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Realised edaphic niche and specialisation of the fern genus *Polybotrya*

Ecology and Evolutionary Biology / Faculty of Science
Master's thesis

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27.01.2025
Turku

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Subject: Ecology and Evolutionary Biology
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Title: Realised edaphic niche and specialisation of the fern genus ***Polybotrya***
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Number of pages: xx pages
Date: 10.12.2024

Abstract:

Understanding species distribution is anchored in ecology as it sheds light on the conditions in which a species occurs. Providing well-defined species ecological niches ensures spotting indicator species and rapid environmental conditions characterisation and grants knowledge on evolutionary mechanisms and diversity patterns. This study aims to delineate the ecological niche of some species of the fern genus ***Polybotrya*** fully nested in the Neotropics. From Costa Rica to the East Atlantic Brazilian Forest, species abundance was recorded, and the edaphic condition was measured to produce their response curves along the nutrient gradient. Species responses were diverse; some appeared specific to the poor edaphic condition, while others harboured more generalist behaviour. This study raises some potential indicator species for soil conditions as well as an insight into the evolutionary history of this genus. Its results are anchored in understanding the Neotropics' diversity patterns and geological and climatic history.

Keywords: Ecology, botany, Pteridophyta, fern, ecological niche, species distribution, soil composition, HOF modelling, evolutionary history, soil map, floristic analysis, realised niche, species optima, species tolerance, Neotropics.

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1 Introduction

Tropics include an extensive diversity of ecosystems, including rainforests, savannas, and coral reefs, each harbouring an extraordinary species richness (Hawkins et al. 2003). However, tropical rainforests stand out among them, leading with the highest species numbers of vertebrates and vascular plants. (Pillay et al. 2022; Sabatini et al. 2022)The major hotspot of biodiversity on earth is the American tropics (which group South and Central America). These regions have an astonishing diversity of vascular plant species, with up to several hundred species of trees per hectare. (Thomas 1999; Francis and Currie 2003; Antonelli 2011). Estimating the diversity of the American tropics supports the idea that they could contain up to 90,000 vascular plant species, with a highly threatened spot of endemic plant species of 20,000 in the tropical Andes identified by Myers. (Myers et al. 2000). Neotropic vascular plant diversity results from tens of millions of years of evolution. (Lundberg et al. 1998). The diversity of biomes, geological context, and interspecific interactions shapes the current high biodiversity.

Throughout history, ecologists have hypothesised several ideas on the underlying drivers that lead Amazonia to host more than 10% of the earth's diversity on less than 1% of the earth's surface. Numerous of them stem from climatic variations. Global biodiversity patterns exhibit that stable climates such as the tropics foster higher species richness. It was suggested that the metabolic energy available in an environment is finite, limiting the coexisting species. (Klopfer 1959; Hutchinson 1959; Brown 1984) Moreover, it implies a consistent correlation between species richness and climatic or ecological drivers. Few studies inferred that this diversity is possible thanks to the specialisation of resource uses. (Bazzaz and Catovsky 2001; Wiens 2011). Vascular plants such as ferns rely extensively on light, water, and soil nutrient resources, as they need those to photosynthesise solar energy into metabolic energy. Consequently, more species in a resource-finite environment involve stronger competition. How can species from tropical ecosystems, especially the extensively rich Amazonia, cope with such intensive competition?

Studying and understanding the ecological niche framework in this area might provide some answers. It has been proposed that in environments with a high density of species, such as the Neotropics, the specialisation of species and their use of resources must also be highly diverse. This diversity arises as species are pushed to adopt different strategies for survival and resource use by evolutionary pressure (i.e. competition). Some species might evolve as generalists, capable of thriving in various conditions and utilising various resources, while others might become specialists, highly adapted to narrow ecological niches. In both scenarios, species behaviour contributes to the ecosystem's global diversity and ensures species' sustainability while avoiding competition. While the evolutionary processes, such as selection and competition, that contribute to the partitioning of resources are relatively well understood in theory, the specific mechanisms driving the current species distribution remain less clear. Studying species niches, traits evolution and interactions with other species can help clarify species distribution and understand the processes that lead to species behaviours and ecosystemic resource partition (Pagani-Núñez et al. 2022).

1.1 Ecological niche theory

In what condition does a species occur? The ecological niche theory answers part of this long-lasting question in ecology. The ecological niche of an organism represents the specific requirements within an ecosystem for its survival and development. During the end of the XIX and beginning of the XX century, several scientists first defined it as the position, habitat, and requirements of species to grow (Packard; Grinnell). This notion was further refined later by Elton and Grinnell (1927;1928) as the function of one species within a community and the interactions or relations with other species. Its definition includes ecosystem and species dynamics and the potential plastic behaviour of the studied species regarding these dynamics.

While this polarised the ecological niche concept to a more functional ecology definition, Grinnell tried to focus on the physical (habitat) space where a species will thrive. By the middle of the XXth century, Hutchinson introduced the current niche theory definition: the n-dimensional hypervolume, which represents the theoretical space where each dimension is an environmental gradient or ecosystemic interaction conditioning the species' occurrence. Each axis weight in the final hypervolume depends on the species' requirement to establish, thrive, and survive.

