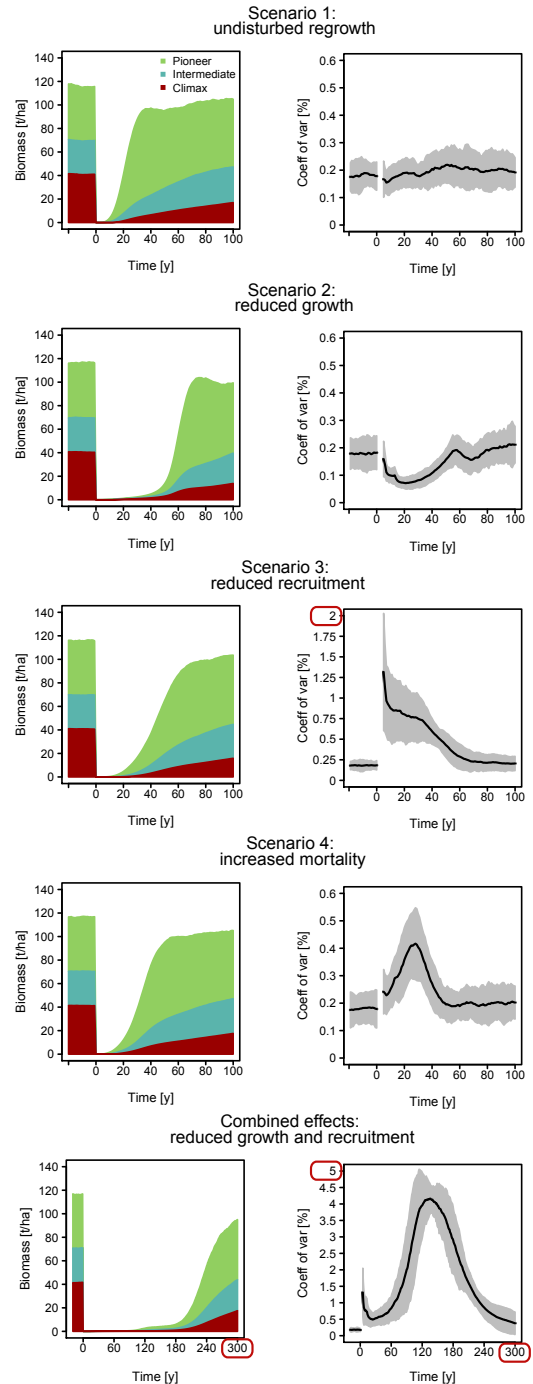

Figure 3: Left column: succession of tree biomass after landslide for different scenarios; mean of 50 simulation runs of one hectare. Right column: spatial variation of biomass on one hectare (between plots of 20 x 20 meter) for the different scenarios: Coefficient of variation of plot biomass over time. Black lines depict the mean of 50 simulations (each one hectare); grey areas mark ± 2-times standard deviation from mean. Note different scales for scenario 3 and the combined effects scenario.

the level of spatial variation in mature forest. To summarize, while the differences in biomass succession for the four scenarios are relatively small (especially for scenario 3 and 4), we find major differences in the spatial variation of biomass within the first decades of succession. After 100 years of succession, for all four scenarios, overall tree biomass is only slightly lower than in the mature forest before the slide; however, species composition is still different from mature forest, with a higher proportion of pioneer and a lower proportion of climax species. Spatial variation in biomass is similar to the variation in mature forest and differences between the four scenarios have levelled out.

In the following, we will investigate in more detail how forest productivity is changed after landslides; for this purpose we analyze the annual production of successional and mature forest. We calculate biomass gains (due to growth and recruitment) and losses (due to mortality) over time for forest without landslides and for the different scenarios after landslide disturbance (Figure 4, small panels). In all scenarios, biomass losses display a higher fluctuation than biomass gains, since losses are determined by mortality of (sometimes large) trees, while biomass gains are driven by smaller entities, namely growth of single trees and biomass of newly recruited trees. Without landslides, annual biomass gains as well as biomass losses fluctuate around 7 tons (organic dry matter) per hectare. After a landslide event, there are no trees on the slide surface, hence biomass production and losses are set to zero. In the course of forest succession, biomass production needs to exceed biomass losses so that biomass accumulates. We observe this in all four scenarios; only for the combination of reduced growth and recruitment both production and losses remain very low (<0.2 tons per hectare) within the first 100 years after landslide. During forest recovery, biomass production temporarily exceeds the production in mature forest, most pronounced in scenario 1 and 2, where the production curve reaches a peak of more than 10 tons per hectare. The accumulated difference between the two curves (biomass gains and losses) describes the biomass accumulation (cf. Figure 3, left column); since biomass losses are on average proportional to standing biomass, the timing of biomass accumulations in Figure 3 coincide with the production curves in Figure 4.

Integrated over the first 100 years of succession after landslide, annual biomass gains and losses are, compared to mature forest without landslides, reduced for all scenarios, except for the undisturbed regrowth scenario, where biomass gain is slightly higher (Figure 4, bar plot). The mature forest is in an equilibrium state, where biomass gains equal biomass losses and thus net production is zero. After a landslide the average annual net production is positive and almost equal for the four scenarios ($\sim$ 1 ton per hectare), whereas the combined scenario yields almost no biomass. Gross biomass production is reduced by 37% for the reduced growth scenario, by 24% percent for reduced recruitment, by 9% for increased mortality and by 99% for the combination of reduced growth and recruitment.

Scenario	Pioneer species	Mid-successional species	Climax species
undisturbed regrowth	28 (0)	50 (2)	202 (11)
reduced growth	65 (1)	85 (2)	218 (11)
reduced recruitment	37 (2)	53 (3)	209 (9)
increased mortality	28 (1)	47 (2)	199 (11)
reduced growth & reduced recruitment	227 (9)	247 (10)	401 (14)

Table 1: Maturation time (years) of successional forest after landslide for different species groups (columns) and different regrowth scenarios (rows). Calculation is based on stem size distributions of mature and successional forest. Results given are mean (and standard deviation) of 50 simulation runs on 1 ha.

In all scenarios, landslides have an effect on forest productivity - within the first decades after the landslide the forest becomes a temporary carbon sink; the magnitude of changes in biomass gains and biomass losses, however, depends on the regrowth scenario.

So far, we have focused at the first 100 years of forest succession after landslides. However, species composition is still different from mature forest after this period (cf. Figure 3 left). To analyze structural differences between mature and transient forest in more detail we utilize stem size distributions of mature and successional forest (for details, see Appendix B). Table 4.4 provides time spans needed for the different species groups to reach a mature structure, i.e. stem size distribution. For all scenarios, the order in which species groups reach the mature state is the same: pioneer species are the first after only few decades of recovery (28 - 65 years), followed by the mid-successional species (47-85 years) and, after a longer period, the climax species (199-218 years). Differences between the four scenarios are relatively small, the reduced growth scenario produces slightly slower maturation times. As already observed (cf. Figure 3 and 4), the combination of reduced growth and reduced recruitment results in a strongly delayed recovery of forest which is also expressed in later maturation of stem size distributions (227-401 years). For all scenarios, the time-lag between maturation time of the different species groups is almost the same: approximately 20 years between pioneer and mid-successional species and 150 years between mid-successional and climax species. This means that once succession sets in and the pioneer species recover, the model predicts similar pathways of succession. In all cases it takes at least 200 years until all species groups have reached a mature stem size distribution, i.e. a forest structure and species composition similar to the pre-landslide situation is restored.

3.2. Landscape level

Until now we have restricted our view to the surface of the landslide. In the following we will broaden our
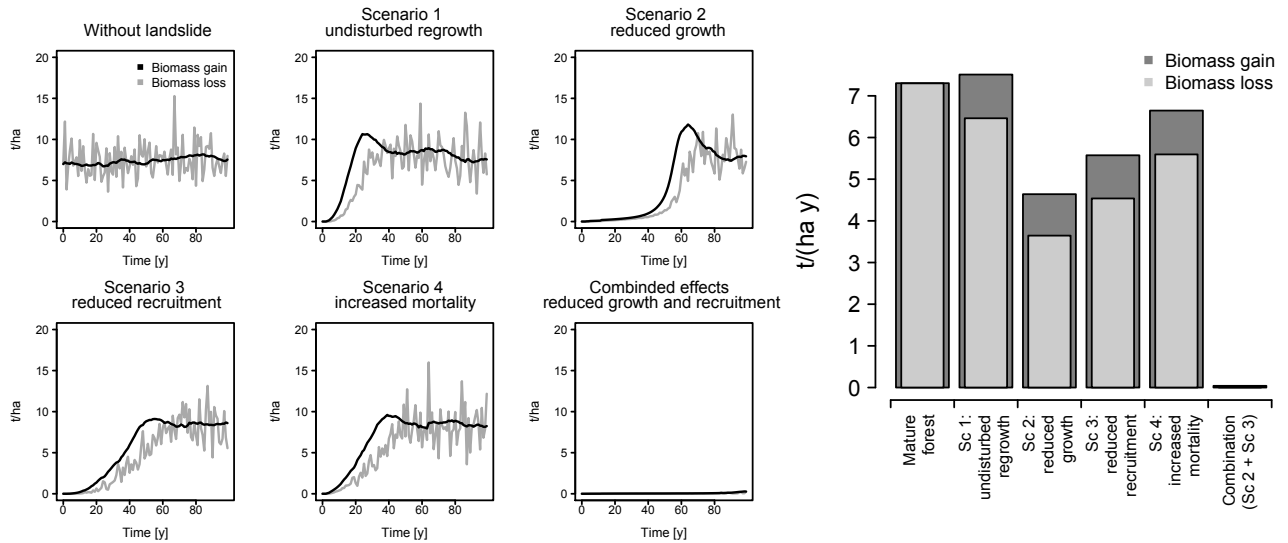
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Figure 4: Small panels: Biomass gains (due to tree growth and recruitment) and biomass losses (due to mortality) after landslide for the different scenarios in one exemplary simulation run. Right: Mean annual build up of biomass and loss of biomass. The first bar depicts dynamics of mature forest where biomass gain equals biomass losses. Remaining bars show dynamics averaged over the first 100 years of forest succession after landslide for the different scenarios (results are based on 50 simulations of one hectare each).

perspective to the landscape level where landslides are a reoccurring disturbance that affects only small parts of the forest. For the rest of this study we select the scenario with reduced recruitment of trees (scenario 3); results for the remaining scenarios are provided in Appendix C. Temporal dynamics for an exemplary simulation run are illustrated in Figure 5. Repeated landslides of different sizes lead to an abrupt reduction in biomass (left panel); with each landslide event, spatial variation in tree biomass increases steeply and returns slowly towards the level of undisturbed forest when no landslide occurs for a longer period (middle panel). Each landslide is marked as a strong peak in biomass losses and biomass production decreases slightly in the years after a landslide (right panel).

For the analysis of landslides on the landscape level, we chose a realistic slide frequency of 0.02 slides per hectare and year. We then compare landslides with the disturbance of gap-building, by switching on and off the gap-building process in FORMIND. While the aboveground biomass decreases with increasing disturbance regime - from 140 tons per hectare without gap-building and landslides to 117 tons with gap-building to 100 tons with gap-building and landslides - forest productivity displays a different dynamic (Figure 6, left and middle). We find the lowest productivity for forest without gap-building (5.6 tons biomass gain per hectare and year), a considerably higher productivity for forest with gap-building (7.3 tons) and a slight reduction of productivity (to 6.9 tons) when in addition to forest gaps also landslides occur. In all

cases, the forest is in a quasi equilibrium state where biomass gains equal biomass losses. The frequency distribution of biomass (on 20 x 20 meter plots) is changed considerably by the different disturbance regimes (Figure 6, right). Without landslide disturbance, the frequency distribution of biomass is unimodal, with plot biomass ranging between 50 and 225 tons per hectare for forest without gap-building, and between 25 and 200 tons per hectare for forest with gap-building. The introduction of landslides results in an increase of plots with low biomass: 13% of plots maintain less than 50 tons tree biomass compared to only 0.1% of plots when only gap-building disturbances are present. In exchange, the fraction of plots with high biomass decreases when landslides are present.

On the landscape scale, landslides reduce aboveground standing biomass and considerably change the spatial heterogeneity of forest biomass.

4. Discussion

4.1. Plausibility of scenarios

We utilized the forest growth model FORMIND and analyzed different hypothetical scenarios of changes in life history traits of trees to provide new insights on the role of landslides for forests regeneration and forest structure. Due to scarcity of data from our study system, the developed scenarios are based on findings from studies in other forests and theoretical considerations (see Methods). Very likely, trees on landslide sites in our study area will respond to the shortage of nutrients: it is well known that
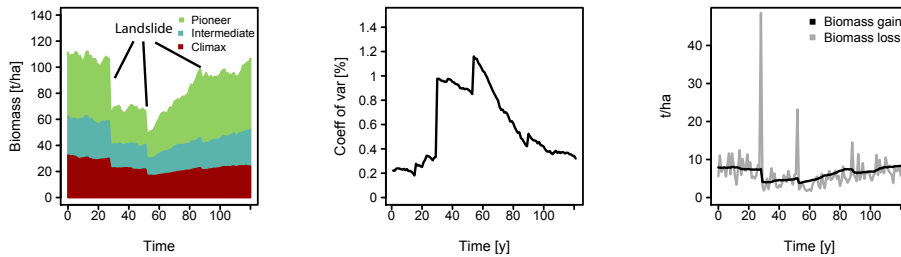
Figure 5: Exemplary simulation of forest dynamics on one hectare with landslide frequency 0.02 per hectare and year under regrowth scenario 3 (reduced recruitment). Left: Biomass dynamics for different species groups. Middle: spatial variation of biomass (between plots of 20 x 20 meter): Coefficient of variation of plot biomass over time. Right: Biomass gains and losses.

nutrient accumulation to pre-landslide levels takes decades (Wilcke et al., 2003) and results of a nutrition experiment (NUMEX) point out that tree growth is nutrient limited in our research area (Wullaert et al., 2010). However, the amount to which tree growth will be reduced in our study system remains speculative. Reduced recruitment can possibly occur due to a dense vegetation layer of early landslide colonists (e.g. ferns). The role of these early colonizers is ambiguous, they might promote the recovery of soil in terms of stabilization and nutrient accumulation, and in this sense act facilitative - on the other hand they might inhibit establishment of trees. Ohl and Bussmann (2004) suggest a combination of tolerance (suggesting all species being equally capable to establish but having different success in population growth) and facilitation for southern Ecuador (Connell and Slatyer, 1977). But even if these early colonizers do not hinder tree establishment, reduced recruitment can also result from continued soil erosion and heterogeneous soil conditions (Walker and Shiels, 2008). Erosion, wind, photo inhibition or increased levels of pathogenes and herbivory could account for increased mortality rates on landslide sites. Empirical evidence for this plausible effect is still missing, in fact Myster (2002) did find high levels of herbivory and pathogenes on landslides but no effect on tree mortality and Fetcher et al. (1996) report moderate levels of photoinhibition for only one of four study species in Puerto Rico. A planting experiment in a Jamaican forest (Dalling and Tanner, 1995) found even higher mortality rates in the understorey compared to mortality on landslide sites, but this result might be influenced by the selection of gap-demanding species.

Presumably, different life history traits of trees will be affected by landslides at the same time. We tested a combination of reduced growth and recruitment and found a strongly delayed recovery process of vegetation. The combination of the two reduction mechanisms amplifies their impact (explanation follows below). Such slow forest recovery has been observed in some forest systems: Restrepo et al. (2003) found only around 25 % of the mature biomass on a 124 year old landslide in Hawai'i and Dalling (1994)

hypothesized that it may take around 500 years until biomass reaches the pre-landslide level for a Jamaican forest.

The four scenarios predict a recovery time of forest biomass close to the pre-landslide level between 30 and 80 years (cf. Figure 3, left column). In the undisturbed regrowth scenario the forest recovers rapidly. Biomass estimations from a single landslide in the study area (C. Dislich, unpublished data) indicate that the scenario with undisturbed regrowth (scenario 1) is too fast: on a 39-46 year old landslide we found approximately 49 tons of biomass per hectare, which is roughly 40% of the mature biomass. This biomass estimation suggests that the reduced growth scenario underestimates biomass recovery while scenario 3 and 4 (reduced recruitment and increased mortality) seem to more or less predict an adequate speed of biomass recovery. The combined scenario of reduced growth and recruitment predicts an unrealistically slow recovery of biomass.

But for none of the scenarios, the structure of the modelled successional forest fully corresponds to the forest structure of this field observation since the model underrepresents the frequency of small trees and overestimates the frequency of larger trees: in the field, almost all individuals had a diameter < 10 cm, and only few individuals were larger than that. This suggests that the maturation times given in Table 4.4 should be considered only as lower bounds. The under-representation of small trees, which does not occur in simulations of the mature forest (see Dislich et al., 2009), may stem from spatial constraints in crown sizes of small trees (allometric relationships).

In summary, a reduced recruitment scenario, a reduced growth scenario with a more moderate reduction in the beginning of succession, or a combination of reduced recruitment and reduced growth with less reduction, all seem to be plausible scenarios. The applied changes in life history traits are quite strong and may be modified, if observations indicate more moderate changes. Currently the quantification of the reduction is difficult due to scarcity of data, however, our approach allows the generation of a range of plausible regeneration times.
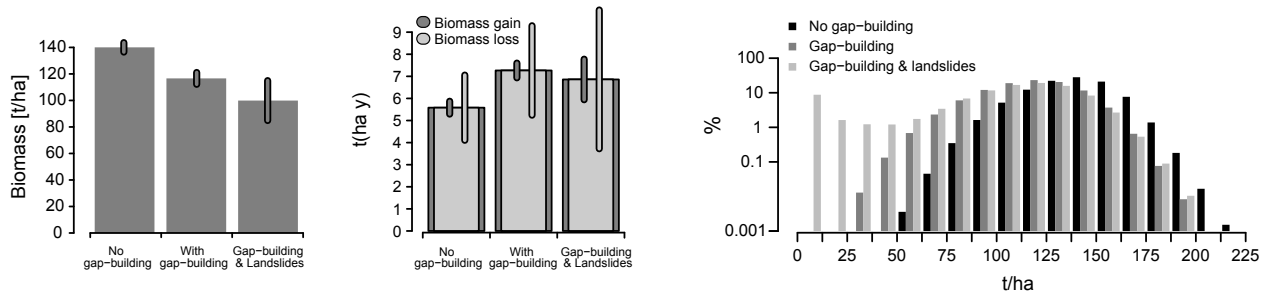
Figure 6: Aboveground biomass per hectare (left) and biomass gains and losses (middle) for forest without gap-building disturbance, for forest with gap-building (falling probability 0.2 for dead trees above 10 cm DBH) and for forest with gap-building and landslide disturbance (frequency 0.02 per hectare and year). Bars show the mean of 50 simulation runs on one hectare for a period of 1000 years; error bars display the standard deviation. Right: Frequency distribution of biomass on plots (20 x 20 m) without gap-building (black) with gap-building (dark grey) and with gap-building and landslides (light grey) respectively. Results with landslides are based on scenario 3 (reduced recruitment).

4.2. Spatio-temporal patterns as an opportunity for identifying mechanisms

The analysis of spatial variation in biomass at the scale of 20 x 20 meter (cf. Figure 3 right column) reveals distinct patterns for the different scenarios. Surprisingly, the spatial biomass variation in the undisturbed regrowth scenario is almost stable throughout succession - one might have assumed that in the early phase of succession all plots have a very similar and low amount of biomass, which would cause a reduction in spatial variation of biomass distribution. However, this is not the case since the fast growing tree species quickly establish a diverse height structure that differs between plots and leads to variations in biomass. If growth rates are reduced after a landslide, we find a low variation of plot biomass within the first decades of succession. In this case, a fast diversification of the canopy structure is suppressed by growth reduction, resulting in a more homogeneous distribution of biomass. The increase in spatial variation of tree biomass for reduced recruitment and increased mortality is not unexpected: with reduced recruitment the few established trees are scattered unevenly by chance at the post-landslide surface, have less competition with other recruits and consequently can grow fast. Due to the feedback of already established vegetation, differences between plots with few recruits and many recruits are further enhanced. Increased mortality acts in a similar way: in the beginning of succession, differences between

plot biomasses are rather small, the heterogenization of biomass distribution only sets in when some plots build up enough biomass to bring the mortality rate almost back to the normal level. Plots with less established trees loose more biomass (due to accelerated mortality rates) compared to plots with more established trees; this feedback enhances differences in plot biomass. Apart from delayed biomass recovery, the combination of reduced growth and recruitment rates leads to a strong increase in spatial heterogeneity of biomass distribution: the combination of the two feedback effects amplifies their impact. Due to recruitment reduction only few plots receive sufficient recruits which then additionally experience a strong growth reduction. Once these plots carry enough biomass so that growth reduction reduces, they build up a mature structure. For a long time the majority of plots remain in the phase where tree biomass is not high enough to overcome growth reduction.

Naturally, one might expect that different mechanisms influence forest recovery on landslide sites at the same time and thus interact with each other like in the above considered combined scenario. Nevertheless, the identified (different) patters of spatial variation in tree biomass raise hope that one could possibly identify the mechanisms that affect forest regrowth with the aid of remote sensing techniques. One possibility would be to fit the parameters of the landslide module with remotely sensed data. In com-

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bination with older aerial photographs that aid in determining the ages of landslides, information on the temporal dynamics of regeneration can be derived. High resolution techniques like Lidar imagery could be used to attain small scale information on the spatial distribution of biomass on single slide surfaces and could thus be compared to model outputs from the different scenarios and combinations. Trusting the structural realism of our model, this comparison could indicate which life history traits are affected by landslides and advise future field experiments to test these hypotheses.

