

**Diversity and distribution of bryophytes along an elevational
gradient on Baru Volcano, Panama**

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In memory of an admirable professor and friend

Prof. Dr. Juan Bernal

(1965-2018)

PREFACE

The idea of carrying out this project originates thanks to previous expeditions made to the top of the Baru volcano, the highest mountain in Panama. The hike to the volcano's top, which lasts around seven to nine hours, provides the opportunity to appreciate changes in the vegetation with the increase in elevation. Interestingly, one of the groups of plants that are frequently observed throughout the ascent is the bryophytes. Towards the top of the volcano, subtle changes in their abundance, colouration and growth forms can be observed in these plants. These observations captured my curiosity about how the diversity and functions of bryophytes within forests change along the mountain slope.

This doctorate was the propitious opportunity to address these and other questions regarding variations in diversity. In this work, in addition to presenting data on ecological patterns of bryophyte diversity, we make suggestions about the importance of considering different substrates and also describe useful methods for analysing information in this type of study. In the same way, we contrast our results with data of the elevational distribution of bryophytes in other tropical mountains, thus providing a literature review of importance for future studies.

Developing and completing this work was a challenging task. Today with joy, I share it, and I hope it is to your complete satisfaction.

Marburg, June 2020

Eyvar Elias Rodríguez-Quiel

**Diversity and distribution of bryophytes along
an elevational gradient on Baru Volcano,
Panama**

**Diversität und Verteilung von Bryophyten
entlang eines Höhengradienten am Vulkan
Baru, Panama**

**Diversidad y distribución de briofitas a lo largo
de un gradiente de elevación en el volcán Barú,
Panamá**



Abstract

Elevational gradients in tropical mountains are suitable systems for studying spatial variations in plant diversity. Due to their great abundance, diversity, and sensitivity to environmental changes, bryophytes are appropriate organisms to explore relationships between diversity patterns and environmental fluctuations. The present study undertakes an analysis of bryophyte diversity and its functions. Moreover, it evaluates the importance of considering bryophytes on different substrates to assess the effects of the microenvironment on the distribution of diversity. The study addresses the following specific questions:

1. How does bryophyte species diversity change with elevation, and how elevational patterns differ between substrate types?
2. How do the community composition and beta diversity of bryophytes on different substrates vary along an elevational gradient? How does elevation influence species association for a particular substrate type along a mountain slope?
3. How do bryophyte biomass and water-holding capacity change with the increase in elevation while accounting for the effect of bryophyte substrates?

The variations in the aspects of diversity and ecosystem functions were assessed along an elevational gradient on the Baru Volcano, Panama. Eight study sites were established from 1900 m to 3300 m, with elevational intervals of 200 m between sites. At each elevation, forest structure and climate data, as well as cover per bryophyte species from six substrate types in 600 cm² plots were recorded. From these plots, bryophyte samples were collected, deposited in plastic bags, and transported to the laboratory where biomass and water-holding capacity were determined and early stages of species identification were carried out.

The obtained results revealed that: *i*) bryophyte species richness consistently decreased towards the highest elevation; *ii*) elevation explains bryophyte community composition along the whole elevational gradient, while substrate types explain variations in short elevation ranges; and *iii*) bryophyte biomass and water-holding capacity consistently increased towards the highest elevation.

The present work demonstrates that bryophytes respond to the environmental variations drawn by a tropical elevational gradient, varying in species richness and community composition. Total richness of species at different elevations and substrate types decreased with increasing elevation. Species richness patterns were dependent on the scale of analysis, and substrates differed from each other only when considering total number of species aggregated per plots. The pattern of decrease in species richness was related to a gradual change in the composition of the communities. Changes in community composition were mainly explained by elevational variations and to a lesser extent by differences related to substrate types. Different substrates were more crucial in explaining community composition only in short elevational ranges (the four lowest and four highest elevations). Environmental aspects related to a transition zone of forest vegetation at 2500 m were associated with high rates of species turnover and differentiation between communities from the higher and lower area of the mountain. The continuous change of species along the

gradient induced a change of typical species per type of substrates and within each elevation. Community turnover results in variations in ecosystem functions that bryophytes perform along the elevational gradient. Bryophyte biomass and its water-holding capacity increased towards higher elevations. Being the terrestrial communities those that registered higher water-holding capacity.

Considering different substrates is relevant in the analysis of the bryophyte diversity since each of these micro-environments provides with different extent of information on the richness of species, composition of communities, and functions within the ecosystem. Species turnover induced a high ecological differentiation between lowest and highest elevation communities, causing modifications even in the association of species for a specific substrate. Bryophyte ecosystem functions varied with elevation due to changes in biomass, with different intensity in each substrate. Consequently, epiphytic and terrestrial bryophyte communities performed functions to different degrees within the mountain. Besides, these functions are performed by different communities at both ends of the gradient and also with varying effectiveness.

Modifications in the climate, such as those expected under climate change scenarios, would imply changes in different aspects of bryophyte diversity and their functions within the mountain ecosystem. If substrates differ in their elevational patterns of species richness, changes in substrate availability present an additional pathway for the climate to shape the diversity of bryophytes on tropical mountains. Therefore, a better understanding of the spatial variation in bryophyte diversity in these mountains is essential to elucidate the effects of environmental change on this crucial group of plants and its implications for ecosystem functioning. Our data suggest that considering the elevational gradient in the tropical mountain is key to the conservation of diversity and maintenance of ecosystem productivity.

Zusammenfassung

Höhengradienten im tropischen Gebirge sind gute Modellsysteme, um räumliche Unterschiede in der Biodiversität zu untersuchen. Wegen ihrer hohen Abundanz, Artenvielfalt und Empfindlichkeit gegenüber Umweltveränderungen sind Bryophyten besonders gut dafür geeignet, um Zusammenhänge zwischen Mustern in der Artenvielfalt und Umweltveränderungen aufzuspüren. Die vorliegende Studie untersucht die Artenvielfalt von Bryophyten sowie deren Funktionen im Ökosystem. Bryophyten von verschiedenen Substraten werden verglichen, um Aufschluss über den Einfluss der Mikrohabitate auf die Verteilung der Artenvielfalt zu gewinnen. Insbesondere werden folgende Fragen untersucht:

1. Wie verändert sich die Artenvielfalt der Bryophyten mit der geografischen Höhe, und wie ändern sich die höhenabhängigen Muster zwischen den verschiedenen Substrattypen?

2. Wie verändern sich die Artengemeinschaft und die Beta-diversität entlang des Höhengradienten? Ändern sich Assoziationen zwischen einzelnen Arten und Substraten entlang des Hanges?

3. Wie ändern sich Biomasse und Wasserspeichervermögen der Bryophyten mit zunehmender Höhe, wenn man den Effekt des Substrates mit berücksichtigt?

Die Unterschiede in den verschiedenen Aspekten von Biodiversität und Ökosystemfunktionen wurden an einem Höhengradienten auf dem Vulkan Baru in Panama untersucht. Acht Untersuchungsstandorte wurden zwischen 1900 und 3300m ü. NN im Abstand von jeweils 200 Höhenmetern festgelegt. An jeder Fläche wurden Waldstruktur und Klimadaten aufgenommen, sowie die Deckungsgrade der verschiedenen Bryophytenarten auf sechs unterschiedlichen Substrattypen, gemessen auf Probeflächen von 600 cm², bestimmt. Auf diesen Probeflächen wurden Proben von Bryophyten entnommen, in Plastiktüten gelagert und in ein Labor transportiert, wo ihre Biomasse und Wasserspeicherkapazität gemessen sowie eine taxonomische Bestimmung durchgeführt wurde.

Die Ergebnisse zeigten, dass i) die Artenvielfalt der Bryophyten mit zunehmender Höhe abnahm, ii) die Zusammensetzung der Bryophytengemeinschaften entlang des gesamten Gradienten durch die Höhe erklärt wurde, wohingegen die Substrattypen Unterschiede innerhalb von kleineren Höhenintervallen erklärten, und iii) Biomasse und Wasserspeicherkapazität mit der Höhe zunahmen.

Die vorliegende Arbeit zeigt, dass Bryophyten auf die Umweltveränderungen entlang des tropischen Höhengradienten mit Veränderungen in Artenvielfalt und -gemeinschaft reagieren. Auf allen Substrattypen sank die Artenvielfalt mit zunehmender Höhe. Verteilungsmuster in der Artenvielfalt hingen von der Größenskala der Analyse ab, und die verschiedenen Substrattypen zeigten hier nur dann unterschiedliches Verhalten, wenn man die Gesamtzahl der Arten auf den Probeflächen betrachtete. Die Abnahme der Artenvielfalt war verbunden mit einer graduellen Veränderung der Artengemeinschaft. Unterschiede in der Artengemeinschaft wurden hauptsächlich durch Höhenunterschiede, in geringerem

Umfang auch durch Unterschiede im Zusammenhang mit den Substrattypen erklärt. Die unterschiedlichen Substrattypen waren entscheidender dabei, die Zusammensetzung der Artengemeinschaft innerhalb kleinerer Höhenintervalle zu erklären (beispielsweise innerhalb der vier niedrigst- und der vier höchstgelegenen Flächen). Die Beta-Diversität zeigte im Zusammenhang mit einer Übergangszone in der Waldvegetation auf 2500m Höhe einen hohen Artenwechsel und eine Differenzierung der Artengemeinschaften ober- und unterhalb dieser Zone an. Der kontinuierliche Wechsel der Arten entlang des Höhengradienten führte auch zu einem Wechsel der für den jeweiligen Substrattyp typischen Leitart. Der Wechsel der Artengemeinschaften führte zu Variationen in den Ökosystemfunktionen, welche die Bryophyten entlang des Umweltgradienten ausführten. Biomasse und Wasserspeicherkapazität nahmen mit der Höhe zu. Bryophyten im Boden besaßen eine größere Fähigkeit, Wasser zurückzuhalten.

Es ist wichtig, die unterschiedlichen Substrate in der Analyse zu berücksichtigen, da jedes dieser Mikrohabitate in unterschiedlichem Maße Informationen über den Artenreichtum, die Artengemeinschaft und die Funktion innerhalb des Ökosystems lieferte. Der Artenwechsel führte zu einer hohen ökologischen Differenzierung zwischen den niedrigst- und höchstgelegenen Gemeinschaften, was auch zu Unterschieden in den Assoziationen verschiedener Arten zu bestimmten Substrattypen führte. Die Ökosystemfunktionen der Bryophyten veränderte sich mit der Höhe aufgrund von Änderungen in der Biomasse, was allerdings in unterschiedlichen Substrattypen unterschiedlich stark ausgeprägt war. Daher erfüllten die Gemeinschaften der epiphytisch und terrestrisch wachsenden Bryophyten Ökosystemfunktionen in unterschiedlichem Maße entlang des Berghanges. An beiden Enden des Höhengradienten werden die Funktionen von unterschiedlichen Gemeinschaften und in abweichender Effektivität ausgeführt.

Änderungen des Klimas, wie sie von den verschiedenen Szenarien des Klimawandels erwartet werden, könnten zu Änderungen in der Vielfalt der Bryophyten und deren Funktionen innerhalb der Bergökosysteme führen. Falls sich die höhenabhängige Verteilung des Artenreichtums zwischen den verschiedenen Substrattypen unterscheidet, dann bildet die Verfügbarkeit dieser Substrattypen ein weiteres Einfallstor für klimatisch bedingte Veränderungen der Biodiversität von Bryophyten im tropischen Gebirge. Daher ist ein besseres Verständnis der räumlichen Variationen der Artenvielfalt der Bryophyten in diesem Gebirgstyp essentiell, um sowohl die Auswirkungen der Umweltveränderungen auf diese so wichtige Pflanzengruppe als auch die daraus resultierenden Implikationen für die Funktionalität des Ökosystems zu erhellen. Unsere Daten legen nahe, den Höhengradienten in seiner jetzigen Form zu erhalten, sowohl im Interesse des Umweltschutzes, als auch zur Erhaltung der Produktivität des Ökosystems.

Resumen

Los gradientes de elevación en las montañas tropicales son sistemas adecuados para estudiar las variaciones espaciales en la diversidad vegetal. Debido a su gran abundancia, diversidad y sensibilidad a los cambios ambientales, las briófitas son organismos apropiados para explorar las relaciones entre los patrones de diversidad y las fluctuaciones ambientales. El presente estudio lleva a cabo un análisis de la diversidad briófitas y sus funciones. Además, evalúa la importancia de considerar las briófitas en diferentes sustratos para evaluar los efectos del microambiente en la distribución de la diversidad. El estudio aborda las siguientes preguntas específicas:

1. ¿Cómo cambia la diversidad de especies de briófitas con la elevación y cómo los patrones de elevación difieren entre los tipos de sustrato?

2. ¿Cómo varía la composición de la comunidad y la beta diversidad de briófitas en diferentes sustratos a lo largo de un gradiente de elevación? ¿Cómo influye la elevación en la asociación de especies por un tipo de sustrato particular a lo largo de la ladera de una montaña?

3. ¿Cómo cambian la biomasa briófitas y su capacidad de retención de agua con el aumento de la elevación mientras se tiene en cuenta el efecto de diferentes sustratos?

Las variaciones en los aspectos de diversidad y funciones del ecosistema se evaluaron a lo largo de un gradiente de elevación en el Volcán Barú, Panamá. Se establecieron ocho sitios de estudio desde 1900 hasta 3300 m, con intervalos de elevación de 200 m entre sitios. En cada elevación, se registraron datos de la estructura forestal y del clima, así como la cobertura por especie de briófitas de seis tipos de sustrato en parcelas de 600 cm². De estas parcelas, se recogieron muestras de briófitas, se depositaron en bolsas de plástico y se transportaron al laboratorio donde se determinó la biomasa, capacidad de retención de agua, y se llevaron a cabo las primeras etapas de identificación de especies.

Los resultados obtenidos revelaron que: i) la riqueza de especies de briófitas disminuyó consistentemente hacia la elevación más alta; ii) la elevación explica la composición de la comunidad briófitas a lo largo de todo el gradiente de elevación, mientras que los tipos de sustrato explican las variaciones en los rangos de elevación cortos; y iii) la biomasa briófitas y la capacidad de retención de agua aumentaron constantemente hacia la elevación más alta.

El presente trabajo demuestra que las briófitas responden a las variaciones ambientales presentes en un gradiente de elevación tropical, variando la riqueza de especies y la composición de las comunidades. La riqueza total de especies a diferentes elevaciones y tipos de sustrato disminuyó con el aumento de la elevación.

Los patrones de riqueza de especies dependían de la escala de análisis, y los sustratos diferían entre sí solo cuando se consideraba el número total de especies agregadas por parcelas. El patrón de disminución en la riqueza de especies se relacionó con un cambio gradual en la composición de las comunidades. Los cambios en la composición de las comunidades se explicaron principalmente por las variaciones en elevación y, en menor medida, por las diferencias de composición relacionadas con los tipos de sustrato. Los diferentes sustratos fueron más cruciales para explicar la composición de las comunidades solo en rangos de elevación cortos (las cuatro elevaciones más bajas y las cuatro elevaciones más altas). Los aspectos ambientales relacionados con una zona de transición de vegetación a 2500 m, se asociaron con altas tasas de rotación de especies y diferenciación entre comunidades de las áreas más altas y más bajas de la montaña. El cambio continuo de especies a lo largo del gradiente produjo un cambio de especies indicadoras por tipo de sustrato y dentro de cada elevación. El recambio de especies en las comunidades produce variaciones en las funciones del ecosistema que las briófitas realizan a lo largo del gradiente de elevación. La biomasa de briofita y su capacidad de retención de agua aumentaron hacia elevaciones más altas. Siendo las comunidades terrestres las que registraron una mayor capacidad de retención de agua.

Tener en cuenta diferentes sustratos es relevante en el análisis de la diversidad de briófitas, ya que cada uno de estos microambientes proporciona información diferente sobre la riqueza de especies, la composición de las comunidades y las funciones dentro del ecosistema. El recambio de especies produjo una alta diferenciación ecológica entre las comunidades de las elevaciones más bajas y más altas, causando modificaciones incluso en la asociación de especies por sustratos específicos. Las funciones que las briofitas desempeñan dentro del ecosistema variaron con la elevación debido a los cambios en la biomasa, con diferente intensidad en cada sustrato. En consecuencia, las comunidades de briofitas epifitas y terrestres realizan funciones en diferentes grados dentro de la montaña. Además, estas funciones son realizadas por diferentes comunidades en ambos extremos del gradiente y también con una eficacia variable.

Las modificaciones en el clima, como las esperadas en los escenarios de cambio climático, implicarían cambios en diferentes aspectos de la diversidad de las briófitas y sus funciones dentro del ecosistema de montaña. Si los sustratos difieren en sus patrones de elevación de la riqueza de especies, los cambios en la disponibilidad de sustratos presentan una vía adicional para que el clima dé forma a la diversidad de briófitas en las montañas tropicales. Por lo tanto, una mejor comprensión de la variación espacial en su diversidad en estas montañas es esencial para dilucidar los efectos del cambio ambiental en este grupo crucial de plantas y sus implicaciones para el funcionamiento del ecosistema. Nuestros datos sugieren que considerar el gradiente de elevación en la montaña tropical es clave para la conservación de la diversidad y el mantenimiento de la productividad del ecosistema.

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CHAPTER 1

General introduction

1 General Introduction

1.1. The relevance of mountain ecosystems

Mountain ecosystems are relevant because they influence the climate (air quality, precipitation regimes), they are the source of many natural resources (water, food, medicines) and also harbour over-proportionally high biodiversity (Egan & Price, 2017; Malhi et al., 2010; Perrigo, Hoorn, & Antonelli, 2019). The growing demand for areas for housing and food has caused overexploitation of the services that these ecosystems provide us. Due to this overexploitation of resources, both the local climate and the existing biodiversity are currently undergoing rapid modification. In consequence, the conservation and understanding of the functioning of mountain ecosystems are of direct relevance to safeguard human populations (Egan & Price, 2017).

Mountains are ecologically highly variable ecosystems, and some of the most predictable variations are environmental changes along mountain gradients (Cavalier, 1996). In response to these environmental changes, both flora and fauna can vary their distribution (for review, see Grytnes & McCain, 2007; McCain & Grytnes, 2010). Furthermore, this variation differs sharply between sites and taxonomic groups, although for some taxonomic groups, the number of sites studied does not yet allow generalizations about geographic variation. The variation of the diversity along a mountain slope is of particular interest, as they may allow a better understanding of the effects of climate change on species distribution, biodiversity and the resulting ecosystem functions. Due to the high diversity they harbor, strong variation in topography and environmental gradients present, the mountains of the tropical region are an appropriate place to carry out studies on the variation of diversity with the increase in elevation (Malhi et al., 2010).

The current diversity of species is the product of numerous processes in time and space that influenced their distribution. Distinguishing the effect of these processes has been an issue that has drawn attention for many years (Mittelbach & McGill, 2019). Processes act on different levels or metrics of diversity, e.g. species richness (alpha, beta and gamma diversity), genetic diversity (genetic variation), functional diversity (ecological importance of species within a community).

Currently, topics of great interest are those that assess the response of species to a climate change scenario and the repercussions that this will imply on the functioning of ecosystems (Laureto, Cianciaruso, & Samia, 2015). The starting point to generate this complex information network is to know the current distribution of the species and the patterns they present in different ecosystems (for example, elevational gradients).

In the Central American region, a mountain of local importance is the Baru Volcano National Park, which is located to the west of the Republic of Panama (08°

48.4°N, 082° 32.4'W), close to the border with Costa Rica (Figure 1-1). This volcano is the highest mountain in Panama, with 3475 m a.s.l. It presents a strong variation of topography and vegetation with the increase in elevation, ranging from tropical montane cloud forests at 1500 m to sub-paramo forests at the top of the volcano. The Baru volcano does not include lowland elevations because the lower part of the mountain is surrounded by small towns, which are dedicated mainly to cattle raising and agriculture. The last eruption of this volcano was approximately 500 years ago (Hopp & Waite, 2016). The protected region and areas near the Baru volcano are the primary source of water and many other resources, both locally and for the entire country.

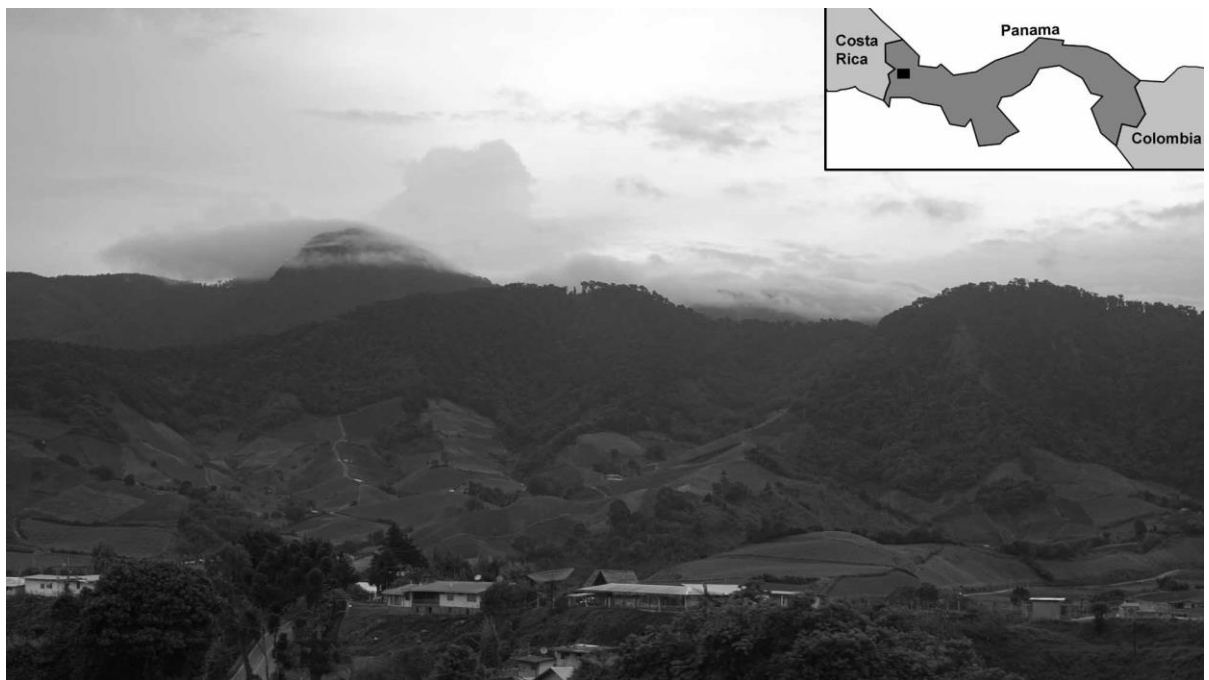


Figure 1-1. Location and panoramic view of the lower part of the Baru Volcano National Park, Panama (ca. 1500 m a.s.l.). Livestock farming and agriculture areas are located in the lower limit of the park (seen from the northern part of the volcanic cone).

1.2 Bryophytes in mountain ecosystems

One of the main characteristics of tropical montane forests is the dense layers of bryophytes present in different substrates from the understory to the small branches on the forest canopy. The bryophytes are an important group of plants within the tropical region, because there is where they reach their greatest species diversity and abundance (Gradstein, Churchill, & Salazar Allen, 2001). Taxonomically they include three groups, Bryophyta, Marchantiophyta and Anthocerotophyta (Goffinet, 2000), throughout this work I will refer to them with only one general category "bryophytes". Each group includes species with anatomical characteristics that have allowed them to proliferate both in high humidity environments and in sites with prolonged droughts

(Glime, 2017c). In this way, they have been able to colonize different natural and urban environments. They can be found growing on stranger surfaces in a natural forest like the leaves of other plants (either in the undergrowth or in the canopy), or in urban areas on iron or cement. For this reason, they are colonizing and substrate-forming organisms relevant for the germination and growth of other plants (Glime, 2019) and even other organisms such as bacteria, insects, molluscs, among others (Glime, 2017a). The success as colonizers of substrates is because the bryophytes are mostly poikilohydric organisms. This strategy means that their state of hydration (and obtaining nutrients) depends on the surrounding environmental conditions. Due to this condition, bryophytes can absorb water and nutrients throughout their entire body. Besides, due to a large number of adaptations related to the poikilohydric strategy (Glime, 2017b; Proctor, 1990), they are plants capable of surviving prolonged periods of drought, as well as being able to produce large amounts of biomass in environments with constant humidity, e.g. peatlands.

Due to this dependence on environmental conditions, bryophytes have been used as indicator organisms of environmental quality (e.g. Benítez, Gradstein, Cevallos, Medina, & Aguirre, 2019; Guerra, Arrocha, Rodríguez, Déleg, & Benítez Chavez, 2020; Holz, Gradstein, Heinrichs, & Kappelle, 2002) and to categorize elevational variations in tropical mountain ecosystems (Churchill, 1991; Dias dos Santos & Pinheiro da Costa, 2010; Enroth, 1990; Frahm, 1987; Frahm & Gradstein, 1991; Gradstein, van Reenen, & Griffin, 1989; Seifriz, 1924).

However, most of the studies above focused on bryophytes that grow on tree bark (epiphytes), and there is little information on the distribution patterns of communities present on other substrates, such as rocks, decaying logs, ground. The substrate types could be a limiting factor for the growth of bryophytes due to the availability of nutrients and chemical properties of each (Bates, 2009). Furthermore, due to their strong dependence on environmental conditions, small variations in their habitat (e.g. in light conditions) affect the presence of certain species, modifying in the long term the communities present in each substrate (Marino & Allen, 1992; Mežaka, Bader, Salazar-Allen, & Mendieta-Leiva, 2020).

Information on the distribution of existing bryophyte diversity in the tropics is currently limited. Some works on the diversity and ecology of bryophytes were carried out in South America, mainly in the Andes (Churchill, 1991; Frahm, 1987; Gradstein et al., 1989; Porrás-López & Morales-Puentes, 2020; Van Reenen & Gradstein, 1983; Wolf, 1993), in Asia in Mt. Kinabalu (Frahm, 1990a), in Southern Thailand (Chantanaorrapint & Frahm, 2011), and Africa nearby Madagascar island (Ah-Peng et al., 2007; Henriques, Borges, Ah-Peng, & Gabriel, 2016; Marline, Ah-Peng, & Hedderson, 2020).

However, as with vascular plants, there is no consensus on the distribution patterns of diversity, and it is shown that these mainly depend on local geographical and environmental conditions. On the other hand, some ecological aspects remain poorly addressed.

In Panama, the works of Gradstein and Salazar Allen (1992), is the only one that details the variation of species diversity with the increase in elevation (elevational range 0-1200 m), providing a detailed elevational zonation based on bryophyte diversity. On the other hand, ecological aspects have been addressed by Wagner, Zotz, Allen, and Bader (2013) that describe how variations in temperature influence the photosynthetic activity of bryophytes and consequently how this environmental factor may affect the elevational distribution of species. Marino and Allen (1992) and Mežaka et al. (2020) also describe how the forest structure dynamics (e.g. canopy openness) influence the composition of epiphyllous bryophyte communities (i.e. grow on shrub or tree leaves). Guerra et al. (2020) details that levels of intervention in highland forests affect the composition of epiphytic bryophyte communities, reaffirming the use of these plants as indicators of environmental quality.

Despite the existence of this reference base, there are currently gaps of information on how the different aspects of diversity (e.g. species richness, species abundances, biomass) behave when there is variation in elevation. This information is crucial to know how important the role of bryophytes is within tropical montane forests and how their ecosystem functions change with increasing elevation.

Studies of the spatial distribution of diversity are based on the simple fact of comparing similar communities that occur in different places. Comparisons allows examinations of the links between current diversity with factors such as climate, light condition, topography. According to the obtained patterns, the occurrence of specific assemblages of species can be predicted, within and in other areas with similar environments.

Thanks to the high sensitivity of bryophytes to changes in climate-related variables, they are organisms that could respond strongly to changes in the environment. The bryophytes could reflect patterns of diversity, variation in community composition, even affectations in the functions that they perform throughout the tropical mountains.

1.3 Structure of the thesis.

The general research goals of the present project were (1) to record and analyse the distribution patterns of bryophytes along an elevation gradient in the Baru Volcano National Park. Also, (2) to determine if these patterns differ when considering different substrates where bryophytes grow. As well, (3) to analyse the relationship of these patterns with environmental conditions.

Following these goals, the spatial distribution of different aspects of bryophyte diversity in the Baru volcano were studied to answer the following questions, which were developed in each of the thesis chapters:

A. How does bryophyte species diversity change with elevation; and how elevational patterns differ between substrate types? (Chapter 2).

