

The ecological niches of two Amazonian understory ferns, *Adiantum tomentosum* Klotzsch and *Lindsaea falcata* Dryand., in relation to light, topography and humus layers.

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Tutkin pro gradu-tutkielmassani *Adiantum*- ja *Lindsaea*-saniaislajien ekolokeroita Amazonian sademetsän kenttäkerroksessa. Maaperän arvioidaan olevan tärkeimpiä näiden lajien esiintymiseen vaikuttavia tekijöitä ja minä tutkin lajien sijoittumista pienemmässä mittakaavassa suhteessa valoon sekä humuskerroksen paksuuteen.

Tutkimus perustui perulaiseen luonnontilaiseen alankosademetsään perustamiini tutkimuslinjoihin. Näiden linjojen varrella mittasin tutkimuslajieni valo-olosuhteita, humuskerroksen paksuutta ja yksilöiden kokoa. Lisäksi dokumentoin topografiaa, metsän rakennetta, valo-olosuhteita ja muuta sanikkaislajistoa, sekä tutkimuslajien runsautta tutkimuslinjojen varrella. Valomittaukset tein digitaalisten latvuskuvien avulla.

Metsän rakenne, valo-olosuhteet ja sanikkaislajisto riippuivat pitkälti topografiasta, kuten tutkimuslajieni esiintymisenkin. *Lindsaea falcata* esiintyi useimmiten kukkuloiden rinteissä, mahdollisesti hieman hämäämmissä paikoissa kuin *Adiantum tomentosum*. Viitteitä tutkimuslajien eriytymisestä valon suhteen saatiin sekä yksilöiden kohdalla tehdyistä suorista mittauksista, että runsauteen pohjautuvasta aineistostani. Valon määrä ei kuitenkaan vaikuttanut *L. falcatan* kasvuun tai lisääntymiseen. *A. tomentosum* oli tutkimusalueen sanikkaislajeista runsaslukuisin ollen harvinainen vain laaksojen pohjalla. Valon määrä ei vaikuttanut lajin esiintymiseen tai runsauteen, mutta valoisammassa kasvavat *A. tomentosumit* olivat useammin itiöiviä yksilöitä. Lisäksi *A. tomentosum* kasvoi keskimäärin paksummassa humuskerroksessa kuin *L. falcata*, mikä voi selittää *L. falcatan* runsautta rinteissä, joissa oli enemmän paljaan maan laikkuja.

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In my master's thesis study I am studying the role of light and humus layers in niche partitioning between ferns of the genera *Adiantum* and *Lindsaea* in the Amazon rainforest understory. Soils have been shown to be among the most important factors in determining the niche space of these species and light was expected to be one of the factors affecting the microhabitats where they are occurring within forests on the same soil type.

The study was based on transects that I established into primary rainforest in Peruvian Western Amazonia. Along these transects I documented light conditions and humus layer depth at the microhabitats of the focal species. Additionally I documented topography, forest structure, light conditions and pteridophyte (ferns and lycophytes) species community composition along the transects. Light conditions were measured using digital hemispherical photographs.

Forest structure, light conditions and pteridophyte species communities were found to be strongly affected by topography, as was the occurrence of the focal species. *Lindsaea falcata* was found to occur mostly on hill slopes, possibly in more shady microhabitats than *Adiantum tomentosum*. The light partitioning hypothesis was supported by both direct measurements at the microhabitats and abundance data. Fertility or size of *L. falcata* was not affected by light. *A. tomentosum* was found to be the most common pteridophyte species in the study area with the species being rarer only in valley bottoms. Occurrence or abundance of *A. tomentosum* was not affected by the amount of light received, although light had a positive effect on the fertility of the species. *A. tomentosum* was also found to occur on deeper humus layers than *L. falcata*, which might explain why *L. falcata* was most common on slopes, as the slope positions seemed to contain more patches of bare soil.

KEYWORDS: Polypodiales, Rain forest ecology, Niche (Ecology), Hemispherical photography

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1. INTRODUCTION

Biodiversity is unevenly distributed and it is widely accepted that regions with high temperatures and precipitation, especially tropical rainforests, are some of the most species-rich ecosystems on earth (e.g. Barthlott et al. 1996, Hawkins et al. 2003). Vascular plants is a group reasonably well documented in comparison to insects for example, and it is estimated that there are some 40 000- 80 000 species of vascular plants in tropical Asia, while tropical Africa harbours around 30 000 species (Raven 1988, Govaerts 2001). The neotropics, that is tropical South and Central America, however are most likely to harbour the highest plant diversity on earth with some 90 000 species of vascular plants (Gentry 1982, Raven 1988, Thomas 1999, Govaerts 2001, Francis & Currie 2003). Also some of the regions with the highest number of endemic species are located in rainforests, with some 20 000 endemic plant species and 1567 endemic vertebrates being found in the Tropical Andes, while Sundaland in South-East Asia has some 15 000 endemic plant species and 701 endemic vertebrates (Myers et al. 2000, Sodhi et al. 2004). Also 15 of the 25 global hotspots of species richness identified by Myers et al. (2000) were in tropical forests.

So what makes it possible for up to 473 different species of trees to occur on a single hectare of Amazonian rainforest (Valencia et al. 1994)? What determines the occurrence of species in ecosystems with such an immense biodiversity? According to the niche partitioning hypothesis species coexistence even in the most diverse ecosystems is made possible through divergence in the use of resources (Wiens 2011). For plants this would mean specialization in their use of light, water and nutrients, the vital resources required for photosynthesis and there is some evidence of each of the three affecting plant niches and distributions in Amazonia (e.g. Poorter & Arets 2003, Kreft et al. 2004, Zuquim et al. 2014).

1.1 EDAPHIC CONDITIONS AS DETERMINANTS OF THE ECOLOGICAL NICHE

It has been suggested that the main drivers of terrestrial plant species distributions in Amazonia could be broad-scale biogeographic variations in rainfall and soils (e.g. Clinebell et al. 1995, Higgins et al. 2011, Zuquim et al. 2014). Out of the 227 tree species dominating Amazonian forests, for example, 121 are edaphic habitat specialists preferring either swamp forests, seasonally inundated forests along white- or blackwater rivers, forests on white sand or completely non-inundated tierra firme forests (ter Steege et al. 2013). Structure and organisation of biodiversity within the apparently uniform tierra firme forests is less well understood than the differences between obviously different habitats, but also tierra firme forests are known to demonstrate a wide variety of edaphic conditions as the soils under these forests are by no means uniform, but of different origins and ages (Tuomisto et al. 1995, Tuomisto & Poulsen 1996, Rebata 2012).

Soil cation concentration, that is the nutrients available for plant growth, has repeatedly emerged as an important factor affecting Melastomataceae, pteridophyte and palm species community composition in Amazonian tierra firme forests (e.g. Suominen et al. 2013, Zuquim et al. 2014, Cámara-Leret et al. 2017). Also tree species communities in tierra firme forests may behave similarly as it seems that geological formations can be deduced from satellite imagery (Tuomisto et al. 1995, Tuomisto et al. 2003a, Ruokolainen et al. 2007, Higgins et al. 2011). Satellite images for example reveal a border of the Nauta and Pebas Formations in Northern Peruvian tierra firme rainforests, where also an abrupt change in pteridophyte and Melastomataceae communities can be observed (Higgins et al. 2011).

There are strong indications that the cation content of tierra firme rainforest soils can be deduced based on species composition, which would make possible classifying forest types based on inventoring readily recognizable pteridophyte or Melastomatacea species (e.g. Tuomisto 1998, Salovaara et al. 2004, Cárdenas et al. 2007, Ruokolainen et al. 2007, Suominen et al. 2013). This is possible because many pteridophyte species seem to be restricted to certain kinds of soils even though their geographic ranges in the Neotropics might be quite large (Tuomisto & Poulsen 1996). Due to similar soils for example Manú in Southern Peru is floristically more similar to Barro Colorado Island in Panama than to many rainforest sites in Northern Peru. Tierra firme forests at least in Western Amazonia may actually consist of a patchy mosaic of forest types occurring on soils with differing edaphic properties (Tuomisto et al. 1995, Tuomisto et al. 2003a, 2003b). This indicates that seemingly uniform Western Amazonian tierra firme forests could be highly variable both among and within regions.

Within regions pronounced differences in plant communities can be observed also at the landscape-scale, in which case they often correlate with topography (Tuomisto et al. 1995, Tuomisto et al. 2003a, Costa 2006, Poulsen et al. 2006). Differences in moisture availability affect plant communities and drainage conditions are affected by topography, which explains part of this landscape-scale variation in plant communities (Svenning et al. 1999, Tuomisto & Poulsen 2000, Costa 2006). In pteridophyte and herb communities on the same geological formations, some species have been found to prefer hilltops, while other species occur on the bottom of valleys or along streams (Tuomisto et al. 1998, Costa et al. 2005). Also tree and palm species communities have been found to differ at the landscape-scale according to topography (Kahn 1987, Clark et al. 1999, Svenning 1999). Indeed different plant communities seem to be affected by these small-scale edaphic differences very similarly with tree, palm, Melastomataceae and pteridophyte communities showing the same kind of responses (Tuomisto et al. 2000). Much of this landscape-scale variation in communities may actually reflect the same soil responses that are found on wider biogeographical scales, because the soils in valleys often differ not only in their moisture, but also in their cation, sand and clay contents from hilltop soils (e.g. Tuomisto et al. 2000, Poulsen et al. 2006, Zuquim et al. 2009).

1.2 LIGHT AND HUMUS LAYERS AS DETERMINANTS OF THE NICHE

From the broad biogeographical scale down to the landscape-scale plant species occurrences in Amazonia thus seem to be determined mostly by edaphic factors, differences caused by geological processes. However, many species may be found on very small areas in Amazonia, for example on plots with similar soils. Kreft et al. (2004) found 146 different epiphyte species on an area of 0.1 ha, 81 of which occurred just on one single emergent *Ceiba pentandra* tree in Yasuní, Ecuador. Small-scale environmental heterogeneity in microhabitats might make it possible for niche diversification within the otherwise apparently homogenous habitat. For example the availability of light and the depth of the organic layer, both of which are determined mostly by vegetation, are some of the factors causing small-scale heterogeneity within habitats (Chazdon & Pearcy 1991, Rodriguez & Costa 2012). Notable is also the scale of the plants themselves, small understory herbs are most likely to have an entirely different habitat patch scale than emergent trees.

Light availability could be expected to be an important factor determining plant niches especially in the rainforest understory where only a few percent of light reaches the forest floor (e.g. Rich et al. 1993, Montgomery & Chazdon 2001). The amount of light reaching rainforest plants varies in space from the canopy to the understorey, as well as in time, with occasional gaps of different sizes creating short-term environments with more light which might result in fierce competition in the understory (Denslow 1980, Koop & Sterck 1994, Montgomery & Chazdon 2001, Lindner 2011). Light and gap dynamics have been shown to be important in structuring tropical forests through niche partitioning as some tree species require gaps and light for recruitment, while others are more tolerant of shady conditions (Denslow 1987, Poorter & Arets 2003, Rüger et al. 2009). Also the abundance of some Amazonian palm species has been shown to be affected by forest structure indicating that treefall gaps may be important for their establishment (Kahn 1987). Under the closed canopy of old-growth tropical rainforests variation in the amount of light is much less, but nevertheless light partitioning affecting growth form and sapling success might happen between Amazonian tree species even in the absence of gaps (Terborgh & Mathews 1999, Montgomery & Chazdon 2002).

Treefall gaps have also been shown to affect the understorey herb community composition in Neotropical rainforests (Dirzo et al. 1992, Lima & Gandolfi 2009). For example sapling success in a species of *Psychotria* in a Colombian cloud forest and in several Melastomataceae-species in a Central American rainforest are positively affected by gaps (Ellison et al. 1993, Amézquita 1998). There are also indications of light partitioning between Melastomataceae species in the rainforest understory with seedling establishment success differing between species in different light regimes (Ellison et al. 1993). Light availability might affect not only seedling establishment, but also later life-history like growth and reproduction success as in two understorey herbs of the order Zingiberales (Westerband & Horvitz 2015).

Actual shade tolerance, the minimum light required for survival, which could be expected to be a key adaptation in the rainforest understory, is not very well understood and it is controversial whether shade-adapted plants maximize their carbon gain in low light or whether they are just able to tolerate shade better than their competitors (Valladares & Niinemets 2008). Traits that are supposed to be associated with shade tolerance are many, for example thin stems, large but thin leaves, high chlorophyll content, low chlorophyll a/b ratio, low dark respiration rate and low net photosynthetic rate. Shade tolerance should also be considered over the whole plant life cycle as reproduction under very shady conditions is often scarce. Many ferns in particular seem to be well adapted to shade and could thus be expected to demonstrate niche partitioning in relation to light, which has indeed been shown to occur among some fern species (Page 2002, Riaño & Briones 2013). For example the spatial distribution of three tree fern species in a Central American cloud forest has been found to be associated with differences in canopy openness, indicating light partitioning even though all three species seemed to be shade adapted (Riaño & Briones 2013). Similarly including canopy openness into models predicting pteridophyte communities in tropical rainforest both in Central America and Amazonia increased their explanatory power, even though clear light partitioning between species was not found (Jones et al. 2006, Zuquim et al. 2009, 2012). Most of the fern species studied by Zuquim et al. (2009) in Amazonia seemed to occur in low light habitats with only a subset of the species occurring also in treefall gaps.

The light regime in rainforests, however is highly dynamic and small herbs in the generally deeply shaded rainforest understory may be exposed to sunflecks, brief pulses of direct sunlight (Le Gouallec et al. 1990, Chazdon & Pearcy 1991). Sunflecks may be an extremely important resource in the understory, contributing to carbon gain or inducing germination, and shade-adapted plants could be expected to be efficient at using sunflecks (Chazdon & Pearcy 1991, Valladares & Niinemets 2008). On the other hand especially longer duration sunflecks may cause a dangerous rise in temperature and transpiration, which will inhibit photosynthesis and cause long-lasting damage to the photosynthetic apparatus (Le Gouallec et al. 1990). Different plant groups may also react differently to sunflecks: epiphytic plants react little to them due to water and carbon dioxide constraints, while light is a limiting factor for terrestrial rainforest plants and they may thus be more efficient at using sunflecks (Zhang et al 2009). Ferns again are restricted by simpler water carrying structure, slower water transport and sparse stomata, wherefore they may respond more slowly to sunflecks as compared to seed plants (Page 2002, Zhang et al. 2009). At the same time germination of fern spores may be inhibited by highly fluctuating temperatures, such as those caused by sunflecks (Pérez-García et al. 2007).