4.3. Effect of landslides on landscape heterogeneity

The disturbance regime of landslides affects larger patches of forest than forest gaps that are produced by falling trees; while typical landslide sizes in our system range between 200 and 1500 m^2 (mean $\sim$ 1100 m^2), sizes of forest gaps range between 20 and 700 m^2, but are most frequently smaller than 200 m^2 (Brokaw, 1985; Yamamoto, 1992). Landslides are also a more severe disturbance than forest gaps since they affect the forest ecosystem above and below ground; they produce a characteristic finger-like signature on the landscape (cf Figure 1). The mosaic landscape structure with forest patches of different successional stages that is created due to landslide disturbances (cf. Figure 6, right), in particular the more open areas, will likely have a positive impact on the diversity of flora and fauna (landslide specialist species), as was suggested in several previous studies (e.g. Yamamoto et al., 1995; Geertsema and Pojar, 2007; Elias and Dias, 2009). Additionally, due to landslides, hotspots of particularly low and high productivity emerge, which do not occur otherwise - young landslides are characterized by low productivity, but during the recovery process, productivity can occasionally exceed the productivity of mature forest (cf. Figure 4).

4.4. Forest productivity and disturbances at the landscape scale

The role of disturbances for the carbon balance of forests is not intuitively clear - due to a disturbance, trees die and carbon stored in vegetation will partly be released and partly be stored in the soil during decomposition. In the case of landslides, vegetation and soil are removed and might come to rest at the lower end of the landslide or be transported out of the system via streams. Soil erosion might continue after landslides (Walker and del Moral, 2003; Walker and Shiels, 2008). The disturbed area offers space where new biomass can accumulate, therefore one can hypothesize that disturbances increase forest productivity. This hypothesis is confirmed in the case of the gap-building disturbance. Without gap-building, standing biomass is high but productivity is low (cf. Figure 6, left and middle panel) since the canopy is permanently closed and light levels in lower strata are low. When dying trees fall over and create gaps, usually not all trees in the gap are damaged, forest soil and seed bank remain intact and

therefore remaining trees can utilize newly available space and rapidly fill in the gap. Consequently, forest productivity increases in the presence of forest gaps.

Our simulation experiments show that the additional disturbance of landslides do not further increase forest productivity. Depending on the regrowth scenario, there is only a short period during succession where gross productivity exceeds productivity of mature forest (cf. small panels in Figure 4); during this period the established young trees can profit from increased available light and space. But integrated over the first century of succession after landslide, aboveground forest productivity is reduced for all scenarios (except the undistubed regrowth scenario) compared to productivity in mature forest (cf. Figure 4, right). Consequently, forest productivity on the landscape scale is also slightly reduced by landslides (cf. Figure 6, middle panel and Appendix C).

The overall standing biomass is reduced by 13 % due to landslide disturbances (cf. Figure 6 left). This relatively high reduction might partly be caused by our simplifying assumption of random landslide locations. In the real landscape, the location of landslides depends on many factors like steepness of the terrain, geomorphological and hydrological factors - therefore certain parts of the forest will be affected stronger by landslides than others.

Measuring forest net primary production (NPP) is a laborious task - it involves estimating different above and below ground components like aboveground biomass increment, litter fall and below ground production (Clark et al., 2001a). A synthesis of 39 tropical forest sites shows a relatively wide variation of NPP even after taken into account different temperatures and precipitation regimes (Clark et al., 2001b). The predicted biomass gains (cf. Figure 4 and 6) represent above-ground coarse wood productivity, which is an important component of NPP, since it dominates above-ground carbon storage dynamics (Chambers et al., 2001). Under the assumption that dry biomass is 50 % carbon, the biomass gain of 5.6-7.3 tons per hectare and year predicted by our model (cf. Figure 6, middle panel) corresponds to 2.8-3.7 tons carbon; these estimated amounts lie well within the range (1.5-5.5 Mg C $ha^{-1}a^{-1}$) of estimated productivities for 104 neotropical forest sites (Malhi et al., 2004).

4.5. Limitations

Presumably, different tree species will show different reactions to the disturbance regime of landslides, for example, Günter et al. (2007) showed that only a limited number of forest species could regenerate on a 38-year old abandoned pasture in our study area. In this study, we applied the same changes of life history traits to all species groups. Potentially one could of course apply different changes for different species groups, but this would require detailed knowledge on how different species react to different environmental conditions, especially nutrient limitations. In

this sense, at this stage, the model is not suitable of testing the effect of landslides on tree species diversity.

In our design of the landslide module, we did not differentiate different zones of landslides. Empirical studies often differentiate between the larger upper "erosional" zone of landslides, where all vegetation is removed, and the smaller "depositional" zone, where the sliding material comes to rest (Walker et al., 1996). In this depositional zone, succession might take place faster than in the erosional zone, since organic material and seeds are present. Our approach neglects differences between zones within landslides for the sake of simplicity and upscaling, and applies the same changes of life history traits on the whole slide surface, assuming that these changes represent changes averaged over the whole slide.

So far, we restricted our analysis to aboveground carbon dynamics. An investigation of the influence of landslides on carbon dynamics of the whole ecosystem requires the inclusion of below ground vegetation dynamics as well as decomposition processes and soil C-dynamics. This is beyond the scope of this study.

4.6. Conclusions and Outlook

Using a process based forest growth model, we found distinct spatial patterns of successional forest depending on changes in different life history traits of trees. Remote sensing techniques will allow quantifying these patterns in the field and will thus aid in designing adequate forest regrowth scenarios in the future. Furthermore, a soil landscape model, as well as a process-based landslide model for the study area are under development. We hope that in the near future the combination of these approaches will aid in gaining a better understanding of the carbon cycle of tropical montane forests.

Appendix A. Adaptations of the previous version of the model

The model utilizes potential growth curves which represent diameter growth under full light without any competition with other trees. We modified the way potential diameter growth curves are assigned to the model. Potential growth curves are modelled as a polynomial function (of degree three, see Appendix in Dislich et al. (2009)). For an easier interpretation of the potential growth curves we now read in the following four parameters: the maximal potential growth, the diameter, at which the maximal potential growth is realized, the potential growth of ingrowing trees and the potential growth of trees that reach their maximal diameter. These four input parameters uniquely define the polynomial of the potential growth curve. The coefficients, which were beforehand read in directly, are now calculated in an initializing procedure. We slightly modified the parameters of the potential growth curve and subsequently updated recruitment and mortality rates. The new input parameter values are depicted in the table below; all other model parameters are the same as in Dislich et al. (2009).

Appendix B. Maturation time of successional forest

To determine the maturation time of successional forest, we first calculate the stem size distribution of mature forest (class width 10 cm). For this we use 50 simulation runs without landslides, and calculate stem size distributions, when all species groups have reached their equilibrium state (for a period of 1000 years). For each diameter class and each species group, we obtain a minimum and a maximum frequency of stems in one hectare of mature forest. This results in three stem size distributions of mature forest: the pioneer, mid-successional and climax species distribution.

For the calculation of maturation time of successional forest, we define the point of maturation as the first year in which stem frequency for all diameter classes of one species group lies within the range between minimum and maximum of the mature stem frequency of this species group.

	PFT 1	PFT 2	PFT 3	PFT 4	PFT 5	PFT 6	PFT 7
maximum potential growth [mm]	10	20	6	6	2	2	2
point of maximal growth [fraction of maximal dbh]	0.33	0.33	0.25	0.33	0.2	0.33	0.33
potential growth at min. dbh [fraction of maximum growth]	0.4	0.8	0.85	0.85	1	1	1
potential growth at max. dbh [fraction of maximum growth]	0	0	0	0	0	0	0
recruitment rates	50	180	130	50	120	310	50
mortality rates	0.05	0.09	0.05	0.05	0.006	0.018	0.008

Appendix C. Landslides on the landscape scale for the different scenarios

Same analysis as in Figure 6 for all scenarios.
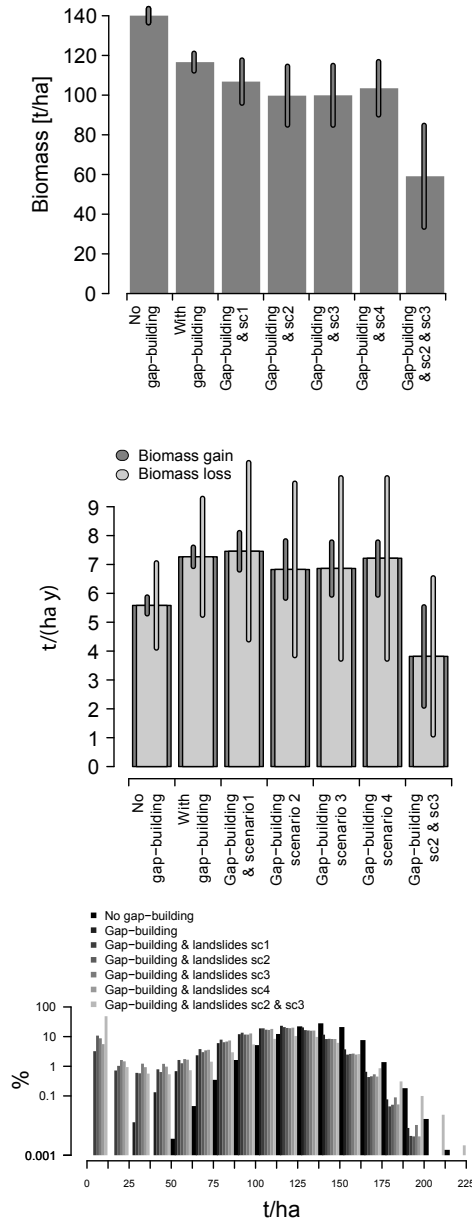
Figure A.7: Same as Figure 6 for all scenarios. Aboveground biomass per hectare (upper left) and biomass gains and losses (upper right) for forest without gap-building disturbance, forest with gap-building and without landslide disturbance and forest with gap-building and landslide disturbance (landslide frequency 0.02 per hectare and year). Below: Frequency distribution of biomass on plots (20 x 20 m) without gap-building, with gap-building, and with gap-building and landslides (landslide frequency 0.02 per hectare and year)

References

Brokaw NVL, 1985. Gap-phase regeneration in a tropical forest. Ecology 66, 682–7.

Brummitt N, Lughadha EN, 2003. Biodiversity: Where's hot and where's not. Conserv Biol 17, 1442–8.

Bussmann R, Wilcke W, Richter M, 2008. Landslides as Important Disturbance Regimes - Causes and Regeneration. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, editors. Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies Vol. 198, p. 319–30.

Chambers JQ, dos Santos J, Ribeiro RJ, Higuchi N, 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. For Ecol Manage 152, 73–84.

Chaudhry S, Singh SP, Singh JS, 1996. Performance of seedlings of various life forms on landslide-damaged forest sites in Central Himalaya. J Appl Ecol 33, 109–17.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, 2001a. Measuring net primary production in forests: Concepts and field methods. Ecol Appl 11, 356–70.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA, 2001b. Net primary production in tropical forests: An evaluation and synthesis of existing field data. Ecol Appl 11, 371–84.

Connell JH, Slatyer RO, 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111, 1119–44.

Dalling JW, 1994. Vegetation colonization of landslides in the Blue Mountains, Jamaica. Biotropica 26, 392–9.

Dalling JW, Tanner EVJ, 1995. An experimental study of regeneration on landslides in montane rain forest in Jamaica. J Ecol 83, 55–64.

Davis TJ, Klinkenberg B, Keller CP, 2004. Evaluating restoration success on Lyell Island, British Columbia using oblique videogrammetry. Restor Ecol 12, 447–55.

Dislich C, Günter S, Homeier J, Schröder B, Huth A, 2009. Simulating forest dynamics of a tropical montane forest in South Ecuador. Erdkunde 63, 347–64.

Elias RB, Dias E, 2009. Effects of landslides on the mountain vegetation of Flores Island, Azores. J Veg Sci 20, 706–17.

Fetcher N, Haines BL, Cordero RA, Lodge DJ, Walker LR, Fernandez DS, Lawrence WT, 1996. Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. J Ecol 84, 331–41.

Frizano J, Johnson AH, Vann DR, Scatena FN, 2002. Soil phosphorus fractionation during forest development on landslide scars in the Luquillo Mountains, Puerto Rico. Biotropica 34, 17–26.

Geertsema M, Pojar JJ, 2007. Influence of landslides on biophysical diversity - A perspective from British Columbia. Geomorphology 89, 55–69.

Günter S, Weber M, Erreis R, Aguirre N, 2007. Influence of distance to forest edges on natural regeneration of abandoned pastures: a case study in the tropical mountain rain forest of Southern Ecuador. Eur J Forest Res 126, 67–75.

Groeneveld J, Alves LF, Bernacci LC, Catharino ELM, Knogge C, Metzger JP, Pütz S, Huth A, 2009. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. Ecol Model 220, 2450–9.

Guariguata MR, 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. J Ecol 78, 814–32.

Homeier J, Werner FA, 2007. Spermatophyta checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S-Ecuador). In: Liede-Schumann S, Breckle SW, editors.. Provisional Checklists of Flora and Fauna of the San Francisco valley and its surroundings (Estación Científica San Francisco), Southern Ecuador. Ecotropical Monographs 4, p. 15–58.

Homeier J, Werner FA, Gradstein SR, Breckle SW, Richter M, 2008. Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, editors. Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies Vol. 198, p. 87–100.

Kessler M, 1999. Plant species richness and endemism during natural landslide succession in a perhumid montane forest in the Bolivian Andes. Ecotropica 5, 123–36.

Köhler P, Chave J, Riera B, Huth A, 2003. Simulating the long-term response of tropical wet forests to fragmentation. Ecosystems 6, 114–28.

Lin CY, Lo HM, Chou WC, Lin WT, 2004. Vegetation recovery assessment at the Jou-Jou Mountain landslide area caused by the 921 Earthquake in Central Taiwan. Ecol Model 176, 75–81.

Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, Di Fiore A, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Montoya LMM, Monteagudo A, Neill DA, Vargas PN, Patino S, Pitman NCA, Quesada CA, Salomao R, Silva JNM, Lezama AT, Martinez RV, Terborgh J, Vinceti B, Lloyd J, 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biol 10, 563–91.

Moser G, Röderstein M, Soethe N, Hertel D, Leuschner C, 2008. Altitudinal Changes in Stand Structure and Biomass Allocation of Tropical Mountain Forests in Relation to Microclimate and Soil Chemistry. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, editors. Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies Vol. 198, p. 292–42.

Myster RW, 2002. Foliar pathogen and insect herbivore effects on two landslide tree species in Puerto Rico. For Ecol Manage 169, 231–42.

Myster RW, Fernandez DS, 1995. Spatial gradients and patch structure on two Puerto Rican landslides. Biotropica 27, 149–59.

Ohl C, Bussmann R, 2004. Recolonization of natural landslides in tropical mountain forests of Southern Ecuador. Feddes Repetorium 115, 248–64.

Pickett STA, 1989. Space-for-time substitutions as an alternative to long-term studies. In: Likens GE, editor. Long-term studies in ecology. Springer, New York, p. 110 –35.

Reddy VS, Singh JS, 1993. Changes in vegetation and soil during succession following landslide disturbance in the Central Himalaya. J Environ Manage 39, 235–50.

Restrepo C, Vitousek P, Neville P, 2003. Landslides significantly alter land cover and the distribution of biomass: an example from the Ninole ridges of Hawai'i. Plant Ecol 166, 131–43.

Restrepo C, Walker LR, Shiels AB, Bussmann R, Claessens L, Fisch S, Lozano P, Negi G, Paolini L, Poveda G, Ramos-Scharron C, Richter M, Velazquez E, 2009. Landsliding and its multiscale influence on mountainscapes. Bioscience 59, 685–98.

Rüger N, Williams-Linera G, Kissling W, Huth A, 2008. Long-term impacts of fuelwood extraction on a tropical montane cloud forest. Ecosystems 11, 868–81.

Russell AE, Raich JW, Vitousek PM, 1998. The ecology of the climbing fern Dicranopteris linearis on windward Mauna Loa, Hawaii. J Ecol 86, 765–79.

Shiels AB, West CA, Weiss L, Klawinski PD, Walker LR, 2008. Soil factors predict initial plant colonization on Puerto Rican landslides. Plant Ecol 195, 165–78.

Shugart HH, 1998. Terrestrial Ecosystems in Changing Environments. Cambridge University Press, Cambridge, U.K.

Singh KP, Mandal TN, Tripathi SK, 2001. Patterns of restoration of soil physicochemical properties and microbial biomass in different landslide sites in the sal forest ecosystem of Nepal Himalaya. Ecol Eng 17, 385–401.

Stern MJ, 1995. Vegetation recovery on earthquake-triggered landslide sites in the Ecuadorian Andes. In: Churchill SP, Balslev H, Forero E, Luteyn JL, editors. Biodiversity and conservation of neotropical montane forests. New York, p. 207–20.

Stoyan R, 2000. Aktivität, Ursachen und Klassifikation der Rutschungen in San Francisco/Südecuador. Master's thesis. Institut für Geographie der Friedrich-Alexander-Universität Erlangen-Nürnberg.

Velazquez E, Gomez-Sal A, 2008. Landslide early succession in a neotropical dry forest. Plant Ecol 199, 295–308.

Vorpahl P, Dislich C, Elsenbeer H, Märker M, Schröder B, submitted. Modeling vegetation landslides - an extension to the infinite slope

model to accommodate thick organic layers.

Walker L, del Moral R, 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, UK.

Walker LR, 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. J Veg Sci 5, 525–32.

Walker LR, Shiels AB, 2008. Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides. Plant Soil 313, 205–16.

Walker LR, Velazquez E, Shiels AB, 2009. Applying lessons from ecological succession to the restoration of landslides. Plant Soil 324, 157–68.

Walker LR, Zarin DJ, Fetcher N, Myster RW, Johnson AH, 1996. Ecosystem development and plant succession on landslides in the Caribbean. Biotropica 28, 566–76.

Wilcke W, Valladarez H, Stoyan R, Yasin S, Valarezo C, Zech W, 2003. Soil properties on a chronosequence of landslides in montane rain forest, Ecuador. Catena 53, 79–95.

Wullaert H, Homeier J, Valarezo C, Wilcke W, 2010. Response of the N and P cycles of an old-growth montane forest in Ecuador to experimental low-level N and P amendments. For Ecol Manage 260, 1434–45.

Yamamoto S, Nishimura N, Matsui K, 1995. Natural disturbance and tree species coexistence in an old-growth beech - Dwarf bamboo forest, southwestern Japan. J Veg Sci 6, 875–86.

Yamamoto SI, 1992. The gap theory in forest dynamics. Botanical Magazine-Tokyo 105, 375–83.

Zarin DJ, Johnson AH, 1995. Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. Soil Sci Soc Am J 59, 1444–52.

The following second author publication is produced in connection with this PhD:

Paper IV

Peter Vorpahl, Claudia Dislich, Helmut Elsenbeer, Michael Märker and Boris Schröder

Shallow translational landslides in tropical montane forests - a hint towards biotic control?

Earth Surface Processes and Landforms
in preparation for resubmission after major revision

Peter Vorpahl and I developed the idea for this paper together. I undertook preliminary analyses of a classical factor of safety model and additionally supported the editing of the manuscript.

Shallow translational landslides in tropical montane forests - a hint towards biotic control?

Peter Vorpahl[*]   Claudia Dislich[†]   Helmut Elsenbeer[*]   Michael Märker[‡]
Boris Schröder[*§]

March 17, 2011

Abstract

We investigated landslides in a South Equadorean montane forest to gain insights in possible biotic and abiotic factors that trigger these slides and found evidence for the occurrence of very shallow translational landslides that do not involve apparent quantities of mineral soil. This supports presumptions of a strong coupling and interaction of biotic and abiotic processes in tropical montane environments and implies the necessity to regard vegetation dynamics in shallow slope stability models for these areas to a stronger extent.

In tropical montane environments, roots of plants tend to grow in a massive organic layer atop the mineral soil rather than penetrating it. Thus their contribution to slope stability differs from other regions. Considering these differences, we introduced an independent organic layer atop the mineral soil into a standard model for shallow slope stability.

We applied the model to our own measurements on and close to eleven landslides in the Andes of Southern Ecuador, among which three were very shallow. Being able to reproduce our findings, the model implies that in case of very shallow landslides, the rapid mass movement event is likely to have been caused by the vegetation itself.

Introduction

Apart from their hazardousness for human live and infrastructure, landslides can provide a beneficial ecological effect: In tropical montane rain forests, landslides represent one of the most important ecosystem disturbances (Lozano et al., 2005; Köhler and Huth, 2007; Bussmann et al., 2008). Their size and frequency contribute to the high levels of vascular plant diversity in these areas, since landslide scars provide habitats for pioneer species (Connell, 1978; Sheil and Burslem, 2003). From an ecological point of view, knowledge on the driving mechanisms of landslides is a prerequisite for understanding and predicting potential future changes in the general conditions for biodiversity in tropical montane ecosystems, which can aid in the planning of conservation measures.

To counteract the threat landslides represent for human activity and to provide tools for planning of sustainable infrastructure measures, the prediction of the spatial occurrence probability of landslides has turned into a major research effort (e.g Montgomery and Dietrich, 1994; Wu and Sidle, 1995; Guzzetti et al., 1999; Guzzetti, 2004; Guitierres et al., 2010). The conceptual abstraction underlying most process-based models of shallow translational landslides is that of an infinite slope segment covered with vegetation (Wu et al., 1979; Buchanan and Savigny, 1990; Sidle and Wu, 1999; Xie et al., 2004). Mohr-Coulomb's failure criterion prescribes that the factor of safety (FoS) for a slope segment is given by the ratio of stabilizing and destabilizing forces, where $FoS < 1$ indicates instability conditions.

$$FoS = \frac{\text{Stabilizing forces}}{\text{Destabilizing forces}} \tag{1}$$

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Most implementations of this concept include vegetation by an increase of soil cohesion due to root networks that grow perpendicular through a potential sliding plane, while the destabilizing effects of aboveground biomass or the effect of wind forces as transferred by trees into the ground via a turning moment mostly are assumed to be negligible. As a consequence, the stabilizing effect of roots of different plant species has been subject to field experiments (Wu et al., 1988a; Abernethy and Rutherfurd, 2001; van Beek et al., 2005) and laboratory tests (Wu et al., 1988b; De Baets et al., 2008) and lead to slope stability models that, for example, allow to investigate the influence of different forms of land use on landslide distribution and frequency (Schmidt et al., 2001; Siddle and Dahkal, 2003). Other investigations additionally regarded the influence of vegetation on slope hydrology (Casadei et al., 2003; Keim and Skaugset, 2003).