B. How do the community composition and beta diversity of bryophytes on different substrates vary along an elevational gradient? How does elevation influence species association for a particular substrate type along a mountain slope? (Chapter 3).

C. How do bryophyte biomass and water-holding capacity change with the increase in elevation while accounting for the effect of bryophyte substrates? (Chapter 4).

In each chapter, also was analysed the effect of climatic fluctuations and forest structure on each ecological aspect considered.

Chapter 2. How does bryophyte species diversity change with elevation; and how elevational patterns differ between substrate types?

Bryophytes are highly diverse and abundant in tropical mountains. However, the diversity is not homogeneously distributed, mainly due to the great variety of ecosystems that occur over short distances. The elevational distribution patterns of the bryophyte species diversity (species richness and community structure) were described and related to elevation, substrate types, and environmental drivers at different scales (aggregated per plot, substrate type or elevation). Also, direct contrast among substrate types using the relative abundance of the species was explored to know how the structure of the communities varied with the increase in elevation.

Chapter 3. How do the community composition and beta diversity of bryophytes on different substrates vary along an elevational gradient? How does elevation influence species association for a particular substrate type along a mountain slope?

The substrates represent different ecosystems in which bryophytes can grow. Therefore, it is expected that due to these different microenvironments, community composition changes with the increase in elevation. These patterns of species turnover (beta diversity) and community composition give us an idea of the relationship between current diversity and environmental conditions. The role of elevation and substrates was primarily evaluated, explaining the community composition along the elevational gradient. Also, it was examined to what extent these species turnover imply a change or loss of species with the increase in elevation. Likewise, it was evaluated if species show a specific association for certain elevations or substrate types along the gradient.

Chapter 4. How do bryophyte biomass and water-holding capacity change with the increase in elevation while accounting for the effect of bryophyte substrates?

Within tropical mountains, bryophytes cover extensive layers from the understory to the forest canopy. The abundance of these plants suggests that they perform essential functions within the mountains. However, how does the ecological relevance of bryophytes and their ecosystem roles (e.g. water retention) change with the increase in elevation? It was analysed how the biomass (as a measure of abundance) and water-holding capacity (ecosystem function) of bryophyte and lichen

layers changes along the gradient. Lichens were included in this chapter due to their close relationship with bryophytes, mainly towards the volcano's top. Also, were evaluated the differences between the patterns shown by samples collected on different substrates. The obtained patterns were associated with climatic variations.

CHAPTER 2

Elevational patterns in tropical bryophyte diversity differ among substrates.

A case study on Baru volcano, Panama

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with, Jürgen Kluge, Glenda Mendieta-Leiva and Maaïke Y. Bader

Elevational patterns in tropical bryophyte diversity differ among substrates. A case study on Baru volcano, Panama

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Abstract. — Bryophytes attain their highest diversity in tropical mountains. Although distribution patterns have been described, little emphasis has been placed on comparing patterns among substrates (e.g. terrestrial, epiphytic). Understanding these patterns is important, because they determine not only the pool of genetic resources, but also ecosystem functioning of mountain ecosystems. Therefore, we studied how bryophyte species diversity changes with elevation and how elevational patterns differ between substrate types, and relate elevational trends to environmental drivers. At eight elevations in the Baru Volcano, Panama, between 1900 and 3300m, bryophytes were collected from six substrates with four replicates per substrate. The cover of species was registered to determine relative abundances. Species richness and community structure were determined and related to elevation, substrate types, and environmental drivers at different scales (aggregated per plot, substrate type or elevation). Bryophytes species richness from different substrates decreased towards the highest elevations, at all scales of analysis. However, at the plot-scale this pattern differed between substrates, with terrestrial bryophytes peaking at higher elevations than the other substrates. Relative humidity explained richness similarly and slightly better than elevation. Uneven communities were present at the lowest elevations, due to the presence of many little-abundant species. In studies on the spatial distribution of bryophyte diversity, it is essential to consider different substrates, the spatial scale and the aspect of diversity. If substrates differ in their elevational patterns of species richness, changes in substrate availability present an additional pathway for climate to shape the diversity of bryophytes on tropical mountains. Therefore, a better understanding of the spatial variation in bryophyte diversity in these mountains is essential to elucidate the effects of environmental change on this crucial group of plants and its implications for ecosystem functioning.

Keywords. — bryophytes, species richness, community structure, elevational gradient, tropical mountains, substrates.

2. Elevational patterns in tropical bryophyte diversity differ among substrates. A case study on Baru volcano, Panama

2.1 Introduction

Mountains play a significant role in determining global and regional climates, are the source of many natural resources, and harbour an over-proportionally high biodiversity (Perrigo et al., 2019). Because of these and other functions, understanding the functioning of mountain ecosystem is of direct relevance to safeguarding human populations in large parts of the globe (Egan & Price, 2017). Mountain ecosystems are spatially highly variable, and some of the most predictable variation is the environmental change along elevational gradients. Changes in species richness and other dimensions of biodiversity in response to this variation have been found to differ strongly between taxonomic groups and sites (for review, see Grytnes & McCain, 2007; McCain & Grytnes, 2010), although for some taxonomic groups the number of sites studied does not yet allow generalisations about geographic variation. These elevational changes are of particular interest, as they may allow a better understanding of the effects of climate change on species distributions, biodiversity, and resulting ecosystem functions.

In the wet tropics, mountain vegetation generally changes from rainforest on the lower slopes to cloud forest on the higher slopes. Cloud forests are characterised by the presence of dense layers of bryophytes, which can cover all types of substrates from the ground to the forest canopy (Gradstein et al., 2001). In the wet tropical Andes, bryophyte cover (Van Reenen & Gradstein, 1983), biomass (Frahm, 1987; Wolf, 1993), and species richness (Churchill, 1991; Frahm & Gradstein, 1991; Gradstein et al., 1989) tend to peak on the higher slopes in the so-called mossy forest (between ca. 2000 and 3000m). Within this cool and moist environment, bryophytes are crucial organisms in terms of ecosystem functions, diversity and productivity (Slack, 2011). Due to their strong dependence on local climatic conditions, bryophytes have been used to define the elevational zonation of forest types all around the world (e.g. Churchill, 1991; Dias dos Santos & Pinheiro da Costa, 2010; Enroth, 1990; Frahm, 1987; Frahm & Gradstein, 1991; Gradstein et al., 1989; Seifrizz, 1924).

Another important determinant of bryophyte species composition and diversity is the type of substrate (Bates, 2009; Richards, 1984). Since bryophytes do not have roots and can take up water and nutrients through their aerial surfaces, they are able to grow on a wide range of substrates, including soil, plants, leaves, deadwood, and rocks. However, so far, there are few studies on elevational diversity patterns that include and explicitly distinguish both terrestrial and epiphytic substrates (Van

Reenen & Gradstein, 1983). Most studies have considered epiphytic bryophytes (e.g. Ah-Peng et al., 2012; Wolf, 1993), or have merged diversity from all available substrates into one dataset (e.g. Cacia-Toledo, Serrano-Cardozo, & Ramirez Pinilla, 2018; Churchill, 1991; Gradstein, 1995; Gradstein et al., 1989). As a result, it is unclear how different substrates contribute to elevational patterns in bryophyte diversity.

Bryophyte species richness and biomass are both highest at cloud-forest elevations (Pócs, 1980; Rodriguez-Quiel, Mendieta-Leiva, & Bader, 2019; Wolf, 1993), but it is unclear how these properties are related to each other. Although both decrease towards the tropical lowlands (Wolf, 1993), this decrease is more pronounced for biomass than for diversity, and some low-biomass lowland communities can contain high numbers of species, e.g. from the very small-statured but diverse liverwort family of Lejeuneaceae (Gehrig-Downie, Obregon, Bendix, & Gradstein, 2013). Conversely, some high-biomass bryophyte communities are strongly dominated by a few very productive species (e.g. *Sphagnum*-dominated peatlands) and show a relatively low species richness (Bedford, Walbridge, & Aldous, 1999; Mason, Zeldin, Currie, Raffa, & McCown, 2014). So, although a positive relationship between biomass and diversity is suggested at large scales, this pattern does not appear to be universal. This issue is not unique to bryophytes but also found for communities dominated by vascular plants, where at a global scale the most highly productive communities like tropical forests have the highest species richness (Mittelbach & McGill, 2019), but at smaller spatial scales the productivity-diversity relationships tend to be variable (Gillman & Wright, 2006), possibly due to confounding effects of diversity on productivity and of biomass on diversity (Grace et al., 2016).

In this paper, we present the elevational patterns in the diversity of bryophytes growing on different substrates on Baru Volcano, Panama. Our first research question was how substrates differ in their pattern of bryophyte species richness along elevation and what environmental variables best explain these patterns. Based on the above-mentioned patterns found in the Andes (Cacia-Toledo et al., 2018; Churchill, 1991; Frahm, 1987; Gradstein, 1995; Gradstein et al., 1989; Van Reenen & Gradstein, 1983; Wolf, 1993), we expected to find a peak in species richness at high elevation, possibly with a different position of the peak for different substrates due to the different microclimatic conditions at these substrates. As little previous information is available about substrate-specific diversity patterns, we could not further specify this hypothesis. Our second question addressed how other aspects of diversity, increasingly considering species relative abundances, differ among substrates and along elevation. We hypothesised that communities would be more uneven at sites with high numbers of species, and because of that abundant species show less pronounced elevational trends than species richness. Our third question addressed the relationship between previously reported biomass patterns along the elevational gradient (Rodriguez-Quiel et al., 2019) with the species richness patterns reported

here. Based on large-scale patterns observed elsewhere, we expected a positive correlation along elevation. We tested this and whether such a correlation was also present when correcting for elevation, so at the smallest scale of plots on different substrates. By better understanding the diversity and functional patterns of tropical bryophytes, our goal is to be better able to predict responses to environmental changes and, subsequently, to better inform conservation measures.

2.2 Material and methods

Study area

This study was conducted in Baru Volcano National Park, western Panama (Figure 2-1). The protected part of Baru ranges from 1500 to 3475 m a.s.l. (below the lower boundary there is agriculture and above the highest boundary transmission antennas are located; thus these areas were not taken into consideration for the study because of the level of disturbance). The last eruption of Baru volcano was roughly 500 years ago (Hopp & Waite, 2016).

The study sites were established along the western slope of the volcano, every 200 m along an elevational gradient, at eight elevations in total (Figure 2-1). We selected sites based mainly on the dominant arboreal vegetation at each elevation. Sites with a strong topographic variation like exposed ridges were avoided as much as possible. At the lowest four elevations, relatively flat sites were selected while at the highest four elevations, slopes were steeper and more exposed.

Climate

From February to October 2017 we sampled bryophytes from 600-cm² plots on each of six substrates: soil, rock, decomposing log, tree base, tree trunk (at breast height), and understorey branch. At each of the eight study sites (i.e. elevations), four replicates were located randomly on each substrate type, and at least 10 m apart so that they had a certain degree of independence. The trees selected for the study had a diameter at breast height (dbh) between 20 and 60 cm. The base and trunk samples were taken at the Northern side of the trunk from each of the four trees at 0.5 and 2 m height, respectively. To evaluate the relative species abundance, we estimated the cover of each species or morpho-species per 600-cm² plot before collecting the samples. Because bryophytes and lichens were found growing on the same substrates, lichen cover was also recorded, but it was not included in the species-richness analyses. A total of 192 samples was collected.

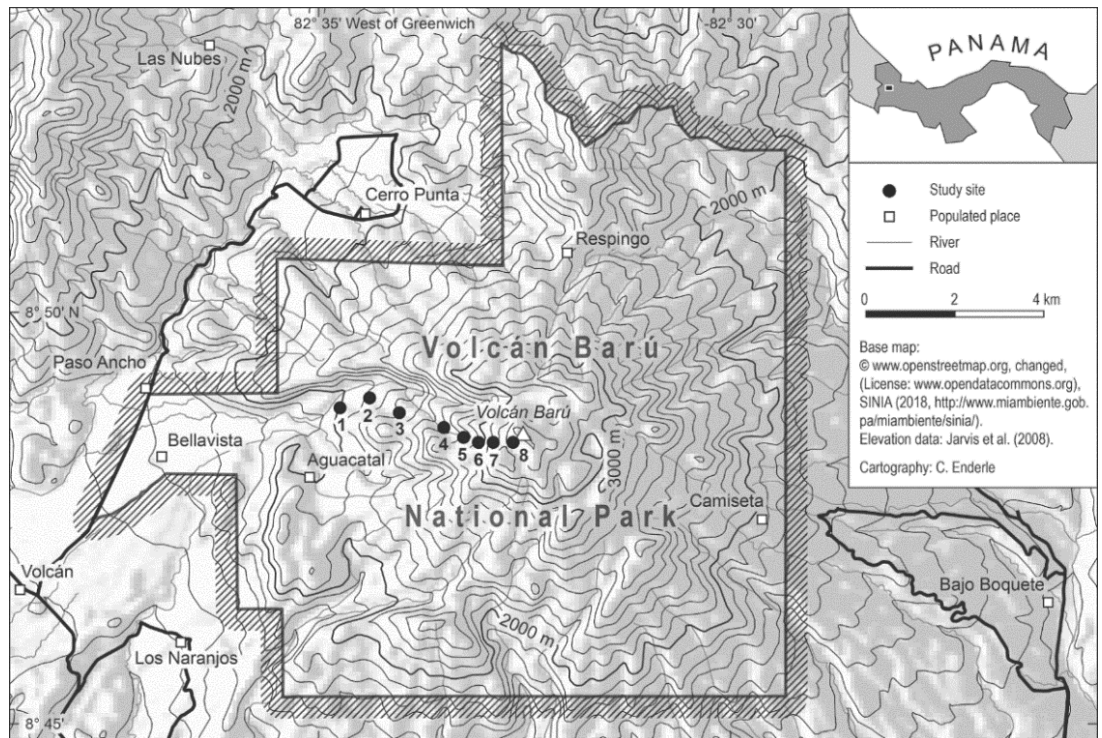


Figure 2-1. Study sites established along an elevational gradient on the Baru Volcano National Park, Panama. Elevational gradient with sites every 200 m, in which plots of 600-cm² for each of the six types of substrates, with four replicates for each substrate, were established.

Species identification

Samples were examined microscopically in the laboratory to search for tiny species that were missed in the field and to identify all species encountered to the lowest possible taxonomic level. Several taxonomic and floristics papers and books for Neotropical bryophytes (e.g. Gradstein, 2016; Gradstein et al., 2001; Gradstein & Pinheiro da Costa, 2003; Gradstein & Uribe, 2011) were used. Specimens were deposited in the herbarium of the “Universidad Autónoma de Chiriquí” (UCH). Bryophyte nomenclature and family classification follow the online database of TROPICOS (Tropicos.org, 2019) for hornworts and mosses, and Bernal, Celis, and Gradstein (2016) for liverworts. Voucher specimens for difficult taxa were examined by specialists (see acknowledgements).

Data analysis

- *Species richness patterns*

To assess changes in the species richness along the elevational gradient at different scales, generalised linear models (GLMs) were used at the plot level and linear models at the substrate and site level. For the plot- and substrate-level models, the substrate type was included as a co-variable to evaluate whether the species richness pattern along elevation differed between substrates. In the plot-level model, the Poisson family distribution was used (Crawley, 2007). The full models included the explanatory variables substrate (if applicable), elevation and elevation squared (to allow for unimodal elevational patterns), and the interactions of the simple and quadratic elevation terms with substrate type (if applicable).

Species richness as a function of climatic and forest-structure variables was tested at the plot level only. Three separate models were evaluated (with temperature, relative humidity and forest structure data as independent variables), as they were strongly mutually correlated (Appendix F 1). These models were compared to the model using elevation as the independent variable (see above) to assess whether any of the environmental variables was a stronger predictor than elevation (comparing their Akaike information criterion [AIC] and R^2 values), which might indicate a causal relationship.

We addressed the scale at which diversity was added to the elevations, either at the plot or at the substrate level, by calculating the β diversity (sensus Whittaker, 1960). Linear models were used to determine changes in the β diversity (for both substrate and plot-level) along elevation.

For all GLMs and linear models, model selection was carried out using backward stepwise selection successively removing the least-significant terms. Simplified and more complex models were compared using the *anova* function in R (Crawley, 2007), and we stopped removing terms when the removal started causing a significant difference between the models.

- *Community structure patterns*

Diversity and community-structure patterns along elevation were assessed at the substrate level by calculating Hill numbers. Hill numbers are a mathematically unified family of diversity indices where the order of " q " (from $q=0$ to $q=2$) indicates the sensitivity of the diversity metric to species relative abundances (Chao et al., 2014). When $q=0$, abundance does not count at all and diversity is equivalent to species richness. When $q=1$, species are weighted in proportion to their relative abundance and diversity is interpreted as the number of "typical species" (analogous to the exponential of the Shannon index), and when $q=2$, abundant species are weighted more strongly than rare species and diversity can be interpreted as the number of "very abundant species" (analogous to the inverse Simpson concentration). Hill numbers are portrayed as a function of order q in diversity profile curves. The slope of this curve reflects the unevenness of the communities (Gotelli & Chao, 2013). A steep slope indicates an uneven community, where the species richness is

made up by few abundant species and many accompanying low abundances to rare species. In the opposite case, when the slope is flat, all species are similarly represented within the community (even community). After $q=3$, there tend to be very few changes in the profile; therefore, we do not show results at these orders of q . We evaluated the first three discrete orders of q (though q is a continuous variable) as a function of elevation and substrate using linear models. For these models, a structure equivalent to those previously described was used (see substrate-level model).

- *Diversity-biomass relationships*

For calculating the correlation between species richness and biomass per area, macrolichen morphospecies (23 in total) were added to the bryophyte species numbers, because the biomass was determined for the epiphyte layer including both bryophytes and lichens. Lichen cover in the plots generally increased from less than 5% per plot at the lowest elevations to about 30% at 2700m, so that they also contribute significantly to biomass in some plots. For this analysis, bryophyte and lichen biomass data, previously reported by Rodriguez-Quiel et al. (2019), from the same plots along the elevational gradient were used. We first calculated the correlation (Pearson) between species richness and biomass at the site level, i.e. correlation along elevation, and at the plot level, i.e. assessing a mixture of elevational as well as more local patterns. Then, to study the correlation of species richness and biomass not related to elevation, we modelled species richness as a function of biomass at the plot level with a generalized linear mixed model (GLMM), with elevation as random effect and Gamma distribution, using the package “lme4” (Bates, Mächler, Bolker, & Walker, 2015). All analyses were performed with the statistical software R 3.6.1. (R-Core Team, 2019) and the packages “vegan” (Oksanen et al., 2007).

2.3 Results

Along the elevational gradient, 43 families (25 Bryophyta, 17 Marchantiophyta and 1 Anthocerotophyta), 84 genera (54 Bryophyta, 29 Marchantiophyta and 1 Anthocerotophyta) and 166 species (91 Bryophyta, 68 Marchantiophyta and 1 Anthocerotophyta) were identified. Six species were new records for Panama (Appendix T 1, list of species).

Species richness patterns

The total species richness per site, i.e. including all substrates, showed a clear decreasing trend ($F = 6.33$, $p < 0.05$, $R^2 = 0.43$). Looking at it more closely we can discern an outlier at 2500m (76 species, Figure 2-2) and a stable level above 2700m. At 2500m, the transition zone between the taller forest up to 2500m and shorter and

more open vegetation above 2900m begins, and vegetation is more heterogeneous than at the other sites. Therefore, although the plot-level richness is not exceptional at this site (Figure 2-4b), all substrates except decomposing logs show a particularly high species richness (Figure 2-4a). We thus expected a high β diversity among plots within substrate types at this elevation, but this was not the case (Appendix F 2b). Not only species richness per substrate, but also β diversity among substrates was relatively high at this elevation, which will have contributed even more to the high overall species richness at this elevation (Appendix F 2a).

At the substrate level species richness also decreased with elevation ($R^2 = 0.41$; $F = 34.01$; $p < 0.001$; Figure 2-3a). Substrates did not differ in their species richness or in the slope of the elevational decrease (no substrate-elevation interaction; Figure 2-3a). The scale of analysis is crucial, and this was demonstrated when analysing richness patterns at the plot level. At this level, substrates differed in their mean species richness per plot, and the shape of the elevational pattern varied according to the substrate types (Figure 2-3b and Table 1). Epiphytes on branches showed the strongest decrease and epiphytes on the tree base the weakest. The terrestrial bryophytes stand out, as their richness did not decrease with elevation but peak at intermediate elevation (Figure 2-3b).

In contrast to α diversity at different scales, within-elevation β diversity did not show an elevational trend ($F = 0.06$; $p = 0.79$ for β diversity among substrates; Appendix F 2a. $F = 0.84$; $p = 0.39$ for β diversity among plots within substrates; Appendix F 2b).

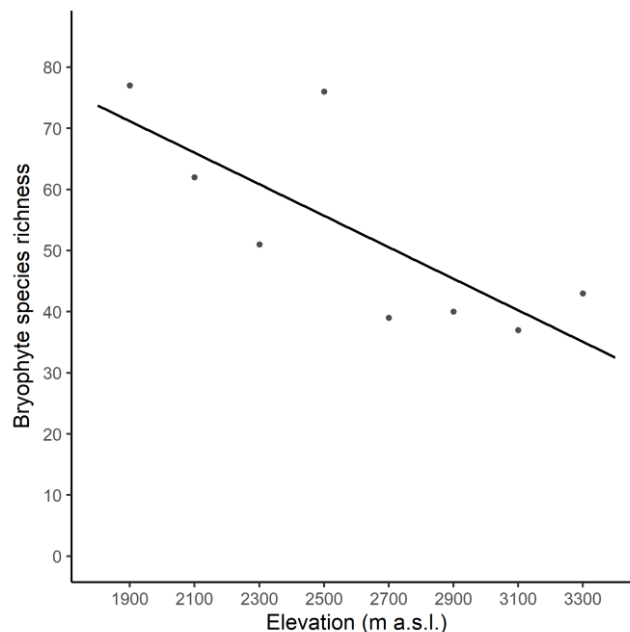


Figure 2-2. Variation in the total bryophyte species richness on six substrate types along an elevational gradient on Baru Volcano, Panama. Elevation had a negative effect ($F = 6.33$, $p < 0.05$, $R^2 = 0.43$), while the quadratic term of elevation did not improve the model.

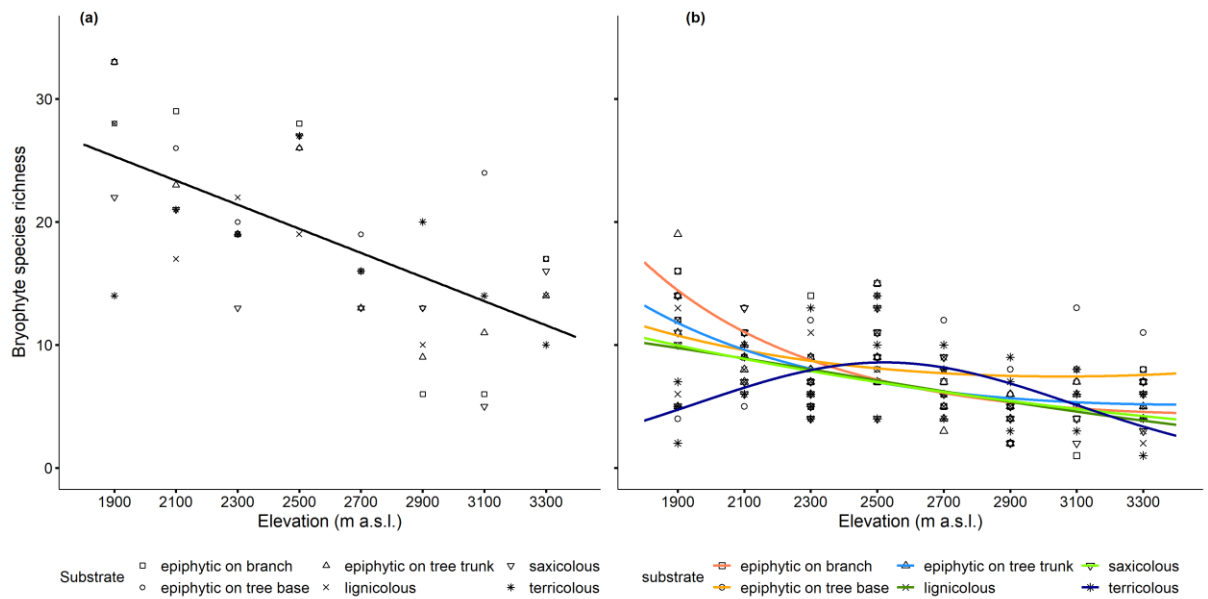


Figure 2-3. Change in bryophyte species richness on different substrates along an elevational gradient on Baru Volcano, Panama. A: variation at the substrate level, i.e. total number of species found in four 600-cm² plots per substrate per elevation (line based on a linear model, no significant differences between substrates at this level); B: variation at the plot level, i.e. number of species found per 600-cm² plot (lines based on a GLM, see Table 2-1). The quadratic term of elevation was useful to improve the model at the plot level only.

The environmental factors that may explain the elevational patterns are all highly correlated with each other and with elevation (Appendix F 1), so it is hard to distinguish their effects. Explaining species richness by mean daily relative humidity, temperature (both taken at the site level) or the forest structure (taken at the plot level) showed that the relative humidity best explains the variation in the bryophyte species richness, although the differences between the models were not large (Table 1-1). Interestingly, the quadratic term of relative humidity did not improve the model, as it did for elevation. The models show that the species richness was higher at higher air humidity, higher temperature, and where the forest canopy was most closed and highest (Appendix F 3). These conditions corresponded to the lower elevations along the transect. The model using relative humidity had a slightly lower *AIC*, i.e. provided more explanatory power with a simpler model, than the model using elevation (Table 1-1).

Table 2-1. Analysis of Deviance models of the generalised linear models (GLMs) explaining the variation in species richness at the plot level of bryophytes from different substrates according to variation in the climatic and forest structure data on the Baru Volcano, Panama.

Model	Included factors	LR Chisq	Df	p-value
Elevation $R^2 = 0.40$ $AIC = 943$	Elevation	0.12	1	0.72
	Elevation ²	0.13	1	0.72
	Substrate	12.40	5	<0.01
	Substrate: Elevation	19.18	5	<0.001
	Substrate: Elevation ²	17.65	5	<0.001
Relative humidity $R^2 = 0.40$ $AIC = 936$	Mean daily relative humidity	82.23	1	<0.001
	Substrate	12.40	5	<0.01
	Substrate: Mean daily relative humidity	28.20	5	<0.001
Temperature $R^2 = 0.34$ $AIC = 961$	Mean daily temperature	0.01	1	0.89
	Mean daily temperature ²	0.67	1	0.41
	Substrate	12.40	5	<0.01
	Substrate: Mean daily temperature	18.42	5	<0.01
	Substrate: Mean daily temperature ²	20.42	5	<0.01
Forest structure factors $R^2 = 0.36$ $AIC = 959$	Canopy-cover	0.36	1	0.55
	Height of the canopy	4.54	1	<0.01
	Substrate	6.60	5	0.25
	Substrate: Canopy-cover	15.74	5	<0.001
	Substrate: Canopy-cover ²	17.52	6	<0.001

Notes: The full models were (1) Species richness ~ elevation * substrates + elevation² * substrates; (2) Species richness ~ relative humidity * substrates + relative humidity² * substrates; (3) Species richness ~ temperature * substrates + temperature² * substrates; (4) Species richness ~ canopy-cover + height of the canopy + substrate + canopy-cover : substrate + height of the canopy : substrate + canopy-cover² : substrate + height of the canopy²: substrate, respectively. *LR Chisq* = Person's Chi-squared value for a Poisson family distribution; *Df* = degree of freedom; *p-value* = level of significance.

Community structure patterns

At the lowest elevation, substrates showed highly uneven communities, particularly epiphytic communities on the base and the trunk of the trees (see the profiles at 1900m, Figure 2-4). However, with increasing elevation, most of the profiles became flatter, indicating that communities were more even.

Like species richness ($q=0$), the richness of typical species ($q=1$) at the substrate level decreased with elevation ($R^2 = 0.13$; $F = 7.86$; $p < 0.01$), though to a lesser degree (Appendix F 4 A and B). In contrast, the number of very dominant species ($q=2$) remained similar along elevation ($p = 0.16$; Appendix F 4 C). The shapes of the elevational patterns did not differ between substrate types (no substrate-elevation interaction, Appendix F 4) and the quadratic term of elevation did not improve the models.