Depth of the humus layer, i.e. the amount of decaying leaf litter covering the rainforest floor, is another factor that varies both in space and time affecting predation of seeds, germination, establishment, growth and diversity of understory plants, thus providing

opportunities for niche partitioning at small scales (Molofsky & Augspurger 1992, Cintra 1997, Xiong & Nilsson 1999). Leaf litter influences the moisture, nutrients, temperature and light available for plants, while the amount of litter is affected by the amount of aboveground vegetation, topography, speed of decomposition and disturbance (Xiong & Nilsson 1999, Rodriguez & Costa 2012). Understory herbs are mostly negatively affected by litter and locations with less litter accumulation, such as slopes, may provide more chances for their establishment (Xiong & Nilsson 1999, Rodriguez & Costa 2012). Especially fern spores have been shown to require light for germination and thus their establishment may be greatly dependent on litter-free sites (Pérez-García et al. 2007, Rodriguez & Costa 2012). Many understory herbs growing under the closed canopy of old-growth rainforests may actually require litter gaps created through small-scale disturbance of the forest floor, rather than canopy gaps (Metcalf & Turner 1998).

Topographic position might affect plants not only through edaphic factors, but also the disturbance regime, i.e. light conditions and litter depth may vary according to topography (Gale 2000, Rodriguez & Costa 2012). Tree species composition, canopy height and density of tree stems, all of which might affect light conditions, have been shown to differ between different topographic positions (Kahn 1987, Svenning et al. 1999). Also the occurrence of gaps depends on topography as especially slope positions, but sometimes also valleys or plateaus, have been shown to have a higher frequency of treefall gaps than the surrounding forest (Kahn 1987, Denslow 1995, Gale 2000). Topography has also been shown to affect litter accumulation, with steeper slopes providing more possibilities for herb establishment as they have shallower humus layers and more litter gaps (Rodriguez & Costa 2012). At the same time canopy gaps with more light tend to accumulate less litter because of less vegetation, further complicating the separation of light and litter effects on understory plants and tree seedlings (Molofsky & Augspurger 1992).

1.3 AIMS OF THE STUDY, THE STUDY SPECIES

In this master's thesis study I investigate the small-scale heterogeneity affecting understory plants in the rainforest, more specifically if understory plant species differ in relation to their light environment and humus layers. To test this hypothesis I measured light conditions at the microhabitats of the study species as compared to the rainforest background, as well as compared depth of the organic layers at the microhabitats of the study species. Also the effect of light on the reproductive status of the study species was evaluated. Because topography was expected to affect not only the measured variables, but also occurrence and abundance of the study species, sampling was done in such a way as to include as much topographic variation as possible. Variation in soils was assessed indirectly with the help of clinometric profiles and pteridophyte (ferns and lycophytes) species inventories.

The reason why light conditions in rainforests have not been studied more often lies within the difficulty in measuring them exactly and in a repeatable manner. Hemispherical photography, if done correctly, is considered a quite reliable way of measuring indirectly the light conditions in tropical forests (Rich et al. 1993). One of the benefits of hemispherical photography in measuring light conditions is that it is possible to separate direct and indirect light quantifying the relative amount of light transmitted through the canopy over the course of a year (Anderson 1964). Taking hemispherical photographs is, however very laborious and it is therefore that the so-called canopy-scope has been suggested by Brown et al. (2000) as a more simple and rapid way of estimating light conditions in forests. The canopy-scope is a dot array on a transparent plastic plate, which is used to score forest openness on a scale of 1-25 based on the largest gap visible. My research will use both of these methods in data collection in order to evaluate their usefulness in documenting small-scale variation in light environments.

The study species are ferns of the genera *Adiantum* and *Lindsaea*, because they were known in advance to be common in the research area. Moreover soil preferences of fern species in these genera are already quite well-documented and my study was expected to provide further insight into the niche space of them especially in relation to light availability and humus layers. *Adiantum* and *Lindsaea* both belong to the order Polypodiales (PPG I 2016). The genus *Adiantum*, belonging to the family Pteridaceae, includes around 225 extant species occurring in tropical to boreal zones on all continents except Antarctica (PPG I 2016, GBIF.org). The genus *Lindsaea* is classified under the family Lindsaeaceae and includes around 180 species occurring on all tropical continents with some species extending also to the subtropics (PPG I 2016, Lehtonen et al. 2010). In Amazonia species of both genera seem to have diverged onto a gradient of soil nutrient content (Tuomisto & Poulsen 1996, Zuquim et al. 2014).

Adiantum was the most species-rich fern genus found by Zuquim et al. (2014) in a large-scale study done in central Amazonia and included 17 species, of which *A. argutum* and *A. pulverulentum* belonged to the most abundant species. Also in studies done in Western Amazonia *Adiantum* species have been among the most frequently encountered pteridophytes with *A. tomentosum* being the dominant species at various sites in Peru and *A. humile* in Yasuní, Ecuador (Tuomisto & Poulsen 1996, Tuomisto et al. 2002). Nine out of the 17 *Adiantum* species found in Zuquim et al. (2014) were indicators of rich soils with *A. phyllitidis* being the pteridophyte species with the highest cation concentration optimum. Also *A. pulverulentum* has been reported to be restricted to soils with relatively high cation concentrations, where it may be very frequent, while *A. humile* and *A. terminatum* have been found to occur on intermediate soils, with *A. terminatum* extending also to poorer soils (Tuomisto & Poulsen 1996, Tuomisto et al. 1998, Zuquim et al. 2014). *A. tomentosum* has been reported to occur on poor loamy soils at the lower end of the cation concentration gradient, while no *Adiantum* species has been found growing on the very poorest sandy soils (Tuomisto et al. 1998, Zuquim et al. 2014).

Similarly *Lindsaea* species of Amazonian rainforests have been shown to differ in occurrence along a gradient of soil fertility. Only one species of the genus, *L. phassa*, has been reported to grow only on rather rich, clayey soils (Tuomisto & Poulsen 1996, Tuomisto 1998). The highest diversity of *Lindsaea* species has been found on poorer, loamy soils which is interesting as it is opposite to the general pattern of highest pteridophyte species diversity on richer soils (Tuomisto 1998, Tuomisto et al. 2014). Of these species for example *L. divaricata* has been found to be most abundant on waterlogged or sandy soils with extremely low cation content while *L. digitata* has been found mostly on well-drained soils, being absent from locations with the lowest cation contents, even though the two species are morphologically similar and have previously been considered to belong to the same species (Lehtonen & Tuomisto 2007). Two of the *Lindsaea* species, *L. tetraptera* and *L. hemiglossa*, have been found to be restricted to the poorest sandy soils (Tuomisto 1998).

Interestingly there are indications, in some of the *Lindsaea* species growing on intermediate soils, that they have diverged on other niche axes than soils (Tuomisto 1998). *L. falcata* and *L. guianensis* have been reported to often grow on decaying organic matter, which indicates that deep humus layers and decaying wood plays an important role in forming their ecological niches. Furthermore *L. falcata* was reported by Tuomisto & Ruokolainen (1994) to occur on loamy as well as on sandy soils, which could indicate that the thick humus substrate makes the species less sensitive to soil properties. Also *L. bolivarensis* and *L. taeniata* have been found to often occur on similar soils but for some reason rarely in the same locations (Tuomisto 1998).

2. MATERIALS AND METHODS

2.1 STUDY AREA AND STUDY SITES

The study area was in lowland non-inundated (tierra firme) tropical rainforest in Peru (Figs. 1, 2). The climate in the region is humid tropical with a total annual rainfall of 2450-3000 mm and a mean temperature of +26.5°C (Marengo 1998, Fick & Hijmans 2016). Half of the annual rain falls in the time between December and April with June-August being a slightly drier period with ca. 120-180 mm monthly rainfall. The study area is on the Nauta Formation, which consists of beige muddy sands to grey or reddish mud, soils of late Miocene estuarine origin (Rebata 2012). The concentration of extractable bases (sum of Ca, K, Mg and Na) in the topmost, weathered layers of the Nauta Formation has been reported to be around 40 µg/g or 0.12 cmol/kg, which in the regional context means intermediate to poor soils (Tuomisto & Poulsen 1996, Tuomisto et al. 1998, Rebata 2012). The landscape in the study area consists of small hills intersected by stream valleys ca. 30-40 meters deep.

The area for the study was chosen to be along the Iquitos-Nauta highway providing easy accessibility and still a relatively natural state of the forests. In the end the study was conducted close to km 82 on the highway, 10 km north of the town Nauta (Fig. 1). Most areas of the rainforest close to the highway had been cleared or selectively logged in recent years and therefore the first five days of field work were used to explore the area in order to find potential study sites representing primary rainforest with as little human disturbance as possible (Fig. 2). At the same time we studied the pteridophyte species in the area to find the most abundant *Adiantum* and *Lindsaea* species and to make sure that the study sites would be comparable in terms of their pteridophyte species composition, i.e. soils. Also a 225 m pilot transect was established in order to test and fine-tune the methodology. Access to the rainforest was provided by footpaths used by the locals for hunting.

In each site chosen for the study we made a campsite in order to use as effectively as possible the morning and evening lights necessary for taking the hemispherical photographs. Transects were established in primary forest in patches where *Adiantum* or *Lindsaea* species were found to occur and the minimum distance between transects was 20 meters. As true primary forest without signs of selective logging was patchy in the research area, sites got quickly exhausted of suitable transect sites, after which the campsite had to be moved to a new location. In the end 12 transects were thus established in three different sites. These

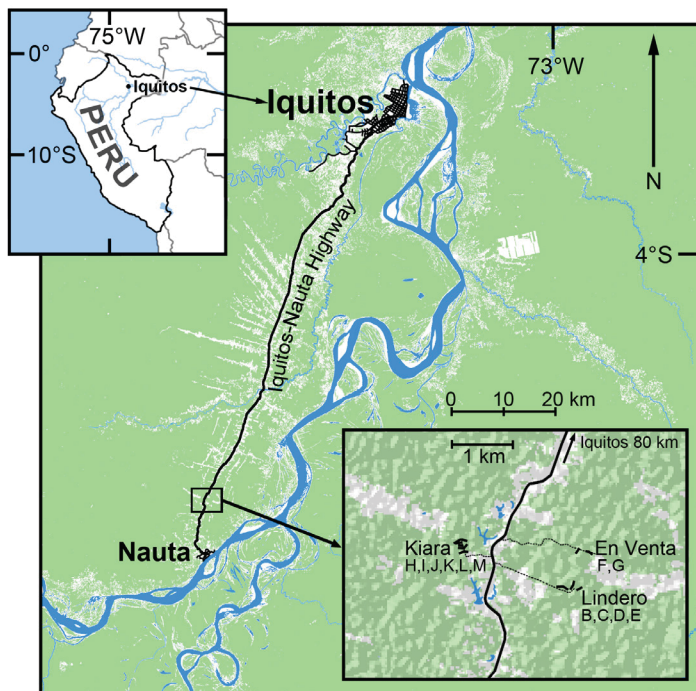


Figure 1. Location of the study area in Peru. Forested areas are in green, while deforested or naturally treeless environments are in white (Hansen et al. 2013). Water is in blue and the main roads in black. The three sites, which can be seen in the lower right map insert with hillshading (USGS 2004), are named after the footpaths leading to them, which are marked with a dashed line. The 12 transects are marked as black lines in their corresponding locations.

sites will hereafter be referred to by the names of the footpaths leading to them: Lindero, transects B-E ($4^{\circ} 24' 46.800''$ S, $73^{\circ} 35' 16.799''$ W), En Venta, transects F and G ($4^{\circ} 24' 50.813''$ S, $73^{\circ} 34' 16.813''$ W) and Kiara, transects H-M ($4^{\circ} 24' 47.973''$ S, $73^{\circ} 35' 19.107''$ W). Transect A was the pilot transect with slightly differing methods of data collection so it is left out of the analyses. Based on own GPS measurements and USGS (2004), the approximate altitudes in Kiara and Lindero ranged from 115-125 to 160 m above sea level and in En Venta from 130 to 170 m. Minimum distance between Lindero and En Venta was 460 m, while Kiara was a bit further away, a minimum of 1490 m from Lindero and 1760 m from En Venta.

2.2 DATA COLLECTION

I studied species of the genera *Adiantum* and *Lindsaea* in advance at the herbarium of the University of Turku and during the first days of fieldwork my supervisor Hanna Tuomisto then confirmed my first identifications of living plants. We collected the actual data between 27.5. and 9.6.2016 with a team consisting of Francisco Farroñay (FF) as my research assistant, Essau Shapiyama (ES) as our field assistant and me as the team leader. In order to account for topographic variation the transects were always established perpendicular to hillslopes, either up a hill or downwards (Fig. 2). While ES opened up the transects with a machete, avoiding to cut treelets and palms as far as possible, FF and I spanned a rope. The red rope had marks every 5 meters and meters written on it every 25 meters. Thereafter the side of the rope with more individuals of *Adiantum* or *Lindsaea* species was chosen to be the transect. The transects were continued until a stream valley bottom or hilltop was encountered, but if the transect was still quite short and the forest didn't change too much, transects were sometimes continued until the next hilltop or valley bottom.

In order to account for soil variation along the transects ES and I documented the clinometric profile of the transects using a Suunto-clinometer, while FF documented all pteridophyte species occurring in 10 m subplots within 5 m along the transect (epiphytic pteridophytes growing at an altitude of >2 m from the ground were excluded). Additionally FF documented the number of living trees with >30 cm diameter at breast height (dbh, as estimated in three classes: I: 30-60 cm, II: 60-90 cm, III: >90 cm) in 10 m subplots and within 10 meters on both sides of the rope. The number of trees in the three dbh classes was documented in order to evaluate forest structure and human disturbance of the forest, as primary forest without signs of selective logging was somewhat difficult to find in the area.



Figure 2. Data collection. Me standing next to transect F in En Venta surrounded by typical understory vegetation of the study area. On the right side of the photograph the red rope used for marking the transect line in the forest. (Photograph by Francisco Farroñay)

During establishment of the transects FF searched and marked *Adiantum* and *Lindsaea* species individuals along the transect with a white paper label so that they could be

identified again when measuring them and documenting their microhabitat characteristics. Only individuals growing within 0.5-2.5 meters on one side of the rope were chosen for the study because the area right around the rope had often quite a disturbed understorey as we walked back and forth along the transect and this was expected to have an effect on the hemispherical photographs. Individuals were defined as any group of leaves some distance apart that were not obviously growing from the same rhizome. If there was more than one individual of a species of interest in a 5 m subplot, only the one with the longest leaf was chosen for the measurements in order to avoid unnecessary repetition, but the total number of individuals in the subplot was still documented.