However, all modeling approaches implicitly assume that roots grow into the mineral soil and hence enhance its mechanical properties. Prandini et al. (1977) pointed out that this implicit assumption does not apply universally, and it certainly does not in those tropical montane environments where tree roots grow preferentially within a massive organic layer above the mineral soil. Thus, in these regions, roots do not necessarily act as slope stabilizers by increasing the soils shear resistance or cohesion. Instead, they may be considered part of a separate layer with its own mechanical properties.

Endeavoring to contribute to the understanding of this different situation in tropical montane environments, our study is located in a tropical montane rain forest in the Andes of Southern Ecuador (Fig. 1), where we found very shallow translational landslides that did not involve apparent quantities of mineral soil. Shallow translational slides, mainly or exclusively consisting of organic material imply a strong biotic control as has been proposed by Richter et al. (2009) and hint towards an additional self organization mechanism in tropical montane ecosystems. Thus, based on a slightly modified standard model for shallow slope stability, our work focuses on the explanation of the very shallow translational landslides we observed.

Standard models for shallow slope stability do not allow for landslides that do not involve mineral soil, nor do they accommodate a thick organic layer. Thus, as a first step, we extend a standard model for shallow slope stability by the addition of an organic layer atop the mineral soil and introduce the mass of this layer as a destabilizing component. Using the model to reproduce the critical minimum soil depth, as necessary for failure, we explore the conditions that lead to single slope failures in the study area.

Hypothesizing that a) the situation close to a landslide reflects the situation on the landslide before the event and b) our model will reproduce the observed depth of failure if parametrized with measurements from the landslide, we apply the model to our measurements, conducted on and close to eleven landslides in the study area (Fig. 1). Based upon our measurements, we further apply a sensitivity analysis to the model to explain the nature of the very shallow translational slides we observed.

Study area

The data we use here were collected in the *Reserva Biósfera de San Francisco* (RBSF), part of the biosphere reserve *Podocarpus - El Condor*, in the Andes of Southern Ecuador (3^o58'S, 79^o04'W, Fig. 1). The study area consists of several low-order catchments south of Rio San Francisco and comprises 8.4 km^2, ranging in altitude from 1,870 to 3,165 m a.s.l. Steep slopes (up to 70°) are covered by an evergreen lower ($< 2,150$ m a.s.l.) and upper broad-leaved montane rain forest up to the tree line between 2,700 m and 3,000 m a.s.l. At higher elevations, a sub páramo shrubland emerges (Beck et al., 2008).

In this mountainous ecosystem, shallow translational landslides are a frequent, natural phenomenon (Lozano et al., 2005; Bussmann et al., 2008; Dislich et al., 2009; Restrepo et al., 2009; Richter et al., 2009) and visible landslide scars permanently cover approximately one to three percent of the study area, as deduced from aerial photographs (taken in 1962, 1969, 1976, 1989 and 1998, respectively). Most landslides within the study area can be classified as rockslides, earthflows and shallow translational landslides. Rockslides and earth flows occur close to anthropogenic inference (such as roads), while within the undisturbed parts of the area all rapid mass movements have been classified as shallow translational landslides (Bussmann et al., 2008).

In addition to this, massive organic layers above the mineral soil exist, that mainly consist of dead organic matter woven with plant roots, while containing only very small amounts of mineral soil. We found these layers, whose mass may reach to up to 700 t ha^{-1} (Wilcke et al., 2002), preferentially on steep slopes in the intermediate altitudinal ranges within the study area (2,100 to 2,700 m a.s.l.).
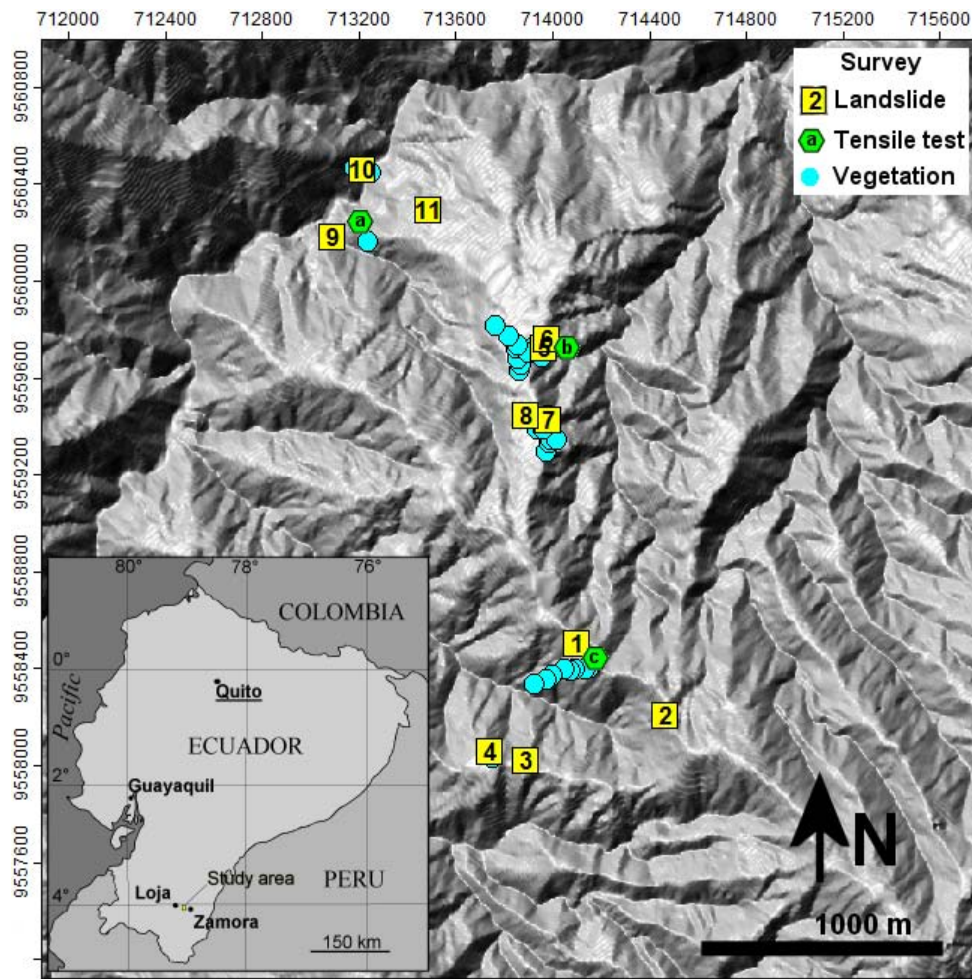
Figure 1: Location of the study area in Southern Ecuador east of Loja. Eleven investigated landslides are marked by yellow rectangles, surveys of vegetation related parameters by light blue circles and locations of organic layer tensile resistance measurements by green hexagons. Annotated UTM-WGS84 coordinates.

Field investigations

During three field campaigns from September 2008 to November 2010, we investigated a total of eleven landslides in the study area (numbered yellow rectangles in Fig. 1) at three distinct altitudinal ranges (below 2,150 m a.s.l, 2,150 to 2,350 m a.s.l. and above 2,350 m a.s.l., respectively). Soil physical parameters, such as in situ and dry density (ρ_s), water content (Θ), soil cohesion (C_s) and internal angle of friction (φ) were assessed in soil profiles, that were created at the top edge of ten landslides. We assessed vegetation related parameters, such as aboveground biomass (M_B), organic layer thickness (h_o, light green circles in Fig. 1) and measured the organic layer's resistance (C_o, green hexagons in Fig. 1). Geographic coordinates as well as altitude above sea level were recorded in UTM WGS84 format by the aid of a hand-held GPS device of type Garmin etrex vista HCx with an integrated barometric altimeter.

Landslide surveys

We based a rough estimate of landslide age on the successional state of the vegetation on the landslide scar and used the terms 'fresh' for landslides without vegetation and 'old' for others since an exact determination of landslide age was not possible.

With the aid of a total station, as well as by manual measurements with compass, clinometer and tape measure,

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relative 3D-coordinates of approximately hundred points on each landslide were recorded. These points served as data source for a three-dimensional reconstruction of the landslides' failure planes, from which topographic information, such as landslide lengths (L) and median widths (W), were derived by projection onto a horizontal plane. Average slope angles (α) were calculated by a linear regression through a projection of all points onto a vertical plane.

Dry and in situ soil bulk densities (ρ_s) and soil water content (Θ) were calculated from undisturbed soil samples from different depths of soil profiles, which we created at the top edge of ten of the eleven landslides. Where possible, we took three samples per soil layer, which were weighted, dried (24h at 80°C), and weighted again. Landslide depths (h_s) were estimated by visually fixing the intersection of the landslide surface with the vertical soil profile.

Soil cohesion was measured in situ by a Geonor H-60 hand-held vane tester three times per identifiable soil layer within each profile. Dry soil bulk densities (ρ_s), water content (Θ) and cohesion measurements (C_s) were used to create depth profiles of these parameters for each landslide. The method of measuring soil shear resistance with a small torsion probe (like the Geonor H-60) tends to overestimate soil cohesion if the soil contains skeleton, which was the case in our soil profiles, where soil textures ranged from clays over silty sands to fine sand, while grain size of the soil skeleton ranged from millimeters to decimeters in diameter.

To compensate the effect of relatively small stones in the soil, we applied a method to simultaneously measure soil cohesion and the internal angle of friction. This approach follows a common method for in-situ measurement of soil shear resistance as applied by several other researches (cf. Wu et al., 1988a; Comino and Duretta, 2009), but uses a much smaller device.

A steel cylinder ($d = 72$ mm) was used to horizontally shear out soil of a reproducible cross section, while measuring the maximum force applied by a spring balance with a drag indicator (Fig. 2). Different vertical loads were superimposed to the soil in the cylinder by a forcer, whose diameter was slightly smaller than the inner diameter of the cylinder. The forcer was attached to the bottom of a bucket, allowing to vary the superimposed load. This procedure was repeated at least twice per superimposed load and with at least two different loads.
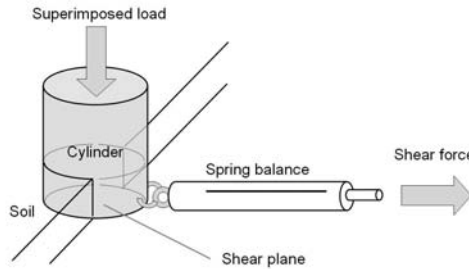

Figure 2: Device for measuring soil shear resistance under different loads.

After Mohr-Coulomb, the soil's shear resistance results from a normal load applied to the soil and its cohesion:

$$\tau = \sigma \tan \varphi + C_s \tag{2}$$

Where τ is the shear resistance [N m^{-2}]; σ the normal load [N m^{-2}]; φ the internal angle of friction and C_s the soil cohesion [N m^{-2}].

Thus, a linear regression through all measurements is used to determine the soil's internal angle of friction (φ) and its cohesion (C_s):

$$\frac{F_{shear}}{r^2\pi} = \frac{F_{load}}{r^2\pi} \tan \varphi + C_s \tag{3}$$

Where F_{shear} is the applied maximum force to shear out the probing cylinder [N]; r the radius of the probing cylinder [m] and F_{load} the additional weight force applied to the soil in the probing cylinder [N].

Our method still is sensitive to coarse stones in the sample. Thus we were able to use it on seven of the eleven landslides (i.e. #1, #2, #5, #6, #7, #9 and #11 in Fig. 1). On four landslides (i.e. #2, #5, #6, #7 in Fig. 1), we applied the method in the soil profile close to the estimated depth of failure. On two landslides (#1 and #9

in Fig. 1), we were able to apply the method in several depths of the soil profile and on the oldest landslide (i.e. #11 in Fig. 1), we conducted measurements on the surface itself.

As has been mentioned by Anderson and Howes (1985), field measurements of soil cohesion and internal friction angle do perhaps not accurately reflect the strength of the residual soils examined since they depend on matrix suction. Thus on landslide #11, we additionally assessed changes of soil cohesion and the internal friction angle as result from saturation with water.

Vegetation related parameters

In the absence of knowledge about the real situation preceding a sliding event, we investigated vegetation-related parameters close to landslides, assuming that the situation there is quite similar to that on the slide before the event. Standard approaches to assess aboveground biomass, require surveys in homogeneous forest stands of at least 1 ha (100 m x 100 m) in extent (Brown et al., 1989; Brown, 1997; Leuschner et al., 2007). Shallow translational landslides, however are initiated at a smaller scale (10 to 30 m). Thus we were interested in possible local biomass aggregations at this scale and assessed vegetation biomass and vertical thickness of the organic layer in circular areas, with a diameter of 10 m around several single points close to landslides (point investigations, light green circles in Fig. 1). Since our measurements were conducted on steep slopes, we additionally measured the upslope and downslope slope angle (α) by a clinometer.

A special sampling design was not applied and as a consequence of the relatively small survey area (78.5 m^2 per site), we expected our results to highly vary between the single point investigations. Thus, we aggregated all measurements from point investigations in one altitudinal level and used the resulting mean values in further calculations.

To calculate aboveground tree biomass, we estimated the average tree height from measurements with tape measure and clinometer and calculated stem diameters at breast height (1.3 m, DBH) of all trees within the area (radius = 5 m) from stem perimeters, measured by a tape measure.

Following Leuschner et al. (2007), we applied two different allometric equations for the estimation of average tree biomass, which, after Brown and Iverson (1992) and Brown (1997), are suitable for american tropical wet forests:

$$M_t^a = e^{-3.375 + 0.948 \ln(\overline{DBH}^2 \, \overline{h})} \tag{4}$$

$$M_t^b = 21.297 - 6.953\overline{DBH} + 0.740\overline{DBH}^2 \tag{5}$$

Where M_t is the biomass per tree [kg], $\overline{DBH}$ is the average stem diameter [cm] at breast height (130 cm) and $\overline{h}$ is the average tree height [m] in the circle (radius = 5 m).

We additionally calculated a basic estimate by assuming all trees to be cylinders of mean DBH and mean height with a constant wood density of $\rho_{\text{wood}} = 600$ kg m^{-3}, which, after Brown (1997), is an appropriate average value for tropical montane forests. In this manner we arrived at an estimate on average tree mass:

$$M_t^c = \rho_{\text{wood}} \, \overline{h} \left(\frac{\overline{DBH}}{200} \right)^2 \pi \tag{6}$$

Where ρ_{wood} is the bulk density of wood [kg m^{-3}].

The aboveground biomass density was then calculated by multiplication of the average tree mass by the number of trees in the circle, divided by the investigated area, projected onto a horizontal plane.

$$M_B = \frac{M_t \, n}{\pi r^2 \cos \alpha} \tag{7}$$

Where M_B is the biomass density [kg m^{-2}], n the number of trees in the circle [1], α is the slope angle [^{o}] and r the radius of the investigated area [m].

Organic layer properties

Within each point investigation, we conducted up to 20 measurements of vertical organic layer thickness by vertically probing the layer with a pole at different, random locations within the circle (radius = 5 m). By using

our slope angle measurements, we then calculated organic layer thickness perpendicular to the slope (h_o).

In order to estimate organic layer bulk densities, 64 samples were taken at 5 different locations in the study area (close to landslides #4 and #5 in Fig. 1 at an altitude of $\approx 2,300$ m a.s.l.) by excavating rectangular blocks (30 cm x 30 cm) through the complete organic layer down to the mineral soil and measuring their volume. The excavated organic layer material was weighted in situ. Fifteen samples (three per location) were saturated with water and weighted again in order to estimate the maximum organic layer bulk density under rainfall conditions.

We assessed organic layer tensile resistance in situ close to landslides (green hexagons in Fig. 1) by repeated application ($n = 903$) of rupture tests. Following De Baets et al. (2008), a large number of fine roots contribute more to the total tensile resistance than a small number of big roots. Thus we measured the tensile resistance of the fine root matrix in the organic layer, not considering plant roots with diameters significantly greater than 5 mm.

Organic layer rupture tests were conducted in vertical profiles through the organic layer, starting at the top of the profile and were subsequently executed down to the mineral soil (see. Fig. 3).
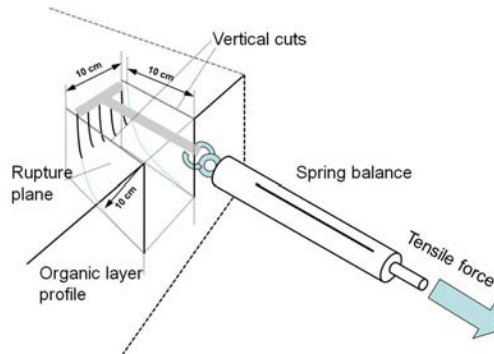

Figure 3: Organic layer tensile test.

Each rupture test started with the preparation of a block of organic layer material of reproducible size (10 cm X 10 cm) by sawing two vertical, parallel cuts. A small rake served as gripper and was hooked into the material from above in a way that it covered a depth of 10 cm. While horizontally pulling out the specimen, we measured necessary forces with a spring balance equipped with a drag indicator. We assumed the rupture plane to roughly follow a circular path with a radius of 10 cm (Fig. 3) and calculated its area to 157.1 cm^2.

While conducting tests at different depths within the organic layer, we distinguished between measurements in the layer and at the boundary to the mineral soil. Expecting high variations in tensile resistance, we conducted up to 100 repetitions per profile.

Model

Following Gabet and Dunne (2002) and Casadei et al. (2003), we idealize a slope failure by a shallow, rectangular block on an inclined plane (Fig. 4). The destabilizing force results of the downhill component of the block's weight force, while the block is stabilized by shear resistance at it's basal plane and at the sides and by tensile resistance at the upper perimeter. A shallow slope stability model that includes lateral forces, implicitly violates the infinite slope assumption since it is sensitive to the failure dimensions. Thus we respect these dimensions in our model, namely by the length (L) and width (W) of the failure.

During our field surveys, we found massive organic layers not containing obvious quantities of mineral soil. Usually the transition to the underlying mineral soil was very sharp and the number of roots, we found in the uppermost layer of the mineral soil was negligible. Thus, our mechanical setup consists of two, non-overlapping layers (Fig. 4), which are assumed to be homogeneous. An overlapping of these layers, indicating a rooting depth, however, would not change the mathematical description. The difference to other approaches is that we explicitly allow the thickness of the organic layer to exceed that of the mineral soil. By mechanically decoupling the two layers we are able to describe even very shallow translational slides that involve no mineral soil.
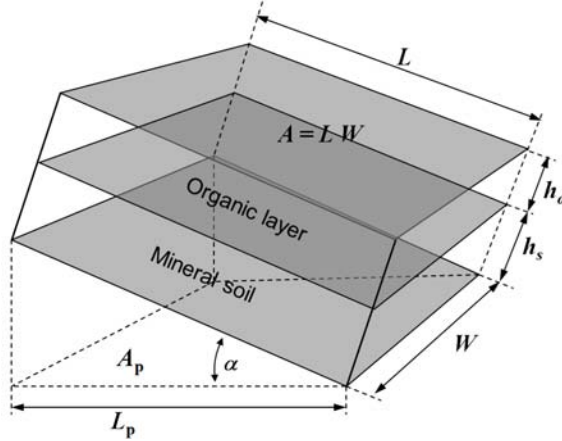
Figure 4: Mechanical setup. Slope-parallel length (L) and width (W) of the sliding block; h_s: Height of mineral soil; h_o: Thickness of organic layer.

The factor of safety for our setup, again, is the ratio of stabilizing and destabilizing forces.

$$FoS = \frac{F_b + F_l}{F_G \sin \alpha} \tag{8}$$

Where FoS is the factor of safety [1]; F_b the basal resistance force [N]; F_l the lateral resistance force [N]; F_G the block's total weight force [N] and α the slope angle [^{o}].

We introduce the weight of the organic layer atop the mineral soil as additional, destabilizing component. Thus, the system's total weight force comprises aboveground biomass, the mass of the organic layer and the mass of soil down to the depth of failure:

$$F_G = (M_B + h_o \rho_o + h_s \rho_s) \, g \, L \, W \tag{9}$$

where g is the earth's acceleration [m s^{-2}]; M_B the aboveground biomass density [kg m^{-2}]; h_s the thickness of the mineral soil [m]; h_o the thickness of the organic layer [m]; ρ_o the bulk density of the organic layer [kg m^{-3}] and ρ_s the bulk density of soil [kg m^{-3}].

We substitute the weight force per area (($M_B + h_o \rho_o + h_s \rho_s)g$) by a pressure load ($G$).

$$F_G = G \, L \, W \tag{10}$$

As prescribed by Mohr-Coulomb's failure criterion, the resistance force in the basal area of the block results from internal friction, soil cohesion and the cohesion provided by roots, penetrating the basal plane. We did not find many torn roots on the slip surface of the landslides, we surveyed. Thus we assume the additional root cohesion at the slip surface to be a fraction of the maximum cohesion, as present in the organic layer. In most cases, this fraction can be assumed to be zero.

$$F_b = F_N \tan \varphi + L \, W (C_s + x C_o) \tag{11}$$

where F_N is the effective normal component of the block's weight force [N]; φ is the internal friction angle of the soil [^{o}]; C_s soil cohesion [N m^{-2}]; C_o is the maximum root cohesion in the organic layer [N m^{-2}]; x is the fraction of roots contributing to basal cohesion [1] and α is the slope angle [^{o}].

The saturated fraction of the vertical soil column causes a pore water pressure (U) at the basal plane, which reduces the effective normal force.

$$U = \rho_w \frac{m \, h_s}{\cos \alpha} g \tag{12}$$

where U is the pore water pressure at the failure plane [N m^{-2}]; m is the saturated fraction of the soil column [1] and ρ_w is the bulk density of water [kg m^{-3}].

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Thus the effective normal force results to:

$$F_N = \left(M_B + \rho_o\, h_o + \left(\rho_s - \frac{m\,\rho_w}{\cos\alpha} \right) h_s \right) g\, L W\, \cos\alpha \qquad (13)$$

$$F_N = (G - U) L W \cos\alpha \qquad (14)$$

The laterally stabilizing force results from soil cohesion and from the organic layer's cohesion. It is effective at both sides and at the upper perimeter of the block.

$$F_l = (2L + W)(h_s C_s + h_o C_o) \qquad (15)$$

where C_o is the organic layer's cohesion [N m^{-2}].