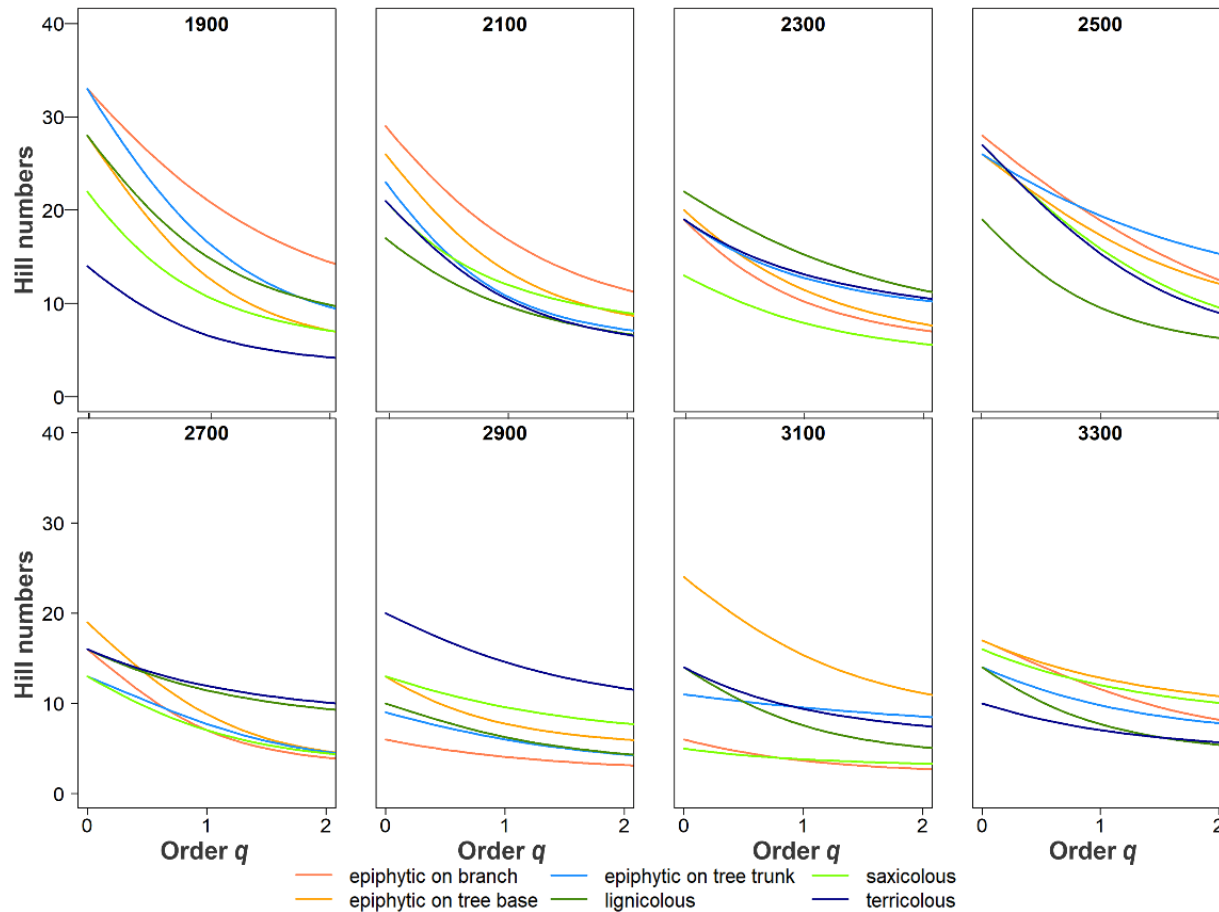


Figure 2-4. The bryophyte diversity profiles based on the cover (abundance) of each species per substrate (total of four 600-cm² plots) along the elevational gradient on Baru volcano, Panama. The asymptotic diversity profile considers the order q based on the observed data, where: $q = 0$ is the total species richness; $q = 1$ captures typical species (exponential of the Shannon index); and $q = 2$ captures very abundant species (inverse of the Simpson concentration).

Diversity-biomass relationships

There was no relationship between species richness and biomass per plot when including elevation as a random factor ($F = 0.24$; $p = 0.63$. Figure 2-5). Also, no significant correlation was found at the site level, i.e. along elevation ($r = -0.57$; $p = 0.14$; Appendix F 5). This appears to be due to the low statistical power at this level ($n = 8$), because at the plot level a simple correlation analysis, not correcting for elevation, indicates a negative correlation ($r = -0.25$, $p < 0.001$. Figure 2-5). The disappearance of this relationship when correcting for elevation (by including it as a random factor) indicates that it was caused by the confounding correlation of both variables with elevation rather than a functional relationship.

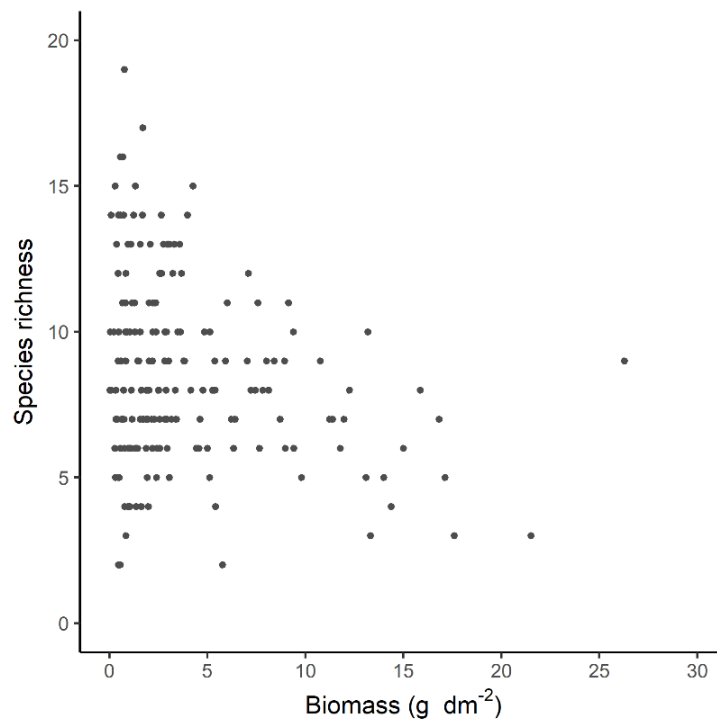


Figure 2-5. Bryophyte and lichen species richness in relation to biomass per 600-cm² plot on six substrate types along an elevational gradient on Baru Volcano, Panama. Species richness is negatively related to biomass at this level, but when correcting for elevation this relationship is no longer observed.

2.4 Discussion

As the first study explicitly studying differences of bryophyte vegetation among substrate types, we demonstrate that elevational patterns in the species diversity of bryophytes on a tropical mountain can differ among substrates, with terrestrial

bryophytes peaking at high elevation, unlike those growing as epiphytes or on rocks or deadwood, which we inferred to peak below our transect. We additionally show that the patterns found can depend on the spatial scale of analysis and on the aspect of diversity considered. This is important to take into account when interpreting elevational patterns, as each aspect of biodiversity may provide relevant information to understand the functions that bryophytes play on tropical mountains.

Species richness patterns

In the Northern Andes, in Colombia, a peak of bryophyte diversity has been found close to the treeline, at around 2500-3190 m (Wolf, 1993), for epiphytic bryophytes with ca. 130 species, and also between 3000-3700m on the western slope of the Central Cordillera, where bryophytes from different substrates reached a peak with ca. 195 bryophyte species (Gradstein et al., 1989). In our study, it appears that for most substrates the transect started at or above the elevation of maximum species richness, i.e. the top of the expected hump in species richness, showing no peak but a steady decline in richness with elevation. Patterns in bryophyte richness further down the volcano could not be studied due to the lack of undisturbed ecosystems below the national park. However, a sharp decline in species richness is the most likely pattern, based on the increasingly dry and hot climate, conditions that support little bryophyte richness, as shown in other tropical areas (Churchill, 1991; Dias dos Santos & Pinheiro da Costa, 2010; Wolf, 1993). The peaks in richness, even that of terrestrial bryophytes at ca 2500 m, thus lie at lower elevations than expected based on the available previous studies in tropical mountains, thereby pointing at the high variability in elevational patterns between regions and the need to collect more data on these patterns in different parts of the tropics.

Lower species-richness peaks have also been reported within the northern Andes on an eastern slope of the Central Cordillera (Colombia) with 260 species between 1200 and 3000m (Gradstein et al., 1989), Piton des Neiges volcano (Réunion Island) with 116 species at 1150m (Ah-Peng et al., 2012), and Marojejy National Park (north-eastern Madagascar) with 105 species at 1250m (Marline et al., 2020). The local climatic conditions were held responsible for these relatively low elevation species-richness peaks. In Colombia, these were the relatively dry conditions on the eastern slope of the Central Cordillera, in contrast to the more humid slope where the peak of richness was between 3000 and 3700m. On Réunion and Madagascar, an inversion layer causes dry conditions at high elevation, shifting the wettest zone to lower elevations than in more continental mountains.

On Baru, being an isolated peak, precipitation due to orographic lift of moist air masses is not as pronounced as in some parts of the Colombian Cordilleras. Even though not as isolated or oceanic as Réunion and Madagascar islands, an inversion layer is, in fact, present and keeps the top of the volcano out of clouds most of the time (pers. obs.). As a result, there is very likely a rainfall gradient with decreasing

rainfall towards higher elevations. Even though fog is likely more frequent at high elevations, the lower sites along the Baru transect were more humid (Appendix F 6), which is likely due to the more sheltered conditions in the tall forest compared to the shorter and more open forest at high elevation. Bryophyte species richness thus likely responded to this humidity gradient, as indicated by the higher explanatory power and more linear relationship of relative humidity compared to the other variables tested. This confirms that the water availability (e.g. rain, fog) is an essential variable in the distribution of bryophyte species (Benítez et al., 2019; Callaghan & Ashton, 2008).

The higher elevation of the richness peak for soil than for the other substrates may be related to the stronger litterfall in the tall closed forest at the lowest elevations. This forest is also darker, which may reduce bryophyte growth, but this argument would apply to all near-soil substrates, i.e. also to rocks, deadwood and stem bases. However, all of these substrates are slightly elevated above the forest floor, which does not change the light levels much but it does change the level of coverage in leaf litter. In these evergreen forests, leaves are shed by and by all year round, which can severely hamper the growth of bryophytes on the forest floor and is commonly assumed to be the main reason for the near-absence of bryophytes on tropical lowland forest floors (Corrales, Duque, Uribe, & Londono, 2010).

Diversity-biomass relationships

Although at the large scale, biomass and diversity tend to correlate positively, with a decrease in both, from cloud forests towards tropical lowlands (Wolf, 1993). However, from cloud forest to higher elevation forest, this pattern changes. We found a tendency to a negative correlation with the increase in elevation. It was coinciding with the pattern found in the Central Cordillera in Colombia (Wolf, 1995), where both aspects presented a weak negative correlation between 2500 and 3700 m. The non-correlation was weak at both mountains, due to the elevational range included and to the fact that biomass peaked at the highest elevations (Rodríguez-Quiel et al., 2019). At the Baru volcano, when controlling for the effect of elevation, the correlation was absent, because there was a considerable variation in the number of species, mainly at elevations with low biomass (Figure 2-5). In fact, there was a considerable variation in the number of species at a given biomass level, in particular at low biomass (Figure 2-5). This variation occurred because the layer of dominant bryophyte or lichen species may or may not be accompanied by rich communities of smaller species (e.g. Lejeuneaceae, *Frullania* spp or *Metzgeria* spp). In our study, such rich communities were found mostly at the lower elevations, which contained uneven communities with many little-abundant species. At the highest elevations, communities were more even and also tended to have a higher biomass. Here, plots mostly contained large-sized species along with only few small-sized species, resulting in high biomass and low species richness values (Rodríguez-Quiel et al., 2019). However, we cannot conclude whether the high biomass caused the low species richness (e.g. through strong competition), or whether the coincidence of large species and low richness was due to

independent responses of species to the high-elevation conditions. The latter is suggested by the lack of a correlation when correcting for elevation. This highlights that relationships reported between biomass or productivity and species richness depend on the scale of analysis and that large-scale patterns do not imply functional relationships between productivity and diversity (Gillman and Wright 2006). The lack of clear functional relationships means that the loss of biodiversity also does not always imply a loss in productivity (Thuiller, 2007). However, even if productivity is maintained, other ecosystem functions may still be compromised by biodiversity losses (Mittelbach & McGill, 2019).

2.5 Conclusion

The different patterns found on different substrates highlight that environmental-change effects on bryophyte species richness are likely driven not only by direct climate effects, but by various inter-connected changes within the ecosystem including changes in forest structure that modify the microclimate as well as substrate availability. Better understanding the spatial variation in bryophyte diversity and abundance in these mountains, including elevational as well as within-forest patterns, is thus essential if we want to understand effects of environmental change on this important plant group and the implications of such effects for ecosystem functioning.

CHAPTER 3

The role of substrates and elevational changes on the bryophyte beta diversity along a tropical mountain

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with Maaïke Y. Bader, Jürgen Kluge and Glenda Mendieta-Leiva

The role of substrates and elevational changes on the bryophyte beta diversity along a tropical mountain

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Abstract. — Bryophytes diversity on tropical mountains changes with elevation, while within elevation species are also not uniformly distributed, given that bryophytes can grow in a variety of substrates. The relative importance of substrate diversity and elevation in determining the composition of the bryophyte community and beta diversity are poorly understood. Therefore, we assess how bryophyte communities and dissimilarity change along an elevation gradient and among different substrates. We also evaluated whether the association of certain species with particular elevations or substrates varies along the gradient. At eight elevations (from 1900 to 3300 m) on Baru volcano, Panama, we collected bryophytes from six different substrates. We recorded the relative abundance of the species in 600-cm² plots, with four replications. The role of elevation and different substrates shaping patterns of bryophyte community composition were evaluated using ordination analysis and multivariate analyses of variance. The possible change in the association of species with particular elevations and substrate types was evaluated using an indicator species analysis. Elevation and substrates both had a strong influence on the composition of the bryophyte communities, and substrates gained in relative importance when analysed in shorter elevational ranges. Both elevation and substrates lead to species turnover along the gradient, but species turnover associated with elevational changes was higher. Species turnover along the gradient involved changes in indicator species by elevations and also in their preference for substrate types. The high species turnover of bryophyte communities both along elevation and among substrates confirm the strong dependency of these plants on specific environmental conditions, suggesting a high sensitivity to environmental change. Monitoring the changes of the most specific and hence the most sensitive species may be a useful tool to evaluate the impact of global warming on bryophyte communities or the mountain environment more generally.

Keywords. — beta diversity; bryophytes; elevational gradient; indicator species; nestedness; substrates; tropical montane cloud forest; turnover

3. The role of substrates and elevational changes on the bryophyte beta diversity along a tropical mountain

3.1 Introduction

The mountains of tropical America are important centres of plant species diversity (Grytnes & McCain, 2007), harbouring over 20 % of the world's plant diversity (Corlett, 2016; Rudmann-Maurer, Spehn, & Körner, 2014 & Körner, C. 2014). At the same time, many tropical mountain ecosystems are severely threatened by global warming and land-use changes (Kohler, Wehrli, & Jurek, 2014). Potential effects of climate change include an upwards migration of low-elevation species, which may displace high-elevation species (Cuesta et al., 2017). High-elevation species, in turn, may also move higher up, but only if suitable habitat is available, i.e. if the mountains are high enough and if suitable substrates are found there. For most plants, a suitable substrate consists of sufficiently developed soil. However, some plants depend on specific substrates that may require a whole forest to develop first. In particular, these are epixylic (growing on dead wood) plants, which are usually bryophytes, and epiphytes (growing on stems and branches of other plants). Therefore, such species, which are particularly abundant in tropical high-elevation forests, may be particularly threatened by global warming (Kohler et al., 2014). To be able to predict how mountain plant communities will change under climate change, it is essential to understand the current structure and distribution of communities within and along elevational gradients (Graham et al., 2014).

Within tropical mountain regions, bryophytes are a species-rich group with considerable biomass (Gradstein, Homeier, & Gansert, 2008; Rudmann-Maurer et al., 2014). Because of their high sensitivity to subtle changes in climate-related variables (e.g. light level, temperature, and water availability), bryophytes are expected to respond strongly to variations in environmental conditions, as reflected in patterns of abundance and diversity along environmental gradients (e.g. Berdugo, Quant, Wason, & Dovciak, 2018; Guerra et al., 2020; Sierra, Toledo, Nascimento, Pereira, & Zartman, 2019). One of the most known spatial patterns for tropical bryophytes is that their species richness and biomass decrease towards the lowlands, most likely due to an increase in temperature (He, He, & Hyvönen, 2016; Zotz & Bader, 2009). Bryophyte richness can also decrease from the middle towards highest elevations (Rodriguez-Quiel, Kluge, Mendieta-Leiva, & Bader, in review; Wolf, 1993), although with an increase in biomass production (Rodriguez-Quiel et al., 2019; Wolf, 1993).

Patterns of distribution of diversity are associated with ecological processes (e.g. species dispersal capacity, habitat filtering, extinction, biogeographic dispersal) that act at different scales and shape the structure of communities (Kraft et al., 2011). One way to assess these effects is by studying patterns of species turnover (beta

diversity). Beta diversity is a measure of the relationship between local diversity, regional diversity, and spatio-temporal changes in the environment (Baselga, 2010; Kraft et al., 2011). Currently, global warming and human impact threaten to modify the distribution of species along tropical mountains. Thus, to foresee whether these changes will result in a loss of species, it is relevant to know whether climatic variation results in loss of species towards less-diverse elevations, which should be reflected by nestedness, or whether species replacement along elevation, that is turnover, takes place (Baselga, 2010). Bryophytes are interesting organisms to assess these responses, due to their sensitivity to environmental changes, their high diversity and abundance in mountain ecosystems (Nascimbene & Spitale, 2017).

The strong contribution of bryophytes to the diversity of tropical mountains is because these plants manage to colonise different substrates within the forest, which have been shown to increase the overall species pool at a given elevation (Rodriguez-Quiel et al., in review). The relative contribution of this source of environmental variability, relative to elevational variation, to overall species richness is not known, however. In other words, it is not known whether beta diversity is highest between substrates within elevations, or within the same substrate at different elevations. Beta diversity, and its components species replacement or species loss and/or gain, can bring to light the extent and manner in which species partition habitats (Baselga, 2010; Schluter & Robert, 1993). Knowing these patterns is also essential for the conservation of local diversity, as regions of high species turnover require the preservation of multiple areas rather than a single large area (Nascimbene & Spitale, 2017).

To better understand patterns of bryophyte diversity and community composition along elevation on a tropical mountain, we addressed the following research questions:

(1) How does the community composition of bryophytes on different substrates vary along an elevational gradient? Do bryophyte communities differ more among substrates or along elevation? And are these differences (i.e. beta diversity) dominated by nestedness or turnover?

(2) Are bryophyte species associated with specific substrates or elevations? Does the nature of the associations of species with types of substrate change along elevation?

3.2 Material and methods

Study area

The study was carried out in Baru Volcano National Park, western Panama (Figure 3-1). Baru volcano is the highest mountain in the country. Its last volcanic activity was approximately 500 years ago (Hopp & Waite, 2016). The studied elevational gradient is located on the western slope of the volcano, from 1900 to 3300 m asl. The lower and upper parts of the volcano were excluded due to the high degree of disturbance in the forests, caused by agricultural activity and the construction of transmission antennas, respectively. The study sites were established every 200 m of elevation, considering a total of eight sites (i.e. elevations) along the gradient. The main criteria for site selection were elevation-typical arboreal vegetation and topography (relatively flat sites, if possible). Forest canopy varied from 25 m height and 91% cover on average at the lowest elevations, down to 4 m height and ca. 76% cover on average at the highest elevations (Figure 3-1 and Appendix F 6). Temperature and relative humidity decreased with increasing elevation (Appendix F 6). For a detailed description of the elevational gradient see (Rodriguez-Quiel et al., 2019).

Sampling method

Bryophytes were collected from February to October 2017. At each elevation, six substrate types were considered: soil, rock, decomposing log, tree base, tree trunk (at breast height), and understory branch. Four replicates for each substrate type were sampled randomly within elevations. The replicates were at least 10 m apart from each other. Samples taken on the tree base and trunk (at 2 m high) were collected from the same tree, trees had a diameter between 20-60 cm. To evaluate the relative species abundance, we estimated the cover of each species or morpho-species per 600-cm² plot before collecting the samples. A total of 192 samples was collected. The taxonomic identification and nomenclature information of the collected specimens followed the procedures described in Rodriguez-Quiel et al. (in review). Bryophyte samples were deposited in the herbarium of the Autonomous University of Chiriquí (UCH).

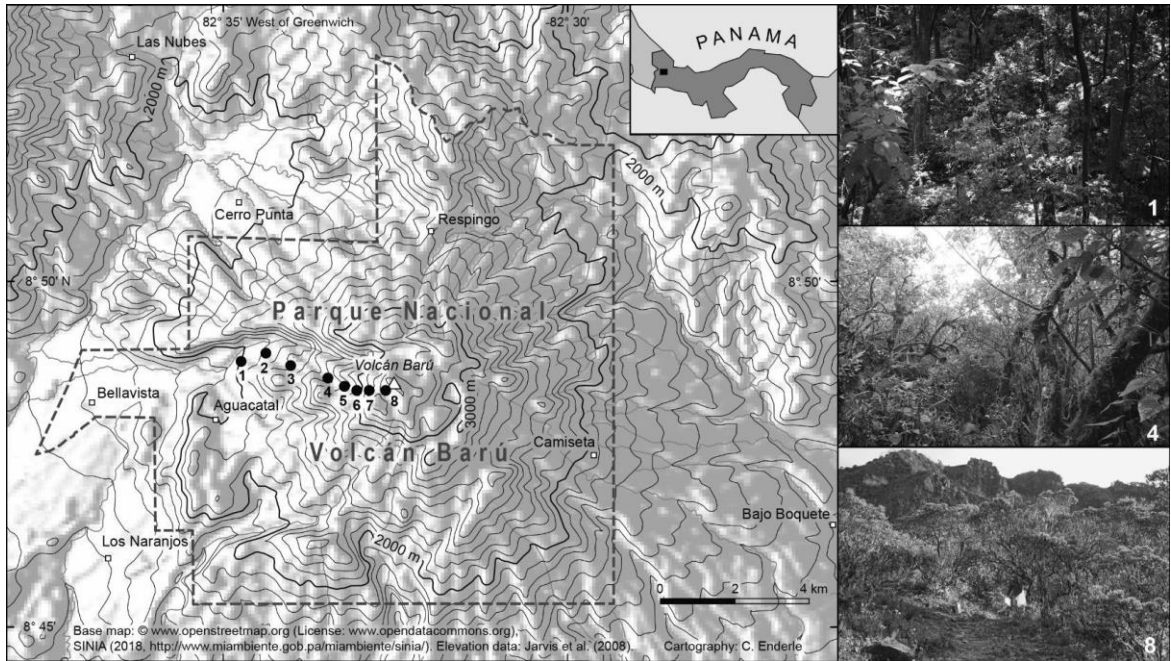


Figure 3-1. Location of the study sites established along an elevational gradient on the Baru Volcano National Park, Panama. The variation in forest structure with the increase in elevation is shown, specifically for elevations 1900m (1), 2500m (4) and 3000m (8).

Data analysis

- *Community composition dissimilarity*

To evaluate community dissimilarity patterns between study sites and substrate types along the elevational gradient, we used an ordination analysis and a multivariate analysis of variance considering the species abundances (cover). We ran a nonmetric multidimensional scaling ordination (NMDS) using the function *metaMDS* (Oksanen et al., 2007) and the Bray Curtis index (Beals, 1984). The NMDS ordination (Appendix F 7) showed a very clear differentiation of the elevational gradient between the lowest and highest elevational ranges, also sustained by a permutational multivariate analysis of variance (PERMANOVA) by means of the *adonis* function with 999 permutations; which were then used to evaluate community variability and species association to elevations and substrates (following sections).

- *Role of elevation and substrates on bryophyte community variation*

The role of elevation and substrate types shaping bryophyte community structure was evaluated using canonical correspondence analysis (CCA) with the function *cca* (Oksanen et al., 2007). We ran a CCA including elevation and substrate types as constraining variables, and to assess the significance of their effects we used the *anova.cca* function (Oksanen et al., 2007). Two additional CCAs were run with

the same baseline factors, but instead of a full elevational gradient, we divided it into two short elevation ranges as indicated by the NMDS and PERMANOVA (see the previous section), the lowest (1900-2500m) and highest elevations (2700-3300m). CCAs including other possible factors explaining the variation in bryophyte community structure (e.g. climate and forest structure) were also tested, but these environmental factors did not explain bryophyte community structure variability better. Changes in community composition and role of elevation and substrates shaping the structure of the bryophytes communities were evaluated using the "vegan" package (Oksanen et al., 2007).

- *β-diversity patterns*

To understand the nature of dissimilarity obtained among elevations along the elevational gradient, we calculated the two components of beta diversity (β -diversity): turnover and nestedness. Turnover implies species replacement, possibly due to environmental sorting or spatial constraints. Nestedness occurs when the poorest community is a subset of the richest one (Baselga, 2012). Beta diversity and its components was calculated using the functions *beta.pair* to calculate pair-wise dissimilarity ("betapart v1.5.1" package. Baselga, 2010). Thus, beta diversity was evaluated along the gradient (comparing elevations), first between pairs of adjoining elevations (1900m-2100m, 2100m-2300m, ..., 3100m-3300m), and comparing each elevation pair for each substrate separately.

- *Indicator species*

To detect variations in association of species to specific substrates, we calculated indicator species for substrates and elevations using the whole elevational range, and for substrates within the upper and lowest elevational ranges. The analyses were carried out using the R package "indicspecies" (Cáceres & Legendre, 2009). These analyses are based on the frequencies and relative abundances of species. The index *IndVal.g* function was used to determine the degree of association between species to elevational ranges, elevations and/or substrate types. For the selection of the indicator species, we considered the output of three values. First, the *specificity value* (A value, 0-1), which indicates to what extent the selected species occurred only in the focal elevation (or elevational range) or substrate (or group of substrates). The second value is the *local fidelity* (value B, 0-1), which indicates if the species occurred everywhere within the focal group (e.g. at all elevations within the range for which it is an indicator or all substrates within an elevation), or if its presence is more specific within the group ($B < 1$). The third is the indicator value, which indicates the degree of association of the species to the chosen elevation (or elevational range) or substrate (or group of substrates), summarising the A and B values. The three values range from 0 to 1, where 0 indicates a random or ubiquitous species distribution and the 1 indicates a strong association of the species to the selected group. The statistical significances of the indicator values were assessed using 999 permutations. All analyses were performed using R version 3.6.1. (R-Core Team, 2019).

3.3 Results

Along the elevational gradient, we identified 166 bryophytes species (91 Bryophyta, 68 Marchantiophyta and 1 Anthocerotophyta), belonging to 43 families (25 Bryophyta, 17 Marchantiophyta and 1 Anthocerotophyta), 84 genera (54 Bryophyta, 29 Marchantiophyta and 1 Anthocerotophyta), collected from 192 plots. Bryophyte species richness decreased with elevation, both when aggregated per substrate and per elevation, but at the elevation scale it decreased more rapidly (Appendix F 8, Rodriguez-Quiel et al., in review)

Dissimilarity between bryophyte communities along the elevational gradient

The composition of bryophyte communities was differentiated in an ordered manner along the first CCA axis, which correlated strongly with elevation (Figure 3-2a). Communities were less easily distinguished by substrate than by elevation, at least when taking the data from all the elevations together (Figure 3-2b). According to the CCA ordination, the elevational gradient explained slightly more of the variation in the community composition (3%), than the substrates (2%, Figure 3-2a and 2b). However, when assessing the community composition separately per short elevational ranges (1900-2500m and 2700-3300m), the substrates gained in explanatory power and were more clearly distinguished in the CCA space, both at the lowest (3%, Figure 3-3a) and highest elevation ranges (4.8%, Figure 3-3b).