At each measured *Adiantum* and *Lindsaea* species individual per 5 m subplot I made, in addition to the hemispherical photographs, the following measurements: canopy-scope and relascope readings above the individual, length of the longest leaf, reproductive status (fertile or sterile) and depth of the humus layer under the individual (measuring the organic layer in a hole made with a knife). The relascope (1:60 ratio) measurements gave an approximation of the basal area in m^2ha^{-1} . If two individuals were closer than 0.5 meters to each other, the same relascope and canopy-scope readings were taken for both. Additional notes were made if the individual was for example growing epiphytically atop of a log or at the very base of a tree. To compare the species microhabitats to the forest background I also took hemispherical photographs, as well as canopy-scope and relascope readings at every 10 meters and at the start- and endpoints of the transects, 2.5 meters from the rope. These points will hereafter be referred to as background points. All the data collected was transferred from paper notes into Microsoft Excel tables shortly after the field work mainly by FF.

I took all the hemispherical photographs at a standard height of 56.5 cm (lens height) with a tripod above each measured *Adiantum* and *Lindsaea* species individual and at the background points. The camera used was a *Sony α -5000* digital camera combined with a *Yasuhara Madoka 180 7.3 mm f/4* fisheye lens that produced a roughly orthographic 180° projection. The photos were taken perpendicularly up (as determined with a circular bubble scale fixed to the camera body) and magnetic north was marked with a pale stick which was fixed on the upper side of the lens. All the photos were taken with aperture 5.6, focus ∞ and ISO 800 at 5 MP resolution. Shutter speed was adjusted manually such that all photos were underexposed by ca. -1.7 stops in order to reach maximum contrast between sky and the leaves/branches. If the stick marking north was not visible in the photo another one was taken with less underexposure for northing. If a leaf of the understorey would cover the lens entirely, the leaf was removed. To avoid direct sunlight in the hemispherical photographs, they were only taken in the morning between sunrise and 08:00 and in the afternoon between 16:30 and sunset, except on cloudy days, when the time for taking the hemispherical photographs could be extended by ca. 2 hours. The photographs were linked to the corresponding fern individuals and transect points by individual codes.

2.3 LIGHT MEASURES

Before analysis I had to process all hemispherical photographs in such a way that white pixels would correspond to visible sky and black pixels would correspond to leaves, branches and trees obstructing light (Fig. 3a-d). Based on this ratio of white to black pixels as back-projected to the hemisphere photographed it was possible to calculate not only canopy openness, but also the relative amount of sunlight that was transmitted through the canopy.

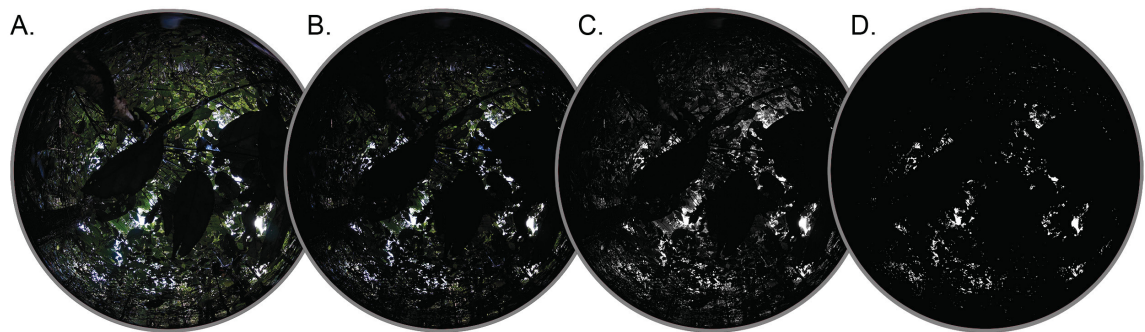


Figure 3. An example of the processing of the hemispherical photographs. The original photograph (a) was first back-corrected for its gamma-function (b), after which only the blue channel was retained (c) and thresholded (d). This photograph was taken on transect F and canopy openness calculated from it was 1.02 % and the Direct Site Factor 1.97 %.

All the hemispherical photographs were rotated such that north was up and after this I processed them as recommended by Chianucci & Cutini (2012). First I back-corrected the photographs gamma-function to the linear function originally recorded by the digital camera's sensor (Fig. 3b). This was done in Adobe Photoshop CS4 with a semi-automated process back-correcting the gamma function of 2.2, transformed by the digital camera, with a function of 0.45 to 1 ($1/2.2=0.4545\dots$). In the same semi-automated process also the red and green channels were removed from the RGB images (Fig. 3c). This was done in order to produce monochrome images of only the blue band, as the contrast between the green foliage and the sky is highest in these wavelenghts (Jonckheere et al. 2005, Chianucci & Cutini 2012, Glatthorn & Beckshäfer, 2014).

2.3.1 TRESHOLDING THE HEMISPHERICAL PHOTOGRAPHS

The next step was to binarize the hemispherical photos for analysis (Fig. 3d). An automated procedure was preferred both to avoid subjectivity, and because there were more than 700 photographs to be thresholded and analyzed, which would have been very laborous to do manually. The literature about thresholding hemispherical photographs is inconsistent as to what would be the best method. According to Jonckheere et al. (2005) the IsoData algorithm, which is based on the Ridler & Calvard 1978 clustering method, would be best suited for distinguishing between vegetation and sky, whereas other authors preferred the minimum algorithm (Glatthorn & Beckshäfer 2014).

Due to this inconsistency in literature I decided to make a small comparison of manual thresholding to the automated algorithms IsoData and minimum. I thus compared means and variation of canopy openness in photographs taken in the same place with different exposures and thresholded by different algorithms with a two-way ANOVA (analysis of variance). The place effect was used in the analysis as the factor tested for and exposure and thresholding methods were included as nominal factors. Post-hoc comparisons were conducted with a Tukey's HSD-test. For further comparisons of resolution between the thresholding methods two-way analyses of variance were also conducted separately for canopy openness derived with the different thresholding methods. Here place was the effect tested for and exposure was used as a second nominal factor. These tests were conducted using built-in functions of R version 3.1.3 (R Core Team) in RStudio version 0.98.1103 (RStudio team).

Based on a test set of 24 photos it seemed that exposure ($p < 0.0001$, $F_{(1,57)} = 25.34$) as well as thresholding ($p = 0.0010$, $F_{(2,57)} = 7.78$) had a strong effect on the canopy openness derived from the hemispherical photographs, but nevertheless the place effect persisted ($p < 0.0001$, $F_{(11,57)} = 10.15$). The thresholding algorithm IsoData exaggerated canopy openness as compared to both, the manually thresholded photos ($p = 0.0035$) as well as the photos thresholded with the minimum algorithm ($p = 0.0032$), while there was no difference between photographs thresholded manually versus using the minimum algorithm ($p = 0.9994$). In underexposed photographs the difference between thresholding methods was smaller and the effects of place and exposure also differed within thresholding methods. In photographs thresholded with the algorithm IsoData no place effect was detected, but exposure had an effect on canopy openness ($p = 0.0284$, $F_{(1,11)} = 6.36$). With the algorithm minimum only a marginal place effect was detected ($p = 0.0975$, $F_{(11,11)} = 2.25$) and the effect of exposure persisted ($p = 0.0302$, $F_{(1,11)} = 6.19$). With manual thresholding the marginal place effect was also detected ($p = 0.0688$, $F_{(11,11)} = 2.54$), while the effect of exposure was diminished ($p = 0.0831$, $F_{(1,11)} = 3.63$). In summary it thus seems, based on this small dataset of 24 photographs, that manual thresholding is the best method, as it is even able to diminish the effect of exposure on the results, but the minimum algorithm didn't perform much worse than manual thresholding. In the end the slightly underexposed hemispherical photos were therefore automatically thresholded using the minimum-algorithm in the program ImageJ, version 1.51j8 (Rasband 1997).

2.3.2 FROM HEMISPHERICAL PHOTOGRAPHS TO LIGHT MEASURES

After thresholding all the hemispherical photographs I could proceed to analysing them. The results that I used for statistical testing were percent canopy openness and percentage of light transmitted through the canopy, which was further divided into direct and diffuse light. The canopy openness-value simply describes the ratio of white to black pixels as back-projected from the hemispherical photograph to the sky. The transmitted light measure again takes into account the latitude and northing of the image calculating the relative

amount of light transmitted through the canopy over the course of a year. Transmitted light consists of indirect light, which is scattered light transmitted through the canopy, as well as of direct light, which is only transmitted through the canopy along the path of the sun. The direct light component, which is biologically very relevant as it is, in the form of sunflecks, providing most of the light in the understory, will hereafter be referred as the Direct Site Factor or DSF (Anderson 1964). The measures derived from the hemispherical photographs will hereafter be collectively referred to as light measures, except where it is relevant to separate the different effects.

All photographs did not have exactly the same relative exposure and therefore I had to subjectively choose them so that they would be comparable with each other and the effect of exposure on the results would be diminished. Choosing the photographs without compromising the amount of data was possible because I had usually taken more than one photograph at each fern individual or background point. For each photograph pair, or group of photographs I thus chose the one corresponding to the apparent exposure of all photographs on average. For some 43 problematic photograph pairs, in which one photograph was over- and one severely underexposed, relative to the other photographs, I calculated averages for the light measures of both photographs in Microsoft Excel.

I did the analyses of the thresholded hemispherical images with the program Gap Light Analyzer, version 2.0 (Frazer et al. 1999). Magnetic declination in the research area was set to be 6,00° W (<https://www.ngdc.noaa.gov/geomag-web/> 17.3.2017 with the date 1.6.2016 and model WMM2015). Latitude of the transects was averaged to 4°24'55" S and elevation of the transects was rounded to 130 m (USGS 2014). The resolution chosen was 18 zenith rings and 24 azimuth sectors. Solar time step was 10 minutes and solar radiation calculations were made for the whole year. Projection was calibrated to the *Yasuhara Madoka 180*-lens, as this projection differed slightly from the theoretical orthographic projection.

2.4 ANALYSIS

2.4.1 PRELIMINARY DATA ANALYSIS

I started the initial data analysis by plotting the clinometric profiles, species richnesses, abundances of the *Adiantum* and *Lindsea* species, light measures and relascope readings along the transects to get a preliminary understanding of possible patterns. I also calculated species-wise mean leaf lengths and proportion of epiphytic and fertile individuals for the measured *Adiantum* and *Lindsaea* species individuals. In order to determine the distribution types of the different variables I explored the data with the help of histograms. The first statistical tests on the data were done to verify correlations between the light measures and canopy-scope scores. Thus I tested for linear correlations between canopy-scope scores and light measures derived from the hemispherical photographs. I did all the statistical testing in R version 3.1.3 (R Core Team) using RStudio version 1.1.453 (RStudio team) and the packages used will be mentioned at the respective analyses.

2.4.2 ANALYSIS OF PTERIDOPHYTE COMMUNITY AND TOPOGRAPHIC DATA

To understand the pteridophyte species communities as well as to find possible topographic effects I used my data on the 124 transect subplots. This dataset consisted of basal areas, light measures, pteridophyte species and the total number of *Adiantum* and *Lindsaea* species individuals found in 10 m subplots along the transects. For the light measures, canopy-scope scores and basal areas I calculated means between the background points corresponding to the start- and endpoints of the subplots so that they would represent the mid-value found in the 10 m subplots. In order to understand the topographic effects and make statistical comparison possible I classified the 10 m subplots into four topographic positions. This classification was made on the basis of the clinometric profile such that the highest and lowest subplots of the transects were classified as hilltop and valley habitats respectively and the slope subplots were divided into upper and lower slope habitats at approximately half height (Fig. 6a, b).

Based on the species communities, which were represented as the presence/absence of all pteridophyte species found in the 10 m subplots, I generated a Jaccard dissimilarity matrix. From these Jaccard distances I computed and visualized a 2-dimensional Nonmetric Multidimensional Scaling (NMDS) as well as an unweighted arithmetic average clustering. In order to understand and interpret the structure of the cluster analysis I cross-tabulated the occurrence of species according to topographic positions and cluster groups. For better understanding of the communities I also calculated mean pteridophyte species richness (the mean number of species per subplot) in each cluster group and topographic position. The Jaccard dissimilarity matrix, the NMDS-ordination and the cluster dendrogram were generated using the R-package “vegan” (Oksanen et al. 2016).

To understand the effect of topography on the pteridophyte species richness, light measures, basal areas and number of trees in the three dbh classes, as well as to verify that the three sites were comparable, I conducted two-way ANOVAs (analyses of variance). Topography and site and their interaction were used as the nominal factors. Type I sums of squares are found to be inappropriate for ANOVAs conducted on unbalanced data (e.g. Shaw & Mitchell-Olds 1993). Furthermore type II sums of squares are found to be more powerful than type III sums of squares when there are no interactions between the nominal factors (Shaw & Mitchell-Olds 1993, Langsrud 2003). Because my data was severely unbalanced as there was not the same number of observations in each topographic position nor site and there was no reason to expect interactions, i.e. that different measurements would behave differently in different slope positions according to site or vice versa, I conducted the two-way ANOVAs using type II sums of squares using the R-package “car” (Fox & Weisberg 2011). A significance level of $p < 0.05$ was accepted as being statistically significant in all statistical tests and assumptions of the models were verified with the help of residual plots. Post-hoc comparisons were conducted with a Tukey’s HSD-test if a significant difference was first found in the ANOVA.

In order to compare the severely non-normally distributed canopy-scope scores I used a non-parametric Kruskal-Wallis tests, in which I tested if the distribution of canopy-scope scores differed between sites or topographic positions.

2.4.3 ANALYSIS OF DATA ON THE FOCAL SPECIES

For these statistical tests I used only the data we had collected on *A. tomentosum* and *L. falcata* individuals, the species which will hereafter be referred as the focal species. Other species of the genera *Adiantum* and *Lindsaea* had to be excluded from statistical testing as there were too few individuals detected for meaningful comparisons.

In order to test if the focal species differed in abundance in the 10 m subplots in relation to topographic position and the Direct Site Factor, I used analysis of covariance, ANCOVA. In the first step topographic position was used as a factor and the DSF as the covariate, testing also for their interactions. If no interactions were found the regressions were assumed to be homogenous, which in practice meant using the same regression slope for the different factors (topographic positions). Only after this I proceeded to the second step where interactions were excluded from the final model and the intercepts of the regressions for the factors were determined. Because of inbalance type II sums of squares were used to test the final models using again the R-package “car” (Fox & Weisberg 2011). A significance level of $p < 0.05$ was accepted as being statistically significant and assumptions of the models were verified with the help of residual plots.