Substituting into equation 8 leads to the final factor of safety:

$$FoS = \frac{[M_B + \rho_o h_o + (\rho_s - \frac{m\rho_w}{\cos\alpha})h_s]g\cos\alpha\tan\varphi + C_s + x\,C_o + \frac{2L+W}{LW}(h_s C_s + h_o C_o)}{(M_B + h_o\rho_o + h_s\rho_s)g\sin\alpha} \qquad (16)$$

For our analysis, we are especially interested in the critical minimum soil depth, as is necessary for failure. Thus we set the factor of safety (Eq. 16) to one and solve the equation for h_s.

$$h_s^{\mathrm{crit.}} = \frac{(M_B + h_o\rho_o)g\,(\cos\alpha\tan\varphi - \sin\alpha) + C_s + x\,C_o + h_o C_o \frac{2L+W}{LW}}{[m\rho_w\tan\varphi + \rho_s(\sin\alpha - \cos\alpha\tan\varphi)]\,g - C_s\frac{2L+W}{LW}} \qquad (17)$$

Model parametrization and sensitivity analysis

As a first step, we assume a most instable situation as given by complete saturation of the soil column ($m = 1$) and calculate minimum factors of safety (FoS, Eq. 16) and the minimum critical soil thickness (h_s^{crit}, Eq. 17) for all landslides, where we have a complete set of parameters and compare the results to the observed landslide depths.

Then, regarding the spatial variability at the scale of meters in parameters related to soil strength, we estimate value ranges of soil cohesion (C_s), soil density (ρ_s) and internal friction angle (φ) based upon our measurements and use these value ranges to calculate ranges for FoS and $h_s^{\mathrm{crit.}}$ for all landslides we surveyed. Again, we compare the results to our observations.

Finally, using plausible mean values of model parameters, we apply a sensitivity analysis to the model and explore the requirements for very shallow translational landslides by varying h_s, while all other parameters are held constant.

Results and discussion

We evaluated relative 3D coordinates, measured on landslide surfaces and derived landslide dimensions and average slope angles. Planar landslide lengths (L_p) varied between 7 and 62 m and median widths (W) ranged from 8 to 23 m, while we found average slope angles (α) from 31° to 55° (Tab. 2). We visually estimated the depth of each of the eleven landslides and found h_s to range from below 10 cm up to 1.3 m (Tab. 2); two of the landslides (#4 and #5) were extremely shallow and one landslide (#8) exposed a depth of failure of about 20 cm.

We assessed dry soil density and in situ soil water content in undisturbed samples, taken from different horizons of ten soil profiles, which we created atop of landslides #1 to #10 and measured in situ soil shear resistance with a torsion probe (Tabs. 3 and 4). Soil cohesion (C_s), as obtained from these measurements ranged from 8.1 to 70 kPa (30.9±16.1 kPa, mean ± standard error of mean, n =119). We calculated dry soil densities (ρ_s) of $1,342$±220 kg m^{-3} (mean ± standard error of mean, n =33). According to Jahn et al. (2006), we conducted field assessments of soil texture and soil skeleton in all soil horizons (Tabs. 3 and 4).

As we suspected, measurements with a small torsion probe overestimated the soil cohesion. We calculated much smaller values by our method to simultaneously determine soil cohesion and internal friction angle, which we applied on seven landslides (Tab 5). Here we found soil cohesion (C_s) to range from 4.5 kPa up to 20.8 kPa

(10.7 ± 5.0 kPa, mean $\pm$ standard error of mean, n =17) and internal friction angles (φ) ranging from 25° up to 51° ($37^o \pm 8^o$, mean $\pm$ standard error of mean, n =17).

Both methods are sensitive to small scale soil inhomogeneities, while this effect is smaller in our method due to the comparably bigger shear plane. We think that our method still overestimates soil cohesion if coarse stone fragments are present in the shear plane. Thus we recommend it for soils without or at least with only small stones ($d < 5$ mm) in the soil skeleton. The results for φ, however should not be affected by this systematic overestimation of shear resistance. Due to the low weight and small size of the device, the method proved especially useful for the application in rough, mountainous terrain.

On landslide #11, we assessed changes in soil shear resistance and internal friction angle on the failure surface due to saturation by conducting two series of measurements. We found no obvious change of C_s, but a reduction of φ by 39% (from 40.2 ^{o} to 24.7 ^{o}). Even though, the two measurements have been conducted in the same soil layer close to each other, it is possible that small scale soil inhomogeneities have caused this decrease of φ. Thus further repetitions of the experiment are required to quantify the effect.

We conducted 39 point investigations of vegetation related parameters (Tab. 7) and calculated aboveground tree biomass estimates of 49 to 92 t ha^{-1} in the lower altitudinal range ($< 2,050$ m a.s.l.), of 35 to 66 t ha^{-1} in the intermediate altitudinal range (2,050 to 2,350 m a.s.l.) and of 13 to 24 t ha^{-1} in the upper altitudinal range ($> 2,350$ m a.s.l.).

As we expected, we found strong variations in tree densities and vegetation composition even by point investigations conducted in one and the same altitudinal range. Nonetheless have we been able to reproduce the decrease of aboveground biomass with altitude a.s.l., as has been reported by other studies. Leuschner et al. (2007), for example, estimated aboveground tree biomass to 132 up to 199 t ha^{-1} at an altitude of 1890 m a.s.l. and to 74 up to 127 t ha^{-1} at 2,380 m a.s.l. by using the same allometric equations. Moser et al. (2008) used a different allometric equation for the estimation of an above ground tree biomass of 173 t ha^{-1} at 1,890 m a.s.l. and of 100 t ha^{-1} at 2,380 m a.s.l. Our estimates of aboveground tree biomass, lie below values of both studies, which is not surprising, since we conducted our measurements close to landslides, mainly on steep open slopes and not in small valleys or gorges, where due to sediment and nutrient accumulation a higher aboveground biomass can develop (Oesker et al., 2008).

Organic layer thickness varied strongly between the single sites and amounted to 35 ± 21 cm (mean $\pm$ standard error of mean; $n = 306$). In situ organic layer density, as calculated from 64 samples and a total sample volume of 2.81 m^3 resulted to 208.1 ± 89.0 kg m^{-3} (mean$\pm$standard error of mean). Density of saturated organic layer, as derived from 15 samples and a total sample volume of 0.59 m^3 resulted to 278 ± 86.7 kg m^{-3} (mean$\pm$standard error of mean). Using these values, we calculate the average mass of the organic layer to 728 ± 187 t ha^{-1} (up to 973 ± 182 t ha^{-1} under wet conditions), which compares pretty well to Wilcke et al. (2002), who estimated the mass of the organic layer in the study area to up to 713 t ha^{-1}.

We conducted a total of 903 in situ organic layer rupture tests in nine organic layer profiles at three altitudinal levels of the study area (Tab. 6) and found organic layer tensile resistance to vary from 1.84 kPa to 2.69 kPa (2.17 ± 1.16 kPa, mean $\pm$ standard error of mean). Tests conducted in the layer yielded 2.26 ± 1.2 kPa and tests conducted at the boundary to the mineral soil yielded 2.07 ± 1.09 kPa, which is a significant reduction by 8.5% (Welch two sample t-test, p-value=0.012, significance level: 95%). A comparison of tensile tests conducted in the distinct altitudinal ranges, however, did not reveal a significant difference.

Model application

The number of torn roots on the failure surfaces of the investigated landslides in our study area was negligible. Thus, we assume that there is no root contribution to basal resistance ($xC_o = 0$). A first calculation of the factor of safety (Eq. 16) and of the critical soil depth ($h_s^{\text{crit.}}$, Eq. 17) from the complete set of parameters, we have for five of the eleven landslides (i.e. #1, #2, #6, #7 and #9, Tab. 1), revealed a potential slope instability on landslides #1 and #9. Here, the calculated minimum soil depths lie within centimeters in the range of our observations. In the other three cases, the factors of safety were greater than 2 and the minimum critical soil depths, as necessary for instability exceeded the observed landslide depths by up to 2.8 m.

At first sight, two out of five is a bad result. But if our measurement results were purely random, the almost perfect prediction of failure depths of landslides #1 and #9 cannot be explained. Thus, we can assume that our method was appropriate but applied at the wrong spot or at the wrong time in three out of five cases and we owe

Table 1: Model application to five landslides, model parameters, critical minimum soil depths ($h_s^{\text{crit.}}$) and factors of safety (FoS).

#	L [m]	W [m]	M_B [kg m^{-2}]	α [^{o}]	φ [^{o}]	ρ_s [kg m^{-3}]	C_s [kPa]	$h_s^{\text{obs.}}$ [m]	h_s^{crit} [m]	FoS [1]
1	30.8	7.8	1.9	53.1	25.8	1,265	4.7	**0.42**	**0.45**	**1.06**
2	35.4	7.0	1.9	49.1	50.9	1,504	10.2	0.39	1.29	2.43
6	31.3	10.6	5.2	37.1	41.4	1,200	14.3	0.60	3.37	3.45
7	43.2	10.1	5.2	37.0	46.4	1,120	12.9	0.40	2.74	4.46
9	34.9	22.6	7.0	33.0	27.0	1,326	7.7	**1.33**	**1.36**	**1.02**

$C_o = 2.17$ kPa; $h_0 = 0.35$ m

the comparably high soil cohesions and internal friction angles, we measured on landslides #2, #6 and #7 either to the high spatial heterogeneity of these parameters or to their dependency on soil water content (Anderson and Howes, 1985).

Sidle and Swanston (1981) stated that conservative values of apparent soil cohesion should be used for factor of safety calculations, if the measured accuracy is questionable. Facing a similar situation, namely by a high variability of our parameters related to soil strength, we estimated appropriate value ranges to calculate FoS and $h_s^{\text{crit.}}$ for all eleven landslides. Our measurements of C_s varied from 4 up to 20 kPa, while we suspect a slight overestimation of C_s by the method we applied. Values of φ ranged from 25° up to 51° and values of ρ_s ranged from 800 up to 1800 kg m^{-3}. Thus, we estimated a value range for soil cohesion of $C_s = 5 \pm 3$ kPa and for the internal friction angle of $\varphi = 30 \pm 4^o$ which lie within our measurement ranges and comply with values used by Collison and Anderson (1996). Similar, we assumed a value range for soil density of $\rho_s = 1,400 \pm 100$ kg, as derived from mean values and standard errors of mean of our measurements.

As a result, calculated value ranges for the critical soil thickness cover the observed depth of failure in all but three cases (#4, #5 and #8 in Fig. 5, right), which were the shallowest landslides in our study. Here factors of safety also did not reach a critical value below one.
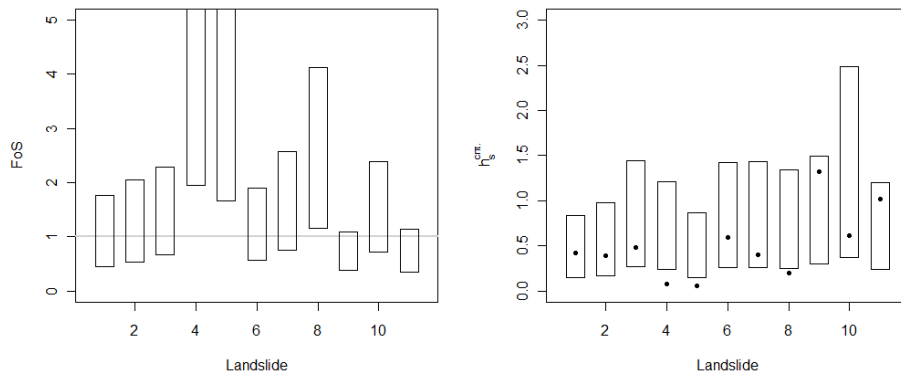

Figure 5: Factors of safety (FoS, left) and critical minimum soil thickness ($h_s^{\text{crit.}}$, right). The horizontal grey line marks the critical FoS of one and the black dots represent observed landslide depths (h_s).

Sensitivity analysis

To explore the prerequisites for a factor of safety below one even for the three very shallow landslides in our study, we first express the factor of safety (Eq. 16) as a sum of four components:

$$FoS = \underbrace{\frac{\tan\varphi}{\tan\alpha}}_{\substack{\text{Internal friction} \\ FoS_A}} - \underbrace{\frac{U\,\tan\varphi}{G\,\tan\alpha}}_{\substack{\text{Pore water} \\ FoS_B}} + \underbrace{\frac{C_s + x\,C_o}{G\sin\alpha}}_{\substack{\text{Basal resistance} \\ FoS_C}} + \underbrace{\frac{2L+W}{LW}\frac{h_s C_s + h_o C_o}{G\sin\alpha}}_{\substack{\text{Lateral resistance} \\ FoS_D}} \tag{18}$$

The critical minimum soil depth is highly sensitive to the slope angle (α). Given mean values of our measurements it ranges from 56 cm ($\alpha = 45^o$, vertical thick line in Fig. 6) to 86 cm ($\alpha = 35^o$, vertical thin line in Fig. 6). Varying the soil depth (h_s, Fig. 6), it becomes obvious that the factor of safety is mainly determined by basal resistance (FoS_C), which gains importance with smaller soil depths. The lateral resistance (FoS_D) also gains
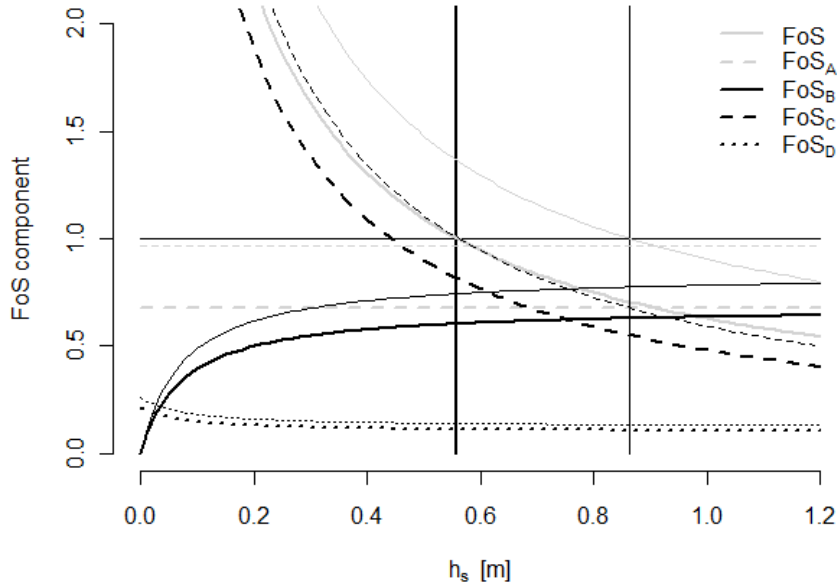

Figure 6: Factor of safety components as a function of available soil depth (h_s) for two different slope angles (thin lines: $\alpha = 35^o$, thick lines: $\alpha = 45^o$), while all other parameters are held constant ($L = 37$ m, $W = 12$ m, $\varphi = 34^o$, $M_B = 4.5$ kg m^{-2}, $h_o = 0.35$ m, $C_s = 5$ kPa, $x = 0$, $C_o = 2.2$ kPa, $\rho_o = 279$ kg m^{-3} and $\rho_s = 1,400$ kg m^{-3}). The vertical lines indicate critical minimum soil depths ($h_s^{\text{crit.}}$).

importance with smaller soil depths but it's absolute contribution remains at a low level depending on the ratio of perimeter and basal plane.

The relative contribution of uplift by pore water pressure to slope instability (FoS_A) is higher at lower slope angles. FoS_A looses importance for the factor of safety with smaller soil depths unless we allow for a perched water table above the mineral soil at the bottom of the organic layer (for example by by setting $m > 1$). However, this is a hypothetic scenario, since we rather observed surface runoff through tubular preferential flowpaths at the base of the organic layer than perched water tables during heavy rain events.

Thus, to allow for very shallow translational landslides, the basal resistance term (FoS_C) has to be minimized. Schmidt et al. (2001), who conducted their study on colluvial soils, assumed no root contribution at the basal plane ($xC_o = 0$) and set C_s to zero. They justified their assumptions by the colluvial nature of their soils, which consisted of cohesionless loose material. φ then represents the angle of repose. If we apply these assumptions to

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our example, we calculate a critical minimum soil depth ($h_s^{\text{crit.}}$) below 1 cm, given the above parameters.

Decreasing the values of soil related parameters (h_s and C_s) down to zero, the uplift by pore water pressure (Fos_B) looses influence and the factor of safety (Eq. 18) finally reduces to a factor of safety for the organic layer alone, querying a basic assumption of all process-based models for shallow slope stability, namely that the failure has to take place in the mineral soil.

$$
FoS^* = \underbrace{\frac{\tan\varphi}{\tan\alpha}}_{\substack{\text{Friction}\\ FoS_A^*}} + \underbrace{\frac{x\,C_o}{(M_B + \rho_o h_o)g\sin\alpha}}_{\substack{\text{Basal resistance}\\ FoS_C^*}} + \underbrace{\frac{2L+W}{LW}\,\frac{h_o C_o}{(M_B + \rho_o h_o)g\sin\alpha}}_{\substack{\text{Lateral resistance}\\ FoS_D^*}} \tag{19}
$$

This factor of safety can reach values below one under the assumption that $\tan\varphi$, which now represents the static physical friction between the two layers, is significantly smaller than $\tan\alpha$.

The second prerequisite is that the anchorage of roots in the underground (xC_o) is sufficiently small. Prandini et al. (1977) stated that water fluxes at the boundary between mineral soil and organic layer may decrease the physical connection of the two layers over time due to erosive processes. It is plausible then, that this connection is highly variable in space and time and the situation may arise that $xC_o = 0$. Thus, for our analysis, we assumed $xC_o = 0.1$ kPa.

Taking these prerequisites as given, the factor of safety (FoS^*) mainly depends on the thickness of the organic layer and aboveground biomass density (Fig. 7) and thus, is subject to biological processes, as has been proposed by Richter et al. (2009). From our calculations, we deduce that aboveground tree biomass only contributes from 4% up to 12% to the total organic mass.
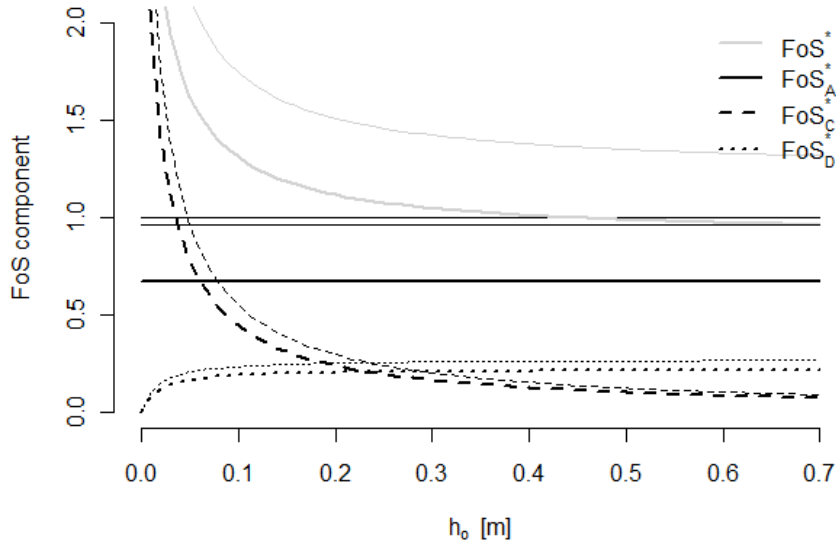

Figure 7: Sensitivity of factor of safety components for the organic layer alone (FoS^*) to variations in organic layer thickness (h_o) for two different slope angles (thin lines: $\alpha = 35^o$, thick lines: $\alpha = 45^o$). All other parameters are held constant ($L = 37$ m, $W = 12$ m, $\alpha = 45^o$, $\varphi = 34^o$, $M_B = 4.5$ kg m^{-2}, $xC_o = 0.1$ kPa, $C_o = 2.2$ kPa and $\rho_o = 279$ kg m^{-3}).

As can be seen by the above considerations, very shallow translational landslides without the involvement of apparent quantities of mineral soil are not unlikely in our study area. They are favored by steep slopes in combination with a topographic situation indicating surface erosion, which leads to a reduced connection of organic layer and mineral soil with time (Prandini et al., 1977).

Conclusion

We showed that a slight modification of a standard model for shallow slope stability is sufficient to explain even the very shallow translational landslides, we observed in our study area. By explicitly allowing the thickness of the organic layer to exceed that of the mineral soil, we implicitly introduced vegetation dynamics into the slope stability model, which gains control of slope stability in the marginal case of very shallow translational slides.

In two out of five cases our model reproduced observed depths of failure within the range of centimeters, supporting the hypothesis that the situation close to a landslide reflects that on the slide before the event. Reliable field measurements of parameters related to soil strength proved hard to obtain due to spatial heterogeneities and their dependency on soil water content (Anderson and Howes, 1985).

Parametrized with plausible parameter ranges for soil strength, the model reproduced slope instability for eight out of eleven landslides we surveyed. The remaining three landslides were very shallow and using a sensitivity analysis, we outlined the prerequisites for slope failure in these cases, as given by steep slope angles and surface erosion at the boundary of organic layer and mineral soil.

Even though our contribution is but a small step towards a broader understanding of processes and interactions in tropical montane environments, we think that or approach is worth consideration for further modeling of geomorphological processes in these areas.

Acknowledgements

References

Abernethy, B. and Rutherfurd, I. D.: The distribution and strength of riparian tree roots in relation to riverbank reinforcement, Hydrological Processes, 15, 63–79, 2001.

Anderson, M. G. and Howes, S.: Development and application of a combined soil water-slope stability model, Quart J Eng Geol Hyd, 18, 225–236, doi:10.1144/GSL.QJEG.1985.018.03.04, 1985.

Beck, E., Makeschin, F., Haubrich, F., Richter, M., Bendix, J., and Valerezo, C.: The Ecosystem (Reserva Biológica San Francisco), in: Gradients in a Tropical Mountain Ecosystem of Ecuador, edited by Caldwell, M., Heldmaier, G., Jackson, R., Lange, O., Mooney, H., Schulze, E.-D., Sommer, U., Beck, E., Bendix, J., Kottke, I., Makeschin, F., and Mosandl, R., vol. 198 of *Ecological Studies*, pp. 1–13, Springer Berlin Heidelberg, doi:10.1007/978-3-540-73526-7_1, 2008.