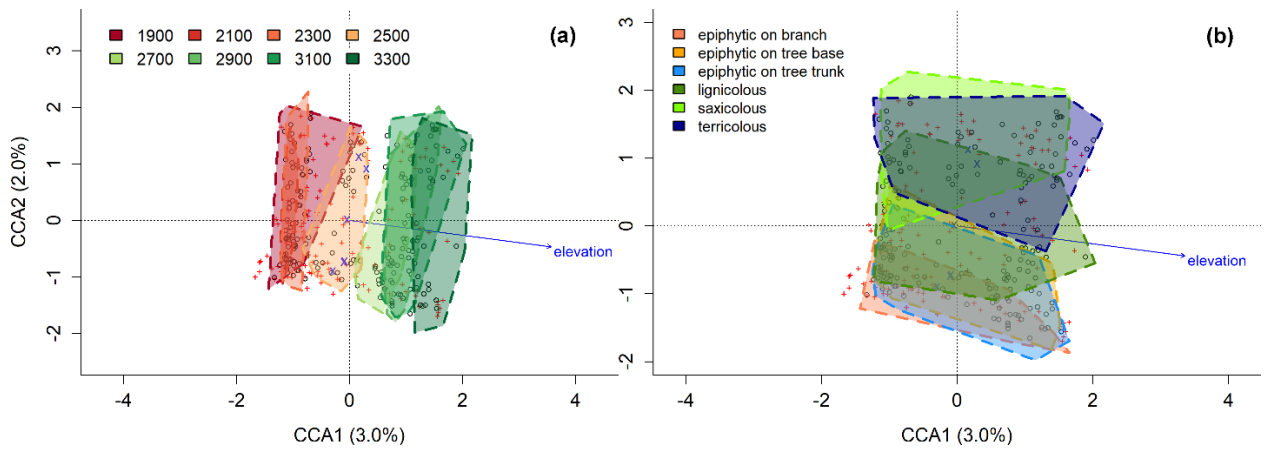


Figure 3-2. Constrained correspondence analysis (CCA) explaining the variation in community composition according to variation in elevation and substrate type along the elevational gradient on Baru volcano, Panama. The constraining variables (elevation and substrates) explained 7.4% of the variation. Polygons represent how plots were grouped based on elevation (a), and substrate types (b).

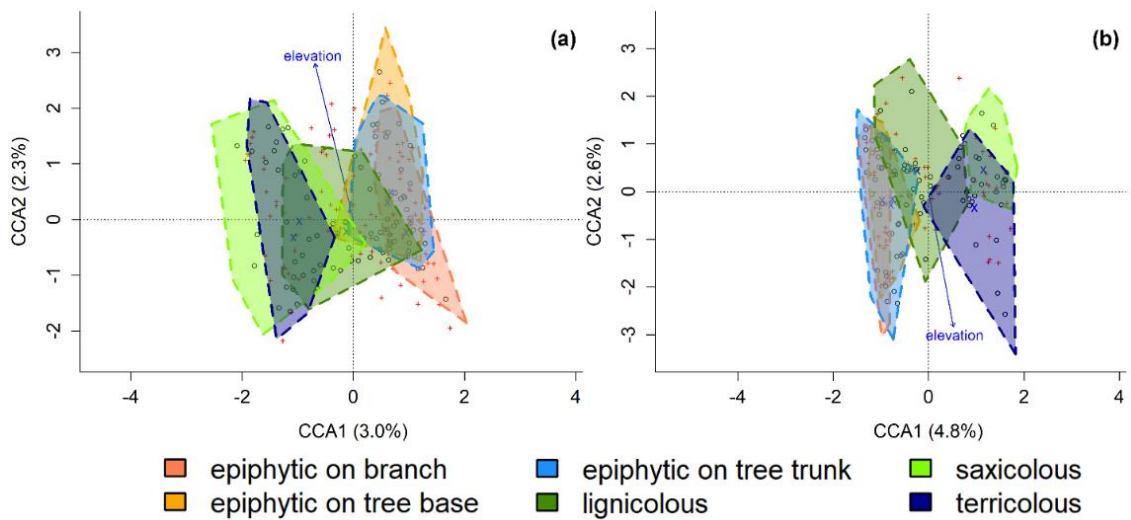


Figure 3-3. Constrained correspondence analysis (CCA) explaining the variation in community composition within two short elevational ranges separately along the western slope of the Baru volcano, Panama. The constraining variables (elevation and substrate) explained 9.5% and 12.7% of the variation for the lowest and highest elevational range, respectively. Polygons represent how plots were grouped based on substrate types within the lowest- (a) and highest-elevation plots (b).

Dissimilarity (beta diversity) was relatively high on all scales and was mainly due to turnover and, to a lesser extent, nestedness. Middle elevations showed the highest beta diversities among them (Figure 3-4 and Appendix T 4). The dissimilarity in species composition between adjoining elevations increased with the increase in elevation (Figure 3-4 and Appendix T 4). When assessing beta diversity between adjoining elevations of each substrates (Figure 3-5), dissimilarity along the gradient was higher than the overall, but without a clear trend with elevation or between substrates.

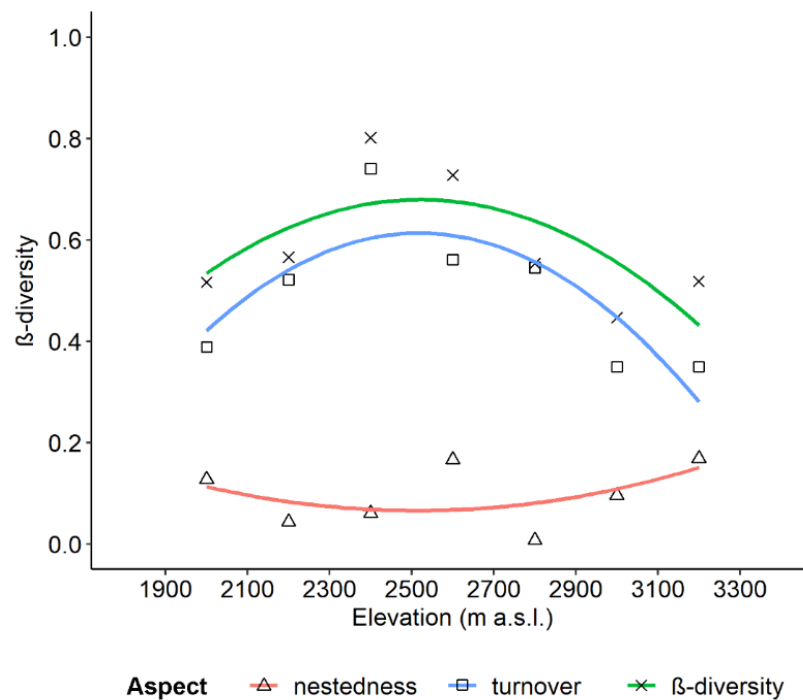


Figure 3-4. Variation at the substrate level among adjoining elevations in the Jaccard dissimilarity (β -diversity) and their components species turnover and nestedness along an elevational gradient on Baru volcano, Panama. Trend lines along the gradient were set with locally weighted regressions (LOWESS).

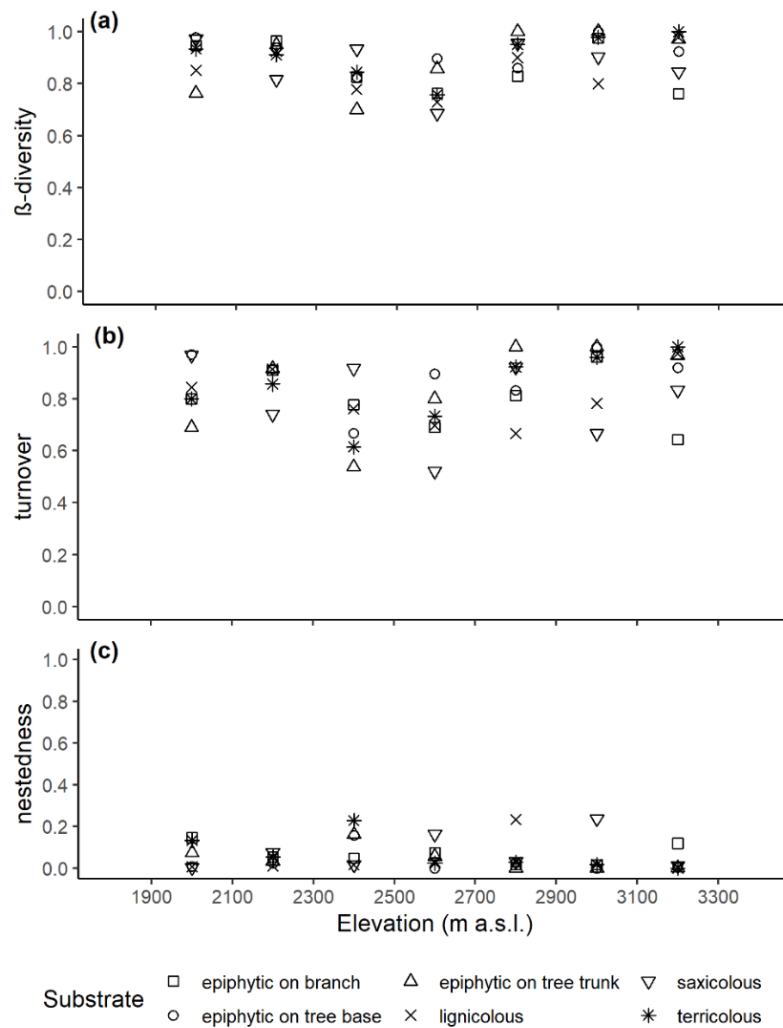


Figure 3-5. Variation at the plot level among adjoining elevations in the Jaccard dissimilarity (β -diversity) and their components species turnover (b) and nestedness (c) along an elevational gradient on Baru volcano, Panama.

Association of species to specific elevations and substrates

We obtained 20 indicator species for six elevations out of eight (Table 3-1) and ten indicator species for four substrates for the short elevational ranges (Table 3-2). Specificity values were high for all of these species. However, only four species (*Meteoridium remotifolium*, *Rhynchostegium serrulatum*, *Aptychella prolifera* and *Pseudomarsupidium decipiens*) had also relatively high local fidelity values, suggesting that they were strongly associated to their respective elevations (2100, 2300, 2500 and 3300m). When comparing the lowest and upper elevation ranges, we found a completely different set of indicator species for the same substrates (Table 3-2).

Table 3-1. Bryophyte indicator species for different elevations on Baru volcano, Panama. A = specificity value, B = local fidelity, both range from 0 to 1.

Elevation	Species	A	B	Indicator value	p-value
1900	<i>Dicranolejeunea axillaris</i>	0.91	0.25	0.48	***
	<i>Frullania obscura</i>	0.86	0.21	0.42	**
2100	<i>Meteoridium remotifolium</i>	0.69	0.83	0.76	***
	<i>Lophocolea muricata</i>	0.70	0.17	0.34	**
2300	<i>Rhynchostegium serrulatum</i>	0.91	0.42	0.61	***
	<i>Fissidens zollingeri</i>	0.91	0.21	0.44	***
	<i>Neckera ehrenbergii</i>	0.80	0.21	0.41	**
	<i>Prionodon densus.</i>	0.80	0.17	0.37	**
	<i>Porotrichum longirostre</i>	1.00	0.12	0.35	**
	<i>Porotrichum usagarum</i>	0.89	0.12	0.33	**
	<i>Aptychella prolifera</i>	0.74	0.46	0.58	***
2500	<i>Caribaeohypnum polypterum</i>	0.97	0.17	0.40	***
	<i>Leptoscyphus amphibolius</i>	0.76	0.17	0.36	**
	<i>Plagiochila adianthoides</i>	1.00	0.12	0.35	**
	<i>Bryum procerum</i>	0.91	0.12	0.34	*
	<i>Racomitrium subsecundum</i>	0.66	0.29	0.44	***
2700	<i>Frullania exilis</i>	0.76	0.25	0.44	***
	<i>Pseudomarsupidium decipiens</i>	0.89	0.42	0.61	***
3300	<i>Drepanolejeunea araucariae</i>	1.00	0.25	0.50	***
	Pottiaceae2	1.00	0.17	0.41	**

Used acronyms: A: specificity value; B: local specificity value (1 = the species was exclusive for an elevation, 0 = random or ubiquitous species distribution); Indicator value: indicator species values for the whole elevational gradient. Significance codes: <0.05 (*), <0.01 (**), <0.001 (***).

Table 3-2. Bryophyte indicator species list considering substrate types within the two obtained elevational range along the elevational gradient on the Baru volcano, Panama.

Elevational range	Species	A	B	Indicator value	<i>p-value</i>
1900 to 2500m					
Epiphytic on branch	<i>Neckera ehrenbergii</i>	0.72	0.31	0.47	*
	<i>Dicranolejeunea axillaris</i>	0.64	0.31	0.45	*
Epiphytic on tree trunk	<i>Frullania intumescens</i>	0.71	0.25	0.42	*
Saxicolous	<i>Racopilum tomentosum</i>	0.78	0.38	0.54	**
	<i>Fissidens asplenioides</i>	1.00	0.25	0.50	**
	<i>Bryum billardierii</i>	0.80	0.19	0.39	*
2700 to 3300m					
Epiphytic on branch	<i>Metzgeria</i> spp	0.66	0.38	0.50	**
Saxicolous	<i>Racomitrium subsecundum</i>	0.74	0.31	0.48	**
	<i>Anomobryum julaceum</i>	1.00	0.19	0.43	*
Terricolous	<i>Breutelia tomentosa</i>	0.93	0.25	0.48	**

Used acronyms: A: positive predictive value corresponding to the selected elevational range; B: fidelity or sensitivity of the species as an indicator for the selected elevational range; *Indicator value*: indicator species values for the whole elevational gradient; significance codes: <0.05 (*), <0.01 (**), <0.001 (***)

3.4 Discussion

The composition of the bryophyte communities was ordered along elevation and differed among substrates, with differences among substrates becoming clearer when considering smaller elevational ranges. It is thus clear that both factors contribute strongly to the overall bryophyte diversity of the studied mountain, and that the relative contribution depends on the scale: the longer the elevational gradient, the stronger the contribution of elevation relative to substrates. For the elevational steps and substrate types used, the contributions had a similar magnitude. Beta diversity was very high overall and dominated by turnover, indicating that for effective species conservation, forests along the entire elevational range need to be conserved.

Elevation or substrate – which adds more species?

Considering the entire elevational gradient, variation in elevation resulted in a higher beta diversity than the substrates alone and explained slightly more of the species composition variation than the substrates. In the middle of our gradient, communities of the lowest and highest part of the gradient diverged floristically, as indicated by the CCA result and the higher values of beta diversity. Habitat heterogeneity, from one type of natural vegetation to another (i.e. transition zone), leads to high community differentiation and beta diversity (Cuesta et al., 2017). These elevations constitute a transition zone in terms of forest structure and topography, from tall forests on gentle slopes to shorter forest on steeper slopes. From elevation 2500 m, slopes presented a considerable inclination and this has been a condition that produced high dissimilarity among bryophyte communities (Benítez et al., 2019). High community differentiation could also be related to a change in climatic conditions, for example the occurrence of more extended periods of fog at mid-elevations towards the mountain's top (Cavelier & Goldstein, 1989). All these differences in environmental conditions make the top of the volcano a highly variable environment, in which only species tolerant of these fluctuations prevail. Thus, the species turnover at 2500 m implies that species from the lowest elevation likely could be replaced by species at the very top of the gradient (Nascimbene & Spitale, 2017).

Previously to our study, very few studies have tried to distinguish the contribution of within-forest variability and large-scale geographic patterns or environmental gradients in determining the species composition and diversity of tropical bryophyte communities. In contrast to our study, studies in Amazonian lowland forests found that bryophyte communities were more different between vertical zones along a host tree than at large-scale gradients, even though sites were up to 2800 km apart across the Amazon basin (Mota de Oliveira & ter Steege, 2015; Mota de Oliveira, ter Steege, Cornelissen, & Gradstein, 2009). The difference to our study may lie in the fact that environmental gradients across these sites are much more subtle. Although elevation varied between sites, the maximum difference was only about 3300 m, and the highest elevations still had numerous lowland floristic components (Mota de Oliveira & ter Steege 2015). Therefore, differences in community composition were not attributed totally to elevation, but to environmental variability and geographical distance. On the Baru volcano, the elevational gradient (with the environmental variability it implies) is strong enough to make elevation the main factor adding species to bryophyte diversity.

In contrast to Mota de Oliveira & ter Steege (2015), who found no spatial structure in community dissimilarity, we noticed that elevations which were farther apart were more dissimilar to each other. These differences may be due to the elevational distance as well as the environmental similarity between nearby elevations. Comparing beta diversity relative to the lowest elevation, like Wolf (1993) did for epiphytic bryophytes in the Colombian Andes, we obtain a similar pattern of

increase in beta diversity with elevation, i.e. with distance to the lowest elevation. The elevational distance between sites, together with the heterogeneity of landscapes and climate over short distances in forests and tropical mountains, are the leading promoters of species turnover in the tropical region (Condit et al., 2002; Kraft et al., 2011).

Our results highlight that we should not underestimate the effect of different substrates promoting differences in community composition and hence species diversity. Habitat heterogeneity promoted by substrate diversity generated considerable beta diversity within elevations equally throughout the elevational gradient. Across elevations, substrates sustain different sets of bryophyte species. For instance, when sectioning the gradient into two shorter elevational ranges, substrates better explained the variation in community composition. Returning to the Amazon forest, Mota de Oliveira and ter Steege (2015), also sectioned the elevation gradient into individual sites and showed that the vertical distribution along the host trees mostly explained the differences between bryophyte communities. Locally, species-specific dispersal limitation is likely one of the leading promoters of community structure, both in vertical gradients (Mota de Oliveira & ter Steege, 2015; Wolf, 1995) as well as in the understory of the Baru volcano. A detailed evaluation of the propagation abilities of bryophytes (e.g. growth forms, production of propagules) would provide more information to corroborate possible limitations.

Variation in species association

Species associated with certain elevations may be related to specific environmental conditions, though high association may also be due to dispersal limitations (Mota de Oliveira & ter Steege, 2015). For species associated with particular substrates, dispersal is unlikely to explain the association, which is more likely due to specific physical and chemical properties of the substrate (Bates, 2009; Schuster, 1984; Wolf, 1995). The indicator species are potential ecological indicators for vegetation types or environmental conditions (Dufrêne & Legendre, 1997). Changes in the distribution and abundance of these species could reveal the effect of climate or land-use change (Gradstein, 2008). The occurrence of indicator species for specific elevations and substrates reflects the high capacity of bryophytes to track habitats (Glime, 2017c). In this context, it is essential to learn what functional traits drive the limitation of some species to specific elevations or substrates? Future studies should focus on these questions to provide a better understanding of bryophyte-environment relationships in scenarios of climate change.

At the tree line it has been observed that epiphytic bryophytes grow in substrates close to the ground (Wolf, 1993) and even submerged in a glacial lake (Gradstein, Vanderpoorten, van Reenen, & Cleef, 2018). We therefore, checked if any species in our transect showed the same behaviour, i.e. a shift from epiphytic to terrestrial substrates from lower to higher elevation (or between elevations in general).

However, this phenomenon was not observed. Although, at 3300 m, some families and genera that usually occupied soils managed to establish on epiphytic habitat with similar abundance, this was the case of some Pottiaceae, *Herbertus* and *Plagiochila* species (Gradstein et al., 2001).

3.5 Conclusion

We demonstrated the important contribution that substrates make, along with elevation, to the beta diversity of bryophyte communities along an elevation gradient in the Baru volcano. The patterns were scale-dependent, with substrates becoming increasingly more important in explaining bryophyte community variation at shorter elevational ranges. The high species turnover along elevation resulted in a complete change of indicator species for different substrates when comparing the lower and upper half of the elevational range. Our results support the fact that bryophytes have a close relationship with the environment. The remarkable diversity and abundance of bryophytes on tropical mountains allowed us to study not only the species richness but also the mechanisms shaping the distribution of tropical diversity in space and time. Our results provide crucial information to understand bryophyte distribution patterns in tropical ecosystems. We suggest assessing bryophyte communities further adding phylogenetic and trait-based approaches. These approaches will allow us to infer mechanisms underlying diversity in mountain ecosystems fully, and to understand how bryophytes contribute to ecosystem services as well as their capacity to respond to environmental changes.

CHAPTER 4

Elevational patterns of bryophyte and lichen biomass differ among substrates in the tropical montane forest of Baru volcano, Panama

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Elevational patterns of bryophyte and lichen biomass differ among substrates in the tropical montane forest of Baru volcano, Panama

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Abstract. — Tropical montane forests support a high abundance and diversity of bryophytes and lichens on different substrates. However, quantitative information about how their biomass and water-holding capacity change with elevation is scarce. The current project assessed variation in the biomass and water-holding capacity of bryophytes and lichens on Baru Volcano, Panama. On the western slope, the bryophyte and lichen layer was collected from 600-cm² plots on six substrate types with four replications at eight elevations along a gradient from 1900 to 3300 m a.s.l. We recorded the thickness, water-holding capacity and biomass of all samples, as well as environmental parameters. At lower elevations substrates had a similar biomass and water-holding capacity per area, but with increasing elevation terricolous substrates showed the strongest increase (highest values at 3100 m). These patterns are associated with climatic variation along the gradient. At the highest elevations, the forest was of low stature and more light reached the forest floor. Also, at these high elevations fog provides a daily wetting of the bryophytes and lichens. At lower elevations the water supply is increasingly in the form of rain, which is less frequent than the fog. The apparent strong coupling of biomass variations to precipitation regimes implies a high sensitivity of the bryophytes and lichens to climatic warming and changes in the cloud base elevation. Furthermore, our data suggest that the importance of bryophytes and lichens for regulating ecosystem water fluxes increases with elevation, which underlines the necessity to conserve intact montane forests.

Keywords. — biomass; bryophytes; elevational gradient; hydrology; lichens; tropical montane cloud forest; water-holding capacity.

4. Elevational patterns of bryophyte and lichen biomass differ among substrates in the tropical montane forest of Baru volcano, Panama

4.1 Introduction

Tropical montane cloud forests are generally recognised as important centres of biodiversity and regulators of regional climate and hydrology, but unfortunately many of these forests are severely threatened by human-induced changes, in particular in land use and climate (Ah-Peng et al., 2012; Leon-Vargas, Engwald, & Proctor, 2006). The forests of the Baru Volcano National Park in Panama are no exception. The limited knowledge and awareness of the environmental services these forests provide contribute to this worrying situation.

Some of the most important ecological roles that tropical montane forests play are those related to the capture, storage and gradual release of water from rain or fog (Holscher, Kohler, van Dijk, & Bruijnzeel, 2004; Kohler, Tobon, Frumau, & Bruijnzee, 2007). Also, they control biogeochemical cycles (e.g. carbon, nitrogen) and contribute to maintaining regional rainfall patterns by assuring a continuous release of water into the atmosphere (Ah-Peng et al., 2017). Within these forests, bryophytes and lichens play an especially important role (Ah-Peng et al., 2017; Kohler et al., 2007; Leon-Vargas et al., 2006; Pentecost, 1998). These organisms are particularly good at capturing and storing water, thanks to their poikilohydric nature. They can vary in water content from nearly zero to over 1000% of their dry weight in some species (Proctor, 2008). Because of their strong dependence on moisture, both groups tend to respond strongly to microclimatic variation, caused either by heterogeneity in forest structure, by elevational or other topographic gradients, or by climatic changes through time (Zotz & Bader, 2009).

Several plot-based diversity studies on elevational gradients consider bryophytes and/or lichens (Ah-Peng et al., 2007; Ah-Peng et al., 2012; Cacua-Toledo et al., 2018; Churchill, 1991; Dias dos Santos & Pinheiro da Costa, 2010; Frahm & Gradstein, 1991; Gradstein & Salazar Allen, 1992; Grau, Grytnes, & Birks, 2007; Henriques et al., 2016; Kessler, 2000; Van Reenen & Gradstein, 1983; Wolf, 1993). All of these studies describe a common pattern of increase in diversity with increasing elevation, with a decrease starting at about treeline elevation. Next to diversity, bryophyte cover has also been studied in several tropical mountains and has been suggested as a suitable parameter for distinguishing tropical forest types or as an indicator of air humidity in tropical forests (Churchill, 1991; Dias dos Santos & Pinheiro da Costa, 2010; Frahm & Gradstein, 1991; Gradstein & Salazar Allen, 1992; Karger et al., 2012; Van Reenen & Gradstein, 1983). However, only very few studies

have addressed elevational patterns in biomass or water-holding capacity (Chantanaorrapint & Frahm, 2011; Frahm, 1990c; Wolf, 1993), despite the importance of these parameters for understanding the role of bryophytes and lichens in ecosystem functioning. Additionally, most plot-based studies consider only epiphytic bryophytes (Chantanaorrapint & Frahm, 2011; Frahm, 1990c; Kürschner & Parolly, 2004; Pypker, Unsworth, & Bond, 2006a, 2006b; Wolf, 1993), while in range-based studies epiphytic and terrestrial species are combined (Van Reenen & Gradstein, 1983). However, as shown for seed plants (Khine, 2018; Kluge et al., 2017), epiphytic and terrestrial species can strongly differ in their response to elevation. More generally, we expect bryophytes and lichens on diverse substrates to differ in their response to climatic conditions because of differences in the exposure to climatic influences (rain, fog, solar radiation, wind) and different hydrological properties of the substrates.

Consequently, they should differ in the elevational patterns of their biomass and importance for ecosystem functioning. Reasons for elevational patterns in bryophyte and lichen biomass are suggested by studies on the physiological activity of these groups in dependence of temperature and other environmental factors (Hedderson & Longton, 1996; Wagner et al., 2013; Zotz & Bader, 2009). In the tropical lowlands, where bryophyte biomass is particularly low, a restricted diel carbon balance likely limits growth. Low and frequent negative diel carbon balances were measured in a tropical macro-lichen (Zotz, Schultz, & Rottenberger, 2003), while for tropical lowland bryophytes no comparable data are available. At higher elevations, lower temperatures and more favourable moisture conditions allow longer activity and thereby higher photosynthetic carbon gain (Wagner, Bader, & Zotz, 2014). The previously hypothesised role of high respiration rates at high temperatures (Frahm, 1990d; Richards, 1984; Zotz, 1999) appears to play a lesser role, as respiration rates across elevations are adapted to the respective ambient temperatures (Wagner et al., 2013).

In this paper we aim to quantify the distribution of biomass and water-holding capacity of bryophytes and lichens, as important contributors to hydrological regulation, along elevation and among substrate types within the forests on Baru Volcano. The following research questions are addressed: (1) how do biomass and water-holding capacity of bryophyte and lichen layers change with elevation? (2) How do these changes vary according to different substrate types? The answers to these questions have important implications for understanding the current and potential future role of bryophytes and lichens in forest hydrology and for the interpretation of elevational transect studies focusing on one or few substrate types only.

4.2 Materials and methods

Study area

Sampling was carried out along an elevational transect in the Baru Volcano National Park (08°48.4'N, 082°32.4'W), located in western Panama (Figure 4-1). This volcano is the highest mountain in Panama and the protected part of Baru ranges from 1500 to 3475 m a.s.l. (below there is agriculture and above there is a small peak just reaching above the treeline ecotone). This gradient thus does not include the warm tropical lowlands, but nonetheless it shows strong climatic and compositional changes. At different elevations, the amount and type of water input (rain vs fog) and the hydrological properties of the forest are expected to differ (Cavelier, Solis, & Jaramillo, 1996), but few data are available on either property or generally on the climate of this area. The last eruption of Baru volcano was roughly 500 years ago (Hopp & Waite, 2016). The forests in which we established our plots are estimated to be at least 300 years old.

Study sites were established along the western slope of the volcano (Figure 4-1), every 200 m along an elevational gradient, at eight elevations in total (1900, 2100, 2300, 2500, 2700, 2900, 3100 and 3300 m a.s.l.). The structure of the forest along the gradient is variable due to the heterogeneous relief. We selected sites based mainly on the dominant arboreal vegetation, looking for sites representative of the zonal forest type at each elevation. Areas with strong topographic effects and azonal vegetation, like wet depressions or exposed ridges, were avoided as much as possible. At the lowest four elevations, relatively flat sites could be selected while at the highest four elevations, slopes were steeper and more exposed.