To study more specifically the focal species microhabitat requirements I used the data we had collected directly at the fern individuals and at the background points. To normalize the DSF-measures I log-transformed them using the formula $\log_{10}(x+1)$ and after testing the means and standard errors were back-transformed for interpretation. Differences in log-transformed DSF between the focal species and them and the background points were tested for using a linear mixed effects model in order to take into account the inbalance and the nested structure in the data, as well as the differences between sites and topographic positions (Zuur et al. 2009). Site was used in the test as a random categorical variable, under which the factors *A. tomentosum*, *L. falcata* or background and topographic position were nested. Estimations were done using restricted effects maximum likelihood (REML). Model fit was evaluated with the help of residual plots for the model in general and for the factors separately. The R-code used to generate the model as well as the residual plots will be presented in the appendices. A significance level of $p < 0.05$ was accepted as being statistically significant. This linear mixed effects model was conducted using the R-package “nlme” (Pinheiro et al. 2015).

Because humus layer depths under the two focal species were severely non-normally distributed, they were compared with a non-parametric Kruskal-Wallis test and epiphytic individuals were excluded. Also differences between topographic habitats and within-species differences among topographic habitats were tested for using Kruskal-Wallis tests. Significance levels of $p < 0.05$ were accepted as being statistically significant.

Within the focal species fertile and sterile individuals were compared with ANCOVA where the DSF was tested against length of the longest leaf accounting for the categorical variable of reproductive status (0 or 1). A difference in intercept was interpreted to indicate a difference between fertile and sterile individuals if $p < 0.05$.

3. RESULTS

3.1 PRELIMINARY DATA ANALYSIS

After five days of preparatory fieldwork we spent 13 days establishing 12 transects with a total length of 1220 meters. Four of the transects were in Lindero (410 m), two in En Venta (175 m) and six in Kiara (635 m). In the total area of 0.244 ha sampled for *Adiantum* and *Lindsaea* species we found a total of 713 individuals belonging to two *Adiantum* and to four *Lindsaea* species (Table 1). Hemispherical photographs, as well as canopy-scope and basal area measurements were taken at 383 measured *Adiantum* and *Lindsaea* species individuals and additionally at 136 background points. Of the measured fern individuals 199 belonged to *A. tomentosum* (Fig. 4a) and 149 to *L. falcata* (Fig. 4b), while the third most common species, *A. terminatum* was represented by only 24 measured individuals. I took and processed a total of 744 hemispherical photographs, 553 of which were included into the analyses after removing duplicates. In the area of

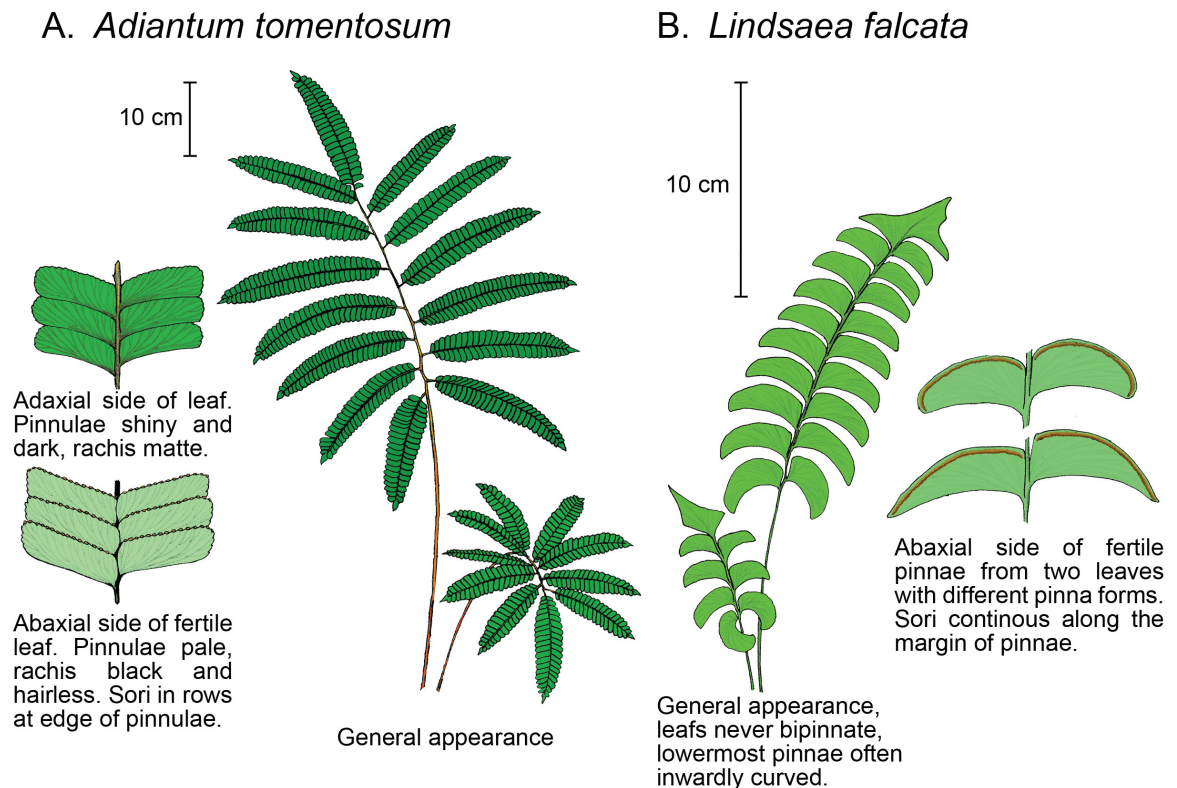


Figure 4. *Adiantum tomentosum* (a) and *Lindsaea falcata* (b), the focal species of this Master's thesis study. Note the different scales of the two illustrations. Drawing by Aslak Eronen.

Table 1. Characteristics of the *Adiantum* and *Lindsaea* species found in this study. Number of measured individuals out of all individuals encountered, mean leaf lengths with standard deviations, proportion of fertile and epiphytic individuals.

Species	n (measured/all)	Leaf length (cm \pm SD)	Fertile (%)	Epiphytic (%)
<i>Adiantum tomentosum</i> Klotzsch	199 / 408	63 \pm 26	31	2
<i>A. terminatum</i> Kze.; Miq.	24 / 38	29 \pm 10	63	0
<i>Lindsaea falcata</i> Dryand.	149 / 250	17 \pm 8	65	11
<i>L. digitata</i> Lehtonen & Tuomisto	8 / 14	32 \pm 16	63	0
<i>L. guianensis</i> (Aubl.) Dryand.	2 / 2	80 \pm 2	0	0
<i>L. taeniata</i> K.U.Kramer	1 / 1	53	100	0

0.610 ha along the transects where pteridophyte species composition was documented, we found a total of 28 pteridophyte species belonging to 15 genera (Table 2). In the area of 2.44 ha along the transects where big trees were inventoried, we found 296 trees with dbh 30-60 cm, 114 trees with dbh 60-90 cm and 28 trees with dbh >90 cm.

The six *Adiantum* and *Lindsaea* species found in the study differed substantially in abundance and size. While *A. tomentosum* and *L. falcata* were among the most common pteridophyte species found, *A. terminatum* and *L. digitata* were quite rare (Tables 1 & 2). *L. guianensis* and *L. taeniata* again seemed to be very rare species in the research area. *A. tomentosum*, *L. guianensis* and *L. taeniata* were rather large ferns in relation to the three other species and especially *L. falcata* was often quite small (Table 1). Roughly one third of the *A. tomentosum* individuals measured and about two-thirds of the *L. falcata*, *A. terminatum* and *L. digitata* individuals were in the fertile life-history stage. While the other *Adiantum* and *Lindsaea* species were almost exclusively terrestrial, 11 % of the *L. falcata* individuals were found to be epiphytic (Table 1.). On the other hand 24 % of *L. falcata* individuals were found growing on bare soil, while 10 % of the *A. tomentosum* individuals and 38 % of the *A. terminatum* individuals were growing on bare soil.

The mean canopy openness found in the study was 1.33 % (range 0.32-3.28 %), the mean transmitted light was 2.14 % (range 0.43-6.53 %) and the mean Direct Site Factor was 2.36 % (range 0.42-7.73 %). Out of the 519 canopy-scope measurements 453 scored 1, 46 scored 2 and only 20 measurements had a score >2, while the two maximum canopy-scope scores measured were 5. The canopy-scope scores were found to correlate with canopy openness, but correlation with the DSF was substantially higher (Figs. 5a, b).

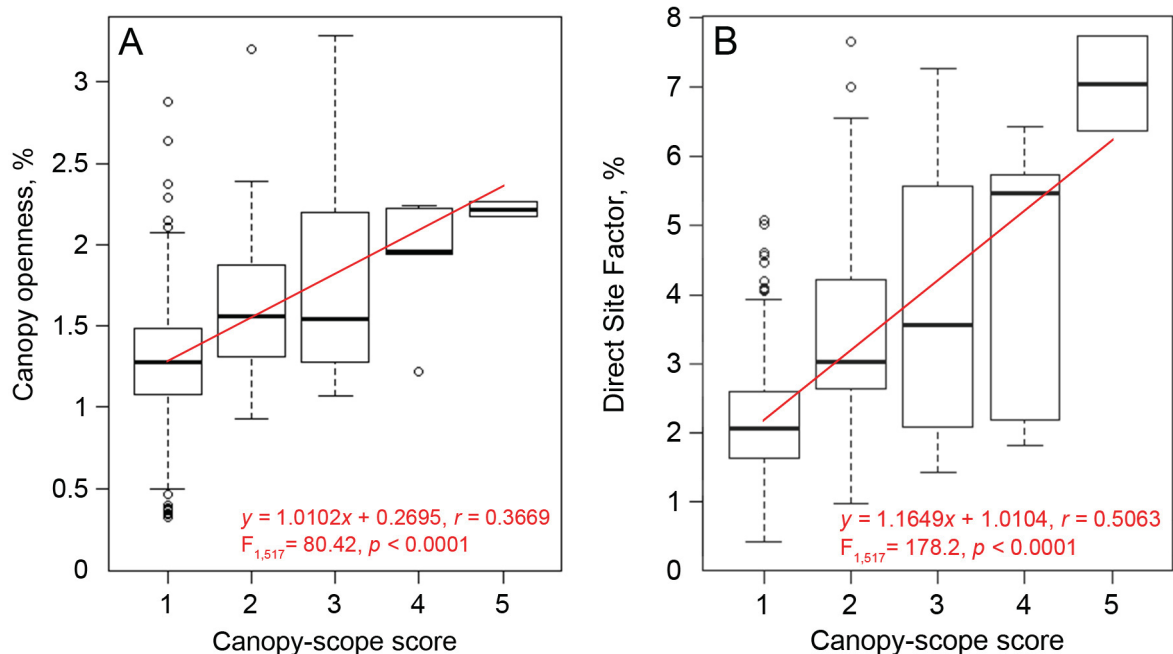
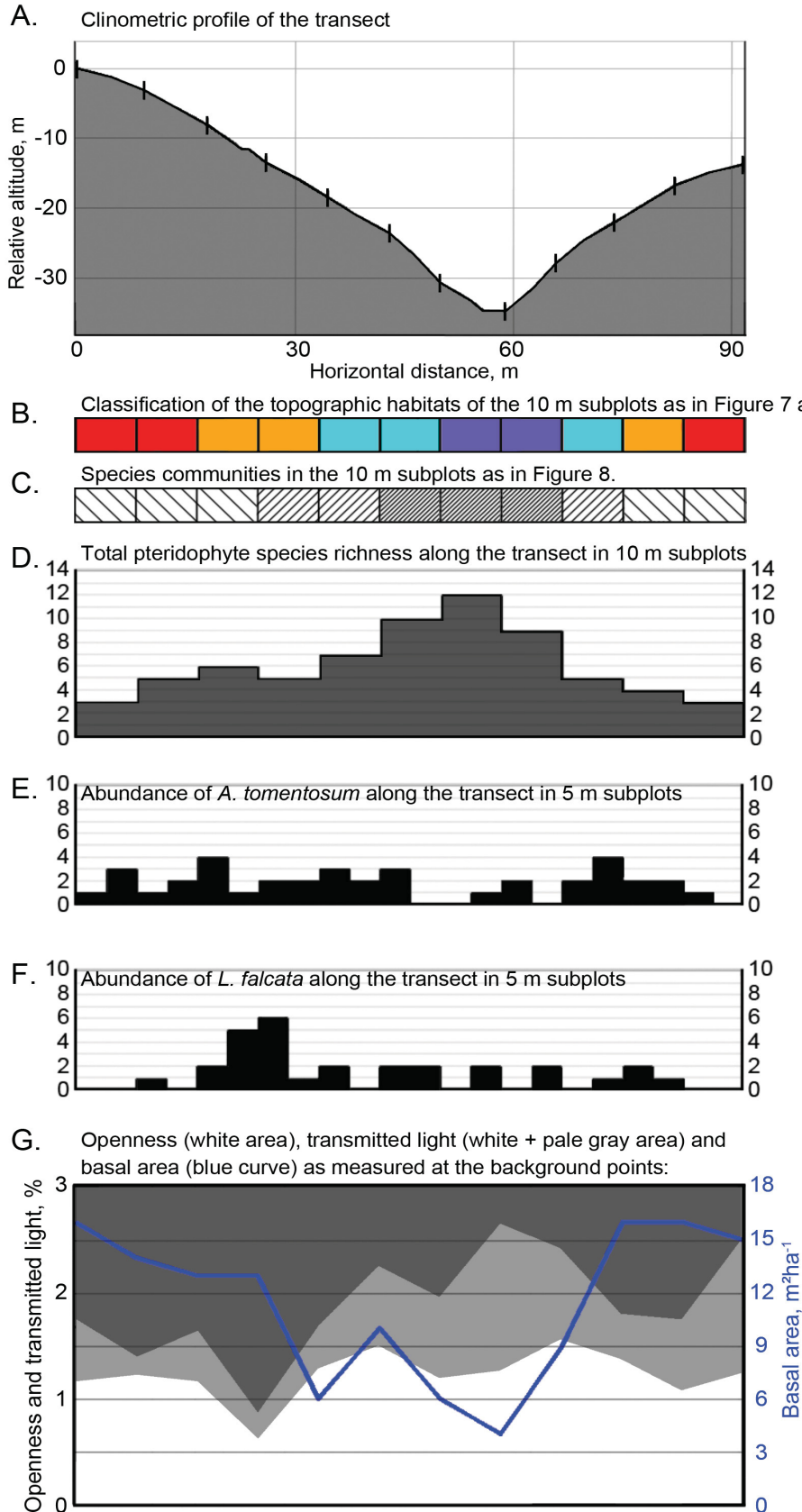


Figure 5. Canopy openness (a) and the Direct Site Factor (b) plotted against canopy-scope scores (x-axes) for all the 519 measurement points of the data. The median values are represented by thick black lines in the boxplot, while the boxes represent the 25th to 75th percentiles, the interquartile range. The whiskers represent 1.5 times the interquartile range and outliers are marked as circles. Linear regression lines and formulae of the regressions with r -, F - and p -values are marked in red.