Brown, S.: Estimating Biomass and Biomass Change of Tropical Forests: a Primer, vol. 134 of *FAO Forestry paper*, FAO, Rome, 1997.

Brown, S. and Iverson, L. R.: Biomass estimates for tropical forests, World Resources Review, 4, 366–384, 1992.

Brown, S., Gillespie, A. J. R., and Lugo, A. E.: Biomass Estimation Methods for Tropical Forests with Applications to Forest Inventory Data, Forest Science, 35, 881–902, 1989.

Buchanan, P. and Savigny, K. W.: Factors controlling debris avalanche initiation, Can. Geotech. J., 27, 659–675, 1990.

Bussmann, R. W., Wilke, W., and Richter, M.: Landslides as Important Disturbance Regimes Causes and Regeneration, in: Gradients in a Tropical Mountain Ecosystem of Ecuador, edited by Caldwell, M., Heldmaier, G., Jackson, R., Lange, O., Mooney, H., Schulze, E.-D., Sommer, U., Beck, E., Bendix, J., Kottke, I., Makeschin, F., and Mosandl, R., Ecological Studies, pp. 319–330, Springer Berlin Heidelberg, doi: 10.1007/978-3-540-73526-7_31, 2008.

Casadei, M., Dietrich, W. E., and Miller, N. L.: Testing a model for predicting the timing and location of shallow landslide initiation in soil-mantled landscapes, Earth Surface Processes and Landforms, 28, 925–950, 2003.

Collison, A. J. C. and Anderson, M. G.: Using a combined slope hydrology/stability model to identify suitable conditions for landslide prevention by vegetation in the humid tropics, EARTH SURF PROC LAND, 21, 737–747, doi:10.1002/(SICI)1096-9837(199608)21:8⟨737::AID-ESP674⟩3.0.CO;2-F, 1996.

Comino, E. and Duretta, A.: In situ Shear Tests of Soil Samples with Grass Roots in Alpine Environment, American Journal of environmental sciences, 5, 474–485, 2009.

Connell, J. H.: Diversity in Tropical Rain Forests and Coral Reefs, Science, 199, 1302–1310, 1978.

De Baets, S., Poesen, J., Reubens, B., Wemans, K., Baerdemaeker, J. D., and Muys, B.: Root tensile strength and root distribution of typical Mediterranean plant species and their contribution to soil shear strength, Plant Soil, 305, 207–226, doi:10.1007/s11104-008-9553-0, 2008.

Dislich, C., Günter, S., Homeier, J., Schröder, B., and Huth, A.: Simulating forest dynamics of a tropical montane forest in South Ecuador, Erdkunde, 63, 347–364, 2009.

Gabet, E. J. and Dunne, T.: Landslides on coastal sage-scrub and grassland hillslopes in a severe El Niño winter: The effects of vegetation conversion on sediment delivery, Geological Society of America Bulletin, 114, 983–990, doi:10.1130/0016-7606(2002)114⟨0983:LOCSSA⟩2.0.CO;2, 2002.

Guitierres, F., Soldati, M., Audemard, F., and Balteanu, D.: Recent advances in landslide investigation: Issues and perspectives, Geomorphology, 124, 95–101, doi:10.1016/j.geomorph.2010.10.020, 2010.

Guzzetti, F.: Book review of "Catastrophic Landslides: Effects, Occurrence, and Mechanisms", NAT HAZARD EARTH SYS, 4, 531–531, 2004.

Guzzetti, F., Carrara, A., Cardinali, M., and Reichenbach, P.: Landslide hazard evaluation: a review of current techniques and their application in a multi-scale study, Central Italy, Geomorphology, 31, 181–216, doi:10.1016/S0169-555X(99)00078-1, 1999.

Jahn, R., Blume, H.-P., Asio, V. B., Spaargaren, O., and Schad, P.: Guidelines for soil description, FAO, Rome, 4. edn., 2006.

Keim, R. F. and Skaugset, A. E.: Modelling effects of forest canopies on slope stability, Hydrological Processes, 17, 1457–1467, 2003.

Köhler, P. and Huth, A.: Impacts of recruitment limitation and canopy disturbance on tropical tree species richness, ECOL MODEL, 203, 511–517, doi:10.1016/j.ecolmodel.2006.11.023, 2007.

Leuschner, C., Moser, G., Bertsch, C., Röderstein, M., and Hertel, D.: Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador, Basic and Applied Ecology, pp. 219–230, doi:10.1016/j.baae.2006.02.004, 2007.

Lozano, P., Bussmann, R. W., and Küppers, M.: Landslides as ecosystem disturbance - their implications and importance in South Ecuador, Lyonia, 8(1), 67–72, 2005.

Montgomery, D. R. and Dietrich, W. E.: A physically based model for the topographic control on shallow landsliding, WATER RESOUR RES, 30, 1153–1171, doi:10.1029/93WR02979, 1994.

Moser, G., Röderstein, M., Soethe, N., Hertel, D., and Leuschner, C.: Altitudinal Changes in Stand Structure and Biomass Allocation of Tropical Mountain Forests in Relation to Microclimate and Soil Chemistry, in: Gradients in a Tropical Mountain Ecosystem of Ecuador, edited by Caldwell, M., Heldmaier, G., Jackson, R., Lange, O., Mooney, H., Schulze, E.-D., Sommer, U., Beck, E., Bendix, J., Kottke, I., Makeschin, F., and Mosandl, R., Ecological Studies, pp. 229–242, Springer Berlin Heidelberg, doi:10.1007/978-3-540-73526-7_22, 2008.

Oesker, M., Dalitz, H., Günter, S., Homeier, J., and Matezki, S.: Spatial Heterogeneity Patterns a Comparison Between Gorges and Ridges in the Upper Part of an Evergreen Lower Montane Forest, in: Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies 198, pp. 267–274, Springer-Verlag Berlin Heidelberg, 2008.

Prandini, L., Guidicini, G., Bottura, J. A., Poncano, W. L., and Santos, A. R.: Behaviour of the vegetation in slope stability: a critical review, Bulletin of the International Association of EGINEERING GEOLOGY, 16, 51–55, 1977.

Restrepo, C., Walker, L. R., Shiels, A. B., Bussmann, R., Claessens, S. L. F., Lozano, P., Negi, G., Paolini, G. L. P., Ramos-Scharr'on, C., Richter, M., and Valzquez, E.: Landsliding and its multi-scale influence on mountainscapes, BioScience, 59, 685–698, doi:10.1525/bio.2009.59.8.10, 2009.

Richter, M., Diertl, K., Emck, P., Peters, T., and Beck, E.: Reasons for an outstanding plant diversity in the tropical Andes of Southern Ecuador, Landscape Online, 12, 1–35, doi:10.3097/LO.200912, 2009.

Schmidt, K. M., Roering, J. J., Stock, J. D., Dietrich, W. E., Montgomery, D. R., and Schaub, T.: The variability of root cohesion as an influence on shallow landslide susceptibility in the Oregon Coast Range, Can. Geotech. Journal, 38, 995–1024, 2001.

Sheil, D. and Burslem, D. F. R. D. P.: Disturbing hypotheses in tropical forests, Trends in Ecology and Evolution, 18, 18–26, 2003.

Siddle, R. C. and Dahkal, A. S.: Recent advances in the spatial and temporal modeling of shallow landslides, in: MODSIM2003: International Congress on Modelling and Simulation, pp. 602–607, University of Wales, Nedlands, 2003.

Sidle, R. C. and Swanston, D. N.: Analysis of a small debris slide in coastal Alaska, Can. Geotech., 19, 167–174, 1981.

Sidle, R. C. and Wu, W.: Simulating effects of timber harvesting on the temporal and spatial distribution of shallow landslides, Z GEOMORPHOL, 43(2), 185–201, 1999.

van Beek, L. P. H., Wint, J., Cammeraat, L. H., and Edwards, J. P.: Observation and simulation of root reinforcement on abandoned Mediterranean slopes, Plant and Soil, 278, 55–74, 2005.

Wilcke, W., Yasin, S., Abramowski, U., Valarezo, C., and Zech, W.: Nutrient storage and turnover in organic layers under tropical montane rain forest in Ecuador, European Journal of Soil Science, 53, 15–27, 2002.

Wu, T. H., McKinnell, W. P. I., and Swanston, D. N.: Strength of tree roots and landslides on Prince of Wales Island, Alaska, CAN GEOTECH J, 16, 19–33, doi:10.1016/j.ecoleng.2009.04.006, 1979.

Wu, T. H., Beal, P. E., and Lan, C.: In-Situ Shear Test of Soil-Root Systems, Journal of Geotechnical Engineering, 114, 1376–1394, 1988a.

Wu, T. H., McOmber, R. M., Erb, R. T., and Beal, P. E.: Study of Soil-Root Interaction, Journal of Geotechnical Engineering, 114, 1351–1375, 1988b.

Wu, W. and Sidle, R. C.: A distributed slope stability model for steep forested basins, Water Resources Research, 31, 2097–2110, 1995.

Xie, M., Esaki, T., and Zhou, G.: GIS-Based Probabilistic Mapping of Landslide Hazard Using a Three-Dimensional Deterministic Model, NAT HAZARDS, 33, 265–282, doi:10.1023/B:NHAZ.0000037036.01850.0d, 2004.

Tables

Table 2: Results of landslide surveys. Geographic coordinates (UTM WGS84), elevation a.s.l. (Elv.), estimated landslide age, number of relative 3D coordinates (n), planar length (L_p) and width (W) of landslide, slope angle (α) and visually estimated depth of failure (h_s).

#	UTM WGS84 [m]	Elv. [m a.s.l.]	Age	n [1]	L_p [m]	W [m]	α [^{o}]	h_s [cm]
1	714,096/9,558,503	2,528	fresh	111	30.75	7.79	53.11	42
2	714,460/9,558,210	2,656	fresh	96	35.36	6.97	49.10	39
3	713,883/9,558,019	2,510	fresh	119	62.42	11.95	35.68	49
4	713,736/9,558,058	2,500	fresh	134	51.57	15.71	38.32	8
5	713,961/9,559,726	2,219	fresh	65	6.97	8.78	54.76	6
6	713,973/9,559,758	2,203	old	105	31.27	10.63	37.14	60
7	713,967/9,559,419	2,294	old	125	43.12	10.10	37.00	40
8	713,884/9,559,444	2,136	old	132	41.22	11.51	37.75	20
9	713,084/9,560,181	1,893	old	102	34.92	22.62	32.99	133
10	713,213/9,560,460	1,820	fresh	54	12.38	8.28	31.25	62
11	713,455/9,560,350	1,983	old	99	55.14	15.66	38.60	102

Table 3: Soil profiles (part 1). Number of associated landslide, vertical soil depth (z), Horizon, Texture and Consistency shortcuts after Jahn et al. (2006), size (F: 2..6 mm; M: 6..20 mm; C: 20..60 mm; S: 60..200 mm) and abundance (N-none; V: 0..2%; F:2..5%; C:5..15%; M:15..40%; A:40..80%; D:<80%; S - Stone line) of soil skeleton, Soil cohesion as measured by torsion probe (C_s; Geonor H-60; mean $\pm$ standard error of mean), dry soil density (ρ_s; mean $\pm$ standard error of mean; $n = 3$) and gravimetric soil water content (Θ; mean $\pm$ standard error of mean; $n = 3$).

#	z [cm]	Symbol	Texture	Consist.	Skeleton Size/Abundance	C_s [kPa]	ρ_s [t m^{-3}]	Θ [%]
1	25	O				-	-	-
1	20	Oe				-	-	-
1	-20	Ah	Sil	ko4	FM/F	25.3± 3.1; $n =3$	1.04±0.15	34.4± 4.0
1	-50	A	CL	ko4	FM/F	37.7± 7.5; $n =3$	1.18±0.02	26.8± 3.1
1	-63	Bw	Sil	ko4	FM/F	23.0± 3.6; $n =3$	1.39±0.04	19.0± 0.8
1	-80	B	LS	so	FM/V	23.7±10.8; $n =3$	1.45±0.10	18.6± 2.5
1	-115	Cb	LS	so	FM/S	-	1.50±0.09	17.8± 0.9
1	-135	Cw	LS	lo	FM/M	23.3± 8.1; $n =3$	-	-
1	-200	C		ko2	S	47.7± 7.1; $n =3$	-	-
2	15	O				-	-	-
2	8	Oe				-	-	-
2	-20	Ah	SL	ko4	N	18.7± 4.0; $n =3$	1.41±0.03	24.3± 0.5
2	-80	Bw	Sil	ko2	M/V	33.3±11.9; $n =3$	1.50±0.09	19.2± 1.4
2	-90	B	SL	ko1	N	29.7± 5.1; $n =3$	1.60±0.03	17.8± 1.0
2	-100	Cb			S	43.3± 6.1; $n =3$	-	-
2	-145	Bwb	LS	ko1	FM/C	45.7± 9.5; $n =3$	1.51±0.08	16.2± 1.9
2	-160	Bw	LS	ko1	M/V	41.7± 3.2; $n =3$	1.50±0.06	17.6± 0.2
2	-225	Cw			S	40.7±22.1; $n =3$	-	-
3	15	O				-	-	-
3	10	Oe				-	-	-
3	-5	Ah				16.0± 2.8; $n =2$	-	-
3	-30	Ah	FS		MC/D	41.3± 5.0; $n =3$	-	-
3	-57	Bw	FS	ko1	FM/F	46.0± 1.7; $n =3$	1.68±0.04	16.3± 0.3
3	-102	Cw	VFS	ko1	CS/A	63.3± 6.1; $n =3$	1.56±0.07	17.9± 1.3
3	-130	C	FS	ko1	N	46.0± 2.0; $n =3$	1.72±0.04	16.8± 0.1
4	-10	Ah	L	ko4	N	44.3±13.1; $n =3$	1.44±0.15	20.6± 5.1
4	-140	Cw	FS	ko3	N	63.7±22.2; $n =3$	1.49±0.02	20.0± 0.3
5	10	O				-	-	-
5	-20	Ah	SiL	ko4	N	14.5± 2.8; $n =3$	-	-
5	-100	Cw		-	S	-	-	-

Table 4: Soil profiles (part 2). Number of associated landslide, vertical soil depth (z), Horizon, Texture and Consistency shortcuts after Jahn et al. (2006), size (F: 2..6 mm; M: 6..20 mm; C: 20..60 mm; S: 60..200 mm) and abundance (N-none; V: 0..2%; F:2..5%; C:5..15%; M:15..40%; A:40..80%; D:<80%; S - Stone line) of soil skeleton, Soil cohesion as measured by torsion probe (C_s; Geonor H-60; mean $\pm$ standard error of mean), dry soil density (ρ_s; mean $\pm$ standard error of mean; $n = 3$) and gravimetric soil water content (Θ; mean $\pm$ standard error of mean; $n = 3$).

#	z [cm]	Symbol	Texture	Consist.	Skeleton Size/Abundance	C_s [kPa]	ρ_s [t m^{-3}]	Θ [%]
6	15	O				-	-	-
6	-20	Ah	L	ko4	FM/C	22.7± 1.6; n =3	0.80±0.17	45.3± 7.9
6	-75	Cw	SCL	ko5	MC/A	41.3±25.3; n =3	1.30±0.00	24.1± 0.1
6	-110	C		-	S	70.0±17.8; n =3	1.50	16.8
7	30	O				-	-	-
7	5	Oe				-	-	-
7	-9	Ah	L	ko4	N	13.3± 1.5; n =3	1.04±0.17	36.0± 4.6
7	-40	Bw	SiL	ko4	M/F	10.8± 3.8; n =3	1.00±0.34	37.7±12.7
7	-56	Cw	L	ko3	CS/A	27.8± 2.0; n =3	1.31±0.31	27.7±10.1
7	-95	C			S	48.7±17.8; n =3	-	-
8	150	O				-	-	-
8	-22	Ah	L	ko4	FM/F	32.7± 3.2; n =3	1.20±0.13	26.5± 4.7
8	-75	Cw			S	-	-	-
9	30	O				-	-	-
9	-20	Ah	SC	ko4	C/A	15.8± 3.4; n =3	1.04±0.18	29.9± 8.9
9	-45	Bw	LS	ko1	MC/C	14.5± 8.2; n =3	1.47±0.08	13.1± 2.3
9	-55	Bs	LS	ko1	MC/C	9.7± 4.7; n =3	1.35±0.12	14.4± 1.6
9	-150	Cb	LS	ko1	MC/C	20.0± 7.8; n =3	1.43±0.08	10.8± 1.3
9	-158	Ab	LS	ko1	F/M	43.3±13.3; n =3	1.35±0.06	12.1± 1.0
9	-190	Bwb	Si	ko1	S	19.0± 3.0; n =3	1.38±0.02	38.1± 1.6
9	-230	Bsh	Si	ko1	F/F	15.3± 2.8; n =3	1.15±0.25	43.4± 6.0
9	-235	Cw	Si	ko1	F/F	11.8± 1.3; n =3	1.31	39.0
9	-290	C	Si	ko1	/M	17.3± 2.6; n =3	1.44±0.03	35.5± 5.7
10	5	O				-	-	-
10	-72	Ah	L	ko3	C/M	8.1± 2.1; n =3	0.90±0.13	36.5± 1.7
10	-105	Cw	SCL	ko4	C/M	23.7± 1.6; n =3	1.32±0.06	19.1± 2.1

Table 5: In situ soil shear tests. Associated landslide number, vertical depth within the soil profile (z), total number of shear tests (n), number of different loads (n_{Loads}), soil cohesion (C_s; mean ± standard error of mean) and internal friction angle (φ; mean ± standard error of mean) calculated by linear regression (Eq. 3) and mean soil cohesion, measured with torsion probe Geonor H-60 (C_{vane}).

#	Landslide	z [cm]	n	n_{Loads}	C_s [kPa]	φ [^{o}]	C_{vane} [kPa]
1	1	40	8	4	11.16±2.70	37.5±6.9	37.67
2	1	70	8	4	7.08±0.93	46.3±2.1	23.67
3	1	90	8	4	5.22±2.11	43.0±4.7	16.00
4	1	95	7	2	12.44±1.39	40.0±1.6	28.29
5	1*	125	14	2	4.65±0.97	25.8±1.9	11.64
6	2*	30	6	3	10.21±2.19	50.9±4.3	33.33
7	5*	20	30	5	4.96±6.32	46.9±7.7	14.50
8	6*	30	6	3	14.31±1.13	41.4±5.1	31.67
9	7	23	6	3	15.06±1.97	32.8±8.6	14.00
10	7*	40	6	3	12.86±1.50	46.4±4.8	20.00
11	9	6	6	2	20.79±4.99	27.7±9.2	15.92
12	9	18	6	2	14.61±0.86	30.1±1.6	16.08
13	9	130	8	3	4.53±2.10	32.6±3.5	20.00
14	9	160	9	3	5.31±1.88	37.2±2.7	31.17
15	9*	185	10	4	7.69±2.43	27.0±4.4	42.00
16	11*	120	15	3	16.17±1.91	40.2±3.1	55.00
17	11*,a	120	12	3	15.23±3.26	24.7±7.1	-

*Measurement in estimated failure plane; [a]Saturated conditions

Table 6: In situ organic layer rupture tests. Location id, minimum ($\tau_{m}in$) and maximum ($\tau_{m}ax$) tensile resistance, mean value (τ,)

Location	τ_{min} [kPa]	τ_{max} [kPa]	τ [kPa]	$\log(\tau)$ log([kPa])	n
a	0.89	3.25	2.41±0.88	0.79±0.49	11
Ø	0.89	3.25	2.41±0.88	0.79±0.49	11
b	0.32	5.47	1.89±1.01	0.50±0.53	205
b	0.32	6.24	2.06±1.11	0.58±0.54	101
b	0.89	7.45	2.69±1.04	0.92±0.39	150
b	0.76	11.84	2.29±1.28	0.72±0.44	150
Ø	0.32	11.84	2.22±1.15	0.67±0.50	606
c	0.76	5.60	2.63±1.15	0.87±0.46	39
c	0.48	7.48	2.09±1.36	0.55±0.64	97
c	0.64	3.82	2.04±0.71	0.65±0.37	51
c	0.32	7.51	1.84±1.17	0.45±0.57	99
Ø	0.32	7.51	2.07±1.19	0.58±0.57	286

Table 7: Point investigations, ordered by elevation. Geographic coordinates (UTM WGS84), elevation a.s.l. (Elv.), slope angle (α), thickness of organic layer (h_o; mean $\pm$ standard error of mean; number of samples), estimated mean tree height ($\overline{h}$), tree diameter in breast height (130 cm; DBH; mean $\pm$ standard error of mean; number of samples) and aboveground tree biomass density estimates after equation 4 (M_B^a, Brown and Iverson, 1992), equation 5 (M_B^b, Brown, 1997) and after equation 6 (M_B^c). Below each altitudinal range, mean values are given.