The lower part of the gradient (1900-2300 m) is covered by a tall forest (30-40 m) consisting mainly of trees of the genera *Quercus* and *Ocotea*. Here the understory is dense, formed by diverse species of shrubs (Rubiaceae, Myrsinaceae, among others) and herbaceous plants (Rubiaceae, Commelinaceae, among others). The middle part of the gradient (2500-2700 m) corresponds to a transitional zone. Here medium-tall trees are common, such as *Clusia* spp and *Schefflera* spp; however, some *Quercus* spp, *Comarostaphylis arbutoides* Lindl. and *Buddleja nitida* Benth. of great size stand out. The understory is dense and mainly composed of the fern *Elaphoglossum* spp and abundant Araliaceae and Orchidaceae. In the upper part of the gradient (2900-3300 m), the canopy height is less than 8 m, on average, and consists mainly of *Comarostaphylis arbutoides*. The understory is dominated by the fern *Elaphoglossum* spp, *Hypericum gnidioides* Seem., *Pernettya prostrata* (Cav.) DC. and *Lycopodium* spp. In this part of the gradient, the terrain is formed by steep slopes, covered with rocks on which dense layers of bryophytes and lichens can be found. From 2700-3100 m, most sites harbour dispersed trees and inclined slopes which are exposed to the sun, fog (depending on the time of day and seasonality) and wind. At 3300 m, there is a small valley that corresponds to the main crater, near the volcano's

top. In the volcano's summit area (3475 m), transmission antennas are located, and for this reason, it was not taken into consideration for the study because of the level of degradation of the woodland.

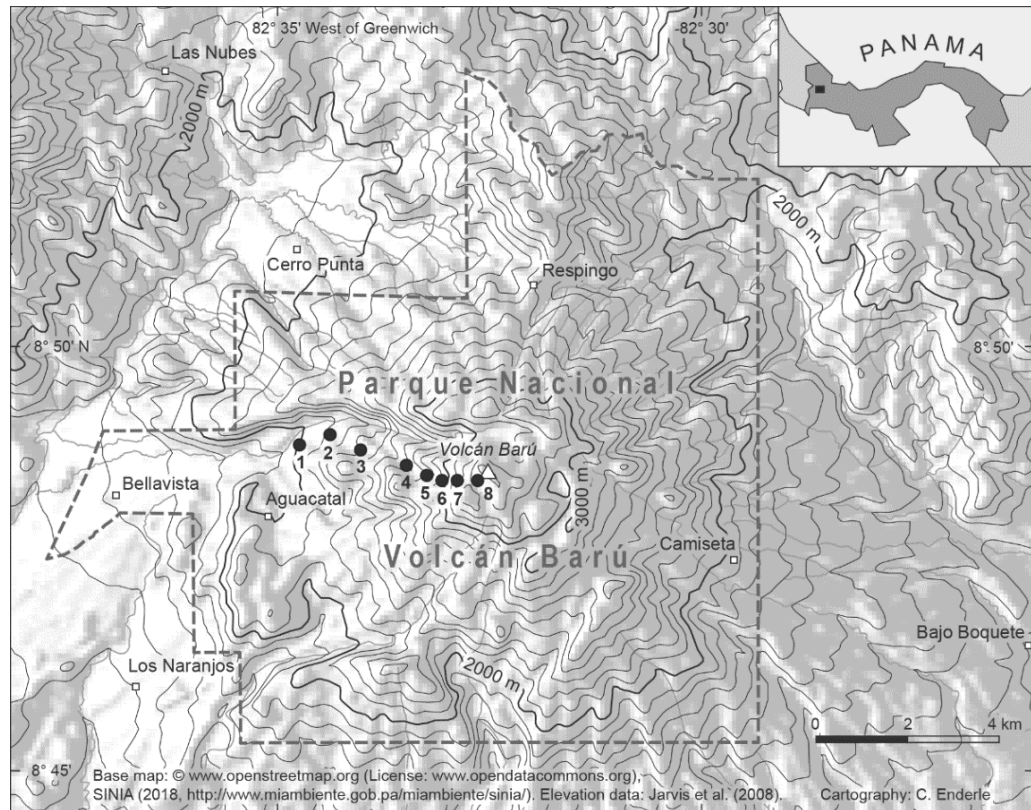


Figure 4-1. Study area established along an elevational gradient on the western slope of the Barú Volcano National Park, in western Panama. Elevation gradient every 200 m, with plots of 600-cm² for each of the six types of substrates and four replicates for each substrate. Source for elevation data: Jarvis, Reuter, Nelson, and Guevara (2008).

Sampling method

From February to October 2017 we sampled bryophytes and lichens from plots on six substrates: soil, rock, decomposing log, tree base, tree trunk at breast height, and understory branch, with four replications. Replicates were located randomly, stratified per substrate, and at least 10 m apart so that they had a certain degree of independence. The trees selected for the study had a diameter between 20-60 diameter at breast height (dbh) and trunk and base samples were taken in duplicates from each of the four trees at 0.5 and 2 m height, respectively. All samples consisted of 600-cm² plots, where the thickness of the bryophyte and lichen layer was recorded and this layer was collected for determining biomass and water-holding

capacity. The cover of bryophytes and lichens was close to or at 100% on all substrates at all elevations, and because of this lack of variation we did not analyse it separately.

The thickness of the layer of bryophytes and lichens was determined by introducing a ruler in the centre of each plot and measuring the distance from the substrate to the tip of the gametophyte or sporophyte (if present). Subsequently, this layer was completely removed from the substrate with the help of a knife, placed in plastic or paper bags and then transferred to the laboratory of the UCH Herbarium for further processing. For the sampling, no distinction was made between dead or living bryophytes and lichens, but dead organic matter coming from other plants was excluded from the samples. A total of 192 samples was collected (8 elevations x 6 substrates x 4 replications).

Biomass and water-holding capacity

The water-holding capacity of the bryophyte and lichen layers was determined gravimetrically in the laboratory. Samples were immersed in water for 5 minutes and left to drip on a wire mesh for 15 minutes. Any excess of water remaining was removed by gently shaking the sample by hand. Samples were then weighed on a balance. Subsequently, these samples were oven dried for 48 hours at 60 °C and then weighed.

The biomass is given in g dry weight per square decimeter of substrate and the water-holding capacity of each sample was calculated as the difference between saturated weight and dry weight. For characterizing the capacity per sample (i.e. per substrate area), it was expressed as g H₂O per square decimeter (g_{H₂O} · dm⁻²), and to characterize the absorptive capacity of the material it was expressed as g H₂O per gram (g_{H₂O} · g⁻¹_{biomass}).

Microclimate characterization

From April to December 2017, temperature loggers (HOBO pendant UA-001-08) or humidity and temperature loggers (DK320 HumiLog ruggedPlus) were installed at all elevations. Logistical problems occurred with the humidity data loggers (DK320 HumiLog ruggedPlus) at 1900 and 2500 m elevation, therefore for these sites we only show records for 110 and 30 days, respectively. The measurements were programmed to take place at 30-minute intervals. These dataloggers were installed under a plastic structure to avoid direct exposure to sun and rain; they were placed in the centre of the study sites at approximately 2 m from the ground avoiding direct exposure to the sun. The microclimatic measurements included both the dry and the rainy season.

The canopy cover above each plot, as a proxy for local light conditions, was estimated with the help of a spherical densiometer. The approximate height of the canopy above each plot was estimated visually.

Data analysis

Changes in the thickness of the bryophyte and lichen layer, in biomass and in the water-holding capacity per area and per gram biomass along the elevational gradient were assessed using generalised linear models (GLMs). The substrate was included as a covariable to assess if the pattern of variation along the gradient differed between types of substrate. Response variables were non-normally distributed; therefore the Gamma family distribution was chosen (Crawley, 2007).

Full models included the explanatory variables canopy height and canopy cover, substrate and elevation and the interaction between the latter two terms. Full models included a quadratic term of elevation to allow for unimodal elevational patterns and an interaction between this quadratic term with substrate. Model selection was carried out using backward stepwise selection, comparing the full model to a simpler one by an analysis of variance (*anova* function) with a Chi-square test, successively removing the least-significant terms. Normality and homogeneity of dispersion were inspected visually using diagnostic plots of the models.

Full models for all response variables showed that the patterns for certain substrates (covariate with six levels: rock, soil, tree base, tree trunk, branch and decomposition log) were similar along the elevational gradient. Therefore, the substrate levels were re-evaluated. We merged levels whenever they did not differ significantly. Significant differences were evaluated comparing the models with separate and joined levels and accepting the model with the joined levels if not significantly different from the more complex model (function *anova* with *Chisq* test) (Crawley, 2007). We also considered ecological affinities between substrates, i.e. we would not have made a group consisting of rock and branch cover, but this consideration did not come into play as the statistical grouping naturally resulted in ecologically meaningful groups.

Additionally, to test whether temperature or relative humidity may explain elevational patterns in biomass better than mere elevation, we tested additional models replacing elevation by either of these variables. We did not include them together in one model or in the models with elevation because of the strong mutual correlations (Appendix F 1).

All analyses were performed with the statistical software R 3.3.2 (R Core Team, 2016).

4.3 Results

Microclimate and forest structure

Temperature decreased gradually with elevation (Appendix F 6), from 15.5 °C to 8.5 °C average temperature. Mean daily temperature maxima were highest at low-elevations and at 2900 and 3100 m. The average daily mean and minimum relative humidity (RH) decreased linearly between 1900 and 3100 m and increased again between 3100 and 3300 m (Appendix F 6). Records from 2700-3100 m correspond to elevations on steeper slopes and forests with scattered trees and sparse vegetation.

The canopy height and cover of the forest decreased with elevation (Appendix F 6). The lower four elevations are characterized by closed *Quercus* forests that decrease gradually in height with increasing elevation. At the higher elevations the forest is shorter and more open, until at the top of the volcano the landscape is dominated by a patchy dwarf forest. Accordingly, light levels at the level of the substrates become higher and spatially more variable at higher elevations, as indicated by the larger variation in canopy cover (Appendix F 6).

Thickness of the bryophyte-lichen layer

Overall, the thickness of the bryophyte and lichen layers increased with elevation, but this pattern differed between substrates (Figure 4-2, Table 2-1). Based on similarities in elevational patterns and confirmed by ecological affinities of the substrates, the base and trunk of the tree were summarized in the “epiphytic on trunk” and saxicolous and terricolous samples in the “lignicolous & saxicolous” group. Branch (renamed as “epiphytic on branch”) and soil (terricolous) substrates showed unique patterns (Figure 4-2).

All the ecological groups had a layer of similar thickness at lower elevations, but with increasing elevation the terricolous group showed the strongest increase, with the thickest layer at 3100 m (though this is not well represented by the model, due to the complex pattern of maxima at 2700 and 3100 with lower values at 2900 and 3300 m, Figure 4-2). In comparison, the lignicolous & saxicolous group showed a relatively weak increase, but with a maximum at 3300 m. The epiphyte group (epiphytic on trunk and epiphytic on branch) had the smallest increase in the thickness of the layer along the elevational gradient and those on branches even showed a slight decrease (Figure 4-2).

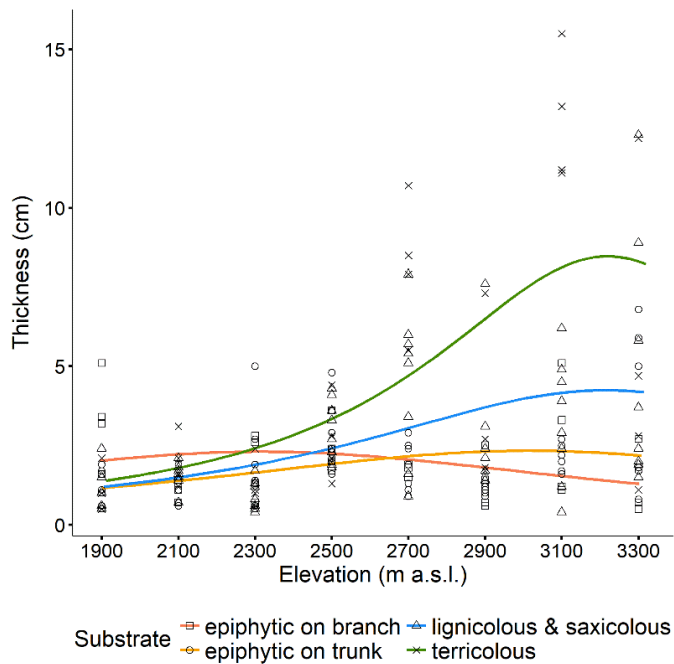


Figure 4-2. Change in thickness of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. Lines represent the predicted thickness of the layer along elevation according to substrate groups. Substrate groups, based on similarity in elevational patterns: epiphytic on branch = on shrub branches, epiphytic on trunk = combination of at the base and at breast height on tree trunks; lignicolous & saxicolous = combination of decomposing log and rock; terricolous = on soil.

Of the vegetation structure parameters, only canopy cover, determined above each sample, had a significant positive effect on layer thickness (Table 4-1), while canopy height had no significant effect.

Table 4-1. Analysis of Deviance models of the most parsimonious generalized linear model (GLM) explaining the variation in the thickness of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. The full model was Layer thickness ~ elevation * substrate + I (elevation ²) * substrate + canopy cover + canopy height. LR Chisq = Person's Chi-squared value for a Gamma family distribution; Df = degree of freedom; p value = level of significance. R² was 40%.

Variables	LR Chisq	Df	p value
Elevation	12.5	1	p<0.001
Substrate	49.5	3	p<0.001
Elevation ²	16.5	1	p<0.001
Canopy cover	6.0	1	p<0.05
Elevation: Substrate	19.6	3	p<0.001

Biomass

Similar to layer thickness, bryophyte and lichen biomass increased along the elevational gradient (Figure 4-3, Table 4-2). However, the grouping of the substrates based on the similarity in their elevational patterns was different than for layer thickness. At the lower elevations, the ecological groups had very similar and low biomass values, while with elevation the saxicolous & terricolous group increased the strongest, with an optimum at 3100 m, and the lignicolous substrate increased more slowly and reached highest values at 3300 m. Biomass of epiphytic substrates continued low until about 2900 m, after which epiphytes on shrub branches stayed low, but those on tree trunks increased in biomass, with the highest values at the highest elevation (Figure 4-3). Canopy cover and canopy height had no significant effect on biomass (Table 4-2).

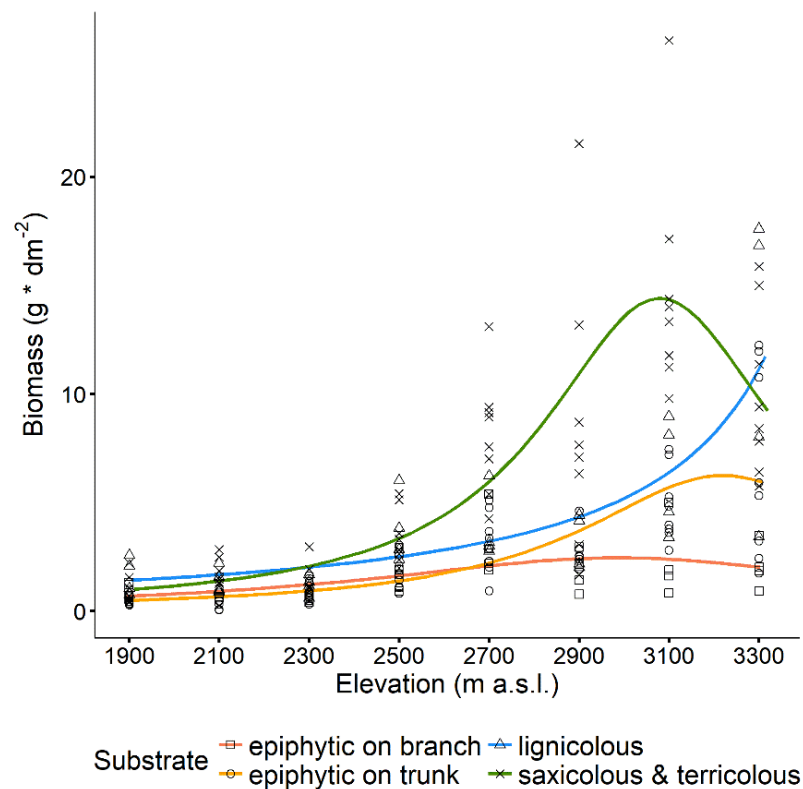


Figure 4-3. Change in biomass of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. Lines represent the predicted biomass per square decimetre along elevation according to substrate groups. Substrate groups, based on similarity in elevational patterns: epiphytic on branch = on shrub branches, epiphytic on trunk = combination of at the base and at breast height on tree trunks; lignicolous = on decomposing log; saxicolous & terricolous = combination of rock and soil.

Table 4-2. Analysis of Deviance models of the most parsimonious generalized linear model (GLM) explaining the variation in the biomass per dm² of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. The full model was Biomass per dm² ~ elevation * substrate + I (elevation ^2) * substrate + canopy cover + canopy height. LR Chisq = Person's Chi-squared value for a Gamma family distribution; Df = degree of freedom; p value = level of significance. R² was 74%.

Variables	LR Chisq	Df	p value
Elevation	92.7	1	p<0.001
Substrate	100.6	3	p<0.001
Elevation ^2	74.9	1	p<0.001
Elevation: Substrate	16.8	3	p<0.001
Elevation ^2: Substrate	15.8	3	p<0.01

Models of biomass as a function of daily minimum relative humidity or mean temperature instead of elevation had a lower explanatory power than models based on elevation (Appendix T 3 and Appendix T 4).

Water-holding capacity

The water-holding capacity per gram bryophyte and lichen biomass changed only moderately along elevation (Appendix F 9) so that the water-holding capacity per sample area (Figure 4-4, Table 4-3) more or less reflected the elevational pattern for biomass (Figure 4-3, Table 4-2). The water-holding capacity per gram biomass also differed between epiphytic vs terrestrial substrate types (terricolous, saxicolous and lignicolous, Appendix S 1), so that the relative importance of the substrates is slightly different for water-holding capacity than for biomass, but the substrate levels were regrouped into the same four ecological groups as for thickness. As with thickness and biomass, groups did not differ much at the lower elevations, and terricolous water-holding capacity increased the strongest with elevation, with a maximum at 3100 m (Figure 4-4). Canopy cover and canopy height did not show a significant effect on water-holding capacity (Table 4-3).

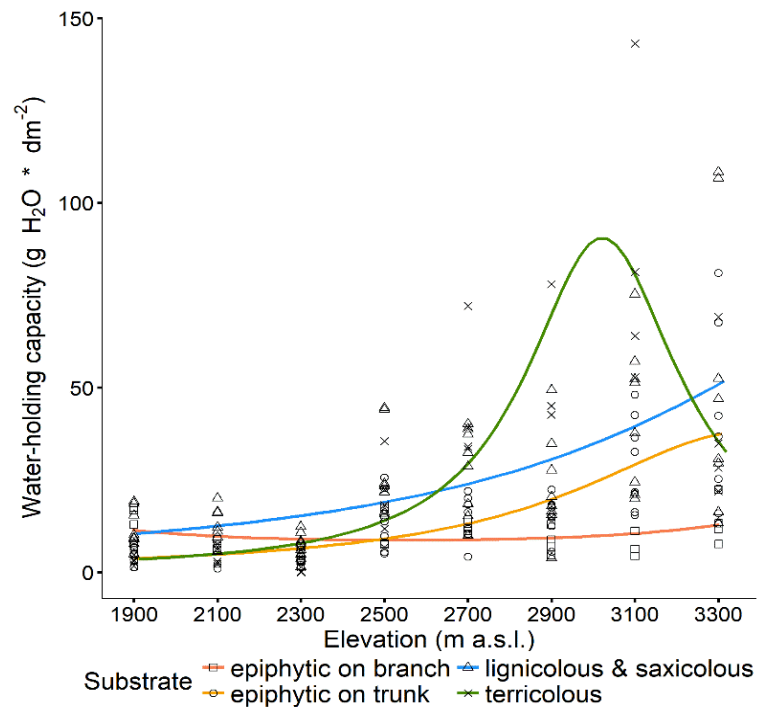


Figure 4-4. Change in water-holding capacity of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. Lines represent the predicted water-holding capacity per square decimetre of the layer along elevation according to substrate groups. Substrate groups, based on similarity in elevational patterns: epiphytic on branch = on shrub branches, epiphytic on trunk = combination of at the base and at breast height on tree trunks; lignicolous & saxicolous = combination of decomposing log and rock; terricolous = on soil.

Table 4-3. Analysis of Deviance models of the most parsimonious generalized linear model (GLM) explaining the variation in the water-holding capacity per dm² of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. The full model was water-holding capacity per dm² ~ elevation * substrate + I (elevation ^2) * substrate + canopy cover + canopy height. LR Chisq = Person's Chi-squared value for a Gamma family distribution; Df = degree of freedom; p value = level of significance. R² was 59%.

Variables	LR Chisq	Df	P. value
Elevation	36.9	1	p<0.001
Substrate	63.2	3	p<0.001
Elevation ^2	28.8	1	p<0.001
Elevation: Substrate	38.4	3	p<0.001
Elevation ^2: Substrate	35.3	3	p<0.001

4.4 Discussion

Biomass, water-holding capacity and thickness of cloud-forest bryophyte and lichen communities all increased with elevation, but this increase differed considerably between substrates. Thereby, patterns differed most between substrate with low ecological similarity such as epiphytic vs terricolous substrates. The results highlight the close but varied relationship of bryophytes and lichens from different substrates with microclimatic variation and shed light on the important role played by these organisms in the hydrological properties of this cloud forest.

Microclimatic variation

The decrease of temperature with elevation is a common pattern worldwide, but most other factors, including the amount of precipitation and relative humidity, are more variable, and even temperature can deviate from the elevational trend due to topographic or vegetation-induced microclimates (Sonnleitner, Dullinger, Wanek, & Zechmeister, 2009; Wolf, 1994). Such effects were clearly measured in our study sites, where the sites with more open vegetation (2900-3300 m) showed higher daytime temperatures and lower relative humidity values than sites in closed forest, even though the latter sites were located at lower elevations (1900-2700 m; Appendix F 1). This is undoubtedly related to the higher solar radiation in this open forest, in combination with the strong winds at this high elevation, which may also reduce air humidity (Wolf, 1993). On the other hand, although air humidity can fall relatively low at the highest elevations, periods of fog around sunrise and sunset are more common here than at lower elevations, where water input is more dominated by rain (Cavelier et al., 1996). Relatively few studies have instrumentally assessed fog occurrence along elevational gradients (Cavelier & Goldstein, 1989; Cavelier et al., 1996), but it is known that the presence of fog is strongly related to tropical forest elevational zonation (Bach & Gradstein, 2011; Gehrig-Downie et al., 2013; Salas-Morales, Meave, & Trejo, 2015). Due to the topography of our study area, we expect fog formation to peak at higher elevations, but below the top of the volcano. A common pattern is for all but the very top of the mountain to be covered in clouds in the early morning as well as the evening (pers.obs.).

Although air humidity did not change linearly with elevation, the correlation between humidity, temperature, and elevation were very strong (Appendix F 3), so that it is practically impossible to distinguish the effects of these different variables on bryophyte and lichen abundance. Most likely, temperature and humidity and other elevation-related variables like slope and vegetation structure interact to determine the elevational pattern, which is thus better captured by elevation than by particular climatic or structural variables.

Cover and height of the canopy describe forest structure, with variation within but also along elevation (Appendix F 1). Forest structure may affect bryophyte and

lichen abundance through variation in microclimate, in particular light availability, as well as substrate availability (not included in our study as similar areas were sampled for each substrate type in each site) and litter input. Litter input is considered an important reason for the almost complete lack of terrestrial bryophytes in tropical lowland forests and may also play a role suppressing them in montane forests (Frahm et al., 2003). In our study area, we did observe a relatively thick litter layer in the lowest site, but even thicker in the highest site. In the lowest site, this may be due to higher litter fall whereas in the highest site slow decomposition at low temperature may be the main reason (Frahm et al., 2003; Frahm, 1990b).

Canopy cover had only a small effect on the thickness of the bryophyte and lichen layers, and canopy height had no effect on either layer thickness, biomass or water-holding capacity. In contrast, several authors have pointed out that light availability or intensity is important in determining the variation in distribution of bryophytes and lichens, both terrestrial and epiphytic (Corrales et al., 2010; Jácome, Gradstein, & Kessler, 2011; Wolf, 1993). In our study, canopy cover correlated negatively with elevation (Appendix F 3), which might have masked a direct effect of light availability on bryophyte and lichen abundance measures other than thickness. Such correlations may take different shapes along other transects, however, and we recommend to always measure this variable, for example using canopy cover as a proxy, in studies aiming to explain cryptogam distribution patterns.

How does biomass change with elevation?

The general elevational pattern of biomass and water-holding capacity on Baru volcano (1900-3300 m) was similar to patterns for epiphytic cryptogam biomass in the Northern Andes [1000-4130 m (Wolf, 1993)], Mt. Kinabalu [20-3400 m (Frahm, 1990c; Frahm & Gradstein, 1991)], in a lower-elevation transect in Southern Thailand [25-1500 m (Chantanaorrapint & Frahm, 2011)] and also similar to patterns of bryophyte cover in the Colombian Sierra Nevada [500-4100 m (Van Reenen & Gradstein, 1983)]. All these transects show an increase of biomass with elevation and a light decrease starting at about treeline elevation. However, our study and that from the Sierra Nevada, the latter presenting cover rather than biomass values, are the only ones that have explicitly distinguished patterns for different substrates. And as we show, these patterns can differ quite drastically.

Most previous studies on elevational patterns have focussed on bryophyte diversity rather than biomass and on epiphytic habitats rather than including more terrestrial substrates (Ah-Peng et al., 2007; Ah-Peng et al., 2012; Churchill, 1991; Dias dos Santos & Pinheiro da Costa, 2010; Frahm & Gradstein, 1991; Gradstein & Salazar Allen, 1992; Grau et al., 2007; Henriques et al., 2016; Kessler, 2000; Van Reenen & Gradstein, 1983; Wolf, 1993). Van Reenen and Gradstein (1983) were the first to include cover as a measure of abundance and distinguished terrestrial and epiphytic substrates, though no lower-level categories within these broad groups. We

show that the increase in biomass is not uniform across substrates, even within terrestrial and epiphytic substrates. The role of bryophyte biomass in improving the water-holding capacity and regulating the flow of water and nutrients in the ecosystem (Ah-Peng et al., 2017; Pypker et al., 2006a, 2006b) likely depends on the position of this biomass within the forest. Therefore, describing elevational patterns per substrate type could strongly improve our understanding of their importance and the effects of changes in these patterns.

How do elevational changes in biomass vary according to different substrate types?

There were clear differences in elevational pattern among substrates, with the largest divergence between terrestrial and epiphytic substrates. In a previous study, estimating phytomass based on bryophyte cover in the Sierra Nevada of Colombia, elevational patterns of bryophytes from the two main substrate groups were less divergent than in our study, both increasing strongly with elevation (Frahm & Gradstein, 1991; Van Reenen & Gradstein, 1983). In that transect, the lower elevations, around 2000 m, were characterised by a stronger development of epiphytic compared to terrestrial bryophyte diversity and cover, whereas in our transect at the lower elevations biomass was similar between these groups. Moreover, on Baru volcano between 2700-3300 m the terrestrial rather than the epiphytic group increased in thickness and biomass, peaking at the one-but-highest elevation at 3100 m, whereas in that study both terrestrial and epiphytic bryophyte cover increased strongly with elevation. In our study, epiphytes on trunks increased more slowly and continued to increase until the highest elevation, while epiphytes on branches hardly increased at all. In contrast, in most other studies, including that in the Sierra Nevada as well as another transect in the Colombian Andes, in Southern Ecuador, on Mt. Kinabalu (with local exceptions, see below), and in Southern Thailand, epiphytic substrates showed a strong increase in bryophyte cover or biomass with elevation (Frahm, 1990c; Frahm & Gradstein, 1991; Van Reenen & Gradstein, 1983; Wolf, 1993).

On Baru volcano, the highest values of biomass and water-holding capacity for bryophytes on terrestrial substrates coincided with the elevational range where the forest begins to open up, and the canopy becomes lower so that more solar radiation reaches the lower strata of the forest. This should benefit trunk, understorey-branch and terrestrial bryophytes alike. Part of the explanation for the relatively low epiphyte cover may lie in the tree species dominating here, *Comarostaphylis arbutoides*, which has a loose bark that may not be a suitable substrate for bryophyte growth. Interestingly, a similar explanation was offered by Frahm (1990a) for the low epiphytic biomass on *Leptospermum* sp. trees at similar elevation on Mt Kinabalu. The peeling bark of high-elevation tropical trees, including *Rhododendron* in the Himalayas and *Polylepis* in the Andes, has been frequently observed to prevent epiphyte growth in spite of high humidity (Miehe et al., 2015).

Like on Mt. Kinabalu, on Baru the particular forest type at this high elevation was related more to geomorphological limitations than to climatic conditions, thus creating a decoupling between the vascular-plant vegetation (strongly affected by factors like soil depth, rock chemistry and slope steepness) and the bryophytes and lichens. However, although we found a similarly small development of epiphytes at these high elevations as on Mt Kinabalu, we could show that this open forest type supported very high bryophyte biomass on other types of substrates.