Figure 6. An example of measures obtained from a typical transect, transect H located in Kiara. The clinometric profile of the transect with the 10 m background points marked with vertical bars is shown in figure (a). Figure (b) demonstrates the classification of topographic positions in the 10 m subplots along the transect with the same colors as in Figure 7a and (c) presents species communities in the subplots with the same patterning as in Figure 8. Figure (d) shows total pteridophyte species richness in the 10 m subplots, while abundance of *A. tomentosum* (e) and *L. falcata* (f) is shown in 5 m subplots. Figure (g) shows measures obtained from the background points: canopy openness and the Direct Site Factor as well as basal areas.



3.2 PTERIDOPHYTE COMMUNITIES AND TOPOGRAPHIC EFFECTS

The non-metric multidimensional scaling, based on the Jaccard distances, which depicts the similarity of species communities in the 10 m subplots, shows some clear patterns (Fig. 7). The first NMDS-axis seems to be related to topography (Fig. 7a), while the three sites (Fig. 7b) are not distinguishable in the ordination. On the first NMDS-axis hilltop and valley communities are on opposite ends, while upper and lower slope positions are intermediate and partially intermixed. Another pattern that can be observed in the NMDS-ordination is that all hilltop subplots are close together meaning that communities in them were quite similar, while community variability especially on the second NMDS-axis increases towards the valley bottom subplots. Stress of the best 2-dimensional NMDS-solution was 0.1804.

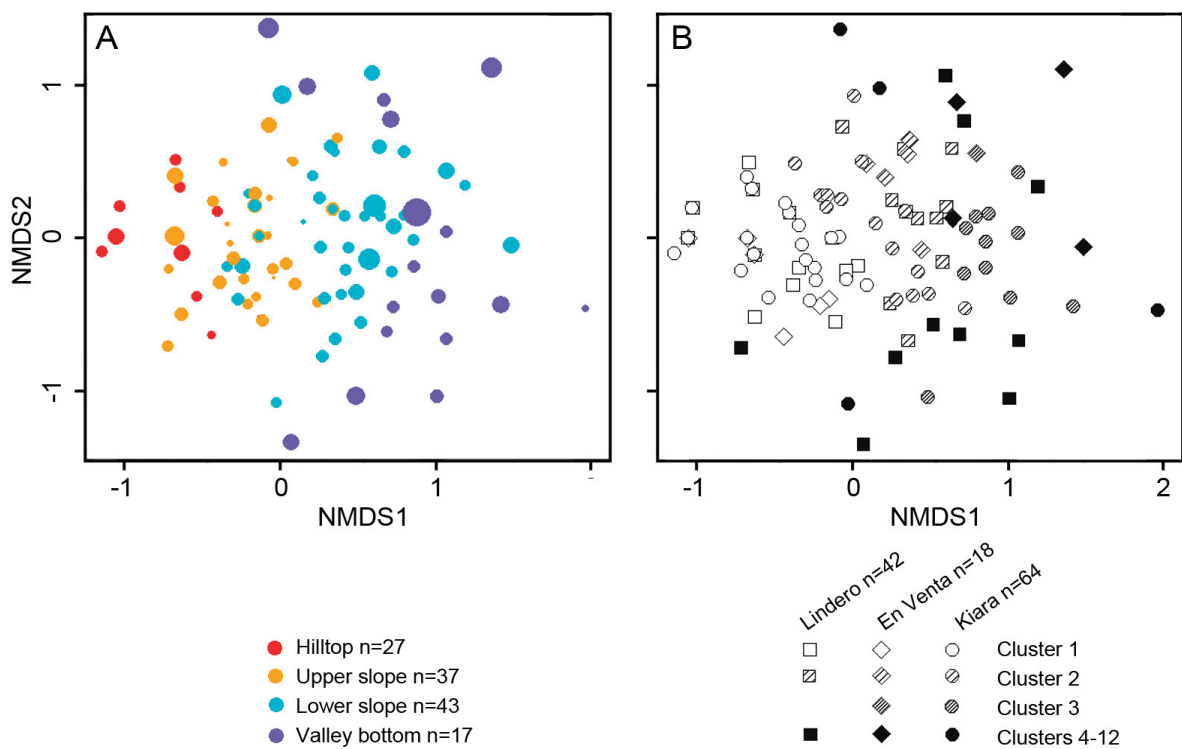


Figure 7. Ordination (Non-metric multidimensional scaling based on Jaccard distances) of pteridophyte species communities in the 124 transect subplots. In (a) the color of the symbols represents topographic positions of the subplots as inferred from the clinometric profiles (see Fig. 6a, b) with size of the dots representing total transmitted light in the subplots, which ranged from 0.67 % to 5.01 %. In (b) the symbols represent the three sites where transects were established and patterning represents the cluster analysis group of the subplots as in Figure 8. Stress of the best two-dimensional NMDS solution was 0.1804.

The unweighted average clustering was visualized as a dendrogram on the basis of which I decided to divide the subplots into 12 groups. The division into 12 groups was decided to sufficiently describe the communities found, as it resulted in three distinct clusters which included 85 % of the subplots and a further nine small clusters (Fig. 8). The first cluster, which is represented by 59 subplots mostly located on hilltops and upper slopes, is characterized by the presence of *Polybotrya sessilisora* and *A. tomentosum* in all the

subplots and *L. falcata* in more than half of the subplots, while the mean number of species in subplots of this cluster is just four. The second cluster, represented by 35 subplots mostly on upper and lower slopes, is characterized by the presence of *A. tomentosum*, *Danaea leprieurii*, *L. falcata*, *Saccoloma inaequale* and *Cyclodium meniscioides* in more than half of the subplots, with the mean number of species per subplot being five. The third cluster, represented by 12 lower slope or valley subplots, all except one in Kiara, seems to consist of more species rich subplots with the mean number of species per subplot being eight and *A. tomentosum*, *L. falcata*, *S. inaequale*, *Trichomanes elegans*, *A. terminatum*, *D. leprieurii* and *Cyathea pungens* being present in more than half of the subplots. Noteworthy is the presence of *P. sessilisora* in nine subplots of the second cluster and the presence of *Polybotrya pubens* in five subplots of the third cluster, as these species never occurred in the same subplots or clusters. The remaining 18 subplots were divided into nine clusters, which included one upper slope, six lower slope and 11 valley subplots, with the mean number of species per subplot ranging from four to six.

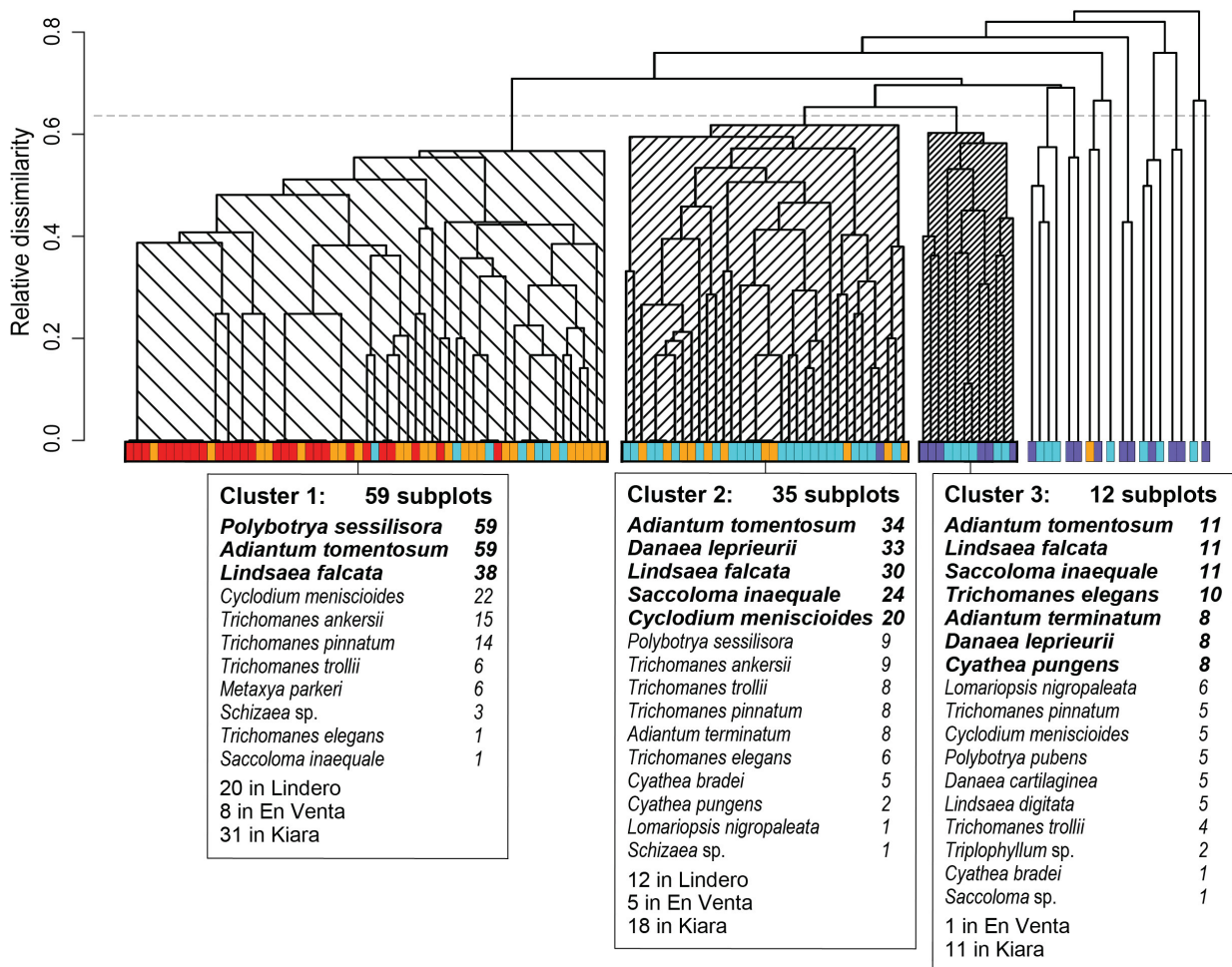


Figure 8. Hierarchical clustering (based on unweighted average clustering of Jaccard distances) of the pteridophyte species communities in the 124 transect subplots. The colored bars under the cluster dendrogram represent topographic positions of the subplots with the same colors as in Figure 7a (see also Fig. 6a, b). Under the three biggest clusters are listed: the number of subplots belonging to the cluster, the number of subplots in the cluster where the fern species listed was present, and the number of subplots in the cluster found in each study site. Species present in more than half of the subplots belonging to a cluster are marked in bold text.

In summary the cluster dendrogram seems to distinguish between relatively species poor but frequently encountered hilltop or upper slope communities and slope communities, while lower slope and especially valley bottom subplots are grouped into several distinct communities.

The topographic positions as classified from the clinometric profiles, had significantly different fern species richnesses, while the three study sites didn't differ from each other in regard to species richness (Tables 2 & 3). Tukey's HSD comparison showed that valleys and lower slopes differed only marginally in species richness ($p=0.0553$), while the other habitats had clearly differing species richnesses. The highest average species richness of 7.2 species per subplot was found in valleys, followed by lower slopes with 6.3 species per subplot, while upper slopes had on average 5.1 species per subplot, with the hilltops being the poorest habitats with an average of only 3 species per subplot (Table 2, see also Fig. 6d).

Table 2. Presences of all pteridophyte species found in the 124 subplots as divided into the four topographic positions. The column marked with *n* shows the number of subplots where the different species were present. The second lowest row shows the number of subplots in each topographic position and the lowest row shows the mean pteridophyte species richness found in subplots of the different topographic positions.

Species	Species present, in % of subplots				n
	Hilltops	Upper slopes	Lower slopes	Valleys	
<i>Polybotrya sessilisora</i>	100	81	28		69
<i>Trichomanes ankersii</i>	26	30	16		25
<i>Adiantum tomentosum</i>	100	100	95	65	116
<i>Metaxya parkeri</i>	4	16	7	6	11
<i>Lindsaea falcata</i>	41	78	88	59	88
<i>Schizaea</i> sp.		11	5	6	7
<i>Selaginella</i> sp.		3	2		2
<i>Lindsaea guianensis</i>		3	7		4
<i>Lindsaea taeniata</i>			2		1
<i>Danaea leprieurii</i>	7	70	77	47	69
<i>Cyclodium meniscioides</i>	7	38	70	53	55
<i>Trichomanes pinnatum</i>	11	27	28	53	34
<i>Trichomanes trollii</i>	4	19	23	29	23
<i>Saccoloma inaequale</i>		22	56	59	42
<i>Cyathea bradei</i>		5	14	24	12
<i>Adiantum terminatum</i>			33	41	21
<i>Trichomanes elegans</i>		5	26	59	23
<i>Cyathea pungens</i>		3	12	29	11
<i>Lomariopsis nigropaleata</i>			12	29	10
<i>Metaxya rostrata</i>			5	12	4
<i>Cyathea lasiosora</i>			2	6	2
<i>Lindsaea digitata</i>			7	24	7
<i>Danaea cartilaginea</i>			7	41	10
<i>Triplophyllum</i> sp.			2	12	3
<i>Polybotrya pubens</i>			2	53	10
<i>Campyloneurum phyllitidis</i>				6	1
<i>Saccoloma</i> sp.				6	1
<i>Thelypteris macrophylla</i>				6	1
Subplots/Habitat type	27	37	43	17	124
Mean richness/subplot:	3.0	5.1	6.3	7.1	

Also the focal species differed in abundance according to topography, while there were no differences between sites (Table 3). There were less *A. tomentosum* individuals in valleys than in other topographic positions and *L. falcata* was significantly more common on upper and lower slopes (Table 2, Fig. 9b, c, see also Fig. 6e, f). The 38 *A. terminatum* and 14 *L. digitata* individuals were all encountered only in lower slope and valley bottom locations (Table 2). Overall the division of the subplots into hilltop, upper slope, lower slope and valley subplots seemed to reflect quite well the pteridophyte community patterns found in the ordination as well as in the cluster analysis (Figs. 6, 7, 8 and Table 2).