#	UTM WGS84 [m]	Elv. [m a.s.l.]	α [^{o}]	h_o [cm]	$\overline{h}$ [m]	DBH [cm]	M_B^a [g m^{-2}]	M_B^b [g m^{-2}]	M_B^c [g m^{-2}]
1	714,150/9,558,405	2,531	38	12.1± 5.7; n =2	4.0	12.57±7.16; n =4	974	3,200	1,875
2	714,162/9,558,420	2,524	30	-	5.0	8.48±7.04; n =8	1,139	1,953	2,130
3	714,133/9,558,397	2,514	28	17.0± 7.2; n =3	3.5	11.94±8.77; n =6	1,166	4,129	2,218
4	714,089/9,558,513	2,505	56	33.7± 2.3; n =3	3.5	5.37±1.82; n =35	1,494	2,915	2,615
5	714,089/9,558,513	2,505	36	33.7± 2.3; n =3	3.0	4.97±1.60; n =18	574	1,421	989
6	714,090/9,558,399	2,492	18	34.3±11.7; n =3	4.0	12.14±6.05; n =8	1,821	5,777	3,494
7	714,069/9,558,390	2,492	24	54.5±38.1; n =3	3.0	10.69±7.23; n =7	953	3,469	1,778
8	713,747/9,558,033	2,478	40	68.8; n =1	12.0	15.01±7.72; n =6	5,793	7,902	12,032
9	713,724/9,558,063	2,469	35	58.7±14.3; n =2	7.0	12.22±8.79; n =5	1,961	3,687	3,877
10	714,047/9,558,399	2,466	40	40.5± 0.0; n =2	4.0	7.27±3.85; n =6	517	930	940
11	714,065/9,558,476	2,440	36	42.6± 7.1; n =3	6.0	6.53±3.36; n =19	1,963	2,229	3,608
12	713,999/9,558,377	2,436	49	21.0± 4.6; n =2	7.0	8.55±2.91; n =8	1,595	2,010	3,038
13	713,970/9,558,355	2,404	47	33.2± 3.4; n =2	3.0	4.77; n =1	30	78	51
14	713,922/9,558,338	2,382	51	24.3± 0.0; n =2	5.5	7.51±3.16; n =12	1,486	2,039	2,757
Ø	Range: 2,382 to 2,531		37.5	35.3±18.2; n =31	5.0	7.84±5.23; n =143	1,310	2,044	2,430
15	713,971/9,559,299	2,331	8	30.4± 9.3; n =17	6.0	8.63±4.06; n =19	3,326	4,900	6,291
16	713,986/9,559,334	2,325	45	61.2±34.8; n =13	4.0	9.43±3.58; n =12	1,693	4,065	3,164
17	713,992/9,559,348	2,303	49	49.4±15.5; n =17	4.0	8.97±3.70; n =23	2,950	6,679	5,485
18	713,936/9,559,392	2,295	28	23.6± 6.6; n =11	10.0	9.16±5.97; n =32	10,187	9,921	19,911
19	713,976/9,559,428	2,294	43	41.0±23.6; n =3	4.0	8.79±2.47; n =8	989	2,187	1,834
20	713,976/9,559,446	2,287	36	15.1±12.0; n =3	3.0	7.43±3.80; n =3	205	494	368
21	713,959/9,559,390	2,285	36	14.6± 4.7; n =10	5.0	10.36±4.87; n =24	4,999	10,826	9,545
22	714,014/9,559,348	2,282	48	18.4± 6.6; n =18	8.0	13.18±6.31; n =21	10,783	19,227	21,634
23	713,860/9,559,631	2,264	36	21.7± 6.0; n =17	2.5	5.53±1.10; n =11	361	947	623
24	713,857/9,559,681	2,256	28	25.6± 4.6; n =12	5.0	7.60±3.33; n =17	1,969	2,997	3,642
25	713,864/9,559,655	2,252	36	40.5±12.4; n =17	6.0	7.06±4.71; n =16	1,915	2,289	3,548
26	713,953/9,559,686	2,243	40	21.0± 1.1; n =2	6.0	10.47±4.78; n =9	2,274	4,192	4,388
27	713,918/9,559,725	2,236	10	28.3± 0.0; n =2	6.4	10.26±4.09; n =13	3,360	5,696	6,492
28	713,896/9,559,704	2,236	15	48.3±14.4; n =18	6.0	9.15±7.93; n =44	8,613	13,596	16,391
29	713,972/9,559,770	2,232	36	61.1±34.9; n =2	5.0	6.57±1.34; n =7	615	833	1,120
30	713,932/9,559,718	2,229	40	20.2± 5.7; n =2	5.0	9.68±3.78; n =15	2,746	5,500	5,206
31	713,982/9,559,756	2,228	35	31.8±43.3; n =3	5.0	7.87±1.91; n =7	865	1,365	1,606
32	713,847/9,559,721	2,225	18	14.1± 4.9; n =17	6.0	11.01±5.84; n =24	6,669	13,000	12,937
33	713,857/9,559,739	2,222	24	58.3±21.7; n =18	7.0	7.26±4.17; n =31	4,527	4,789	8,478
34	713,965/9,559,412	2,214	52	25.9± 5.1; n =9	10.0	11.65±7.75; n =18	9,043	11,544	18,123
35	713,819/9,559,775	2,208	44	58.0±20.8; n =18	7.0	7.67±3.49; n =28	4,543	5,073	8,556
36	713,759/9,559,819	2,192	36	54.1±13.9; n =18	7.0	9.60±4.33; n =20	4,959	7,150	9,559
Ø	Range: 2,192 to 2,331		33.8	37.2±22.2; n =247	5.8	9.15±5.29; n =402	3,459	5,627	6,571
37	713,234/9,560,163	1,915	36	32.4; n =1	5.0	6.87±2.92; n =37	3,533	4,913	6,464
38	713,248/9,560,451	1,843	54	19.8±10.7; n =13	7.0	10.79±4.97; n =18	5,570	9,176	10,870
39	713,179/9,560,469	1,809	45	25.5± 8.1; n =14	6.0	8.94±3.82; n =22	4,121	6,331	7,824
Ø	Range: 1,809 to 1,915		45.0	23.1± 9.7; n =28	6.0	8.38±4.02; n =77	4,897	6,970	9,234

Chapter 4

Conclusion and Outlook

Below we discuss the main findings of this thesis along its two main themes: first the role of life history traits for species coexistence, and then their role in forest recovery after landslides. Each section is organized according to the questions stated in the introduction and closes with potential starting points for further research arising from our findings. In the outlook, we outline future research activities based on this thesis.

4.1 Role of life history traits for species coexistence

Which mechanisms enable coexistence in species rich plant communities?

The question of species coexistence is of general nature and applies to many ecosystems – particularly tropical forests. In the light of insufficient knowledge about such diverse ecosystems, theoretical investigations of potential processes that drive coexistence of trees might be a key to a better understanding of competition. Therefore, in paper 1 we took an idealized approach which extends beyond the specific study system that motivated our question, and developed a theoretical model to investigate the question of species coexistence in forests. While many model studies investigating species coexistence focus on single coexistence mechanisms (e.g. Potthoff et al., 2006; Pronk et al., 2007), the question how different mechanisms interact remains open. We therefore analyzed trade-offs between different species traits (tree recruitment, tree growth, tree mortality), alone and in combination with additional mechanisms that modify local competition (density-dependent mortality, light-dependent regeneration) for their potential to facilitate species coexistence. To this end, we developed a simple spatially explicit forest model. Our main findings from this study are:

- The combination of life history traits is crucial for species coexistence: we find very narrow coexistence ranges for a simulation period of 1000 years (Figure 4 in paper 1). This means that trade-offs need to be 'fine-tuned', i.e show a defined relation, in order to facilitate coexistence. Already small deviations from this relation result in competitive exclusion. However, the considered trade-offs alone do not support long-term coexistence as they have no stabilizing effect – they act only equalizing (Figure 7 in paper 1).

- The narrow coexistence ranges of trade-off communities are considerably broadened by the inclusion of processes that modify local competition (density-dependent mortality, light-

dependent regeneration, cf. Figure 4 and 7 in paper 1). Such mechanisms act stabilizing and constitute an important contribution to coexistence in forest communities.

- The timescale on which different species traits operate in competition can differ considerably. A trade-off between one trait, which has a stronger effect on competition and a second trait which has a weaker effect can result in highly non-linear coexistence areas in the trait space – thus there might be threshold values above or below which we cannot expect functioning trade-offs between strong and weak traits (Figure 4 b,c in paper 1).

Our investigation revealed that the considered trade-offs alone are insufficient for explaining long-term coexistence and thus species diversity. In fact, we were surprised to see how rapidly (within few generations) competitive exclusion takes place if trade-offs are not 'fine-tuned', i.e. show a defined relation (cf. Figure 2a in paper 1). Consequently, in the absences of internal (e.g. density-dependence, speciation) or external (e.g. disturbance, immigration of new species) stabilizing mechanisms, species could not coexist in the long run. On the other hand, simple mechanisms that modify the local competition (e.g. density-dependent mortality) could be sufficient to buffer rapid exclusion. Only few studies examining trade-offs mention the insufficiency of trade-offs alone to support coexistence (Chesson, 2000; Lischke and Löffler, 2006; Banitz et al., 2008). In fact, one prominent class of models investigating the competition-colonization trade-off (Tilman, 1994; Klausmeier and Tilman, 2002; Muller-Landau, 2008) have seemingly showed the opposite – namely, that trade-offs can facilitate coexistence. This seeming contradiction can be settled when examining the mechanisms acting in the different models. Most studies of the competition-colonization trade-off implement an a priori hierarchy of local competition, which is a stabilizing mechanism that may lead to coexistence of a potentially unlimited number of species (Tilman, 1994). In contrast, the trade-offs in physiological traits considered in paper 1 do not bear a stabilizing component, and fitness differences evolve directly from physiological species traits. Compared to the rather indirect parameters of competition and colonization strength of the abovementioned models, our process-based approach uses more direct parameters (growth, mortality, dispersal) which can more easily be observed in the field.

In difference to many classical studies on species coexistence that focus on equilibrium states of ecosystems (e.g. Chave et al., 2002) and often use spatially implicit approaches (e.g. Levins and Culver, 1971; Durrett and Levin, 1994; Tilman, 1994), our model takes a non-equilibrium perspective and is spatially explicit. Thereby, we take into account, first, that space plays an important role in forest ecosystems (as they are not 'well-mixed' systems) and second, that these systems are also affected by both disturbances and environmental (e.g. climatic) changes on different spatiotemporal scales, and therefore are likely never in a real equilibrium state (at medium scales).

Implications for our study system

How do the findings from paper 1 relate to our study system, the species-rich montane forest of the Tropical Andes? At large spatial scales, various biogeographical hypotheses try to explain the high species richness in the tropics compared to lower species richness in higher latitudes (e.g. Willig et al., 2003; Kreft and Jetz, 2007). Climate is involved in different ways in such hypotheses: on the one hand, contemporary climate (e.g. temperature, water availability) is assumed

to be a driver of latitudinal diversity patterns (e.g. water-energy hypothesis[1]; Hawkins et al., 2003; Francis and Currie, 2003). On the other hand, the climate-stability hypothesis assumes that historical dynamics in climate regimes (glacial-interglacial cycles) govern diversity patterns (McGlone, 1996; Dynesius and Jansson, 2000; Jablonski et al., 2006). Naturally, these explanations could apply to our tropical study system. Additionally to these large scale explanations that generally apply to low latitudes, mountain ecosystems, due to their complex topography, are characterized by high levels of environmental heterogeneity and a broad range of climatic conditions compared to lowland ecosystems. This environmental heterogeneity manifests in a diversity of habitat types that is assumed to positively affect species diversity (e.g. Huston, 1994; Rosenzweig, 1995; Dufour et al., 2006). Moreover, our study site is located in a unique area, the Amotape-Huancabamba depression. This depression is a partial interruption of the Andean mountain chain with the lowest point at 2145 m asl in northern Peru. The Amotape-Huancabamba depression has been suggested both to be a migration corridor (Weigend, 2002; Beck et al., 2008a) between the Amazon and the pacific side and a migration barrier in north-south direction (Borchsenius, 1997; Keating, 2008). The extraordinary high species diversity has been increasingly recognized in the last years (Young and Reynel, 1997; Keating, 2008; Richter et al., 2009) and suggests that this region is a meeting point of lowland and upland species (Beck and Richter, 2008)

The abovementioned large scale hypotheses explain rather the formation of diversity but not the maintenance of species richness. Here, the smaller scale of local plant communities, where species interactions like competition, predation and spatial heterogeneity are important, come into play. Therefore, in our study, we focused on interactions between individuals and their effect on population dynamics. In the wet tropics, stable and favourable climate both within the year and historically over long time periods might have allowed for a strong specialization of traits, resulting in narrower partitioning of niches compared to outside the tropics (MacArthur (1972); May (1973), but see also Vazquez and Stevens (2004)). But our findings (from the more local scale) suggest that additional factors might be necessary to explain the maintenance of diversity in species-rich habitats like our study area. Such additional factors could include biotic mechanisms evolving from inter- or intra-specific interactions (e.g. density-dependent mortality), but they could also be connected to abiotic factors like topography (spatial heterogeneity) or disturbances (e.g landslides).

Importance of understanding mechanisms that maintain biodiversity

Biodiversity has both direct and indirect values for humans. Direct values concern economically important environmental services like timber, medicinal and food products. Indirect values are the maintenance of biogeochemical cycles and ecosystem functions like carbon sequestration and regulation of regional climate. Other indirect values are of ethical ('intrinsic value' of biodiversity) and aesthetical nature (Ehrlich and Ehrlich, 1992). Over the past decades, the implications

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[1] The water-energy hypothesis states that "species richness at higher latitudes is controlled by the availability of ambient heat, whereas, in the thermally suitable tropics, water- and humidity-related variables are the main driving factors"(Kreft and Jetz, 2007). It is known that plant species distribution and richness is influenced by the factors energy (e.g. temperature, insolation, potential evapotranspiration) and water, which strongly influence the productivity of a system (Stephenson, 1990; O'Brien, 1993). Potential mechanisms leading to high species richness under ambient energy and water are low extinction rates and high speciation rates (Hawkins et al., 2003).

of biodiversity for ecosystem functions, in particular the role of biodiversity for ecosystem productivity and stability, also with respect to climate change, received growing scientific attention (e.g. Hooper et al., 2005; Nadrowski et al., 2010; Paquette and Messier, 2011). Acknowledging the importance of biodiversity and its rapid loss due to human interventions (Butchart et al., 2010) give rise to the urgent need of concepts to reduce biodiversity loss (Noss, 2001; Heller and Zavaleta, 2009). For the development of such concepts, the understanding of mechanisms maintaining biodiversity are indispensable.

Where to go from here?

One strength of the modelling approach chosen in paper 1 is its flexibility – it can, for example, easily be extended to investigate other coexistence mechanisms. Potential directions for further explorations are:

- Upscaling: from few to multiple species competition. An extension to a multi-species community may provide further insights into how the mechanisms that we identified as important for the two-species system translate into species-rich communities. A first step in this direction has been undertaken in the end of paper 1 (cf. Figure 5).

- Downscaling: incorporating intra-specific differences. Recent studies suggest intra-specific variation to be highly important for species coexistence (Adler et al., 2007; Clark, 2010; Clark et al., 2010). In our study we focused on differences between species, yet, in principle our individual-based approach also allows incorporating differences between individuals of the same species.

- From theoretical towards more applied models: incorporating environmental heterogeneities. One could incorporate spatial heterogeneity (e.g. mountains, landslides) or other potentially relevant gradients (e.g. nutrients) and incorporate species-specific differences in response to such heterogeneities. Such an approach may provide insights into further mechanisms that maintain biodiversity and that are particularly relevant for mountainous systems like our study system.

4.2 Forest dynamics, landslide disturbance and life history traits

How do montane forests react on the disturbance of landslides?

Landslides have received much less scientific attention than other disturbances in forests such as gap-building and fire. Yet, they are a common disturbance in many montane forests (Garwood et al., 1979; Restrepo et al., 2009). In addition, the majority of landslide research focused on local processes on the level of single landslides (e.g. Dalling, 1994; Chaudhry et al., 1996; Fetcher et al., 1996; Kessler, 1999; Ohl and Bussmann, 2004; Velazquez and Gomez-Sal, 2008). While these investigations are important to gain knowledge about the reaction of different species on this particular disturbance, the effect of landslides from the landscape perspective was so far rather neglected (Restrepo et al., 2009). Thus, our study contributes to understanding the effects of landslides on forest structure and dynamics on the local and landscape scale.

On landslide sites, changed environmental conditions like reduced nutrient contents and soil instability are likely to result in slower forest recovery compared to other well-studied disturbances such as tree-fall gaps. Depending on the changes in tree life history traits due to altered

environmental conditions, the pathway (and speed) of local forest regeneration might differ. Due to scarcity of data from our study region, we developed different scenarios to investigate the effect of changed tree life history traits on forest recovery and dynamics. This approach will allow to estimate the impact of landslides on forest dynamics on different spatial and temporal scales.

In paper 2 and 3, we utilized the spatially explicit, individual-based forest simulation model FORMIND, that was parameterized for the ridge forest of our study area, to investigate hypothetical scenarios of forest regrowth after landslides. Each scenario assessed different changes in life history traits resulting from changed environmental conditions following the landslide disturbance. Our main findings are:

- The FORMIND model successfully reproduces the dynamics of the mature ridge forest on different levels of complexity (for example both overall and pft-specific basal area and stem size distribution, cf. Figure 2 and 3 in paper 2)

- While the overall tree biomass may recover within the first century of succession after a landslide, it takes presumably at least 200 years until the recovering forests forms a mature forest structure (stem size distribution) again (cf. Figure 3 and Table 1 in paper 3).

- The spatial variation in tree biomass during forest recovery reveals distinct patterns for different scenarios of changed life history traits (cf. Figure 3 in paper 3) – compared to mature forest, spatial variation in successional forest may increase, if tree recruitment is reduced or tree mortality is increased, or decrease, if tree growth rates are reduced.

- Landslide sites become carbon sinks during forest recovery. Productivity on slide surfaces is likely reduced compared to productivity in undisturbed sites (cf. Figure 4 in paper 3).

- Compared to a forest without landslide disturbances, the overall tree biomass is reduced considerably by landslides (8‑14%, cf. Figure 7a in paper 3). Thus, it is important to incorporate this disturbance regime when investigating the carbon balance of this ecosystem.

- On the landscape scale, landslides increase variation in biomass distribution and thus increase landscape heterogeneity (cf. Figure 6 in paper 3). By creating types of habitat that would not appear without this particular type of disturbance, landslides might have a positive impact on biodiversity.

We calibrated the FORMIND model to reproduce the structure and dynamics of the mature ridge forest. Recalling how difficult it is to obtain stable coexistence of only two species through trade-offs between species traits (paper 1), it is interesting to think about which coexistence mechanisms are present in the FORMIND model. While the model includes some trade-offs which might act equalizing (e.g. differences in growth, recruitment and mortality rates), the most important mechanism enabling stable coexistence is the assumption of constant recruitment rates of small trees (i.e. recruitment rates are independent of species abundance). These recruitment rates can also be interpreted as a density-dependent process of recruitment: when a species is rare, the per capita recruitment rate is high; when it is abundant, the per capita recruitment rate decreases. Variants of the FORMIND model, where recruitment depends on the presence of adult mother trees exist and were applied in studies on fragmented forests (Groeneveld et al., 2009). However, we assume that seed availability and thus recruitment limitation plays a minor role in the recolonization after landslides, since landslides are relatively small scale disturbances with sharp borders. Thus the species pool around such disturbed sites can be assumed to be saturated.
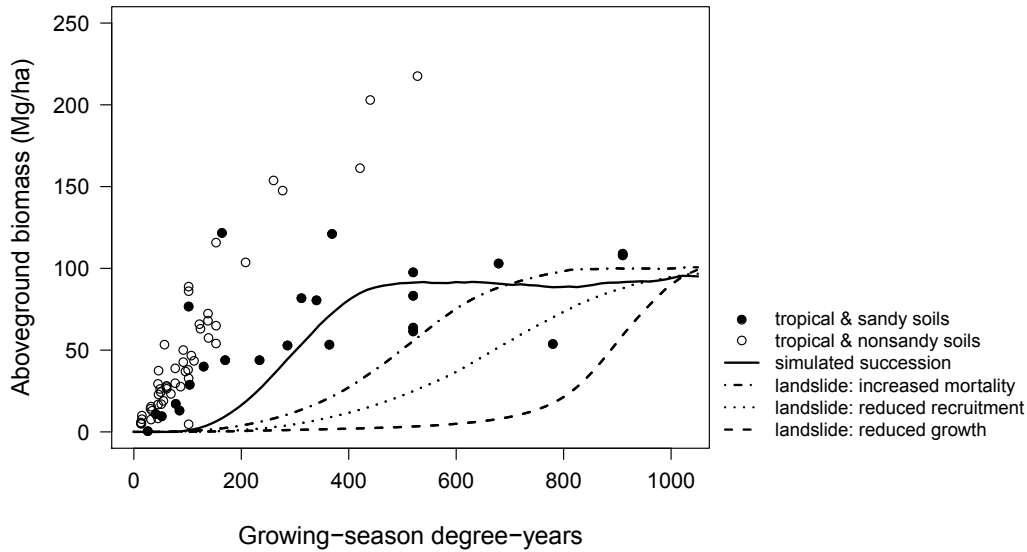
Figure 4.1: Comparison of field data from global secondary forests (Johnson et al., 2000) and simulation output of the FORMIND model. Growing-season degree-years is derived as the product of stand age (years), growing-season temperature (°C) and growing-season length (years). For the RBSF-forest we apply a mean annual temperature of 15 °C (Beck et al., 2008b) and a growing-season length of 1. The solid line depicts 'normal' succession after forest clearance. Dashed lines show succession after landslides with different changes in tree life history traits.

Applications of process-based forest models for species-rich tropical forests have so far concentrated on lowland forests (e.g. Shugart et al., 1980; Kohyama, 1992; Kürpick et al., 1997; Liu and Ashton, 1998; Chave, 1999; Huth and Ditzer, 2001; Groeneveld et al., 2009), which are in general more intensively studied compared to montane tropical forests. This thesis demonstrates that this class of models is also suitable for various applications in montane forests, be it improving our understanding of these complex ecosystems (as demonstrated in paper 2 and 3) or developing adaptive management strategies (see General outlook 4.3).