Similar to other areas in the Cordillera de Talamanca, the upper parts of Baru volcano also likely experience more fog, which increases humidity, but it also experiences strong winds (Morales, Zamora, & Herrera-F, 2007), which decreases humidity when not combined with fog. As a result, the mean and minimum relative humidity were relatively low at the highest elevations. The negative effects of wind and low relative humidity would affect epiphytes more than terrestrial species, epiphytes being more coupled to the atmosphere (Zotz, Mendieta-Leiva, & Wagner, 2014). This, together with the peeling bark of the dominant tree species, may explain much of the difference in bryophyte biomass between terrestrial and epiphytic substrates at the highest elevations.

Not only biomass but also the concurrent water-holding capacity per area was highest in the terrestrial bryophytes, those on soil in particular, at the highest elevations, in spite of a lower water-holding capacity per weight compared to lower elevations or epiphytes (Appendix F 9). For epiphytic bryophytes on the tree trunks, Frahm (1990c) also reported highest recorded water-holding capacity at the upper end of his transect on Mt Kinabalu (at 3400 m – above the zone with small-stature forest discussed above). The water-holding capacity patterns of soil bryophytes on Baru volcano indicate a particularly important role in regulating water fluxes, as also suggested by Frahm et al. (2003) for paramo bryophytes due to their high biomass. The contribution at the ecosystem level will additionally depend on the surface of different substrates available. We did not estimate these areas for our sites, but in studies focussed on ecosystem-level hydrological roles of bryophytes and lichens this is recommended (Gomez-Gonzalez, Rodriguez-Quiel, Zotz, & Bader, 2017; Kürschner & Parolly, 2004).

Notes about bryophyte taxonomic groups, outlook

Although we are not presenting a detailed analysis of taxonomic groups, we did observe a shift in the importance of bryophyte families with elevation. In the lower sites, the greatest contribution in biomass among epiphytic bryophytes comes mainly from families such as Plagiochilaceae and Meteoriaceae. At higher elevations, the epiphytic groups were represented more by Frullaniaceae and Herbertaceae. Within the terrestrial groups, the contribution of biomass at low elevations was mainly by Thuidiaceae and, again, Plagiochilaceae, while at higher elevation Pottiaceae and, again, Herbertaceae become more important. The reasons (response

traits) and the importance for ecosystem functioning (effect traits) of these taxonomic groups and the related functional differentiation along and within the elevational gradient would be exiting topics for future studies.

4.5 Conclusions

We found that substrates close to the ground increased strongly in bryophyte and lichen biomass with elevation while epiphytic substrates showed a lesser increase. These differences underline the importance of considering different substrates when studying biomass patterns along elevational transects. Based on our study, it seems reasonable to reduce the number of substrates sampled from the six sampled here (soil, rock, decomposing log, tree base, tree trunk at breast height, and understory branch) to four: soil, decomposing wood, tree trunk and understory branch. However, although grouped in their biomass development, these grouped substrates (trunk base and trunk at breast height, rock substrates with either soil or decomposing log) may still have very different species compositions. Also, if logistics allow it, sampling the canopy is highly recommended because the contribution of canopy epiphytes to green forest biomass and biodiversity tend to be considerable (Gomez-Gonzalez et al., 2017; Kürschner & Parolly, 2004).

Our data suggest that the importance of tropical bryophytes and lichens as an ecosystem water compartment increases as elevation increases, due mainly to the high biomass. Their suggested sensitivity to climatic conditions implies that bryophytes and lichens in tropical montane forests will need intact forests and continued cloud immersion to maintain this function.

SYNTHESIS AND OUTLOOK

5. Synthesis and Outlook

5.1 Synthesis

Many different habitats coexist over short distances thanks to variations in elevation within tropical mountains. This variety of ecosystems makes these forests reservoirs of high diversity. As a consequence of this climatic variation in the tropical mountains, the diversity present is not evenly distributed. Furthermore, some taxonomic groups are more sensitive than others to changes in the environment.

One of the plant groups that reach high diversity and abundance in tropical mountains are the bryophytes. Bryophytes have three main advantages that make them suitable for analysing the distribution of diversity in response to environmental variations. First, their diversity is relatively manageable compared to vascular plants diversity. However, due to their taxonomic complexity, their importance has been underestimated in conservation programs. Second, due to their poikilohydric character, bryophytes have a close relationship with the environment and respond quickly to habitat changes, varying their distribution and abundance. Third, bryophytes perform crucial ecological functions, especially those related to hydrological and biogeochemical cycles.

Previous studies on the distribution of bryophyte diversity along elevation gradients have mainly considered aspects of species richness, focusing less on the variation in ecosystem functions. Furthermore, most of the previously described patterns correspond mainly to epiphytic bryophytes, underestimating the potential role of considering different substrates to obtain complete information on bryophyte diversity and ecology.

In the present study, a detailed analysis of the variation of ecological aspects and diversity of bryophytes was carried out along the western slope of Baru Volcano National Park, Panama. At the Baru volcano, we established an elevational gradient from 1900 m to 3300 m, with elevation intervals of 200 m, covering eight sites in total (i.e. elevations). Selection of these elevations was based on the selection of relatively flat areas (as far as possible) and dominant arboreal vegetation. Bryophytes from six different microhabitats (i.e. substrates) were collected in 600 cm² plots, with four replicates for each. Climatic data and forest structure were recorded to describe environmental conditions. The relative abundance of the bryophyte species and thickness of the sample layer were recorded in each plot. Subsequently, the samples were collected from the substrates, placed in plastic bags, and transported to the laboratory. Biomass and water-holding capacity were measured, and species identification was performed in the laboratory. The fieldwork was carried out from February to October 2017. The study addressed the following questions:

A. How does bryophyte species diversity change with elevation, and how elevational patterns differ between substrate types? (Chapter 2).

B. How do the community composition and beta diversity of bryophytes on different substrates vary along an elevational gradient? How does elevation influence species association for a particular substrate type along a mountain slope? (Chapter 3).

C. How do bryophyte biomass and water-holding capacity change with the increase in elevation while accounting for the effect of bryophyte substrates? (Chapter 4).

A high species richness and communities with a low number of abundant species (i.e. more uneven communities) were found at 1900 m. With the increase in elevation, the species richness decreased, and the presence of species with high abundance within the communities was a common characteristic for all substrates towards 3300 m. The bryophytes of terrestrial substrates differed from the others by presenting a maximum peak of species richness at 2500 m, subsequently decreasing until presenting a comparable number of species as other substrates. Along with variation in species richness and changes in community structure, there is a high rate of beta diversity (dissimilarity) along the gradient when different substrates are considered. The variation in community composition was mainly explained based on the effect of the elevational changes and to a lesser degree by different substrates. Based on the composition and abundance of the species, we can describe two main groups of bryophyte communities, that is, those in the lower part (1900-2500 m) and the upper part (2700-2900 m) of the gradient. However, within these two short ranges of elevation, the communities are still different from each other. The differences between them were mainly explained considering the substrates in which bryophytes grow, and in the second degree, by elevation.

Species richness patterns and variation in community structure along the elevational gradient were useful diversity metrics for understanding the relationship of bryophytes to environmental changes. However, an elevational gradient includes a massive number of biotic and abiotic factors that could influence the species distribution. Many of these factors correlate with each other or interact with each other to shape diversity patterns, and it is difficult to separate their effects because they also interact at different scales. Elevation alone was considered as a factor to interpret the results. Then the obtained patterns were studied, including environmental factors that were registered along the gradient. In most diversity metrics, elevation alone explained the distribution of diversity better. Relative humidity and minimum temperature explained the elevation patterns of species richness and variation in the structure of communities with comparable effectiveness. In this way, the presence of indicator species can be confirmed and related directly to particular environmental conditions. Fluctuations in environmental conditions also induce changes in the association of species observed along increasing elevation and on specific substrates.

The pattern of decrease in species richness might lead us to suggest that bryophytes were less relevant organisms in the maintenance of the ecosystem towards the volcano's top, but this was not the case. The obtained species richness patterns did not show a correlation with changes in biomass, and therefore also with the water-holding capacity. Both biomass and water-holding capacity consistently increased from 1900 to 3300 m, to a greater extent for terrestrial substrates and less for epiphytic. The ecological importance of bryophytes increased with elevation, thus being more important at the top of the volcano, performing ecosystem functions such as biomass production and the capture and incorporation of water into the forest. Other studies have reported that the relationship between biomass and species richness is highly variable and that it depends on the scale of analysis. In the Baru volcano, it was observed that low species richness occurs in high biomass sites. In the species richness and biomass relationship, the competition between species could be a

determining factor. When the environmental conditions are relatively unstable as those present at the volcano's top (e.g. higher temperature fluctuation during the day), the competition between species was less, due to the presence of fewer species that tolerate these environmental variations. Furthermore, these fluctuation-tolerant species conform groups of uniform communities in terms of species abundance.

This work demonstrates that bryophytes respond to environmental variations included along an elevation gradient, varying species richness and community composition. We show that the scale of data analysis and considering different substrates were relevant aspects. By including bryophytes from different substrates, a high rate of species turnover was obtained along the gradient. Also, there was high ecological differentiation between the communities of the lower and upper parts of the volcano, with modifications in the association of species by specific substrates. With changes in elevation, the functions that bryophytes perform within the ecosystem also change, becoming more critical in the roles of biomass production and water-holding capacity towards the top of the volcano. Furthermore, the functions are performed by different communities at both ends of the gradient and also with different effectiveness.

5.2 Outlook

At the Baru volcano, a decrease in diversity increased biomass, showing no correlation between them. Better use of the light resource by terrestrial bryophytes seems to be one of the factors that were most related to this finding. The costs of this process within the ecosystem implied a decrease in the number of species, an increase in dominant species, and the displacement of low abundance species. Describing these communities and the factors that locally determine their composition, along with controlled experiments removing and adding species to communities (high and low productivity), would help to understand the consequences of changes in diversity in the ecosystem. There are many questions about whether processes within ecosystems depend to a greater extent on the diversity or community structure. With the results obtained at the Baru, we have the basis for developing studies that address these aspects.

Environmental changes at the Baru volcano also showed that some bryophytes could tolerate variations and prevail along the gradient. What characteristics make these groups more resistant than others? A detailed study based on morphological variation and its relationship with environmental conditions would give answers about the functional characteristics that help bryophytes to tolerate modifications in the environment. *Frullania* was an example of these groups, which predominated in epiphytic substrates. *Frullania* presented high species diversity in the lowest part of the gradient but less abundance. Towards 3300 m they were less diverse, but the groups showed great abundance and presence in different substrates. What is the reason for this pattern? The hypothesis that could answer this question could be related to the availability of light. However, at the morphological level, what are the implications of this distribution pattern?

These and other questions have to be addressed to understand the fundamental role of bryophyte diversity in the tropical mountains. However, changing environmental conditions and human impact in different parts of the volcano add additional variables to the study of bryophyte ecology. Are current conservation measures appropriate? How effective is the current zonification for sustainable use of the resources provided by the Baru volcano? As bryophytes are good indicators of environmental conditions, they could be used for diversity monitoring plans.

REFERENCES

6. References

- Ah-Peng, C., Cardoso, A.W., Flores, O., West, A., Wilding, N., Strasberg, D., & Hedderson, T.A.J. (2017). The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. *Journal of Hydrology*, 548(2017), 665-673. <https://doi.org/10.1016/j.jhydrol.2017.03.043>
- Ah-Peng, C., Chuah-Petiot, M., Descamps-Julien, B., Bardat, J., Stamenoff, P., & Strasberg, D. (2007). Bryophyte diversity and distribution along an altitudinal gradient on a lava flow in La Reunion. *Diversity and Distributions*, 13(5), 654-662. <https://doi.org/10.1111/j.1472-4642.2007.00393.x>
- Ah-Peng, C., Wilding, N., Kluge, J., Descamps-Julien, B., Bardat, J., Chuah-Petiot, M., . . . Hedderson, T.A.J. (2012). Bryophyte diversity and range size distribution along two altitudinal gradients: Continent vs. island. *Acta Oecologica-International Journal of Ecology*, 42(2012), 58-65. <https://doi.org/10.1016/j.actao.2012.04.010>
- Bach, K., & Gradstein, S.R. (2011). A Comparison of Six Methods to Detect Altitudinal Belts of Vegetation in Tropical Mountains. *Ecotropica*, 17(1), 1-13.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134-143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, 21(12), 1223-1232. <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. 2015, 67(1), 48. <https://doi.org/10.18637/jss.v067.i01>
- Bates, J.W. (2009). Mineral nutrition and substratum ecology. In B. Goffinet & A. J. Shaw (Eds.), *Bryophyte biology* (pp. 299-356): Cambridge University Press.
- Beals, E.W. (1984). Bray-Curtis Ordination: An Effective Strategy for Analysis of Multivariate Ecological Data. In *Advances in Ecological Research* (pp. 1-55): Elsevier.
- Bedford, B.L., Walbridge, M.R., & Aldous, A. (1999). Patterns in nutrient availability and plant diversity of temperate North American wetlands. *Ecology*, 80(7), 2151-2169. [https://doi.org/10.1890/0012-9658\(1999\)080\[2151:Pinaap\]2.0.Co;2](https://doi.org/10.1890/0012-9658(1999)080[2151:Pinaap]2.0.Co;2)
- Benítez, A., Gradstein, S.R., Cevallos, P., Medina, J., & Aguirre, N. (2019). Comunidades de briófitos terrestres relacionados con factores climáticos y topográficos en un páramo del sur de Ecuador. <https://doi.org/10.15446/caldasia.v41n2.67869>
- Berdugo, M.B., Quant, J.M., Wason, J.W., & Dovciak, M. (2018). Latitudinal patterns and environmental drivers of moss layer cover in extratropical forests. *Global Ecology and Biogeography*, 27(10), 1213-1224. <https://doi.org/10.1111/geb.12778>
- Bernal, R., Celis, M., & Gradstein, S.R. (2016). *Catalogue of the plants and lichens of Colombia*: Universidad Nacional de Colombia, Facultad de Ciencias, Instituto de Ciencias Naturales.
- Cáceres, M.D., & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, 90(12), 3566-3574.
- Cacua-Toledo, C.F., Serrano-Cardozo, V., & Ramirez Pinilla, M.P. (2018). Composición y distribución de hepáticas (Marchantiophyta) en un intervalo altitudinal en la Cordillera Oriental de Colombia. *Rev. Biol. Trop.*, 66(2), 559-570.
- Callaghan, D.A., & Ashton, P.A. (2008). Bryophyte distribution and environment across an oceanic temperate landscape. *Journal of Bryology*, 30(1), 23-35. <https://doi.org/10.1179/174328208X282148>
- Cavalier, J. (1996). Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains. Chapt. 14. In S. S. Mulkey, R. L. Chazdon, & A. P. Smith (Eds.), *Tropical forest plant ecophysiology*: Springer Science & Business Media.

- Cavelier, J., & Goldstein, G. (1989). Mist and Fog Interception in Elfin Cloud Forests in Colombia and Venezuela. *Journal of Tropical Ecology*, 5(3), 309-322. <https://doi.org/10.1017/S0266467400003709>
- Cavelier, J., Solis, D., & Jaramillo, M.A. (1996). Fog interception in montane forest across the Central Cordillera of Panama. *Journal of Tropical Ecology*, 12(3), 357-369. <https://doi.org/10.1017/S026646740000955x>
- Chantanaorrapint, S., & Frahm, J.-P. (2011). Biomass and selected ecological factors of epiphytic bryophyte along altitudinal gradients in Southern Thailand. *Songklanakarin J. Sci. Technol.*, 33(6), 625-632.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., & Ellison, A.M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), 45-67. <https://doi.org/10.1890/13-0133.1>
- Churchill, S.P. (1991). The Floristic Composition and Elevational Distribution of Colombian Mosses. *Bryologist*, 94(2), 157-167. <https://doi.org/10.2307/3243691>
- Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., . . . Villa, G. (2002). Beta-diversity in tropical forest trees. *Science*, 295(5555), 666-669.
- Corlett, R.T. (2016). Plant diversity in a changing world: Status, trends, and conservation needs. *Plant Diversity*, 38(1), 10-16. <https://doi.org/10.1016/j.pld.2016.01.001>
- Corrales, A., Duque, A., Uribe, J., & Londono, V. (2010). Abundance and diversity patterns of terrestrial bryophyte species in secondary and planted montane forests in the northern portion of the Central Cordillera of Colombia. *Bryologist*, 113(1), 8-21. <https://doi.org/10.1639/0007-2745-113.1.8>
- Crawley, M.J. (2007). *The R Book*: Imperial College London at Silwood Park, UK.
- Cuesta, F., Muriel, P., Llambí, L.D., Halloy, S., Aguirre, N., Beck, S., . . . Gosling, W.D. (2017). Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes. *Ecography*, 40(12), 1381-1394. <https://doi.org/10.1111/ecog.02567>
- Dias dos Santos, N., & Pinheiro da Costa, D. (2010). Altitudinal zonation of liverworts in the Atlantic Forest, Southeastern Brazil. *Bryologist*, 113(3), 631-645. <https://doi.org/10.1639/0007-2745-113.3.631>
- Dufrêne, M., & Legendre, P. (1997). SPECIES ASSEMBLAGES AND INDICATOR SPECIES: THE NEED FOR A FLEXIBLE ASYMMETRICAL APPROACH. *Ecological Monographs*, 67(3), 345-366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:Saaist\]2.0.Co;2](https://doi.org/10.1890/0012-9615(1997)067[0345:Saaist]2.0.Co;2)
- Egan, P.A., & Price, M.F. (2017). *Mountain ecosystem services and climate change: A global overview of potential threats and strategies for adaptation*: UNESCO Publishing.
- Enroth, J. (1990). Altitudinal zonation of Bryophytes on the Huon Peninsula, Papua New Guinea. A floristic approach, with phytogeographic considerations. *Bryophyte Diversity and Evolution*, 2, 61. <https://doi.org/10.11646/bde.2.1.6>
- Frahm, J.-P., Pócs, T., O'Shea, B., Koponen, T., Piipo, S., Enroth, J., . . . Fang, Y. (2003). Manual of tropical bryology, chapter 5: Ecology of tropical bryophytes. *Tropical Bryology*, 23, 39-58.
- Frahm, J.P. (1987). Ökologische Studien über die epiphytische Moosvegetation in Regenwäldern NO-Perus. *Nova Hedwigia*, 88, 143-158.
- Frahm, J.P. (1990a). The Altitudinal Zonation of Bryophytes on Mt Kinabalu. *Nova Hedwigia*, 51(1-2), 133-149.
- Frahm, J.P. (1990b). Bryophyte Phytomass in Tropical Ecosystems. *Botanical Journal of the Linnean Society*, 104(1-3), 23-33. <https://doi.org/10.1111/j.1095-8339.1990.tb02209.x>
- Frahm, J.P. (1990c). The Ecology of Epiphytic Bryophytes on Mt Kinabalu, Sabah (Malaysia). *Nova Hedwigia*, 51(1-2), 121-132. Retrieved from <Go to ISI>://WOS:A1990ED63600004

- Frahm, J.P. (1990d). The Effect of Light and Temperature on the Growth of the Bryophytes of Tropical Rain-Forests. *Nova Hedwigia*, 51, 151-164. Retrieved from <Go to ISI>://WOS:A1990ED63600006
- Frahm, J.P., & Gradstein, S.R. (1991). An Altitudinal Zonation of Tropical Rain-Forests Using Bryophytes. *Journal of Biogeography*, 18(6), 669-678.
<https://doi.org/10.2307/2845548>
- Gehrig-Downie, C., Obregon, A., Bendix, J., & Gradstein, R. (2013). Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *Journal of Bryology*, 35, 243-254.
<https://doi.org/10.1179/1743282013Y.0000000070>
- Gillman, L.N., & Wright, S.D. (2006). The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, 87(5), 1234-1243.
[https://doi.org/10.1890/0012-9658\(2006\)87\[1234:Tiopot\]2.0.Co;2](https://doi.org/10.1890/0012-9658(2006)87[1234:Tiopot]2.0.Co;2)
- Glime, J.M. (2017a). The Fauna: A Place to Call Home. Chapt. 1. In J. M. Glime (Ed.), *Bryophyte Ecology* (Vol. 2. Bryological Interaction 1-1-1): Ebook sponsored by Michigan Technological University and the International Association of Bryologists.
- Glime, J.M. (2017b). Introduction. Chapt. 1. In J. M. Glime (Ed.), *Bryophyte Ecology* (Vol. 1. Physiological Ecology): Ebook sponsored by Michigan Technological University and the International Association of Bryologists.
- Glime, J.M. (2017c). Limiting Factors and Limits of Tolerance. Chapt. 6-1. In J. M. Glime (Ed.), *Bryophyte Ecology* (Vol. 1. Physiological 6-1-1): Ebook sponsored by Michigan Technological University and the International Association of Bryologists.
- Glime, J.M. (2019). Tropics: Interactions and Roles. Chapter 8-13. In J. M. Glime (Ed.), *Bryophyte Ecology* (Vol. 4. Habitat and Role): Ebook sponsored by Michigan Technological University and the International Association of Bryologists.
- Goffinet, B. (2000). Origin and phylogenetic relationships of bryophytes. In A. J. Shaw & B. Goffinet (Eds.), *Bryophyte biology* (pp. 124-149). Cambridge: Cambridge University Press.
- Gomez-Gonzalez, D.C., Rodriguez-Quiel, C.E., Zotz, G., & Bader, M.Y. (2017). Species Richness and Biomass of Epiphytic Vegetation in a Tropical Montane Forest in Western Panama. *Tropical Conservation Science*, 10.
<https://doi.org/10.1177/1940082917698468>
- Gotelli, N.J., & Chao, A. (2013). Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (second ed., Vol. 5, pp. 195-211). Waltham: MA: Academic Press.
- Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., . . . Smith, M.D. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529(7586), 390-393.
<https://doi.org/10.1038/nature16524>
- Gradstein, R., Vanderpoorten, A., van Reenen, G., & Cleef, A. (2018). Mass occurrence of the liverwort *Herbertus sendtneri* in a glacial lake in the Andes of Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 42, 221-229. Retrieved from http://www.scielo.org.co/scielo.php?script=sci_arttext&pid=S0370-39082018000300221&nrm=iso
- Gradstein, S.R. (1995). Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. *Biodiversity and conservation of Neotropical montane forests. Proc. symposium, New York Botanical Garden*, 1993, 321-334.
- Gradstein, S.R. (2008). Epiphytes of tropical montane forests - Impact of deforestation and climate change. In S. R. Gradstein, J. Homeier, & D. Gansert (Eds.), *The Tropical Mountain Forest. Patterns and processes in a biodiversity hotspot* (pp. 51-65). Göttingen, Germany: Universitätsverlag.
- Gradstein, S.R. (2016). The genus *Plagiochila* (Marchantiophyta) in Colombia. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 40, 104.
<https://doi.org/10.18257/raccefyn.272>

- Gradstein, S.R., Churchill, S.P., & Salazar Allen, N. (2001). *Guide to the Bryophytes of tropical America*. Bronx, N.Y.: New York Botanical Garden Press.
- Gradstein, S.R., Homeier, J., & Gansert, D. (2008). The tropical mountain forest; patterns and processes in a biodiversity hotspot. In Germany: Universitätsverlag Göttingen.
- Gradstein, S.R., & Pinheiro da Costa, D. (2003). *The Hepaticae and Anthocerotae of Brazil* (Vol. 87).
- Gradstein, S.R., & Salazar Allen, N. (1992). Bryophyte diversity along an altitudinal gradient in Darién National Park, Panama. *Tropical Bryology*, 5, 61-71.
- Gradstein, S.R., & Uribe, J. (2011). A Synopsis of the Frullaniaceae (Marchantiophyta) from Colombia. *Caldasia*, 33(2), 367-396.
- Gradstein, S.R., van Reenen, G., & Griffin, D. (1989). Species richness and origin of the bryophyte flora of the Colombian Andes*. *Acta Botanica Neerlandica*, 38, 439-448. <https://doi.org/10.1111/j.1438-8677.1989.tb01375.x>
- Graham, C.H., Carnaval, A.C., Cadena, C.D., Zamudio, K.R., Roberts, T.E., Parra, J.L., . . . Sanders, N.J. (2014). The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography*, 37(8), 711-719. <https://doi.org/10.1111/ecog.00578>
- Grau, O., Grytnes, J.-A., & Birks, H.J.B. (2007). A Comparison of Altitudinal Species Richness Patterns of Bryophytes with Other Plant Groups in Nepal, Central Himalaya. *Journal of Biogeography*, 34(11), 1907-1915. Retrieved from <http://www.jstor.org/stable/4640656>
- Grytnes, J.A., & McCain, C.M. (2007). Elevational trends in biodiversity. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (Second ed., pp. 149-154). Waltham: MA: Academic Press.
- Guerra, G., Arrocha, C., Rodríguez, G., Déleg, J., & Benítez Chavez, A. (2020). Briófitos en los troncos de árboles como indicadores de la alteración en bosques montanos de Panamá. *Revista de biología tropical*, 68, 492-502.
- He, X., He, K.S., & Hyvönen, J. (2016). Will bryophytes survive in a warming world? *Perspectives in Plant Ecology, Evolution and Systematics*, 19, 49-60. <https://doi.org/10.1016/j.ppees.2016.02.005>
- Hedderson, T.A., & Longton, R.E. (1996). Life history variation in mosses: Water relations, size and phylogeny. *Oikos*, 77(1), 31-43. <https://doi.org/10.2307/3545582>
- Henriques, D.S.G., Borges, P.A.V., Ah-Peng, C., & Gabriel, R. (2016). Mosses and liverworts show contrasting elevational distribution patterns in an oceanic island (Terceira, Azores): the influence of climate and space. *Journal of Bryology*, 38(3), 183-194. <https://doi.org/10.1080/03736687.2016.1156360>
- Holscher, D., Kohler, L., van Dijk, A.I.J.M., & Bruijnzeel, L.A. (2004). The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *Journal of Hydrology*, 292(1-4), 308-322. <https://doi.org/10.1016/j.jhydrol.2004.01.015>
- Holz, I., Gradstein, S.R., Heinrichs, J., & Kappelle, M. (2002). Bryophyte Diversity, Microhabitat Differentiation, and Distribution of Life Forms in Costa Rican Upper Montane Quercus Forest. *The Bryologist*, 105(3), 334-348. Retrieved from <http://www.jstor.org/stable/3244684>
- Hopp, C.J., & Waite, G.P. (2016). Characterization of seismicity at Volcan Baru, Panama: May 2013 through April 2014. *Journal of Volcanology and Geothermal Research*, 328, 187-197. <https://doi.org/10.1016/j.jvolgeores.2016.11.002>
- Jácome, J., Gradstein, R., & Kessler, M. (2011). Responses of Epiphytic Bryophyte Communities to Simulated Climate Changes in the Tropics. In Z. Tuba, N. G. Slack, & L. R. Stark (Eds.), *Bryophyte Ecology and Climate Change* (pp. 191-207): Cambridge University Press.
- Jarvis, A., Reuter, H.I., Nelson, A., & Guevara, E. (2008). Hole-filled seamless SRTM data V4. Tech. rep., International Centre for Tropical Agriculture (CIAT). In, <http://srtm.csi.cgiar.org>