The study sites differed in their canopy openness with Lindero having a more open canopy than the other two sites and canopy openness didn't differ between topographic positions (Table 3, Fig. 9a). Mean canopy openness in Lindero was 1.41 %, in En Venta it was 1.35 % and in Kiara 1.24 %. The canopy-scope scores didn't differ between the three study sites (Kruskal-Wallis $\chi^2=0.2797$, $df=2$ and $p=0.8695$), but valleys had higher

Table 3. Results of the two-way ANOVAs conducted for the effects of site and topographic position as well as their interactions on different variables as in the 124 transect subplots. Sums of squares used are of type II. Columns show: the variables tested for, the nominal factors, nominator degrees of freedom, denominator degrees of freedom, F- and *p*-values. $o=p<0.10$; $*=p<0.05$; $***=p<0.001$.

Tested variable	Nominal factor	nom. df	den. df	F	<i>p</i>
Species Richness	Site	2	112	1.07	0.358
	Topography	3	112	40.28	<0.001 ***
	Site:Topography	6	112	1.03	0.410
Abundance of <i>A. tomentosum</i>	Site	2	112	2.09	0.128
	Topography	3	112	6.39	<0.001 ***
	Site:Topography	6	112	1.03	0.411
Abundance of <i>L. falcata</i>	Site	2	112	0.45	0.638
	Topography	3	112	9.68	<0.001 ***
	Site:Topography	6	112	0.46	0.834
Canopy Openness	Site	2	112	7.85	<0.001 ***
	Topography	3	112	1.37	0.255
	Site:Topography	6	112	1.04	0.406
Total transmitted light	Site	2	112	2.60	0.079 o
	Topography	3	112	9.83	<0.001 ***
	Site:Topography	6	112	0.97	0.450
Direct Site Factor	Site	2	112	1.98	0.142
	Topography	3	112	10.74	<0.001 ***
	Site:Topography	6	112	1.05	0.395
Basal area	Site	2	112	19.46	<0.001 ***
	Topography	3	112	34.00	<0.001 ***
	Site:Topography	6	112	0.19	0.978
Trees with dbh 30-60 cm	Site	2	112	3.25	0.043 *
	Topography	3	112	8.98	<0.001 ***
	Site:Topography	6	112	0.28	0.944
Trees with dbh 60-90 cm	Site	2	112	4.52	0.013 *
	Topography	3	112	3.05	0.032 *
	Site:Topography	6	112	1.80	0.105
Trees with dbh >90 cm	Site	2	112	1.11	0.335
	Topography	3	112	3.68	0.014 *
	Site:Topography	6	112	1.82	0.101

canopy-scope scores than the other topographic positions (Kruskal-Wallis $\chi^2=12.4738$, $df=3$ and $p=0.0059$). The Direct Site Factor didn't differ between the three sites, but similarly than in the canopy-scope measurements, valleys had a higher DSF than the other topographic positions (Table 3, Fig. 9a, see also Fig. 6g).

Basal areas and the number of big trees differed between topographic positions as well as between sites (Table 3). Valleys had the lowest mean basal area of $7.3 \text{ m}^2\text{ha}^{-1}$, followed by lower slopes with a mean basal area of $10.4 \text{ m}^2\text{ha}^{-1}$ and the highest mean basal areas of $12.7 \text{ m}^2\text{ha}^{-1}$ were encountered on upper slopes and hilltops. Hilltops also harboured more trees of 60-90 cm dbh than valleys and more trees of 30-60 cm dbh than either lower slopes or valleys. Lindero had a higher basal area than the other two sites and at the same time the site also harboured more trees of 30-60 cm dbh than Kiara (139 ha^{-1} vs. 107 ha^{-1}). En Venta again harboured less trees of the 60-90 cm diameter class than the other two sites (26 ha^{-1} vs. 50 ha^{-1}). The number of the very largest trees of >90 cm diameter didn't differ between sites, but it needs to added that only 28 trees of this size class were encountered in the whole study.

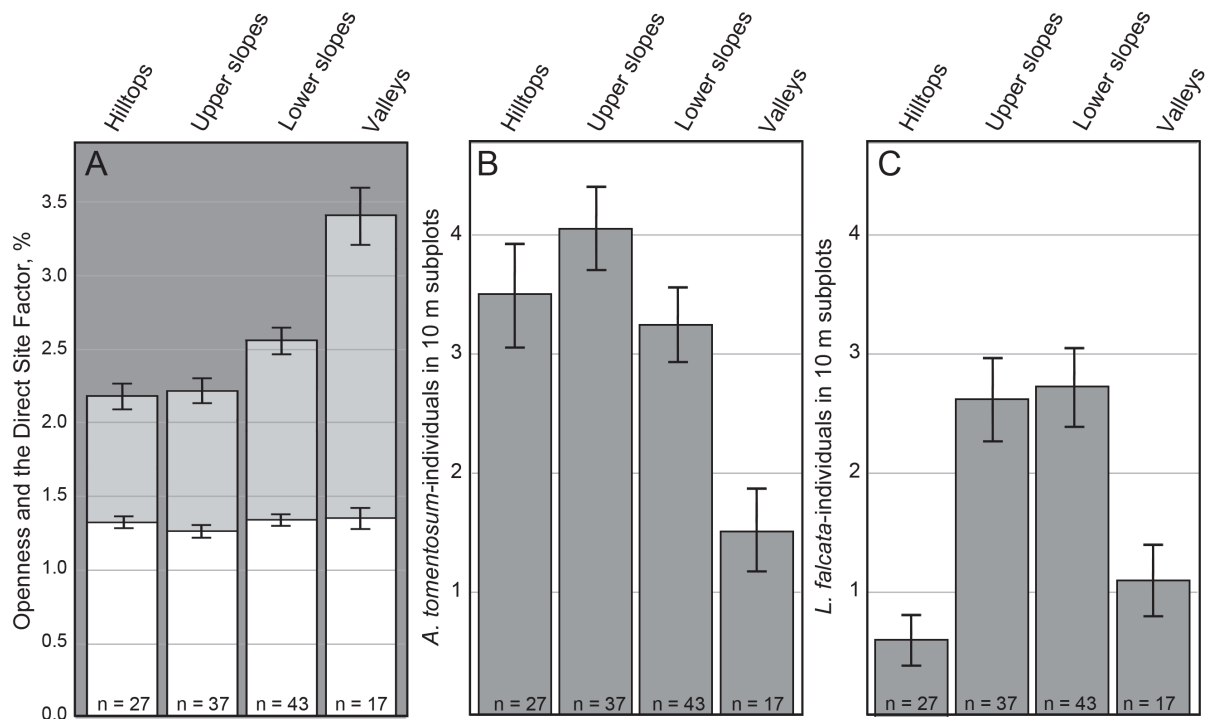


Figure 9. Light regimes (a), abundance of *A. tomentosum* (b) and *L. falcata* (c) in the 124 subplots as divided into the four topographic positions. Bars show means and standard errors. In figure (a) the white bars represent canopy openness and the white and grey bars combined represent the Direct Site Factor.

3.3 CHARACTERISTICS OF THE FOCAL SPECIES

The ANCOVA for *A. tomentosum* showed no interactions (type III ANOVA $p=0.344$ for the interaction term) between the DSF and abundance of the species in 10 meter subplots, which meant that the relation of the DSF with abundance of the species were similar within each topographic position (Fig. 10a). The slopes, however didn't deviate from 0, which indicated that the DSF didn't have effect on the abundance of the species. The intercepts of the slopes differed between topographic positions confirming that *A. tomentosum* was rarer in valleys, as indicated already by the ANOVA (Table 3, Fig. 9b). The residual plots showed no obvious problems in model fit (Appendix, Fig. 1). The ANCOVA for *L. falcata* didn't show any interactions either (type III ANOVA $p=0.1028$ for the interaction term), but the slope was negative (Fig. 10b). This indicates that the DSF might have had a negative effect on abundance of the species even when taking into account the differences in abundance between the topographic positions (Figs. 9c, 10b). The residual-plot however shows heteroscedasticity, an increase in spread of the residuals at higher DSF-values as well as slight deviation from the normal distribution (Appendix, Fig. 2). If using canopy-scope scores instead of the DSF, ANCOVAs of neither species showed statistically significant correlation with the canopy-scope scores.

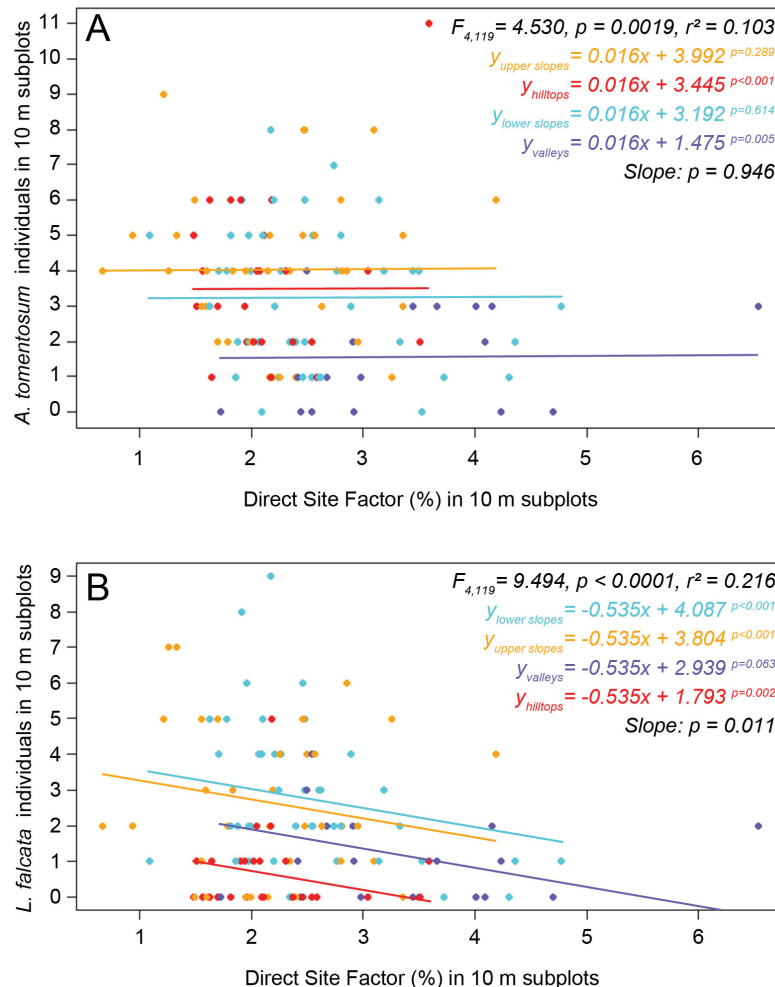


Figure 10. Abundance of *A. tomentosum* (a) and *L. falcata* (b) individuals (y -axes) in the 124 subplots plotted against the Direct Site Factor (x -axes). ANCOVA regression lines and their formulae with F- and p -values are given. Symbols and ANCOVA-regression formulae are color-coded according to topographic position as in Figs. 6b and 7a.

The linear mixed effects model indicated that the log-transformed DSF in microhabitats of *A. tomentosum* and *L. falcata* differed marginally ($p=0.0555$), while the background points log-transformed DSF didn't differ from either species microhabitats (*A. tomentosum* – background $p=0.5893$, *L. falcata* – background $p=0.1424$). Back-transformed mean±standard error DSF for *A. tomentosum* was 2.161±0.030 % and 1.766±0.034 % for *L. falcata*, while the background points mean DSF was 2.115±0.026 %. The residual plots showed no apparent problems of model fit (Appendix, Fig. 3).

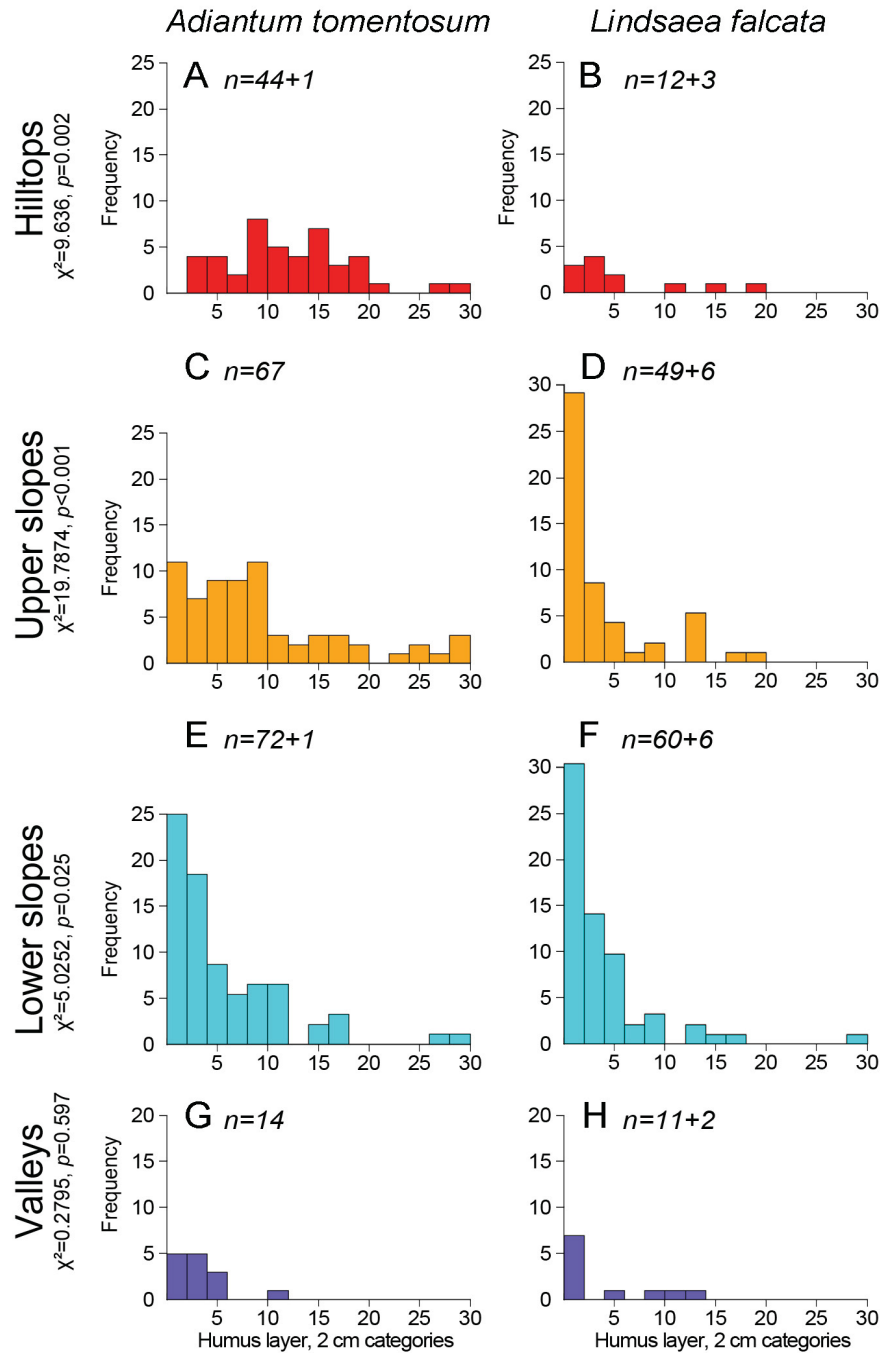


Figure 11. Histograms of humus layer depths under individuals of the focal species as divided into topographic positions. The left column (a, c, e, g) gives humus layers for *A. tomentosum* and the right column (b, d, f, h) for *L. falcata*. Kruskal-Wallis test statistics are given for comparisons of the focal species within topographic positions: hilltops (a, b), upper slopes (c, d), lower slopes (e, f) and valleys (g, h). Total number of individuals within topographic position is given in the figure by n , where the first number stands for terrestrial individuals and the number after + stands for epiphytic individuals.