Aboveground biomass accumulation after disturbance

For calibrating our forest model, we utilized inventory data from mature ridge forest, as well as data on tree growth. The simulated mature forest dynamics reproduces the dynamics of the ridge forest quite well (cf. paper 2). Yet, since empirical data from successional forest was not available, we could not quantify uncertainties in the course of biomass accumulation. In Figure 4.1 we compare the simulated accumulation of biomass of the ridge forest with measured biomass accumulation after disturbance in various forests worldwide (Johnson et al., 2000); in this study data from 54 chronosequence and long-term studies are compiled. Despite the fact that the mature biomass of our montane forest is far lower than the mature biomass of most forests compiled in this study, we find a generally good agreement between the simulated (solid line in Figure 4.1) and observed biomass accumulation on sandy soils. Our study system has a diversity of soils (predominantly loam and silt loam; Mareike Ließ, pers. comm.), and therefore the lower

biomass in our system may relate to other factors (e.g. steep or unstable slopes) that were not addressed by Johnson et al. (2000): the only montane rainforest they included is at 1100 metre above sea level and reaches over 200 Mg/ha. In the first few years of succession our model predicts a slightly slower accumulation of biomass compared to the field data. This could be due to the fact that the sites, where the data were collected, were affected by disturbances that "killed or removed all, or virtually all, aboveground vegetation but left most of the soil organic matter intact" (Johnson et al., 2000). This means that the soil seed bank was likely still unimpaired, in difference to our simulation, where initial conditions assumed no seed bank. Concerning the accumulation of biomass after landslide disturbance, all scenarios with changes in life history traits (dashed lines) predict a considerably slower biomass recovery than most of the observed biomass accumulations from less severe disturbances. Thus, landslide disturbances seem to be qualitatively different from other disturbances, and it is crucial to consider this special type of disturbance for estimating the speed of biomass accumulation on disturbed sites.

Importance of disturbances in forest ecosystems

Disturbances (natural as well as anthropogenic) play an important role in structuring forest ecosystems and their effects have been studied for many decades (e.g. Garwood et al., 1979; Shugart and West, 1980; Suffling et al., 1988; Attiwill, 1994; Zimmerman et al., 1994; Rüger et al., 2007a). Disturbances influence ecosystem dynamics – they increase mortality and disturbed sites offer new space for regeneration. Important disturbance characteristics are size, frequency and intensity (Crawley, 1997b). Since the type of disturbance (e.g. gap-building, fire, landslide, windthrow, hurricane) may affect the pathway of regeneration (Romme et al., 1998; Shorohova et al., 2009), it is important to investigate implications of different disturbance regimes for forests ecosystems. The challenges of climate change further emphasize the relevance of understanding the response of ecosystems to disturbances, since climate change may involve increased frequency and intensity of extreme events (Smith et al., 2009). For example, a higher frequency of droughts may result in changing fire frequency and extent, and a higher frequency of extreme precipitation may result in a higher frequency of landslides in montane forest ecosystems. Such changes may, in the long term, change species compositions and affect ecosystem functioning. Given the difficulty of obtaining detailed empirical data and monitoring complex systems across long time periods, ecological models such as FORMIND are important tools for predicting and quantifying the potential consequences of (future) changes in disturbance regimes. Our findings demonstrate a strong effect of the current landslide regime on carbon dynamics in our study area: the reduction in overall biomass through landslides (8 - 14%, cf. Figure 7a in paper 3) is far higher than the visibly affected area in aerial photographs ($\sim$ 2 - 3%). Therefore, the effect of landslides needs to be taken into account when estimating the carbon dynamics in our study region.

Do forest dynamics influence the triggering of landslides?

Identifying the driving processes that trigger landslide occurrence and understanding how they interact can aid in landslide prediction (e.g. in form of susceptibility maps) and in estimating how landslide regimes might change in a changing environment. Knowledge about landslide risks is particularly important in populated areas and also relevant for the management of montane forest ecosystems.

While in paper 3 we concentrated on the impact of landslides on forest dynamics, paper 4 investigates potential feedbacks of vegetation on the occurrence of landslides. Several studies have analyzed slope stability in forested areas, and it is well-established that different variables, like soil attributes, hydrological factors, slope steepness and vegetation, play a vital role in slope stability (Wu and Sidle, 1995; Glade, 2003; Alcantara-Ayala et al., 2006). Vegetation adds to both stabilizing and destabilizing forces on a slope: tree roots increase soil cohesion and thus stabilize slopes; on the other hand, biomass adds to the weight resting above a potential failure plane, thereby increases shear stress and acts destabilizing.

Studies on slope stability in temperate rainforests found that vegetation stabilizes slopes; in particular, they demonstrated an increase in landslide frequency due to the impact of forest logging (Sidle and Wu, 1999; Jakob, 2000; Montgomery et al., 2000; Dhakal and Sidle, 2003; Imaizumi et al., 2008). In contrast to this view of forest as 'slope-stabilizer', we think that in our tropical rainforest study system, vegetation might also be one of the triggering factors for landslides (see also Richter et al., 2009). One reason for this is that most trees in our system have shallow roots (Soethe, 2006); below this shallow root zone, tree roots do not increase soil cohesion. The major share of roots is accommodated in a thick organic layer above ground (Wilcke et al., 2002), and this 'root carpet' is rather loosely connected to the soil. In combination with strong rainfalls or earthquakes, weak spots in this root carpet could trigger landslide occurrence. Such weak spots could occur due to root ageing or tree mortality, and/or a locally high load of biomass of big trees resting on the carpet. Our hypothesis that forest vegetation could also trigger landslides is supported by the observation that some landslides in our study system involve almost exclusively organic material (cf. paper 4).

In the introduction (section 1.1) we stated one more questions that was not directly answered in the research papers. In the following, we shortly address this question.

Do landslides have an effect on (tree species) diversity?

One important aspect of ecosystem disturbances is that they might be drivers of biodiversity, as they create spatial heterogeneity and form unique habitats (e.g. Connell and Slatyer, 1977; Shea et al., 2004; Johst and Huth, 2005). Since landslides constitute a particular ecosystem disturbance, the question how landslides affect diversity is intuitive. If landslides have a positive feedback on tree species diversity, they should be added to the set of coexistence mechanisms discussed earlier in this chapter (section 4.1). A better understanding of the relationship between landslide disturbances and species diversity will also assist in estimating how diversity might be affected when disturbance regimes shift for example in response to direct human interventions or climate change.

Landslides change a whole set of environmental conditions in a secluded area and initiate primary succession. Successional pathways may depend on abiotic factors like soil stability or substrate quality, and biotic factors like adaptation to the harsh site conditions or recruitment limitation (Walker and del Moral, 2003). The differences compared to undisturbed habitats are most pronounced in the first years after landslide occurrence. Consequently, these early colonization stages on landslides received most scientific attention (e.g. Stern, 1995; Velazquez and Gomez-Sal, 2008; Restrepo et al., 2009). It has been shown that landslides contribute to plant diversity by providing distinct habitat types within the early phase of succession (Kessler, 1999; Elias and Dias, 2009); this was demonstrated also for our study system (Ohl and Bussmann, 2004). Concerning later successional stages, Vittoz et al. (2001) detected changes in tree species composition in forests in New Zealand due to earthquake-induced landslides in the 1920's. In a

Puerto-Rican forest, revegetation on a 38-year-old landslide was still dominated by pioneer tree species and ferns; composition on a 52-year-old slide started to resemble pre-landslide composition (Guariguata, 1990). A study from a Jamaican forest reported very slow biomass accumulation on landslide sites, accompanied by slow changes in structural and species composition: mosses and lichens constituted a major share of biomass on a 15-year-old landslide (Dalling, 1994). Geertsema and Pojar (2007) reviewed several other landslide-vegetation studies and concluded that landslides have an important positive impact on biophysical (i.e. site, soil and habitat) diversity, which likely also reflects on species diversity.

Both field observations (e.g. Dalling, 1994) and our simulations results (Table 1 in paper 3) indicate that also after the first 50-100 years, a landslide-disturbed forest differs from an undisturbed forest. Thus, the long-term effects of landslides exceed a researcher's lifespan – chronosequence studies try to overcome this problem by investigating sites that experienced the same type of disturbance at different times (Pickett, 1989; Guariguata, 1990; Wilcke et al., 2003). Here, ecological models can aid in investigating long-term effects of disturbances.

In our study system, research on landslides has so far focused on relatively young landslides (Wilcke et al., 2003; Ohl and Bussmann, 2004), since old landslides, on which vegetation cover is restored, are invisible in aerial photographs and hard to detect in the steep terrain. Therefore, data on tree species composition on old landslide sites was not available. Our simulation results show that in the first decades of forest recovery, tree species composition is strongly shifted towards fast-growing pioneer species (cf. Figure 3 in paper 3). Thus, on the level of functional types, landslides clearly do have a strong impact on forest composition on the local level of landslides and therefore also affect overall forest composition. On the landscape level, landslides create patches of habitat types that would not exist without this particular disturbance regime. Therefore, landslides increase habitat heterogeneity which may imply a positive effect on overall species diversity (Huston, 1994; Rosenzweig, 1995). A positive impact of landslides on tree species diversity in our study region is supported by the observation that some few tree species are primarily found on landslide sites (Jürgen Homeier, pers. comm.); such species might be absent without the particular disturbance type of landslides.

Note that in our forest model we grouped tree species into plant functional types, i.e. we identify species which are similar concerning selected physiological traits (e.g. maximum diameter, maximum growth rate). Therefore, our forest model in its current form can only analyze diversity on the level of plant functional groups and not on the species level. Modelling each species individually is in principal possible, but requires detailed knowledge about all tree species which is rarely available.

Where to go from here?

The forest model applied in this thesis allows for investigating aboveground forest dynamics on different spatial scales, from single trees to several square kilometres. Depending on specific research questions, we see different interesting starting points on the basis of this thesis:

- Downscaling I: species-specific differences. Due to the lack of empirical data, in paper 3 we assumed equal responses of species to changed environmental conditions after landslides. But likely, different species will respond differently. Therefore, it would be interesting, given that knowledge is available, to combine different responses of species or species groups and investigate the outcome on the pathway of forest regeneration.

- Downscaling II: Local level of landslides. Given the interest in local community dynamics within landslide surfaces, one may wish to look at a finer spatial resolution than the

resolution of our model. In this case, it may be important to distinguish different zones within landslides (upper and lower zone, landslide edges versus centre), as is frequently done in field studies(e.g. Wilcke et al., 2003; Velazquez and Gomez-Sal, 2008).

- Upscaling: Landscape level characteristics of landslides. By incorporating topography and possibly other factors connected to soil characteristics and slope hydrology into the forest model and relating landslide probability to these attributes, one could obtain a realistic spatial distribution of landslides (e.g. landslides density is likely higher in steep areas). This will improve estimations of the effect of landslides on the forest carbon budget (see General outlook 4.3). Comparing realistic landslide maps derived from aerial photographs or other remote sensing techniques with outcomes of the simulation model offers various opportunities for model validation.

- Model extension: below-ground vegetation dynamics. So far our forest model concentrates on the detailed description of aboveground ground forests dynamics. An extension which also includes detailed below-ground vegetation dynamics may be important for various reasons: first, the quantification of the carbon pools of forest ecosystems requires estimations of the carbon stored in tree roots. Secondly, tree roots may play an important role in stabilizing slopes, as mentioned above. Therefore, a process-based, spatially explicit formulation of root distribution may aid in understanding the driving factors for landslides.

4.3 General outlook

In paper 2 and 3 we focused on the ridge forest, one out of four forest types occurring in the RBSF forest. In the near future, we will parameterize the remaining forest types, the ravine forest and the two types at higher elevations. The parametrization of a forest model like FORMIND is a complex and time demanding task, that involves data from different sources. To facilitate the parametrization process and to deal with parameter uncertainty, we will utilize a Bayesian calibration framework which is currently under development (Hartig et al., in preparation). The model versions for all forest types of the RBSF will allow describing forest growth dynamics on the regional scale and estimating aboveground carbon budget. In cooperation with other research groups that investigate soil carbon pools, we further intend to extend our investigation from aboveground vegetation dynamics to the total carbon budget. The incorporation of landslides is an important aspect in this context, since landslides affect carbon dynamics by the relocation of vegetation and soil, as well as by creating new space for vegetation establishment.

Census data, that are commonly used for the parametrization of forest models, are often exclusively collected in undisturbed forest sites. For the validation of forest models that are used to simulate forest dynamics under disturbance, it would be highly important to also have field data from disturbed sites. In future, the increasing availability of remotely sensed data (with high resolution, e.g. 10m) will offer additional opportunities for model calibration and validation. In particular, we plan to use the results of Lidar-imagery for estimating biomass for the whole study area and especially for landslide disturbed sites (Van Den Eeckhaut et al., 2007; Frolking et al., 2009; Köhler and Huth, 2010).

A central aim of the DFG Research Unit 816 is to develop sustainable management scenarios for our study region. Apart from pasture management, this also involves sustainable use of remaining forest and potentially reforestation (e.g. Knoke et al., 2009). Previous experimental studies explored possible management strategies for the study region including targeted felling

of trees to promote economically valuable species and enrichment planting of selected species (Günter et al., 2004; Aguirre et al., 2006; Cabrera Cisneros et al., 2006; Mosandl and Günter, 2008). Our dynamic forest model provides a suitable framework to compare different management options concerning their long-term impact on forest structure and composition (e.g. Huth and Ditzer, 2001; Kammesheidt et al., 2002; Rüger et al., 2007a). Combining ecological models like our forest model with economic models that evaluate the economic benefits of different land use options will enable the development of environmental policies that balance ecological and economic benefits of land use.

Bibliography

Adler PB, HilleRisLambers J, Levine JM, 2007. A niche for neutrality. Ecol Lett 10, 95–104.

Aguirre N, Günter S, Weber M, Stimm B, 2006. Enrichment of Pinus patula plantations with native species in southern Ecuador. Lyonia 10, 33–45.

Alcantara-Ayala I, Esteban-Chavez O, Parrot JF, 2006. Landsliding related to land-cover change: A diachronic analysis of hillslope instability distribution in the Sierra Norte, Puebla, Mexico. Catena 65, 152–165.

Ashton PS, 1993. Conservation Biology. Chapman and Hall, New York. chapter Species richness in plant communities. pp. 4–22.

Attiwill PM, 1994. The disturbance of forest ecosystems - the ecological basis for conservative management. For Ecol Manag 63, 247–300.

Banitz T, Huth A, Grimm V, Johst K, 2008. Clumped versus scattered: how does the spatial correlation of disturbance events affect biodiversity? Theor Ecol 1, 231–240.

Beck E, Kottke I, Bendix J, Makeschin F, Mosandl R, 2008a. Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer, Berlin. volume 198 of *Ecological Studies*. chapter Gradients in a Tropical Mountain Ecosystem - a Synthesis. pp. 467–479.

Beck E, Mosandl R, Richter M, Kottke I, 2008b. Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer, Berlin. volume 198 of *Ecological Studies*. chapter The investigated gradients. pp. 55–62.

Beck E, Richter M, 2008. The Tropical Mountain Forest - Patterns and Processes in a Biodiversity Hotspot. Göttingen Centre for Biodiversity and Ecology. volume 2 of *Biodiversity and Ecology Series*. chapter Ecological aspects of a biodiversity hotspot in the Andes of southern Ecuador. pp. 195–217.

Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvalhais N, Rodenbeck C, Arain MA, Baldocchi D, Bonan GB, Bondeau A, Cescatti A, Lasslop G, Lindroth A, Lomas M, Luyssaert S, Margolis H, Oleson KW, Roupsard O, Veenendaal E, Viovy N, Williams C, Woodward FI, Papale D, 2010. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. Science 329, 834–838.

BIBLIOGRAPHY

Bendix J, Rollenbeck R, Richter M, Fabian P, Emck P, 2008. Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer, Berlin. volume 198 of *Ecological Studies*. chapter Climate. pp. 63–73.

Bolker B, 2008. Ecological Models and Data in R. Princeton University Press.

Borchsenius F, 1997. Patterns of plant species endemism in ecuador. Biodivers Conserv 6, 379–399.

Borga M, Dalla Fontana G, Da Ros D, Marchi L, 1998. Shallow landslide hazard assessment using a physically based model and digital elevation data. Environ Geol 35, 81–88.

Borga M, Tonelli F, dalla Fontana G, Cazorzi F, 2005. Evaluating the influence of forest roads on shallow landsliding. Ecol Model 187, 85–98.

Bossel H, Krieger H, 1991. Simulation-model of natural tropical forest dynamics. Ecol Model 59, 37–71.

Brehm G, Pitkin LM, Hilt N, Fiedler K, 2005. Montane andean rain forests are a global diversity hotspot of geometrid moths. J Biogeogr 32, 1621–1627.

Brooks TM, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C, 2002. Habitat loss and extinction in the hotspots of biodiversity. Conserv Biol 16, 909–923.

Bugmann H, 2001. A review of forest gap models. Climate Change 51, 259–305.

Bussmann R, Wilcke W, Richter M, 2008. Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer, Berlin. volume 198 of *Ecological Studies*. chapter Landslides as Important Disturbance Regimes - Causes and Regeneration. pp. 319–330.

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie JC, Watson R, 2010. Global biodiversity: Indicators of recent declines. Science 328, 1164–1168.

Cabrera Cisneros O, Günter S, Mosandl R, 2006. Dynamics in natural and selectively logged tropical mountain rain forest of South Ecuador. Lyonia 10, 87–97.

Chaudhry S, Singh SP, Singh JS, 1996. Performance of seedlings of various life forms on landslide-damaged forest sites in Central Himalaya. J Appl Ecol 33, 109–117.

Chave J, 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. Ecol Model 124, 233–254.

Chave J, Muller-Landau HC, Levin SA, 2002. Comparing classical community models: Theoretical consequences for patterns of diversity. Am Nat 159, 1–23.

Chesson P, 2000. Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31, 343–366.

Clark J, Dietze M, Chakraborty S, Agarwal P, Ibanez I, LaDeau S, Wolosin M, 2007. Resolving the biodiversity paradox. Ecol Lett 10, 647–659.

Clark JS, 2010. Individuals and the variation needed for high species diversity in forest trees. Science 327, 1129–1132.

Clark JS, Bell D, Chu CJ, Courbaud B, Dietze M, Hersh M, HilleRisLambers J, Ibanez I, LaDeau S, McMahon S, Metcalf J, Mohan J, Moran E, Pangle L, Pearson S, Salk C, Shen ZH, Valle D, Wyckoff P, 2010. High-dimensional coexistence based on individual variation: a synthesis of evidence. Ecol Monogr 80, 569–608.

Condit R, Hubbell SP, Lafrankie JV, Sukumar R, Manokaran N, Foster RB, Ashton PS, 1996. Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots. J Ecol 84, 549–562.

Connell J, 1971. Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands. chapter On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. pp. 298–313.

Connell JH, Slatyer RO, 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111, 1119–1144.

Conservation International, . Biodiversity hotspots. `www.biodiversityhotspots.org`.

Crawley M, 1997a. Plant Ecology. Blackwell Science, Oxford. chapter Structure of Plant Communities. pp. 475–531.

Crawley M, 1997b. Plant Ecology. Blackwell Science, Oxford. chapter Life History and Environment. pp. 73–131.

Cruden D, 1991. A simple definition of a landslide. Bulletin of the International Association of Engineering Geology 43, 27–29.

Dalling JW, 1994. Vegetation colonization of landslides in the Blue Mountains, Jamaica. Biotropica 26, 392–399.

Dalling JW, Tanner EVJ, 1995. An experimental study of regeneration on landslides in montane rain forest in Jamaica. J Ecol 83, 55–64.

Darwin C, Wallace A, 1858. On the tendency of species to form varieties: and on the perpetuation of varieties and species by natural means of selection. J Linnean Society (Zool) 3, 46–50.

Dhakal AS, Sidle RC, 2003. Long-term modelling of landslides for different forest management practices. Earth Surf Proc Land 28, 853–868.

Dirzo R, 2001. Global Biodiversity in a Changing Environment. Springer, New York. volume 152 of *Ecological Studies*. chapter Tropical Forests. pp. 251–276.

Dislich C, Günter S, Homeier J, Schröder B, Huth A, 2009. Simulating forest dynamics of a tropical montane forest in South Ecuador. Erdkunde 63, 347–364.

Dislich C, Johst K, Huth A, 2010. What enables coexistence in plant communities? Weak versus strong species traits and the role of local processes. Ecol Model 221, 2227–2236.

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J, 1994. Carbon pools and flux of global forest ecosystems. Science 263, 185–190.

Dudek A, Ek A, 1980. A bibliography of worldwide literature on individual tree based stand growth models. Staff Paper Series, Dep. of Forest Resources, University of Minnesota 12, 1–34.

Dufour A, Gadallah F, Wagner HH, Guisan A, Buttler A, 2006. Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. Ecography 29, 573–584.

Durrett R, Levin S, 1994. The importance of being discrete (and spatial). Theor Popul Biol 46, 363–394.

Dynesius M, Jansson R, 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc Natl Acad Sci USA 97, 9115–9120.

Ehrlich PR, Ehrlich AH, 1992. The value of biodiversity. Ambio 21, 219–226.

Ek A, Monserud R, 1974. Growth models for tree and stand simulation. Royal College of Forestry, Stockholm, Sweden. volume 30 of *Research Notes*. chapter Trials with program FOREST: Growth and reproduction simulaltion for mixed species even- or unevenaged forest stands. pp. 56–73.

Elias RB, Dias E, 2009. Effects of landslides on the mountain vegetation of Flores Island, Azores. J Veg Sci 20, 706–717.

FAO, 2009. State of the World´s Forests 2009. Rome, Italy.

Fearnside PM, 2005. Deforestation in Brazilian Amazonia: History, rates, and consequences. Conserv Biol 19, 680–688.

Fetcher N, Haines BL, Cordero RA, Lodge DJ, Walker LR, Fernandez DS, Lawrence WT, 1996. Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. J Ecol 84, 331–341.

Francis AP, Currie DJ, 2003. A globally consistent richness-climate relationship for angiosperms. Am Nat 161, 523–536.

Frolking S, Palace MW, Clark DB, Chambers JQ, Shugart HH, Hurtt GC, 2009. Forest disturbance and recovery: A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. J Geophys Res-Biogeosc 114, 1–27.

Garwood NC, Janos DP, Brokaw N, 1979. Earthquake-caused landslides - a major disturbance to tropical forests. Science 205, 997–999.

Geertsema M, Pojar JJ, 2007. Influence of landslides on biophysical diversity - A perspective from British Columbia. Geomorphology 89, 55–69.

Gentry AH, 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann Mo Bot Gard 75, 1–34.

Glade T, 2003. Landslide occurrence as a response to land use change: a review of evidence from New Zealand. Catena 51, 297–314.

Günter S, Stimm B, Weber M, 2004. Silvicultural contributions towards sustainable management and conservation of forest genetic resources in southern ecuador. Lyonia 6 (1), 75–91.

Grace J, 2004. Understanding and managing the global carbon cycle. J Ecol 922, 189–202.