- Karger, D.N., Kluge, J., Abrahamczyk, S., Salazar, L., Homeier, J., Lehnert, M., . . . Kessler, M. (2012). Bryophyte cover on trees as proxy for air humidity in the tropics. *Ecological Indicators*, 20, 277-281. <https://doi.org/10.1016/j.ecolind.2012.02.026>
- Kessler, M. (2000). Altitudinal zonation of Andean cryptogam communities. *Journal of Biogeography*, 27(2), 275-282. <https://doi.org/10.1046/j.1365-2699.2000.00399.x>
- Khine, P.K. (2018). *Biogeographical transect studies in the high elevation mountain areas of Myanmar*. (PhD thesis). University of Marburg.,
- Kluge, J., Worm, S., Lange, S., Long, D., Böhner, J., Yangzom, R., & Miehe, G. (2017). Elevational seed plants richness patterns in Bhutan, Eastern Himalaya. *Journal of Biogeography*, 44(8), 1711-1722. <https://doi.org/doi:10.1111/jbi.12955>
- Kohler, L., Tobon, C., Frumau, K.F.A., & Bruijnzee, L.A. (2007). Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecology*, 193(2), 171-184. <https://doi.org/10.1007/s11258-006-9256-7>
- Kohler, T., Wehrli, A., & Jurek, M. (2014). Mountains and climate change. A global concern. In (pp. 136): Sustainable Mountain Development Series. Bern, Switzerland, Centre for Development and Environment (CDE), Swiss Agency for Development and Cooperation (SDC) and Geographica Bernensia.
- Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., . . . Myers, J.A. (2011). Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science*, 333(6050), 1755-1758. <https://doi.org/10.1126/science.1208584>
- Kürschner, H., & Parolly, G. (2004). Phytomass and water-storing capacity of epiphytic rain forest bryophyte communities in S Ecuador. *Botanische Jahrbücher*, 125(4), 489-504. <https://doi.org/10.1127/0006-8152/2004/0125-0489>
- Laureto, L.M.O., Cianciaruso, M.V., & Samia, D.S.M. (2015). Functional diversity: an overview of its history and applicability. *Natureza & Conservação*, 13(2), 112-116. <https://doi.org/10.1016/j.ncon.2015.11.001>
- Leon-Vargas, Y., Engwald, S., & Proctor, M.C.F. (2006). Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. *Journal of Biogeography*, 33(5), 901-913. <https://doi.org/10.1111/j.1365-2699.2006.01468.x>
- Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P., & Saatchi, S. (2010). Introduction: Elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Global Change Biology*, 16(12), 3171-3175. <https://doi.org/10.1111/j.1365-2486.2010.02323.x>
- Marino, P.C., & Allen, N.S. (1992). Tropical Epiphyllous Hepatic Communities Growing on Two Species of Shrub in Barro Colorado Island, Panama: The Influence of Light and Microsite. *Lindbergia*, 17(4/6), 91-95. Retrieved from www.jstor.org/stable/20149814
- Marline, L., Ah-Peng, C., & Hedderson, T.A.J. (2020). Epiphytic bryophyte diversity and range distributions along an elevational gradient in Marojejy, Madagascar. *Biotropica*, 00, 1-11. <https://doi.org/10.1111/btp.12781>
- Mason, C.J., Zeldin, E.L., Currie, C.R., Raffa, K.F., & McCown, B.H. (2014). Populations of uncultivated American cranberry in sphagnum bog communities harbor novel assemblages of Actinobacteria with antifungal properties. *Botany*, 92(8), 589-595. <https://doi.org/10.1139/cjb-2014-0025>
- McCain, C.M., & Grytnes, J.A. (2010). Elevational gradients in species richness. In eLS (Ed.), *Encyclopedia of life sciences* (pp. 1-10). Chichester, UK: John Wiley and Sons.
- Mežaka, A., Bader, M.Y., Salazar-Allen, N., & Mendieta-Leiva, G. (2020). Epiphyll specialization for leaf and forest successional stages in a tropical lowland rainforest. *Journal of Vegetation Science*, 31(1), 118-128. <https://doi.org/10.1111/jvs.12830>
- Miehe, G., Miehe, S., Böhner, J., Bäumler, R., Ghimire, S.K., Bhattarai, K., . . . Pendry, C. (2015). Vegetation ecology. In G. Miehe & C. Pendry (Eds.), *Nepal. An introduction*

- to the natural history, ecology and human environment of the himalayas (pp. 385-472). Edinburgh: Royal Botanic Garden Edinburgh.
- Mittelbach, G.G., & McGill, B.J. (2019). *Community ecology*: Oxford University Press.
- Morales, J., Zamora, N., & Herrera-F, B. (2007). Análisis de la vegetación en la franja altitudinal de 800-1500 m.s.n.m. en la vertiente pacífica del Parque Internacional La Amistad (PILA), Costa Rica. *Brenesia*, 68, 1-15.
- Mota de Oliveira, S., & ter Steege, H. (2015). Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. *Journal of Ecology*, 103(2), 441-450. <https://doi.org/10.1111/1365-2745.12359>
- Mota de Oliveira, S., ter Steege, H., Cornelissen, J.H.C., & Gradstein, S.R. (2009). Niche assembly of epiphytic bryophyte communities in the Guianas: a regional approach. *Journal of Biogeography*, 36(11), 2076-2084. <https://doi.org/10.1111/j.1365-2699.2009.02144.x>
- Nascimbene, J., & Spitale, D. (2017). Patterns of beta-diversity along elevational gradients inform epiphyte conservation in alpine forests under a climate change scenario. *Biological Conservation*, 216, 26-32. <https://doi.org/10.1016/j.biocon.2017.09.021>
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., & Suggests, M. (2007). The vegan package. *Community ecology package*, 10, 631-637.
- Pentecost, A. (1998). Some observations on the biomass and distribution of cryptogamic epiphytes in the upper montane forest of the Rwenzori Mountains, Uganda. *Global Ecology and Biogeography*, 7(4), 273-284.
- Perrigo, A., Hoorn, C., & Antonelli, A. (2019). Why mountains matter for biodiversity. *Journal of Biogeography*, 00, 1-11. <https://doi.org/10.1111/jbi.13731>
- Pócs, T. (1980). The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Botanica Academiae Scientiarum Hungaricae*, 26, 143-167.
- Porras-López, S., & Morales-Puentes, M. (2020). Distribución altitudinal de musgos en algunos sustratos en Tipacoque, Colombia. *Bol. Cient. MusHist. Nat. U. de Caldas* (0123-3068); (2462-8190). 24, 15-30.
- Proctor, M.C.F. (1990). The physiological basis of bryophyte production. *Botanical Journal of the Linnean Society*, 104(1-3), 61-77. <https://doi.org/10.1111/j.1095-8339.1990.tb02211.x>
- Proctor, M.C.F. (2008). Physiological ecology. In A. J. Shaw & B. Goffinet (Eds.), *Bryophyte biology* (2 ed., pp. 237-268). Cambridge: Cambridge University Press.
- Pypker, T.G., Unsworth, M.H., & Bond, B.J. (2006a). The role of epiphytes in rainfall interception by forests in the Pacific Northwest. I. Laboratory measurements of water storage. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 36(4), 809-818. <https://doi.org/10.1139/X05-298>
- Pypker, T.G., Unsworth, M.H., & Bond, B.J. (2006b). The role of epiphytes in rainfall interception by forests in the Pacific Northwest. II. Field measurements at the branch and canopy scale. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 36(4), 819-832. <https://doi.org/10.1139/X05-286>
- Richards, P.W. (1984). The ecology of tropical forest bryophytes. In R. M. Schuster (Ed.), *New manual of bryology* (Vol. 2, pp. 1233-1270). Nichinan: The Hattori Botanical Laboratory.
- Rodriguez-Quiel, E.E., Kluge, J., Mendieta-Leiva, G., & Bader, M.Y. (in review). Elevational patterns in tropical bryophyte diversity differ among substrates. A case study on Baru volcano, Panama. *Journal of Vegetation Science*.
- Rodriguez-Quiel, E.E., Mendieta-Leiva, G., & Bader, M.Y. (2019). Elevational patterns of bryophyte and lichen biomass differ among substrates in the tropical montane forest of Baru Volcano, Panama. *Journal of Bryology*, 41, 95-106. <https://doi.org/10.1080/03736687.2019.1584433>
- Rudmann-Maurer, Spehn, E., & Körner, C. (2014). Biodiversity in Mountains: Natural heritage under threat. In T. Kohler, A. Wehrli, & M. Jurek (Eds.), *Mountains and climate change. A global concern* (pp. 79-109): Sustainable Mountain Development

- Series. Bern, Switzerland, Centre for Development and Environment (CDE), Swiss Agency for Development and Cooperation (SDC) and Geographica Bernensia.
- Salas-Morales, S.H., Meave, J.A., & Trejo, I. (2015). The relationship of meteorological patterns with changes in floristic richness along a large elevational gradient in a seasonally dry region of southern Mexico. *International Journal of Biometeorology*, 59(12), 1861-1874. <https://doi.org/10.1007/s00484-015-0993-y>
- Schluter, D., & Robert, E. (1993). Species diversity: introduction to the problem. In D. Schluter & E. Robert (Eds.), *Species diversity in ecological communities*: University of Chicago Press.
- Schuster, R.M. (1984). *New Manual of Bryology* (Vol. 2). The Hattori Botanical Laboratory.
- Seifriz, W. (1924). The Altitudinal Distribution of Lichens and Mosses on Mt Gedeh, Java. *Journal of Ecology*, 12(2), 307-313. <https://doi.org/10.2307/2255252>
- Sierra, A.M., Toledo, J.J., Nascimento, H.E., Pereira, M.R., & Zartman, C.E. (2019). Are extinction debts reflected in temporal changes of life history trait profiles? A fifteen-year reappraisal of bryophyte metacommunities in a fragmented landscape. *Biological Conservation*, 238, 108218. <https://doi.org/10.1016/j.biocon.2019.108218>
- Slack, N.G. (2011). The Ecological Value of Bryophytes as Indicators of Climate Change. In L. R. Stark, N. G. Slack, & Z. Tuba (Eds.), *Bryophyte Ecology and Climate Change* (pp. 3-12). Cambridge: Cambridge University Press.
- Sonnleitner, M., Dullinger, S., Wanek, W., & Zechmeister, H. (2009). Microclimatic patterns correlate with the distribution of epiphyllous bryophytes in a tropical lowland rain forest in Costa Rica. *Journal of Tropical Ecology*, 25, 321-330. <https://doi.org/10.1017/S0266467409006002>
- R-Core Team. (2019). R: A language and environment for statistical computing (Version 3.3.2). R Foundation for Statistical Computing, Vienna, Austria.
- R-Core Team. (2016). R: A Language and Environment for statistical Computing (Version 3.3.2). R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>
- Thuiller, W. (2007). Climate change and the ecologist. *Nature*, 448(7153), 550-552. <https://doi.org/10.1038/448550a>
- Tropicos.org. (2019). Missouri Botanical Garden. In, <http://tropicos.org/>
- Van Reenen, G.B.A., & Gradstein, S.R. (1983). Studies on Colombian Cryptogams .20. A Transect Analysis of the Bryophyte Vegetation Along an Altitudinal Gradient on the Sierra-Nevada De Santa-Marta, Colombia. *Acta Botanica Neerlandica*, 32(3), 163-175. <https://doi.org/10.1111/j.1438-8677.1983.tb01698.x>
- Wagner, S., Bader, M.Y., & Zotz, G. (2014). Physiological Ecology of Tropical Bryophytes. In D. T. Hanson & S. K. Rice (Eds.), *Photosynthesis in Bryophytes and Early Land Plants* (pp. 269-289). Dordrecht: Springer Netherlands.
- Wagner, S., Zotz, G., Allen, N.S., & Bader, M.Y. (2013). Altitudinal changes in temperature responses of net photosynthesis and dark respiration in tropical bryophytes. *Annals of Botany*, 111(3), 455-465. <https://doi.org/10.1093/aob/mcs267>
- Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30(3), 280-338.
- Wolf, J. (1995). Non-vascular epiphyte diversity patterns in the canopy of an upper montane rain forest (2550-3670 m), Central Cordillera, Colombia. *Selbyana*, 16, 185-195.
- Wolf, J.H.D. (1993). Diversity Patterns and Biomass of Epiphytic Bryophytes and Lichens Along an Altitudinal Gradient in the Northern Andes. *Annals of the Missouri Botanical Garden*, 80(4), 928-960. <https://doi.org/10.2307/2399938>
- Wolf, J.H.D. (1994). Factors Controlling the Distribution of Vascular and Nonvascular Epiphytes in the Northern Andes. *Vegetatio*, 112(1), 15-28. <https://doi.org/10.1007/Bf00045096>
- Zotz, G. (1999). Altitudinal Changes in Diversity and Abundance of Non-Vascular Epiphytes in the Tropics - An Ecophysiological Explanation. *Selbyana*, 20(2), 256-260. Retrieved from <http://www.jstor.org/stable/41760030>

- Zotz, G., & Bader, M.Y. (2009). Epiphytic plants in a changing world: Global-change effects on vascular and non-vascular epiphytes. In U. Lüttge, W. Beyschlag, B. Büdel, & D. Francis (Eds.), *Progress in Botany* (pp. 147-170). Berlin, Heidelberg: Springer Berlin Heidelberg.
- Zotz, G., Mendieta-Leiva, G., & Wagner, K. (2014). Vascular epiphytes at the treeline - composition of species assemblages and population biology. *Flora*, 209(8), 385-390. <https://doi.org/10.1016/j.flora.2014.06.001>
- Zotz, G., Schultz, S., & Rottenberger, S. (2003). Are tropical lowlands a marginal habitat for macrolichens? Evidence from a field study with *Parmotrema endosulphureum* in Panama. *Flora*, 198(1), 71-77. <https://doi.org/10.1078/0367-2530-00077>

APPENDICES

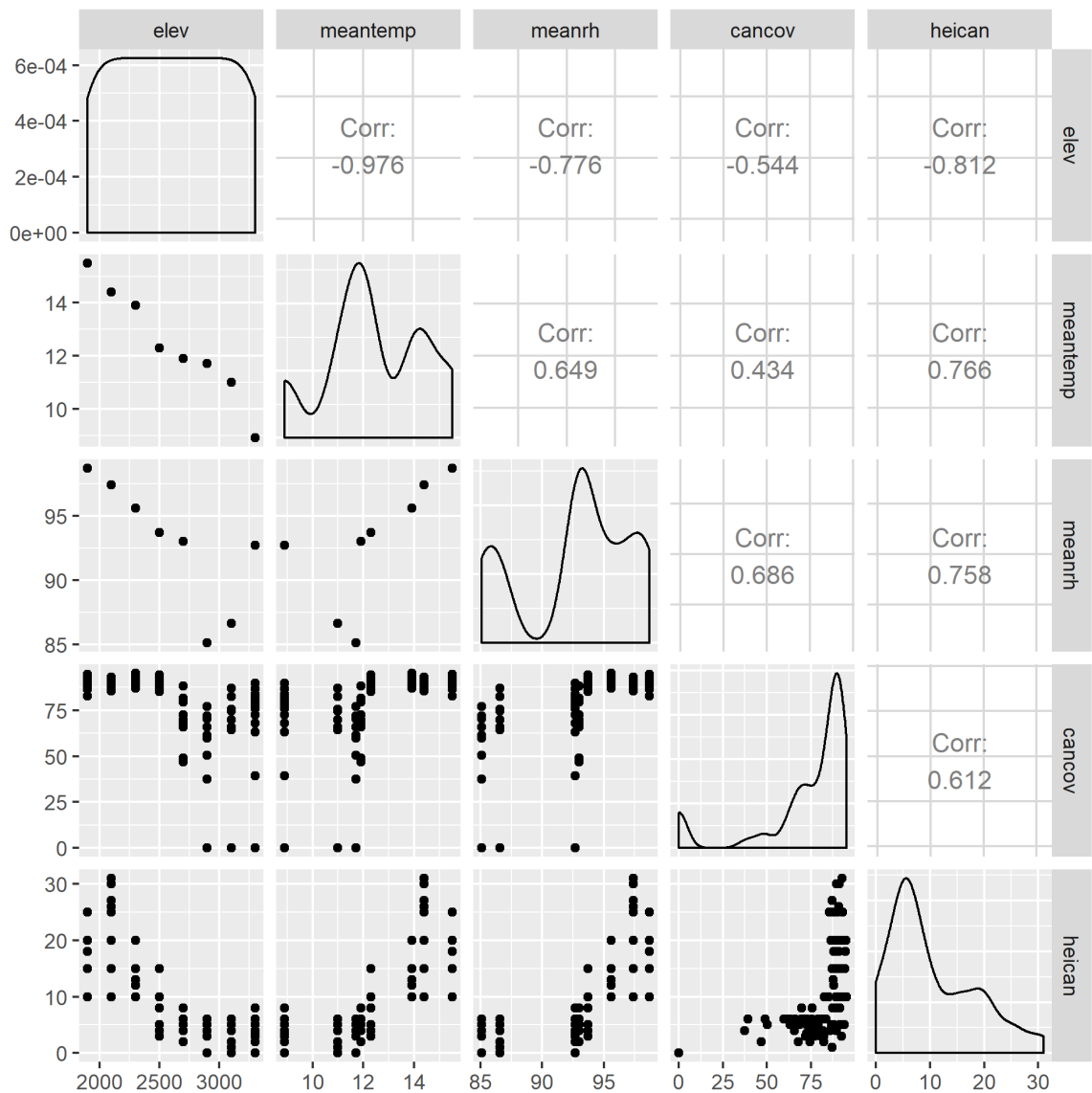
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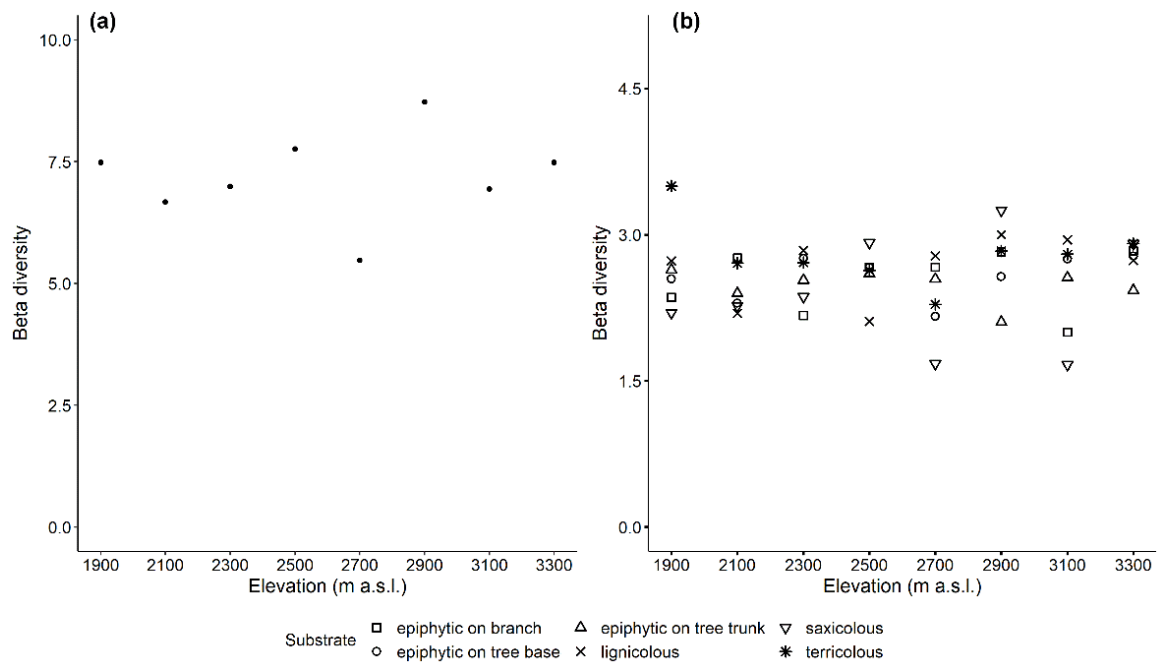
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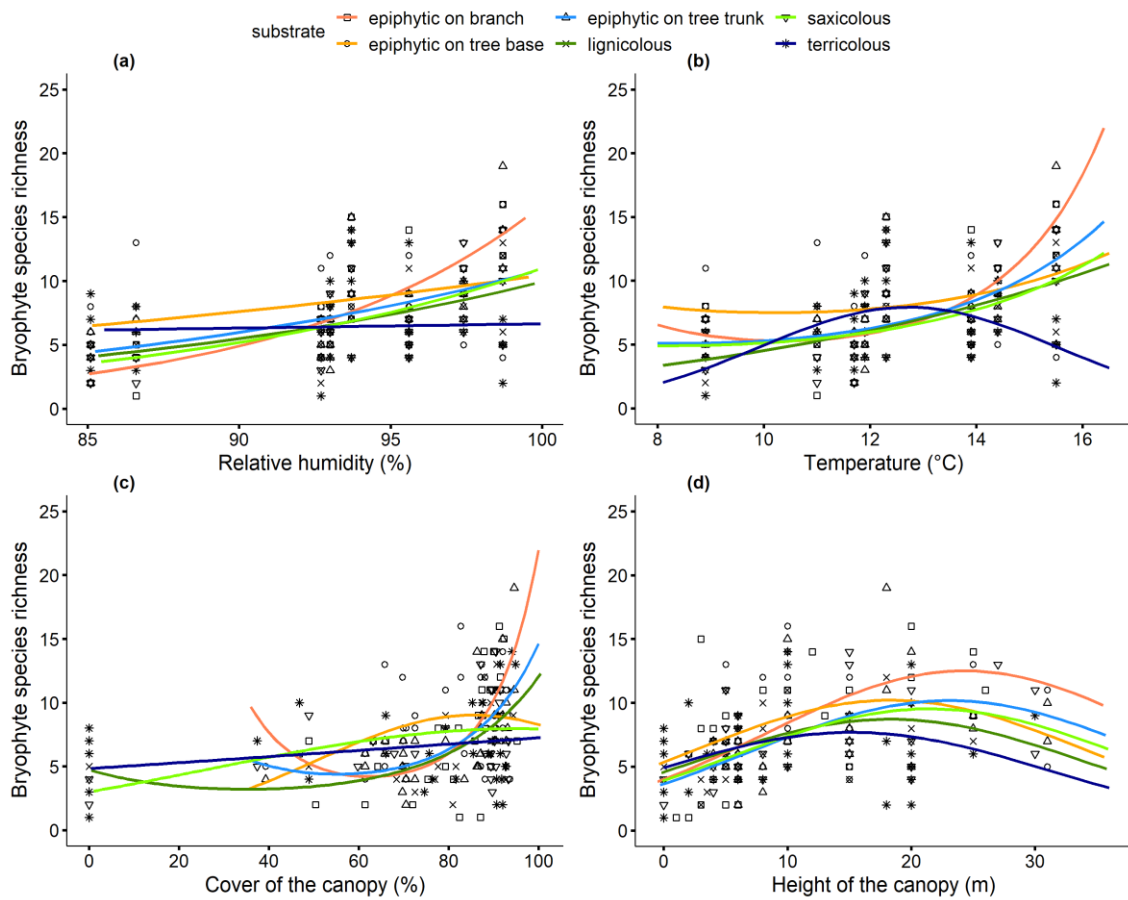
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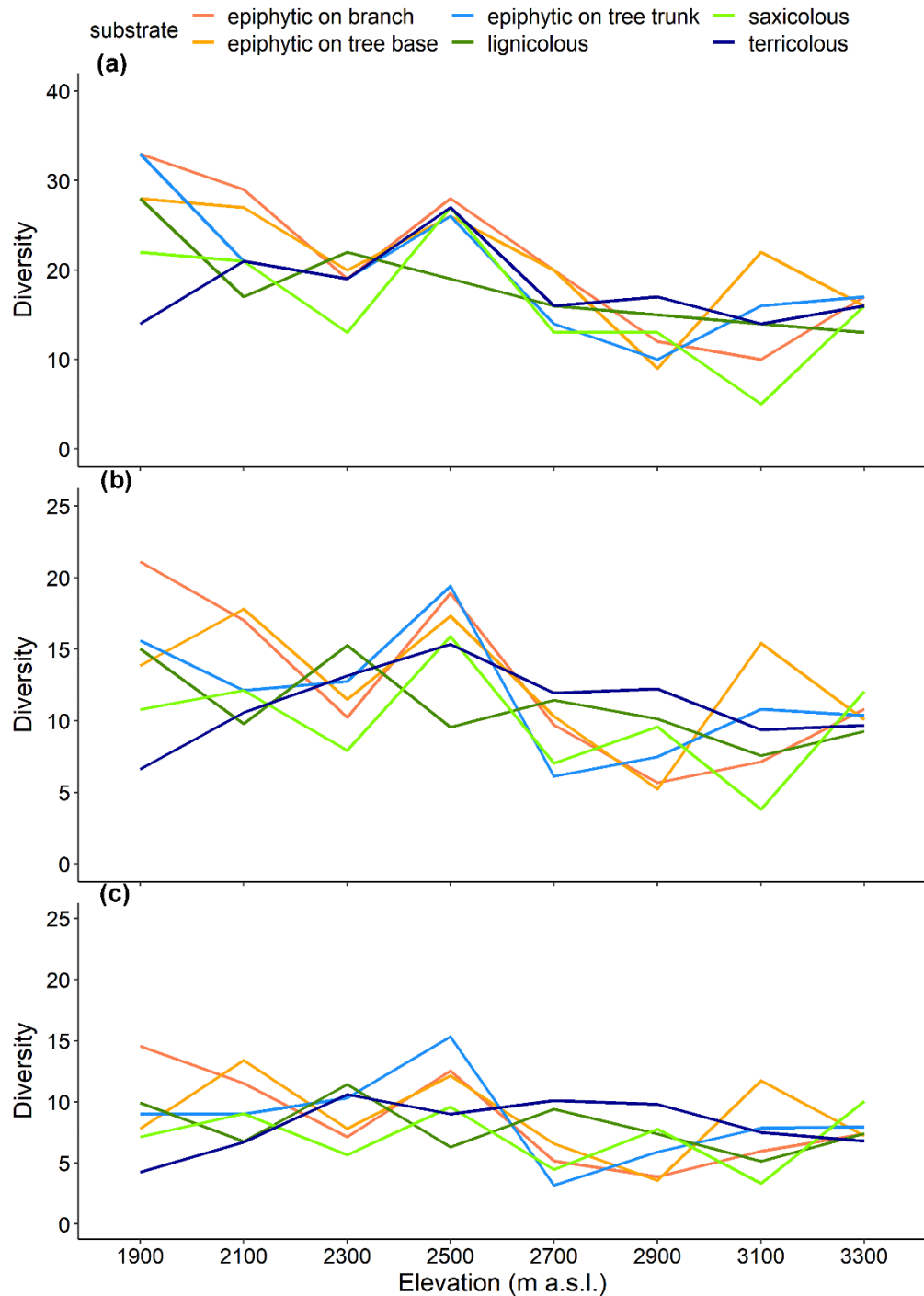
Appendix F 1. Pairwise Spearman Correlations among elevation, climate (mean temperature and mean relative humidity) and forest structure data (canopy-cover and height of the canopy) along an elevational gradient on Barú Volcano, Panama. Left-bottom panels represent scatter plots among factors, diagonal panels represent a density plot for each factor, and right-upper panels show the correlation coefficients. Used acronyms: *elev*: elevation, *meantemp*: mean temperature, *meanrh*: mean relative humidity, *cancov*: canopy-cover, *heican*: height of the canopy.



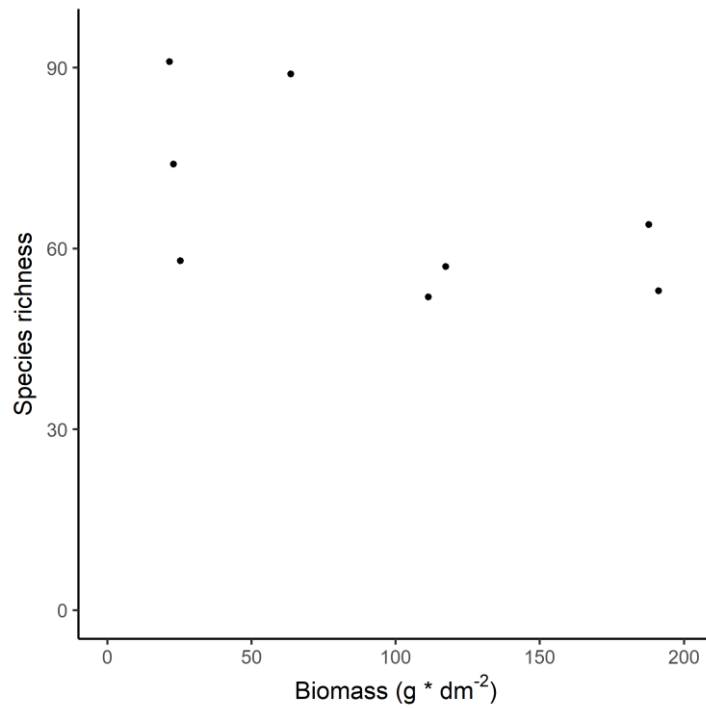
Appendix F 2. Change in bryophyte beta diversity ($\beta = \gamma / \alpha$, sensus Whittaker, 1960) along an elevational gradient on Baru Volcano, Panama. A: Variation in beta diversity among six substrate types per elevation. No significant trend with elevation was detected; B: Variation in beta diversity among plots within substrate types. There was no significant trend along elevation and no difference between the types of substrate.