Humus layer depths under the focal species differed significantly (Fig. 11, Kruskal-Wallis $\chi^2=39.1649$, $df=1$, $p<0.0001$) with *L. falcata* growing on a median humus layer of 3 cm, while the median humus layer of *A. tomentosum* was 7 cm, when epiphytic individuals of both species were excluded. This was not surprising as it was noticed already during data collection that *L. falcata* was often found growing on small patches of bare soil, while *A. tomentosum* was almost always growing on leaf litter or other organic matter. Indeed 24 % of *L. falcata* individuals and only 10 % of *A. tomentosum* individuals were growing on bare soil (humus layer of 0 cm). This difference was obvious also within topographic positions, as *A. tomentosum* was consistently growing in thicker humus layers than *L. falcata* in each topographic position except in valleys (Fig. 11). Especially in slope positions the prevailing humus layers under *L. falcata* were very shallow (Fig. 11d, f). An interesting detail is how on hilltops *A. tomentosum* never occurred in the very shallowest humus layers, while *L. falcata* did, even though the species was rare on hilltops (Fig. 11a, b). At the same time one fifth of the *L. falcata* individuals found on hilltops were epiphytic, more than in other topographic positions, although the sample size for hilltops is quite small, just 15 individuals in total (Fig. 11a). The median humus layer found under *A. terminatum* ($n=24$) was 1 cm and under *L. digitata* ($n=8$) it was 2 cm.

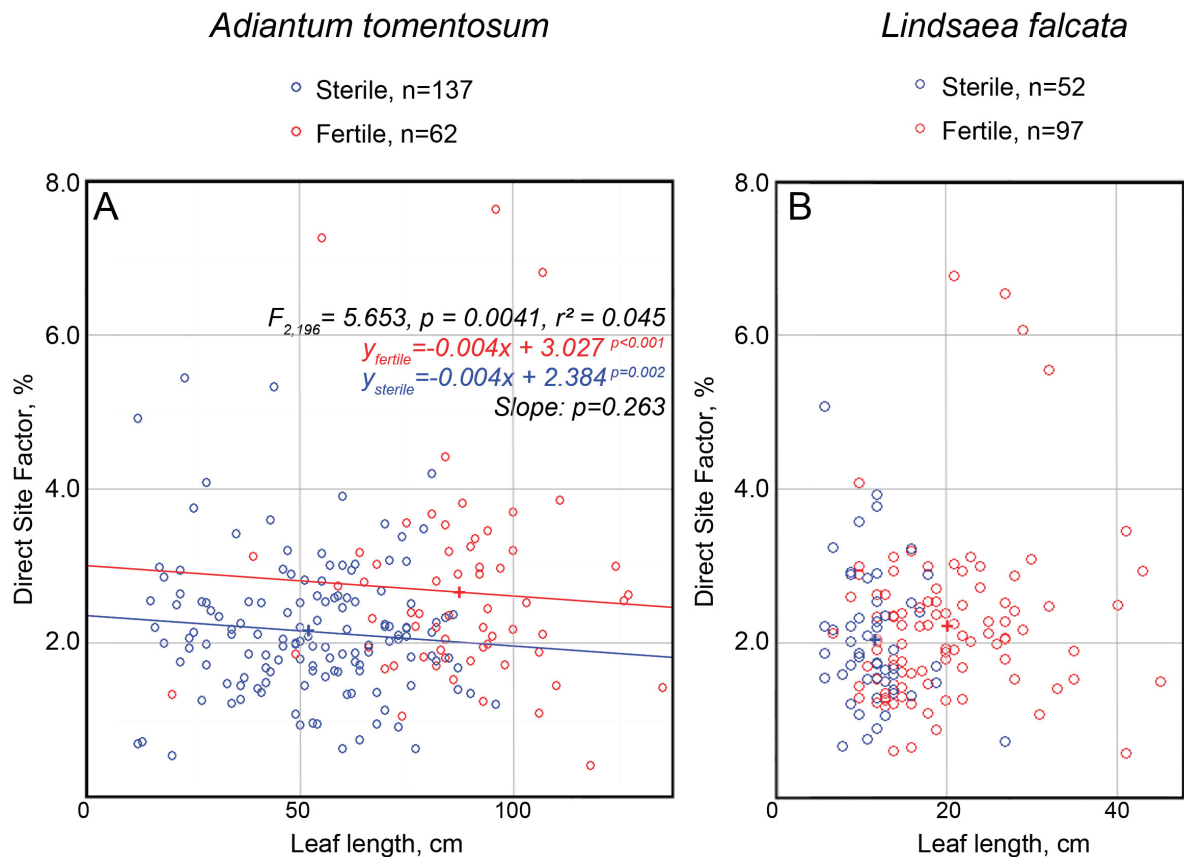


Figure 12. The Direct Site Factor (y-axes) plotted against length of the main leaf (x-axes) of *A. tomentosum* (a) and *L. falcata* (b) taking into account their reproductive status. Sterile individuals are marked as blue circles and fertile individuals as red circles and means of both groups are marked as small crosses. ANCOVA regression lines and their formulae with F- and p-values are given for (a). Note the different scales used for leaf length as the two focal species were substantially different in size.

No statistically significant interaction was found between leaf length and the Direct Site Factor in *A. tomentosum* in relation to the reproductive status ($p=0.709$ for the interaction term). Therefore the same slope was accepted for sterile and fertile individuals and a significant difference was found between their intercepts with the DSF (Fig. 12a). Residual fit was quite good, although the quantile-quantile plot showed a slight deviation from the normal distribution (Appendix, Fig. 4). For *L. falcata* the overall ANCOVA-model was statistically insignificant and additionally there was a marginally significant interaction term, which meant that it was not sensible to test for a difference in intercepts (Type III ANOVA for the model: $F_{3,145}=2.014$, $p=0.1145$ and $p=0.0622$ for the interaction term). Rather it seemed like *L. falcata* would become fertile after reaching a certain size as the mean leaf lengths of fertile and sterile individuals differed clearly (Fig. 12b).

4. DISCUSSION

4.1 PTERIDOPHYTE COMMUNITIES

Pteridophyte communities, forest structure and light conditions were found to be strongly affected by topography along the transects with lower slopes and valley bottoms being the most diverse and species rich habitats exposed to the highest levels of direct light (Table 2, Figs. 6, 7, 8, 9a). Hilltops on the contrary were rather homogenous, species-poor and had quite low levels of light, which was possibly due to higher wood volumes. Generally it seemed that differences between topographic positions were more pronounced than the differences between the three study sites, especially in relation to the pteridophyte communities (Table 3).

The total species richness of 28 pteridophyte species with leaves at an altitude of <2m found in my study on 0.61 ha were comparable with previous studies, especially if accounting for the fact that *Saccoloma*, *Schizaea*, *Selaginella* and *Triplophyllum* were identified only to the genus level. For example Tuomisto & Poulsen (2000) found 32 pteridophyte species in an area of 0.65 ha on the Nauta Formation. Also the topographic distribution of fern species in my study seems consistent with the one reported by Tuomisto & Poulsen (2000) for the Nauta Formation. Presence of *A. terminatum* and *P. pubens* on the lower slopes and in valley bottoms could indicate that the soils in lower locations on the Nauta formation are slightly more nutrient-rich than in upper locations, as these two species have slightly higher soil cation content optima than *A. tomentosum* and *P. sessilisora* (Tuomisto et al. 1998, Tuomisto 2006). The very cation poor Nauta Formation indeed lies on top of the slightly richer uppermost Pebas Formation and the two are floristically different (Higgins et al. 2011, Rebata 2012). Moreover soils in the Allpahuayo-Mishana reserve, just 54 km north from my research area have been found to be layered in a manner where valley bottoms have significantly richer soils than hilltops (Vormisto et al. 2000).

Zuquim et al. (2009, 2012) found slopes to be poor predictors of species communities, which would indicate the community composition to be site-specific, depending not only on topography but rather on variation in sand and nutrient content of the soils along the slopes. In my study the effects of soil moisture and drainage conditions on the pteridophyte communities are impossible to separate from the effects of soil nutrient content because these factors were not measured but can only be deduced based on pteridophyte community composition and topographic position. After all *P. pubens* is not only associated with richer soils, but also with poor drainage whereas *P. sessilisora* is associated with better drained soils (Tuomisto & Ruokolainen 1994). Besides Tuomisto & Poulsen (2000) suspected variable drainage conditions to be important in forming the species communities in forests on the Nauta Formation. In summary it seemed that the topographic habitats along slopes differed most likely in their soil properties and drainage conditions, both of which seemed to affect also forest structure and light conditions and all of these may interact to form the pteridophyte communities.

Even though the two focal species were growing in the same habitat within the wider context of soils, they still occurred in a mosaic of habitat patches with different topography and light conditions. Both, *A. tomentosum* and *L. falcata* were as very common species present in almost all of the topographically distinct pteridophyte communities, being absent only from some of the most distinct valley communities (Figs. 8, 9a, b, Table 2). *A. tomentosum*, however was present in all hilltop communities, which otherwise were relatively species-poor, while *L. falcata* was most frequent on slopes. *A. terminatum* and *L. digitata*, both of which were relatively rare, again were completely restricted to the more species-rich lower slope and valley habitats (Table 2).

Although several ecological patterns and species differences were found in this study, it should be remembered that the data is spatially very restricted as the three study sites were just 0.5-1.7 km apart. Due to this the patterns in pteridophyte communities, as well as the ecological differences among *Adiantum* and *Lindsaea* species may apply only for forests on the Nauta Formation. At the same time the transects in my study were always established into locations where *A. tomentosum* and *L. falcata* were present, which might bias the results into the direction of certain types of forests, excluding some fern species otherwise present. Also between the transects, which were sometimes a mere 20 meters apart, there might be quite a lot of spatial autocorrelation. For example pteridophyte communities in Kiara might seem quite uniform, because all transects traversed the same ridge and five of them crossed the same valley. In Lindero, on the contrary almost all transects crossed different valleys and it could be for that reason why some of the pteridophyte communities there seemed quite distinct.

4.2 THE ECOLOGICAL NICHES OF *A. TOMENTOSUM* AND *L. FALCATA*

It seemed that some differences among the focal species ecological niches were found that were not directly related to soils. There were indications that *L. falcata* could be growing preferentially in more shady environments than *A. tomentosum*. Although the difference in the log-transformed DSF at microhabitats of these species was only marginally significant, the observation was further supported by abundance data, as abundance of *A. tomentosum* was not related to the DSF, while *L. falcata* seemed to be rarer in subplots with a higher DSF even if accounting for topography (Fig. 10a, b). Another difference was that *A. tomentosum* was growing on clearly thicker humus layers than *L. falcata* in all topographic positions, except in valleys where both species were quite rare (Fig. 11).

A. tomentosum was the most common species encountered in this study and it is therefore not surprising that the species was occurring in almost all communities as well as in a wide variety of light conditions. Also in previous studies *A. tomentosum* has often been found to be the dominant fern species when present (e.g. Tuomisto & Poulsen 1996, Tuomisto et al. 1998). Even though *A. tomentosum* was the dominant fern species in our whole research area, it was clearly associated with relatively species-poor hilltop and slope communities where it was present in every subplot, while being less frequent or even absent in valley bottoms. Similar distribution patterns with highest *A. tomentosum* densities on hilltops were found by Tuomisto et al. (1998) in two study sites, but in the third study site the species reached high densities in lower parts of the transect being completely absent from the higher parts. Also in central Brazilian Amazonia Drucker et al. (2008) found *A. tomentosum* occurring only in valley bottoms close to streams. It seems thus that the distribution of *A. tomentosum* in relation to topography might be very site specific and could be rather related to the nutrient and sand content of the soils, or even climatic differences, rather than only drainage of the soils.

Abundance and occurrence of *A. tomentosum* was found to be relatively unrelated to light conditions at least in this low range of ≤ 3.28 % canopy openness. Also Zuquim et al. (2009) found *A. tomentosum* to occur across different canopy openness regimes with the species being possibly slightly more frequent under more closed canopies, but my study didn't include any sites with bigger gaps. *A. tomentosum* was, however by no means totally indifferent to light, as individuals seemed to become fertile if there was more direct light available. Somewhat similar effects on reproduction in two understorey *Zingiberales*-species adapted to low-light conditions were shown by Westerland & Horvitz (2015) in a premontane rainforest in Central America. Growth in both species was negatively affected by light which had a positive effect on reproduction. Liao et al. (2013) again showed light availability to positively affect growth in two chinese *Adiantum*-species, although these species were also adapted to relatively open habitats.

L. falcata was another fern species that was very common in the research area across different habitats, being only slightly rarer than *A. tomentosum*. *L. falcata* showed clear preference towards slope habitats and even within these habitats it was possibly more likely to occur in patches with lower levels of direct light and a shallower humus layer. The preference of *L. falcata* for more shady microhabitats might be related to better survival in places where the individual is less exposed to direct sunlight. Sunflecks, short pulses of direct light transmitted through the canopy, have indeed been shown to induce photoinhibition in some understorey plants (Chazdon & Pearcy 1991). Besides many ferns in general could be expected to escape competition by living in low-light conditions as shade-adapted plants, being at the same time poor at adapting to changing conditions like increased light levels through tree fall gaps (Page et al. 2002, Zhang et al. 2009). *L. falcata* as a very small understorey fern could thus be expected to be well adapted to the shade of the understorey, which again could make the species especially sensitive to photoinhibition. In respect to growth and reproduction *L. falcata*, however seemed indifferent to light conditions and all individuals got fertile after being tall enough.