Grimm V, Railsback S, 2005. Individual-based Modeling and Ecology. Princeton University Press.

Groeneveld J, Alves LF, Bernacci LC, Catharino ELM, Knogge C, Metzger JP, Pütz S, Huth A, 2009. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. Ecol Model 220, 2450–2459.

Grote R, Erhard M, 1999. Simulation of tree and stand development under different environmental conditions with a physiologically based model. For Ecol Manag 120, 59–76.

Guariguata MR, 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. J Ecol 78, 814–832.

Gutierrez AG, Armesto JJ, Aravena JC, Carmona M, Carrasco NV, Christie DA, Pena MP, Perez C, Huth A, 2009. Structural and environmental characterization of old-growth temperate rainforests of northern Chiloe Island, Chile: Regional and global relevance. For Ecol Manag 258, 376–388.

Guzzetti F, Carrara A, Cardinali M, Reichenbach P, 1999. Landslide hazard evaluation: a review of current techniques and their application in a multi-scale study, Central Italy. Geomorphology 31, 181–216.

Hansen MC, Stehman SV, Potapov PV, 2010. Quantification of global gross forest cover loss. Proc Natl Acad Sci USA 107, 8650–8655.

Hartig F, Dislich C, Huth A, in preparation. Approximate bayesian calibration by simulated pseudo-likelihoods for a stochastic model of tropical forests .

Hastings A, 1980. Disturbance, coexistence, history, and competition for space. Theor Popul Biol 18, 363–373.

Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG, 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84, 3105–3117.

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Hogberg P, Huss-Danell K, Joshi J, Jumpponen A, Korner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH, 1999. Plant diversity and productivity experiments in European grasslands. Science 286, 1123–1127.

Heller NE, Zavaleta ES, 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biol Conserv 142, 14–32.

Homeier J, Werner FA, 2007. Provisional Checklists of Flora and Fauna of the San Francisco valley and its surroundings (Estación Científica San Francisco), Southern Ecuador. Society for Tropical Ecology. volume 4 of *Ecotropical Monographs*. chapter Spermatophyta. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S-Ecuador). pp. 15–58.

Homeier J, Werner FA, Gradstein SR, Breckle SW, Richter M, 2008. Gradients in a Tropical Mountain Ecosystem of Ecuador. Springer, Berlin. volume 198 of *Ecological Studies*. chapter Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. pp. 87–100.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA, 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75, 3–35.

Houghton RA, Hall F, Goetz SJ, 2009. Importance of biomass in the global carbon cycle. J Geophys Res-Biogeosc 114, 1–13.

Hubbell S, 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Monographs in Population Biology, Princeton University Press.

Huston M, 1994. Biological Diversity - The coexistence of species in changing landscapes. Cambridge University Press.

Huth A, 1999. Modellierung des Wachstums und der Nutzung von tropischem Regenwald. Habilitationsschrift, Universität Kassel.

Huth A, Ditzer T, 2001. Long-term impacts of logging in a tropical rain forest – a simulation study. For Ecol Manag 142, 33–51.

Huth A, Drechsler M, Kohler P, 2005. Using multicriteria decision analysis and a forest growth model to assess impacts of tree harvesting in dipterocarp lowland rain forests. For Ecol Manag 207, 215–232.

Imaizumi F, Sidle RC, Kamei R, 2008. Effects of forest harvesting on the occurrence of landslides and debris flows in steep terrain of central Japan. Earth Surf Proc Land 33, 827–840.

Jablonski D, Roy K, Valentine JW, 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science 314, 102–106.

Jakob M, 2000. The impacts of logging on landslide activity at Clayoquot Sound, British Columbia. Catena 38, 279–300.

Janzen DH, 1970. Herbivores and the number of tree species in tropical forests. Am Nat 104, 501–528.

Jeltsch F, Moloney K, Schurr F, Kochy M, Schwager M, 2008. The state of plant population modelling in light of environmental change. Perspect Plant Ecol 9, 171–189.

Jeltsch F, Wissel C, 1994. Modelling dieback phenomena in natural forests. Ecol Model 75-76, 111–121.

Johnson CM, Zarin DJ, Johnson AH, 2000. Post-disturbance aboveground biomass accumulation in global secondary forests. Ecology 81, 1395–1401.

Johst K, Huth A, 2005. Testing the intermediate disturbance hypothesis: When will there be two peaks of diversity? Divers Distrib 11, 11–20.

BIBLIOGRAPHY

Kammesheidt L, Köhler P, Huth A, 2002. Simulating logging scenarios in secondary forest embedded in a fragmented neotropical landscape. For Ecol Manag 170, 89–105.

Keating PL, 2008. The floristic composition and biogeographical significance of a megadiverse paramo site in the southern Ecuadorian Andes. J Torrey Bot Soc 135, 554–570.

Kessler M, 1999. Plant species richness and endemism during naturel landslide succession in a perhumid montane forest in the Bolivian Andes. Ecotropica 5, 123–136.

Köhler P, 2000. Modelling anthropogenic impacts on the growth of tropical rain forests. Ph.D. thesis. Univeristät Kassel.

Köhler P, Ditzer T, Huth A, 2000. Concepts for the aggregation of tropical tree species into functional types and the application on Sabah's dipterocarp lowland rain forests. J Trop Ecol 16, 591–602.

Köhler P, Huth A, 2010. Towards ground-truthing of spaceborne estimates of above-ground life biomass and leaf area index in tropical rain forests. Biogeosciences 7, 2531–2543.

Klausmeier CA, Tilman D, 2002. Competition and Coexistence. Springer, Berlin. volume 161 of *Ecological Studies*. chapter 3: Spatial Models of Competition. pp. 43–78.

Kneitel JM, Chase JM, 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol Lett 7, 69–80.

Knoke T, Calvas B, Aguirre N, Román-Cuesta RM, Günter S, Stimm B, Weber M, Mosandl R, 2009. Can tropical farmers reconcile subsistence needs with forest conservation? Front Ecol Environ 7, 548–554.

Kohyama T, 1992. Size-structured multispecies model of rain-forest trees. Funct Ecol 6, 206–212.

Kraft N, Valencia R, Ackerly D, 2008. Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. Science 322, 580–582.

Kreft H, Jetz W, 2007. Global patterns and determinants of vascular plant diversity. Proc Natl Acad Sci USA 104, 5925–5930.

Kürpick P, Kürpick U, Huth A, 1997. The influence of logging on a malaysian dipterocarp rain forest: A study using a forest gap model. J Theor Biol 185, 47–54.

Lehnert M, Kessler M, Salazar L, Navarrete H, Gradstein S, 2007. Provisional Checklists of Flora and Fauna of the San Francisco valley and its surroundings (Estación Científica San Francisco), Southern Ecuador. Society for Tropical Ecology. volume 4 of *Ecotropical Monographs*. chapter Pteridophytes. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S-Ecuador). pp. 59–68.

Levins R, 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15, 237–240.

Levins R, Culver D, 1971. Regional coexistence of species and competition between rare species (mathematical model/habitable patches). Proc Natl Acad Sci USA 68, 1246–1248.

Liess M, Glaser B, Huwe B, 2009. Digital soil mapping in southern ecuador. Erdkunde 63, 309–319.

Lischke H, Löffler T, 2006. Intra-specific density dependence is required to maintain species diversity in spatio-temporal forest simulations with reproduction. Ecol Model 198, 341–361.

Liu JG, Ashton PS, 1998. Formosaic: An individual-based spatially explicit model for simulating forest dynamics in landscape mosaics. Ecol Model 106, 177–200.

Logofet DO, Lesnaya EV, 2000. The mathematics of Markov models: what Markov chains can really predict in forest successions. Ecol Model 126, 285–298.

MacArthur RH, 1972. Geographical ecology. Princeton University Press, Princeton, N. J.

Malhi Y, Baldocchi DD, Jarvis PG, 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ 22, 715–740.

Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li WH, Nobre CA, 2008. Climate change, deforestation, and the fate of the amazon. Science 319, 169–172.

May RM, 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J.

McGlone MS, 1996. When history matters: Scale, time, climate and tree diversity. Global Ecol Biogeogr Lett 5, 309–314.

Mittermeier RA, Robles Gil P, Hoffmann M, Pilgrim J, Brooks T, Goettsch Mittermeier C, Lamoreux J, Da Fonseca G, Alger K, Boltz F, Brandon K, Bruner A, Da Silva J, Carter A, Cavalcanti R, Carter A, Church R, Foster M, Gascon C, Gorenflo L, Gratwicke B, Guerin-Mcmanus M, Hannah L, Knox D, Konstant W, Lacher T, Langhammer P, Langrand O, Lapham N, Martin D, Myers N, Naskrecki P, Parr M, Pearson D, Prickett G, Rice D, Rylands A, Sechrest W, Smith M, Stuart S, Thomson J, Totten M, Ward J, 2004. Hotspots Revisited - Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX Books on Nature. chapter Introduction. pp. 19–68.

Mohren GMJ, Burkhart HE, 1994. Contrasts between biologically-based process models and management-oriented growth and yield models - preface. For Ecol Manag 69, 1–5.

Montgomery DR, Dietrich WE, 1994. A physically-based model for the topographic control on shallow landsliding. Water Resour Res 30, 1153–1171.

Montgomery DR, Schmidt KM, Greenberg HM, Dietrich WE, 2000. Forest clearing and regional landsliding. Geology 28, 311–314.

Mosandl R, Günter S, 2008. The Tropical Mountain Forest - Patterns and Processes in a Biodiversity Hotspot. Göttingen Centre for Biodiversity and Ecology. volume 2 of *Biodiversity and Ecology Series*. chapter Sustainable management of tropical mountain forests in Ecuador. pp. 179–195.

Moser J, 1974. Growth models for tree and stand simulation. Royal College of Forestry, Stockholm, Sweden. volume 30 of *Research Notes*. chapter A system of equations for the components of forest growth. pp. 260–287.

Muller-Landau HC, 2008. Tropical Forest Community Ecology. Blackwell Publishing; 2002. chapter Colonization-related trade-offs in tropical forests and their role in the maintanance of plant species diversity. pp. 182–195.

Münkemüller T, Bugmann H, Johst K, 2009. Hutchinson revisited: Patterns of density regulation and the coexistence of strong competitors. J Theor Biol 259, 109–117.

Murrell DJ, Law R, 2003. Heteromyopia and the spatial coexistence of similar competitors. Ecol Lett 6, 48–59.

Myers N, 1988. Threatened Biotas: "Hot Spots" in Tropical Forests. The Environmentalist 8, 187–208.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J, 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Myster RW, Fernandez DS, 1995. Spatial gradients and patch structure on two Puerto Rican landslides. Biotropica 27, 149–159.

Nadrowski K, Wirth C, Scherer-Lorenzen M, 2010. Is forest diversity driving ecosystem function and service? Current Opinion In Environmental Sustainability 2, 75–79.

Noss RF, 2001. Beyond kyoto: Forest management in a time of rapid climate change. Conserv Biol 15, 578–590.

O'Brien EM, 1993. Climatic gradients in woody plant-species richness - towards an explanation-based on an analysis of southern Africa's woody flora. J Biogeogr 20, 181–198.

Ohl C, Bussmann R, 2004. Recolonization of natural landslides in tropical mountain forests of Southern Ecuador. Feddes Repetorium 115, 248–264.

Pacala SW, Rees M, 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. Am Nat 152, 729–737.

Paquette A, Messier C, 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Global Ecol Biogeogr 20, 170–180.

Parolly G, Kurschner H, Schafer-Verwimp A, Gradstein SR, 2004. Cryptogams of the Reserva Biologica San Francisco (Province Zamora-Chinchipe, Southern Ecuador) - III. Bryophytes - Additions and new species. Cryptogamie Bryol 25, 271–289.

Pickett S, 1989. Long-term studies in ecology. Springer, New York. chapter Space-for-time substitutions as an alternative to long-term studies. pp. 110 –135.

Potthoff M, Johst K, Gutt J, Wissel C, 2006. Clumped dispersal and species coexistence. Ecol Model 198, 247–254.

Pretzsch H, 2001. Modellierung des Waldwachstums. Parey Buchverlag Berlin.

Pronk TE, Duringa HJ, Schievinga F, 2007. Coexistence by temporal partitioning of the available light in plants with different height and leaf investments. Ecol Model 204, 349–358.

Rees M, Westoby M, 1997. Game-theoretical evolution of seed mass in multi-species ecological models. Oikos 78, 116–126.

Restrepo C, Vitousek P, Neville P, 2003. Landslides significantly alter land cover and the distribution of biomass: an example from the Ninole ridges of Hawai'i. Plant Ecol 166, 131–143.

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Restrepo C, Walker LR, Shiels AB, Bussmann R, Claessens L, Fisch S, Lozano P, Negi G, Paolini L, Poveda G, Ramos-Scharron C, Richter M, Velazquez E, 2009. Landsliding and its multiscale influence on mountainscapes. Bioscience 59, 685–698.

Rüger N, Gutiérrez, A.G.and Kissling W, Armesto J, Huth A, 2007a. Ecological impacts of different harvesting scenarios for temperate evergreen rain forest in southern chile - a simulation experiment. For Ecol Manag 252, 52–66.

Rüger N, Williams-Linera G, Kissling W, Huth A, 2007b. Long-term impacts of fuelwood extraction on a tropical montane cloud forest. Ecosystems 11, 868–881.

Richter M, Diertl KH, Emck P, Peters T, Beck E, 2009. Reasons for an outstanding plant diversity in the tropical andes of southern ecuador. Landscape Online 12, 1–35.

Ricklefs RE, 1977. Environmental heterogeneity and plant species-diversity - hypothesis. Am Nat 111, 376–381.

Ricklefs RE, 1987. Community diversity - relative roles of local and regional processes. Science 235, 167–171.

Rodríguez-Mahecha J, Salaman P, Jørgensen P, Consiglio T, Forno E, Telesca A, Suárez L, Arjona F, Rojas F, Bensted-Smith R, Inchausty V, 2004. Hotspots Revisited - Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX Books on Nature. chapter Tropical Andes. pp. 73–79.

Romme WH, Everham EH, Frelich LE, Moritz MA, Sparks RE, 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems 1, 524–534.

Rosenzweig M, 1995. Species diversity in space and time. Cambridge University Press.

Scherer-Lorenzen M, Körner C, Schulze ED (Eds.), 2005. Forest Diversity and Function - Temperate and Boreal Systems. volume 176 of *Ecological Studies*. Springer.

Schwappach A, 1890. Wachstum und Ertrag normaler Fichtenbestände. Julius Springer, Berlin.

Shea K, Roxburgh SH, Rauschert ESJ, 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecol Lett 7, 491–508.

Shorohova E, Kuuluvainen T, Kangur A, Jogiste K, 2009. Natural stand structures, disturbance regimes and successional dynamics in the eurasian boreal forests: a review with special reference to russian studies. Ann Forest Sci 66, 201.

Shugart H, 2002. Forest gap models. Internet-CRES-University of Virginia.

Shugart H, 2003. A Theory of Forest Dynamics - The Ecological Implications of Forest Succession Models. The Blackburn Press, Caldwell, N.J.

Shugart HH, Hopkins MS, Burgess IP, Mortlock AT, 1980. The development of a succession model for subtropical rain forest and its application to assess the effects of timber harvest at wiangaree-state-forest, new-south-wales. J Environ Manage 11, 243–265.

Shugart HH, West DC, 1980. Forest succession models. Bioscience 30, 308–313.

Sidle RC, 1992. A theoretical-model of the effects of timber harvesting on slope stability. Water Resour Res 28, 1897–1910.

Sidle RC, Wu WM, 1999. Simulating effects of timber harvesting on the temporal and spatial distribution of shallow landslides. Annals of Geomorphology 43, 185–201.

Sizer N, Miranda M, Brown P, Johnson N, Malk A, Miller K, 1997. The last frontier forests: Ecosystems and economics on the edge - What is the status of the world's remaining large, natural forest ecosystems? World Resource Institute.

Slatkin M, 1974. Competition and regional coexistence. Ecology 55, 128–134.

Smith JB, Schneider SH, Oppenheimer M, Yohe GW, Hare W, Mastrandrea MD, Patwardhan A, Burton I, Corfee-Morlot J, Magadza CHD, Fuessel HM, Pittock AB, Rahman A, Suarez A, van Ypersele JP, 2009. Assessing dangerous climate change through an update of the Intergovernmental Panel on Climate Change (IPCC) "reasons for concern". Proc Natl Acad Sci USA 106, 4133–4137.

Smith T, Shugart H, Woodward F (Eds.), 1997. Plant Functional Types - their relevance to ecosystem properties and global change. volume 1 of *International Geosphere-Biosphere Programme Book Series.* Cambridge University Press.

Soethe N, 2006. Structure and function of root systems at different altitudes of a south Ecuadorian montane forest. Ph.D. thesis. Humboldt-Universität zu Berlin.

Stearns S, 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

Stephenson NL, 1990. Climatic control of vegetation distribution - the role of the water-balance. Am Nat 135, 649–670.

Stern MJ, 1995. Biodiversity and conservation of neotropical montane forests. New York. chapter Vegetation recovery on earthquake-triggered landslide sites in the Ecuadorian Andes. pp. 207–220.

Stoyan R, 2000. Aktivität, Ursachen und Klassifikation der Rutschungen in San Francisco/Südecuador. Master's thesis. Institut für Geographie der Friedrich-Alexander-Universität Erlangen-Nürnberg.

Suffling R, Lihou C, Morand Y, 1988. Control of landscape diversity by catastrophic disturbance - a theory and a case-study of fire in a canadian boreal forest. Environ Manage 12, 73–78.

Suzuki T, 1971. Mitt. der Forestlichen Bundesversuchsanstalt. Wien. volume 91. chapter Forest transition as a stochastic process. pp. 137–150.

Thomas W (Ed.), 1956. Man's role in changing the face of the earth. University of Chicago Press, Chicago.

Thomson AM, Calvin KV, Chini LP, Hurtt G, Edmonds JA, Bond-Lamberty B, Frolking S, Wise MA, Janetos AC, 2010. Climate mitigation and the future of tropical landscapes. Proc Natl Acad Sci USA 107, 19633–19638.

Tilman D, 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2–16.

Tilman D, 1997. Plant Ecology. Blackwell Science, Oxford. chapter Mechanisms of Plant Competition. pp. 239–261.

Tilman D, Pacala S, 1993. Species Diversity in Ecological Communities. Univerity of Chicago Press; 1993. chapter The Maintenance of Species Richness in Plant Communities. pp. 13–25.

Townsend C, Harper J, Begon M, 2003. Ökologie. Springer, Berlin.

Valencia R, Valslev H, Miño G, 1994. High tree alpha-diversity in Amazonian Ecuador. Biodivers Conserv 3, 21–28.

Van Den Eeckhaut M, Poesen J, Verstraeten G, Vanacker V, Nyssen J, Moeyersons J, van Beek LPH, Vandekerckhove L, 2007. Use of LIDAR-derived images for mapping old landslides under forest. Earth Surf Proc Land 32, 754–769.

Vanclay JK, 1995. Growth-models for tropical forests - a synthesis of models and methods. For Sci 41, 7–42.

Vazquez DP, Stevens RD, 2004. The latitudinal gradient in niche breadth: Concepts and evidence. Am Nat 164, E1–E19.

Velazquez E, Gomez-Sal A, 2008. Landslide early succession in a neotropical dry forest. Plant Ecol 199, 295–308.

Vittoz P, Stewart GH, Duncan RP, 2001. Earthquake impacts in old-growth Nothofagus forests in New Zealand. J Veg Sci 12, 417–426.

Walker L, del Moral R, 2003. Primary Succession and Ecosystem Rehabilitation. Cambridge University Press, UK.

Walker LR, Shiels AB, 2008. Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides. Plant Soil 313, 205–216.

Weigend M, 2002. Observations on the biogeography of the Amotape-Huancabamba Zone in northern Peru. Bot Rev 68, 38–54.

van der Werf GR, Morton DC, DeFries RS, Olivier JGJ, Kasibhatla PS, Jackson RB, Collatz GJ, Randerson JT, 2009. Co_2 emissions from forest loss. Nat Geosci 2, 737–738.

Whitmore TC, 1998. An Introduction to Tropical Rain Forests. Oxford University Press.

Wilcke W, Valladarez H, Stoyan R, Yasin S, Valarezo C, Zech W, 2003. Soil properties on a chronosequence of landslides in montane rain forest, Ecuador. Catena 53, 79–95.

Wilcke W, Yasin S, Abramowski U, Valarezo C, Zech W, 2002. Nutrient storage and turnover in organic layers under tropical montane rain forest in ecuador. Eur J Soil Sci 53, 15–27.

Willig MR, Kaufman DM, Stevens RD, 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annu Rev Ecol Evol S 34, 273–309.

Wissel C, 1989. Theoretische Ökologie. Springer, Berlin.

Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Diaz S, Engelbrecht BMJ, Harms KE, Hubbell SP, Marks CO, Ruiz-Jaen MC, Salvador CM, Zanne AE, 2010. Functional traits and the growth-mortality trade-off in tropical trees. Ecology 91, 3664–3674.

Wu WM, Sidle RC, 1995. A distributed slope stability model for steep forested basins. Water Resour Res 31, 2097–2110.

Xie MW, Esaki T, Zhou GY, 2004. Gis-based probabilistic mapping of landslide hazard using a three-dimensional deterministic model. Nat Hazards 33, 265–282.

Yamamoto S, Nishimura N, Matsui K, 1995. Natural disturbance and tree species coexistence in an old-growth beech - Dwarf bamboo forest, southwestern Japan. J Veg Sci 6, 875–886.

Yodzis P, 1989. Introduction to theoretical ecology. Harper & Row, New York.

Young KR, Reynel C, 1997. Centres of plant diversity: A guide and strategy for their conservation, 3: North America, Middle America, South America, Caribbean Islands. IUCN, Cambridge, England. chapter Huancabamba Region, Peru and Ecuador. pp. 465–469.

Zarin DJ, Johnson AH, 1995. Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. Soil Sci Soc Am J 59, 1444–1452.

Zimmerman JK, Everham EM, Waide RB, Lodge DJ, Taylor CM, Brokaw NVL, 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto-Rico: implications for tropical tree life-histories. J Ecol 82, 911–922.

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