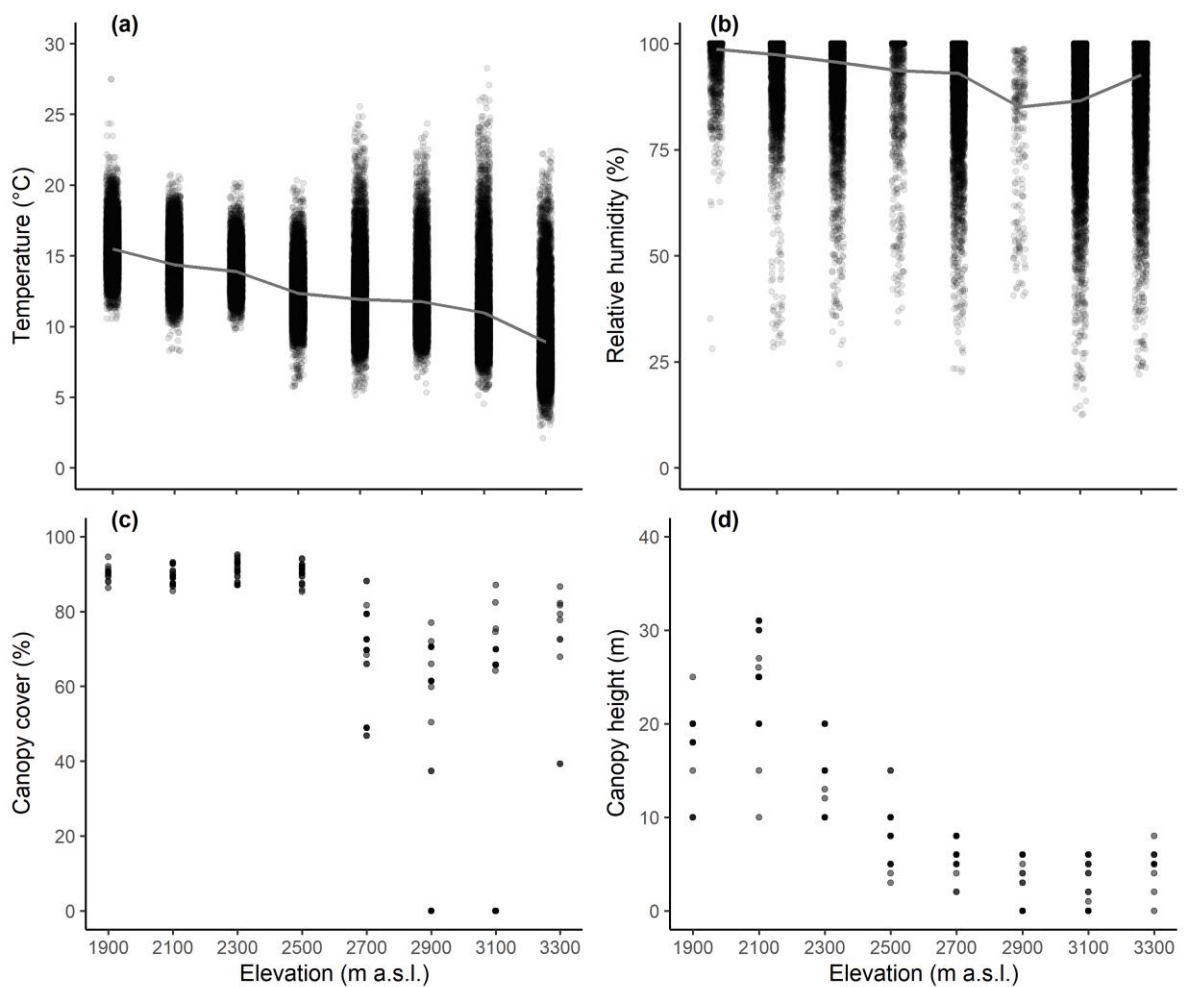
Appendix F 3. Change in bryophyte species richness on different substrates according to the variation in the climate ([a]: mean relative humidity; [b]: mean temperature) and forest structure variables ([c]: canopy cover; [d]: height of the canopy), along an elevational gradient on Baru Volcano, Panama. Lines represent the predicted species richness according to an GLM for each factor considered separately. The analysis was at the plot level, i.e. based on the number of species found per 600-cm² plot.



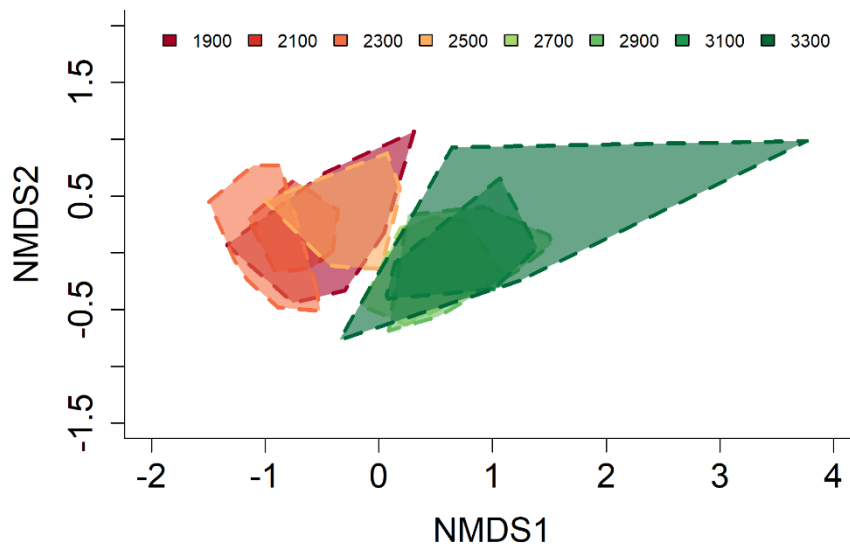
Appendix F 4. Variation of each order of diversity (from Figure 2-4) for bryophytes from different substrates along an elevational gradient on Baru volcano, Panama. Diversity was assessed based on the number of species observed ($q = 0$) and increasingly considering the relative abundance (cover) of the species ($q = 1$ and $q = 2$). **(a)**: diversity order $q = 0$ (total species richness); **(b)**: diversity order $q = 1$ (typical species); and **(c)**: diversity order $q = 2$ (very abundant species). Note: in **b** and **c**, the scale of the y-axis was adjusted to provide a better visual illustration. A significant decrease in diversity with elevation was observed for $q = 0$ and $q = 1$ only. There was no significant difference between substrates.



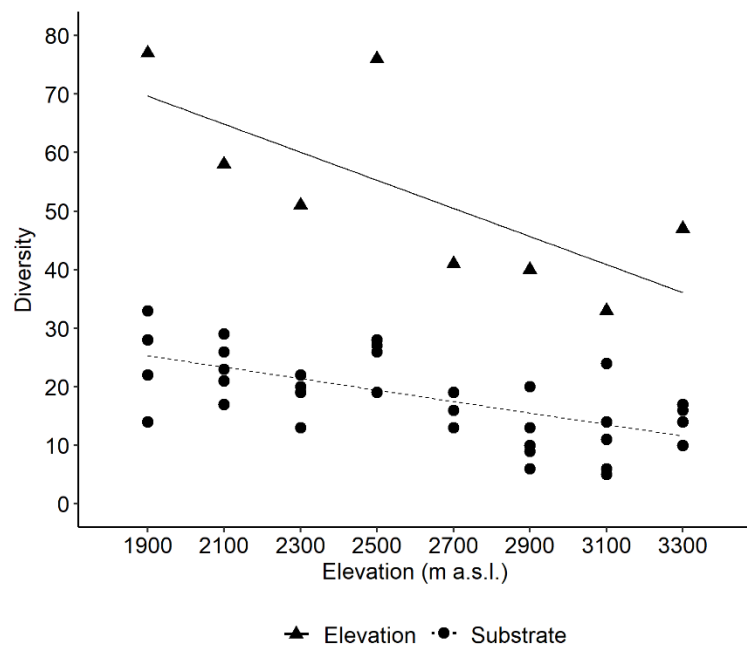
Appendix F 5. Relationship between total bryophyte and lichen species richness per elevation and mean biomass per dm² on six substrate types along an elevational gradient on Baru Volcano, Panama. There is no correlation between total species richness and total biomass per elevation ($r = -0.57, p = 0.14$).



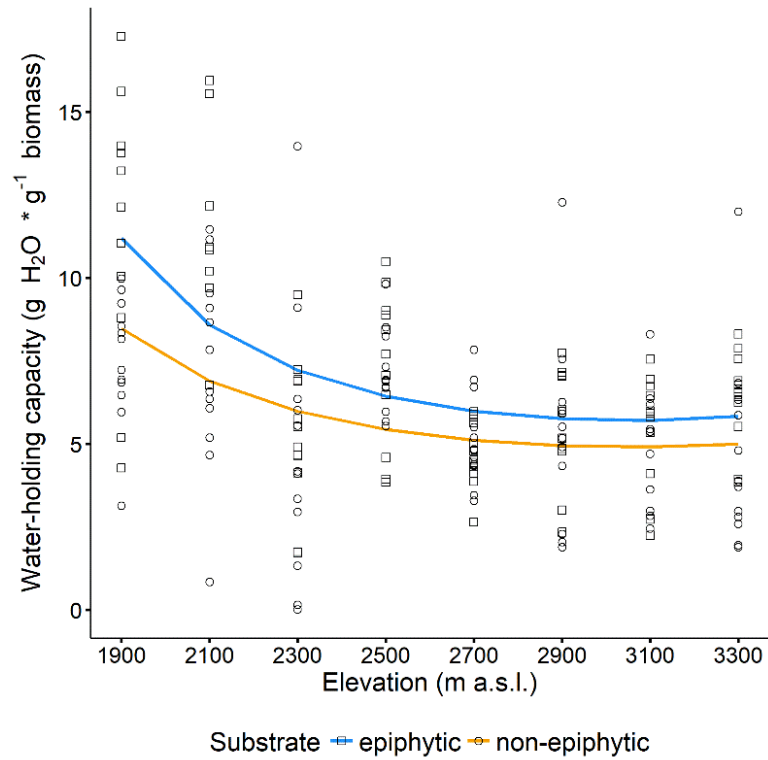
Appendix F 6. Climate and forest structure of the study sites along an elevational gradient on Baru Volcano, Panama (Modified from: Rodriguez-Quiel et al., 2019). The symbols and lines for temperature and relative humidity represent the overall variation and connect the means, respectively (measurements were taken at the site level, from April to December 2017, at 30-minute intervals and including both the dry and the rainy season. Except at 1900, 2500 and 2900 m, where measurements were taken for 110, 30 and 10 days only due to equipment failure). The symbols for canopy-cover and the height of the canopy represent their overall fluctuation (measurements were taken at the plot level, based on 24 measurements per elevation).



Appendix F 7. Nonmetric multidimensional scaling ordination (NMDS), showing how species composition of bryophyte communities differ between the lowest and highest elevations along an elevational gradient on Baru volcano, Panama. Each polygon encloses 24 plots within one elevation and six substrate types. The analysis was based on the relative abundance (cover) of the species (Bray Curtis index as a measurement of similarity).



Appendix F 8. Elevational pattern of bryophyte species richness aggregated by elevations and substrates level, along an elevational gradient on Baru Volcano, Panama. Modified from (Rodriguez-Quiel et al., in review)



Appendix F 9. Change in water-holding capacity per gram biomass of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. Lines represent the predicted model water-holding capacity of the layer per gram biomass along elevation according to substrate groups. Substrate groups, based on similarity in elevational patterns: epiphytic = on shrub branches and base and breast height on tree trunks; no epiphytic = decomposing log, rock and soil.

Appendix T 1. List and distribution of the bryophytes recorded from different substrates along an elevational gradient on Baru Volcano, Panama.

NOTE: * New record for Panama.

Taxa	Elevation (m a.s.l.)							
	1900	2100	2300	2500	2700	2900	3100	3300
Hornworts								
1. <i>Anthocerotaceae</i>								
<i>Nothoceros vincentianus</i> (Lehm. & Lindenb.) J. C. Villarreal			X	X				
Bryophytes								
1. <i>Bartramiaceae</i>								
<i>Breutelia squarrosa</i> A. Jaeger						X		
<i>Breutelia tomentosa</i> (Sw. ex Brid.) A. Jaeger						X	X	X
2. <i>Brachytheciaceae</i>								
<i>Brachythecium ruderale</i> (Brid.) W.R. Buck	X		X	X				
<i>Rhynchostegium serrulatum</i> (Hedw.) A. Jaeger		X	X					
3. <i>Bryaceae</i>								
<i>Anomobryum julaceum</i> (Schrad. ex G. Gaertn., B. Mey. & Scherb.) Schimp.						X		X
<i>Brachymenium</i> sp			X					
<i>Bryum argenteum</i> Hedw.						X		X
<i>Bryum billardierii</i> Schwägr.	X		X	X				X
<i>Bryum procerum</i> Schimp. ex Besch.				X				X
<i>Pohlia papillosa</i> (A. Jaeger) Broth.				X				
<i>Pohlia richardsii</i> A.J. Shaw					X	X		
4. <i>Cryphaeaceae</i>								
<i>Cryphaea jamesonii</i> Taylor			X					
<i>Cryphaea patens</i> Hornsch. ex Müll. Hal.	X							

<i>Dendropogonella rufescens</i> (Schimp.) E. Britton									X
5. <i>Daltoniaceae</i>									
<i>Daltonia</i> cf <i>gracilis</i> Mitt.								X	
<i>Lepidopilum</i> sp									X
6. <i>Dicranaceae</i>									
<i>Campylopus albidovirens</i> Herzog								X	X
<i>Campylopus nivalis</i> (Brid.) Brid.								X	X
<i>Campylopus pilifer</i> Brid.								X	X
<i>Campylopus richardii</i> Brid.								X	X
<i>Dicranum frigidum</i> Müll. Hal.								X	X
<i>Leucobryum subobtusifolium</i> (Broth.) B.H. Allen								X	X
<i>Pilopogon guadalupensis</i> (Brid.) J.-P. Frahm								X	X
7. <i>Entodontaceae</i>									
<i>Entodon serrulatus</i> Mitt.								X	
<i>Erythrodontium longisetum</i> (Hook.) Paris								X	
8. <i>Fissidentaceae</i>									
<i>Fissidens</i> sp								X	X
<i>Fissidens asplenioides</i> Hedw.								X	
<i>Fissidens zollingeri</i> Mont.								X	X
9. <i>Grimmiaceae</i>									
<i>Racomitrium crispipilum</i> (Taylor) A. Jaeger								X	X
<i>Racomitrium subsecundum</i> (Hook. & Grev. ex Harv.) Mitt. & Wilson								X	X
10. <i>Hedwigiaceae</i>									
<i>Braunia squarrulosa</i> (Hampe) Müll. Hal.								X	
11. <i>Hypnaceae</i>									
<i>Caribaeohypnum polypterum</i> (Mitt.) Ando & Higuchi								X	X

<i>Ectropothecium leptochaeton</i> (Schwägr.) W.R. Buck	X	X					
<i>Hypnum amabile</i> (Mitt.) Hampe	X			X	X	X	X
<i>Mittenothamnium reptans</i> (Hedw.) Cardot	X	X	X				
<i>Mittenothamnium scalpellifolium</i> (Müll. Hal.) H.A. Crum		X					
<i>Pylaisiadelpha tenuirostris</i> (Bruch & Schimp. ex Sull.) W.R. Buck					X	X	X
<i>12. Lembophyllaceae</i>							
<i>Porotrichodendron lindigii</i> (Hampe) W.R. Buck			X	X			
<i>13. Meteoriaceae</i>							
<i>Meteorium deppei</i> (Hornsch. ex Müll. Hal.) Mitt.	X	X		X			
<i>Meteorium nigrescens</i> (Sw. ex Hedw.) Dozy & Molk.		X					
<i>Meteoridium remotifolium</i> (Müll. Hal.) Manuel	X	X	X				
<i>Pilotrichella</i> sp			X				
<i>Pilotrichella flexilis</i> (Hedw.) Ångstr.	X	X	X				
<i>Pilotrichella mauiensis</i> (Sull.) A. Jaeger	X						
<i>Squamidium isocladum</i> (Renauld & Cardot) Broth.	X						
<i>Squamidium livens</i> (Schwägr.) Broth.	X			X			
<i>Squamidium nigricans</i> (Hook.) Broth.	X		X				
<i>Toloxis imponderosa</i> (Taylor) W.R. Buck	X	X	X	X			
<i>Zelometeorium patulum</i> (Hedw.) Manuel	X			X			
<i>14. Mniaceae</i>							
<i>Plagiomnium rhynchophorum</i> (Hook.) T.J. Kop.	X	X	X				
<i>Plagiomnium rostratum</i> (Schrad.) T.J. Kop.				X			
<i>15. Neckeraceae</i>							
<i>Neckera</i> sp	X	X	X				
<i>Neckera ehrenbergii</i> Müll. Hal.	X	X	X				
<i>Neckera</i> cf <i>urnigera</i> Müll. Hal.			X				

<i>Porotrichum</i> sp1		X	X	X				
<i>Porotrichum lindigii</i> (Hampe) Mitt.	X		X					
<i>Porotrichum longirostre</i> (Hook.) Mitt.			X					
<i>Porotrichum</i> cf <i>mutabile</i> Hampe		X						
<i>Porotrichum</i> cf <i>usagarum</i> Mitt.		X	X					
16. <i>Orthotrichaceae</i>								
<i>Zygodon</i> cf <i>liebmannii</i> Schimp. *	X	X	X	X		X	X	X
17. <i>Pilotrichaceae</i>								
<i>Cyclodictyon roridum</i> (Hampe) Kuntze					X			
<i>Cyclodictyon</i> cf <i>varians</i> (Sull.) Kuntze			X					
<i>Trachyxiphium guadalupense</i> (Brid.) W.R. Buck					X			
<i>Trachyxiphium repens</i> (Hook. & Grev.) B.H. Allen	X	X	X					
<i>Trachyxiphium subfalcatum</i> (Hampe) W.R. Buck *		X	X					
18. <i>Polytrichaceae</i>								
Polytrichaceae 1						X		
<i>Pogonatum comosum</i> (Müll. Hal.) Mitt.						X		
<i>Polytrichum juniperinum</i> Hedw.					X	X	X	X
<i>Polytrichastrum tenellum</i> (Müll. Hal.) G.L. Sm.						X	X	
19. <i>Pottiaceae</i>								
Pottiaceae1	X	X	X	X	X			
Pottiaceae2								X
<i>Leptodontium</i> sp1	X			X				
<i>Leptodontium exasperatum</i> Cardot	X			X	X	X	X	X
<i>Leptodontium excelsum</i> (Sull.) E. Britton				X	X	X	X	X
<i>Leptodontium flexifolium</i> (Dicks.) Hampe	X				X	X	X	X
<i>Leptodontium</i> cf <i>filicola</i> Herzog						X		

<i>Leptodontium ulocalyx</i> (Müll. Hal.) Mitt.	X			X	X	X	X	X
<i>Trichostomum</i> sp				X				X
<i>20. Prionodontaceae</i>								
<i>Prionodon densus</i> (Sw. ex Hedw.) Müll. Hal.				X	X			
<i>Prionodon fuscolutescens</i> Hampe					X			
<i>21. Pterobryaceae</i>								
<i>Pterobryopsis mexicana</i> (Renauld & Cardot) M. Fleisch.	X							
<i>Renauldia mexicana</i> (Mitt.) H.A. Crum	X	X	X					
<i>22. Racopilaceae</i>								
<i>Racopilum tomentosum</i> (Hedw.) Brid.	X	X	X					
<i>23. Regmatodontaceae</i>								
<i>Regmatodon orthostegius</i> Mont.	X	X						
<i>24. Sematophyllaceae</i>								
<i>Acroporium caespitosum</i> (Hedw.) W.R. Buck					X			
<i>Aptychella prolifera</i> (Broth.) Herzog	X	X		X		X	X	
<i>Pterogonidium pulchellum</i> (Hook.) Müll. Hal.						X		
<i>Sematophyllum</i> sp1						X		
<i>Sematophyllum subsimplex</i> (Hedw.) Mitt.	X	X						
<i>Sematophyllum swartzii</i> (Schwägr.) W.H. Welch & H.A. Crum				X				
<i>Sematophyllum virgatum</i> B.H. Allen					X			
<i>25. Thuidiaceae</i>								
<i>Cyrto-hypnum involvens</i> (Hedw.) W.R. Buck & H.A. Crum	X							
<i>Cyrto-hypnum sharpii</i> (H.A. Crum) W.R. Buck & H.A. Crum	X	X	X	X				
<i>Thuidium delicatulum</i> (Hedw.) Schimp.	X	X	X	X		X		

LIVERWORTS

1. Adelanthaceae

<i>Pseudomarsupidium decipiens</i> (Hook.) Grolle							X	X
2. <i>Arneliaceae</i>								
<i>Stephaniella paraphyllina</i> J.B.Jack							X	X
3. <i>Calypogeiaceae</i>								
<i>Mnioloma cyclostipum</i> (Spruce) R.M.Schust.					X	X		
4. <i>Frullaniaceae</i>								
<i>Frullania</i> sp2	X	X						
<i>Frullania brasiliensis</i> Raddi	X	X	X	X	X	X	X	X
<i>Frullania dusenii</i> Steph.	X							
<i>Frullania ecklonii</i> (Spreng.) Spreng.	X			X				
<i>Frullania ericoides</i> (Mart.) Mont.	X	X		X				
<i>Frullania exilis</i> Taylor						X	X	
<i>Frullania intumescens</i> (Lehm. & Lindenb.) Lehm. & Lindenb.	X	X	X					
<i>Frullania cf kunzei</i> Lehm. & Lindenb.	X	X	X					X
<i>Frullania obscura</i> (Sw.) Nees	X	X		X				
<i>Frullania cf pluricarinata</i> Gottsche			X					
<i>Frullania tetraptera</i> Nees & Mont. *	X					X	X	
5. <i>Herbertaceae</i>								
<i>Herbertus bivittatus</i> Spruce				X	X	X	X	X
<i>Herbertus grossispinus</i> Fulford				X	X	X	X	X
<i>Herbertus juniperoideus</i> (Sw.) Grolle				X		X	X	X
6. <i>Jamesoniellaceae</i>								
<i>Syzygiella rubricaulis</i> (Nees) Steph.							X	X
<i>Syzygiella sonderi</i> (Gottsche) K. Feldberg, Vána, Hentschel & Heinrichs						X	X	X
7. <i>Lejeuneaceae</i>								
Lejeuneaceae1	X	X				X		X

<i>Anoplolejeunea conferta</i> (Spreng.) A.Evans		X			X	X	X
<i>Brachiolejeunea laxifolia</i> (Taylor) Schiffn.	X			X	X		
<i>Ceratolejeunea fallax</i> (Lehm. & Lindenb.) Bonner				X			
<i>Cheilolejeunea</i> sp1	X	X	X	X			X
<i>Cheilolejeunea acutangula</i> (Nees) Grolle	X			X			
<i>Cheilolejeunea filiformis</i> (Sw.) W. Ye, R.L. Zhu & Gradst.	X		X	X			
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & R.L.Zhu	X						
<i>Cheilolejeunea oncophylla</i> (Aongstr.) Grolle & M.E.Reiner					X		X
<i>Dicranolejeunea axillaris</i> (Nees & Mont.) Schiffn.	X	X					
<i>Diplasiolejeunea pauckertii</i> S. Winkl							X
<i>Drepanolejeunea</i> sp1	X			X			
<i>Drepanolejeunea araucariae</i> Steph.							X
<i>Harpalejeunea</i> cf <i>subacuta</i> A. Evans				X			
<i>Lejeunea</i> sp1	X	X	X	X			
<i>Lejeunea laetevirens</i> Nees & Mont.	X	X	X	X			
<i>Lejeunea pallescens</i> Mitt.				X			
<i>Lejeunea pterigonia</i> (Lehm. & Lindenb.) Mont.	X	X	X				
<i>Lejeunea rotundifolia</i> Mitt.	X	X		X			
<i>Lejeunea sporadica</i> Besch. & Spruce *		X					
<i>Lopholejeunea nigricans</i> (Lindenb.) Steph.	X	X					
8. <i>Lepidoziaceae</i>							
Lepidoziaceae							X
<i>Telaranea diacantha</i> (Mont.) J.J.Engel & G.L.Merr.				X			
<i>Bazzania aurescens</i> Spruce		X					
<i>Bazzania hookeri</i> (Lindenb.) Trevis.				X			
<i>Lepidozia cupressina</i> (Sw.) Lindenb.				X			

<i>Telaranea nematodes</i> (Austin) M.Howe				X		X	X		X
9. <i>Lophocoleaceae</i>									
<i>Leptoscyphus amphibolius</i> (Nees) Grolle						X	X		
<i>Leptoscyphus porphyrius</i> Grolle	X	X				X	X	X	X X
<i>Lophocolea bidentata</i> (L.) Dumort.	X	X				X			
<i>Lophocolea muricata</i> (Lehm.) Nees	X	X				X			
10. <i>Metzgeriaceae</i>									
<i>Metzgeria</i> ssp	X	X	X			X	X		X X
11. <i>Monocleaceae</i>									
<i>Monoclea gottschei</i> Lindb.						X			
12. <i>Plagiochilaceae</i>									
<i>Plagiochila adianthoides</i> (Sw.) Lindenb.						X			
<i>Plagiochila bifaria</i> (Sw.) Lindenb.	X					X	X	X	X X
<i>Plagiochila deflexirama</i> Taylor						X			
<i>Plagiochila fuscolutea</i> Taylor									X
<i>Plagiochila heterophylla</i> Lehm.	X	X	X			X	X		
<i>Plagiochila laetevirens</i> Lindenb.	X	X	X			X			
<i>Plagiochila ovata</i> Lindenb.						X			X
<i>Plagiochila punctata</i> (Taylor) Taylor						X	X	X	X X
<i>Plagiochila raddiana</i> Lindenb.	X	X	X			X	X		
<i>Plagiochila trichostoma</i> Gottsche	X					X	X	X	X
<i>Plagiochila vitiana</i> Inoue *									X X
13. <i>Porellaceae</i>									
<i>Porella complanata</i> (Steph.) Swails						X			
<i>Porella crispata</i> (Hook.) Trevis.	X	X	X						
<i>Porella swartziana</i> (F.Weber) Trevis.	X	X	X						

<i>14. Radulaceae</i>						
<i>Radula tectiloba</i> Steph.	X	X				
<i>Radula voluta</i> Taylor	X	X	X			
<i>15. Scapaniaceae</i>						
<i>Anastrophyllum auritum</i> (Lehm.) Steph.				X	X	X X
<i>16. Solenostomataceae</i>						
<i>Solenostoma sphaerocarpum</i> (Hook.) Steph. *				X	X	X X X
<i>17. Trichocoleaceae</i>						
<i>Leiomitra tomentosa</i> (Sw.) Lindb.						X

Appendix T 2. Analysis of Deviance models of the generalized linear model (GLM) based on minimum relative humidity (Mrh) explaining the variation in the biomass per dm² of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. *LR Chisq* = Person's Chi-squared value for a Gamma family distribution; *mrh* = minimum of relative humidity; *Df* = degree of freedom; *p-value* = level of significance. *R*² = 0.67.

Variables	<i>LR Chisq</i>	<i>Df</i>	<i>p-value</i>
Mrh	25.8	1	p<0.001
Mrh ²	27.9	1	p<0.001
Substrate	66.4	5	p<0.001
Canopy cover	3.4	1	p>0.05
Canopy height	4.1	1	p>0.05

Appendix T 3. Analysis of Deviance models of the generalized linear model (GLM) based on temperature explaining the variation in the biomass per dm² of the bryophyte and lichen layer on different substrates along an elevational gradient on Baru Volcano, Panama. *LR Chisq* = Person's Chi-squared value for a Gamma family distribution; *Temperature* = mean of temperature; *Df* = degree of freedom; *p-value* = level of significance. $R^2 = 0.70$.

Variables	<i>LR Chisq</i>	<i>Df</i>	<i>p-value</i>
Temperature	37.5	1	p<0.001
Temperature ²	41.9	1	p<0.001
Substrate	66.0	5	p<0.001
Canopy cover	0.05	1	p>0.05
Canopy height	0.871	1	p>0.05

Appendix T 4. Pair comparisons of the variation of bryophyte species composition among elevations using the Jaccard dissimilarity (β -diversity) along an elevational gradient on Baru volcano, Panama.

	1900	2100	2300	2500	2700	2900	3100	3300
1900	-	0.5	0.7	0.7	0.8	0.9	0.9	0.9
2100		-	0.6	0.8	0.9	0.9	0.9	0.9
2300			-	0.8	0.9	1.0	1.0	0.9
2500				-	0.7	0.8	0.8	0.8
2700					-	0.6	0.5	0.6
2900						-	0.4	0.5
3100							-	0.5
3300								-

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