L. falcata was growing in shallower humus layers than *A. tomentosum*, even though there was a lot of variation. It was also observed that 24 % of *L. falcata* individuals were growing in small patches of bare soil, while 11 % of the individuals were growing epiphytically on the base of trees or atop of fallen logs. This result somewhat contradicts previous research, in which *L. falcata* has been described as a species that often grows on dead plant material or thick humus layers (Tuomisto & Ruokolainen 1994, Tuomisto 1998). On the other hand leaf litter was found by Rodriguez & Costa (2012) to negatively affect sporophyte establishment in general. It could also be possible that the species behaves differently on different soils, such that it would for example grow on thicker humus layers on less optimal soils. Indeed Tuomisto & Ruokolainen (1994) found *L. falcata* to occur not only on clayey, but also on sandy soils. Besides they found *L. falcata* to be most common on well drained clay soils and also in my study the species was most abundant on slopes, which could be assumed to be better drained than flat terrain. Furthermore Rodriguez & Costa (2012) demonstrated that slopes had more bare-soil patches, which may promote sporophyte establishment and this could actually be one of the factors affecting the preference for slope habitats found in *L. falcata*. Interestingly *L. falcata* was also found more often epiphytically on hilltops, where there might have been less patches of bare soil available.

Because the data is spatially restricted and the difference in the DSF at microhabitats of the species were only marginally significant, further detailed studies in different locations about light partitioning among *Adiantum* and *Lindsaea* species should be conducted before generalisations can be made. Nevertheless there were indications of niche partitioning in relation to humus layers and possibly light conditions, which added more dimensions into the suspected niche space of *L. falcata* and *A. tomentosum*.

4.3 COMPARISON OF HEMISPHERICAL PHOTOGRAPHY AND THE CANOPY-SCOPE

I found statistically significant correlations between canopy-scope scores and the light measures obtained from hemispherical photographs. A significant correlation between canopy-scope scores and canopy openness as derived from hemispherical photographs was also found by Brown et al. (2000). On the other hand Hale & Brown (2005) found low correlation between canopy openness and canopy-scope scores especially in very closed canopies of coniferous plantation forests. The spherical densiometer, a tool similar to the canopy-scope, has been found to give poorer correlation with direct light measures than hemispherical photography (Engelbrecht & Herz 2001, Ferment et al. 2001). Interestingly in my study correlation between the canopy-scope scores and the Direct Site Factor, rather than canopy openness, was higher. It is possible that clear gaps visible with the canopy-scope were often located above the observation point, in which case also direct sunlight was higher in them. Scattered openings where there was more diffuse than direct light, while openness was still high, may again always have resulted in a canopy-scope score of 1.

In comparison to the canopy-scope, which was introduced by Brown et al. (2000), hemispherical photography has been used much more widely since Anderson (1964) for estimating light conditions in forests (Roxburgh & Kelly 1995, Promis 2013, but see also Boll et al. 2005, Suominen et al. 2015). As in other studies, the hemispherical photographs were more laborious to take and process than obtaining canopy-scope scores, but in my study they clearly gave much more detailed information on direct and indirect solar radiation especially under very closed canopies (Brown et al. 2000, Hale & Brown 2005). The low resolution of the canopy-scope under a very closed canopy, where most scores were 1, is probably the main reason why the correlation between the DSF and abundance of *L. falcata* remained undetected when using canopy-scope scores. Suominen et al. (2015) successfully used the canopy-scope in similar rainforest than was encountered in my study, but they used it for estimating gap fraction, not to detect subtle ecological differences in light regimes at very local scales under closed canopies, as I did. In summary it seems that hemispherical photographs remain a more reliable tool for estimating rain forest light conditions under very closed canopies even though processing of them is laborious.

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APPENDIX:

Figure 1. Residual plot (a), quantile-quantile plot (b), spread-location plot (c) and residuals vs. leverage plot (d) of the ANCOVA-model conducted on the effect of the Direct Site Factor on abundance of *A. tomentosum* in the 10 m subplots taking into account differences among topographic positions.

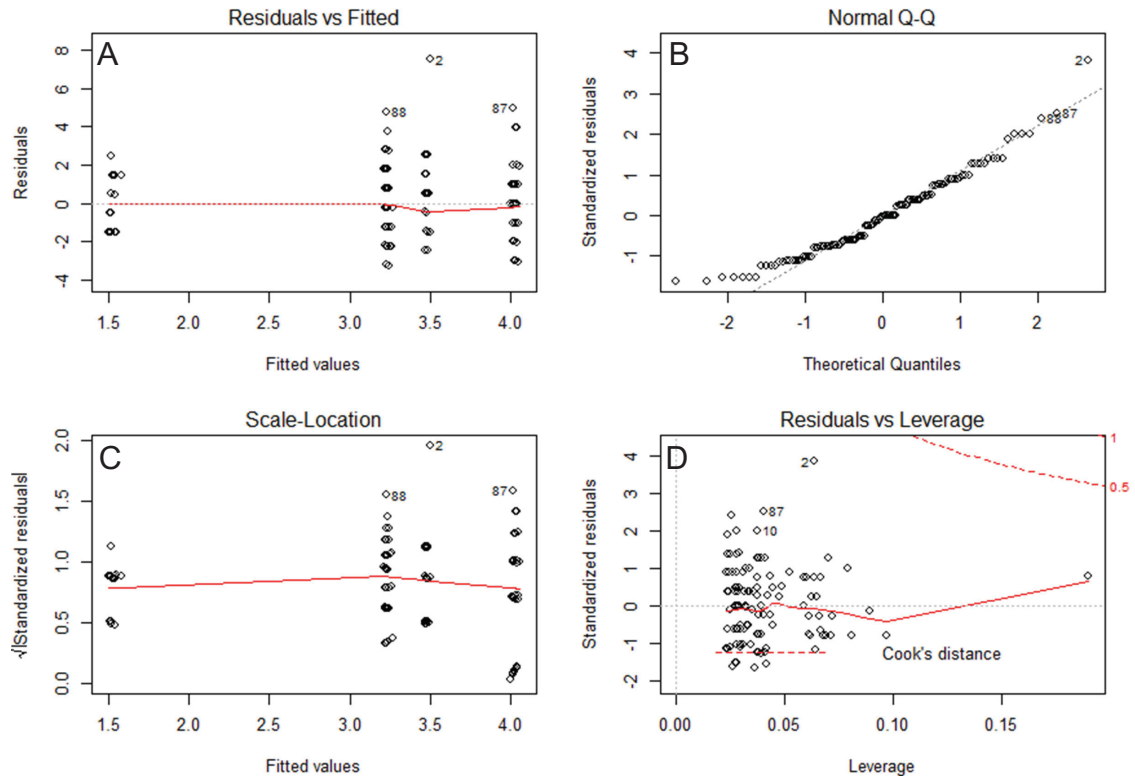


Figure 2. Residual plot (a), quantile-quantile plot (b), spread-location plot (c) and residuals vs. leverage plot (d) of the ANCOVA-model conducted on the effect of the Direct Site Factor on abundance of *L. falcata* in the 10 m subplots taking into account differences among topographic positions.

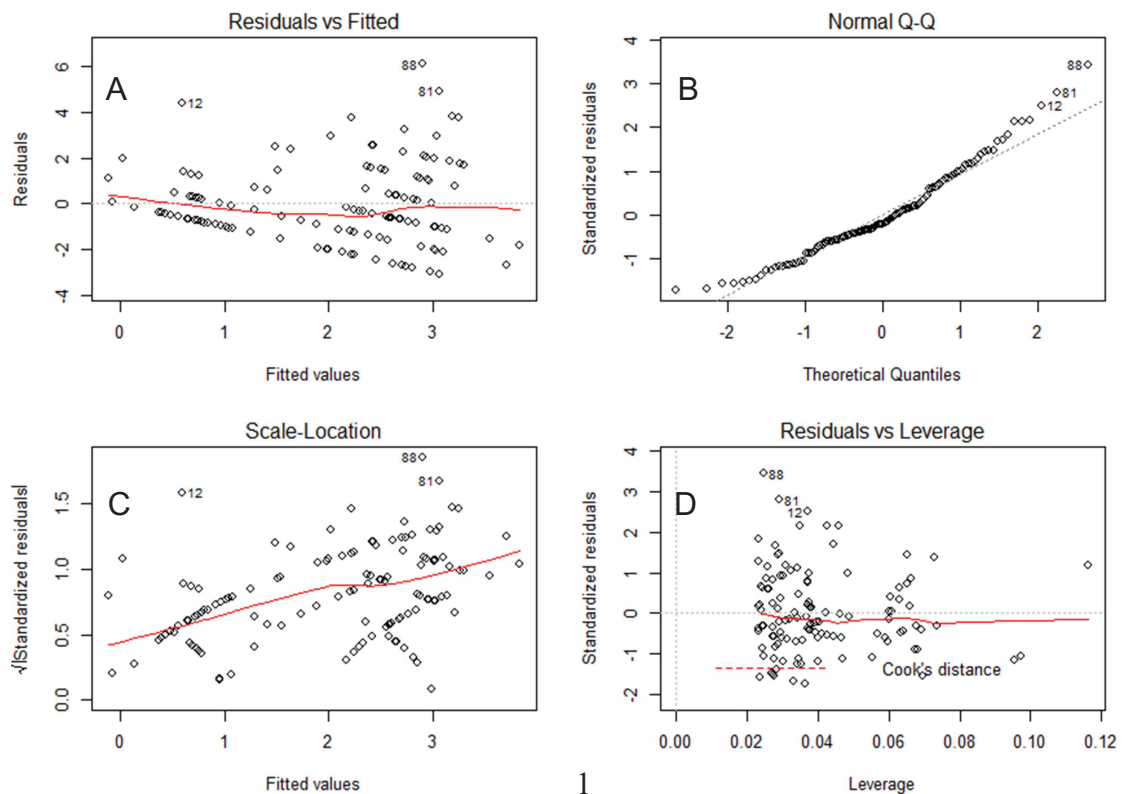


Figure 3. The R-code (a) used for the linear mixed effects model testing for differences in log-transformed Direct Site Factor between microhabitats of *A. tomentosum* and *L. falcata* and them and the background points. Residual plot of the whole model (b), residuals of the factor species (c), residuals of the factor topographic position (d) and residuals of the factor study site (e).

```
A Model <- formula(logDSF ~ SpeciesBackground*Topography)
  TopoSiteModel.Full <- lme(Model, random = ~1 | Site,
    method = "REML", data=Focaldata)
```

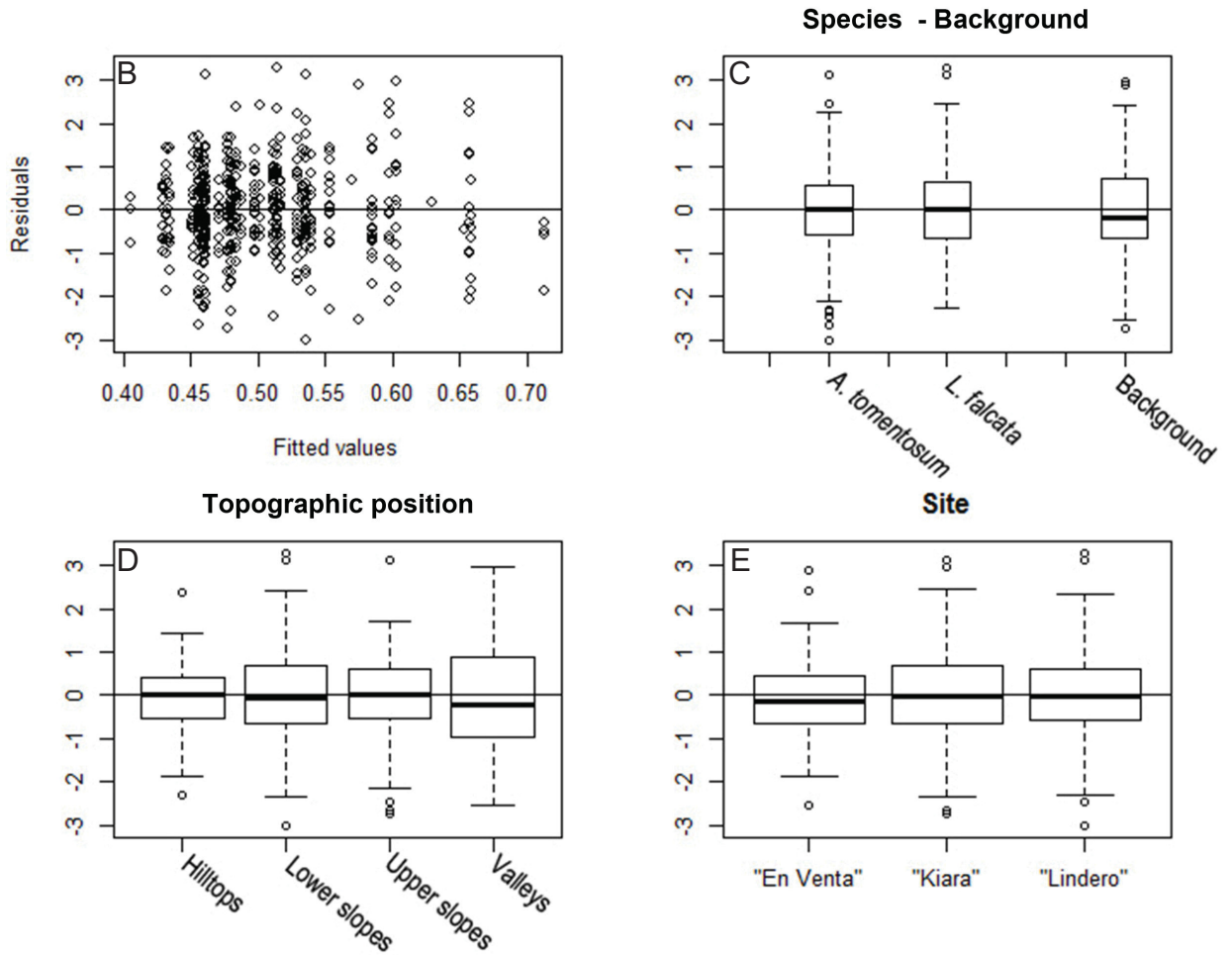


Figure 4. Residual plot (a), quantile-quantile plot (b), spread-location plot (c) and residuals vs. leverage plot (d) of the ANCOVA-model used to compare fertile and sterile *A. tomentosum* individuals microhabitats Direct Site Factor accounting for length of the individuals longest leaf.