The shape of this hypervolume is linked with the physiology of a species (phenotypes). Across this hypervolume, it is expected that the species response is not uniform. Metabolism relies on diverse energy sources and substrates to be pursued. Consequently, species occurrence variation (abundance, cover, growth rate, etc.) depends on the cost-effectiveness of the physiological reactions in specific conditions. For example, for primary producers such as ferns, edaphic conditions and the availability of some specific cation in the ground conditions species' efficiency (Zuquim et al. 2012). The physiological reactions do not necessarily follow a linear response and usually present an optimum, where the phenotype and its associated physiology reach their maximum. Mathematically speaking, this variation can be seen as an unimodal response curve, where the maximum is the optimum value across one environmental gradient. This reaction can show a bell-shaped curve or not. The farther the conditions are from the optimum, the less probable the species will occur or survive in this environment. The threshold of the ecological niche is reached when the outcome of the species occurrence is null.

When looking at a species in different environmental conditions, the observed performance (seen as abundance, presence or productivity) of one individual to another might change a lot. Many environmental variables can affect an individual's productivity (n-dimension). This is even more tangible when one looks at the plants. As they live fixed, these organisms must cope with different environmental factors to ensure their survival and reproduction (i.e., nutrient uptake in poor soil and photosynthesis in fully shaded areas). All these processes have an optimum according to the organism's phenotype, and by compiling the different variables, species' response to the environment can be mathematically modelled as curves again that are more or less skewed and have different weights. Consequently, there is a (or several) theoretical point(s)in the n-dimension space of the affecting environmental variable where the conditions are reaching a maximum(s): This is the species optima. (Franklin et al. 2016). The other parts of the n-dimensional space can be seen as the species' tolerance range, where the species can occur and survive but with lower productivity. As n-dimensional space is not easy to visualise, ecologists can simplify it as a 2-dimensional space where the x-axis represents an n-gradient and the y-axis species response (Figure 1).

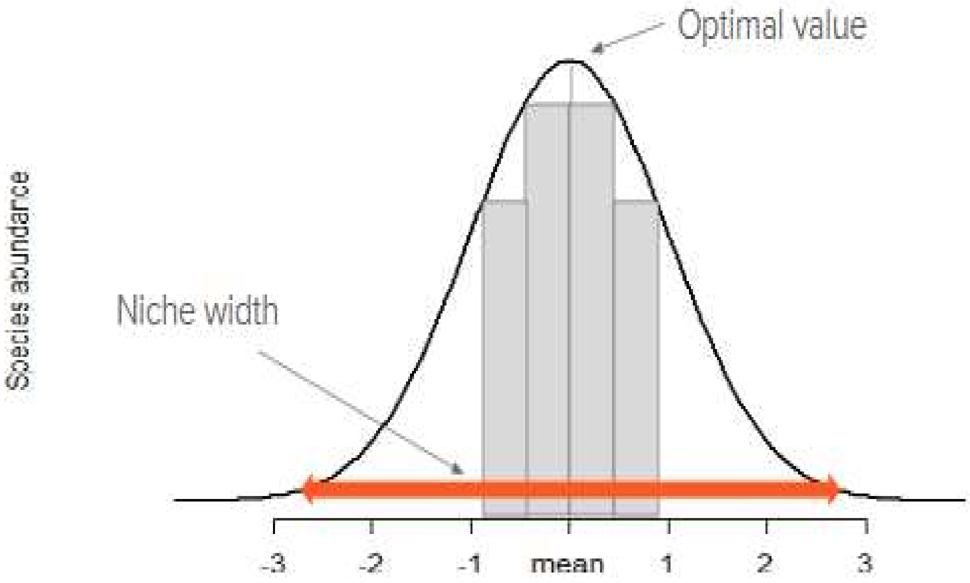


Figure 1: Species response curve across an environmental gradient (here, following a symmetric Gaussian curve). The red arrow covers the niche width (or tolerance range). The maximum of the species response is obtained where abundance reaches its maximum (here, the mean value).

As mentioned earlier, the optimum along one gradient is closely linked with the physiology, functional traits, and the associated genetic background of the organism. Consequently, ecological niches can also be defined at different scales (population or species). The species' optimum is when the sum of individuals’ abundance across environmental variables reaches a maximum, and the species' ecological niche is at every point of the gradient where this sum is not null. The species response curve to an environmental gradient is closely related to the evolutionary history and genetics of the species as they may have acquired functional traits, optimising those physiological processes, increasing the tolerance range or even skewing the species' specialisation toward a part of the gradient. Consequently, the optimum value or the width of the ecological niche from species to one another or from one population to another can be different and enable them to thrive in a distinct physical, ecological space and environment (i.e. ferns across an elevation gradient in South America. (Salazar et al. 2015; Hernandez-Rojas 2018).

Ecological niches are multidimensional spaces driven by different factors (Whittaker 1965; Polechová 2019). The ecological niche can be divided into two aspects. The fundamental niche primarily considers environmental conditions—such as soil nutrients (Hulshof and Spasojevic 2020). However, this niche definition remains incomplete; in a complex ecosystem where species interactions are omnipresent, including those to understand their realised distribution is relevant. The Realised niche emerges, compiling abiotic and biotic aspects, such as competition, predation, and facilitation (Hutchinson 1959). The realised niche subset of the fundamental niche across diverse environmental gradients and ecosystems, as different interactions might reduce it. While the fundamental ecological niche aims to include all the potential habitats for a species, the realised niche does not include environments with favourable conditions that the species cannot reach or where the adverse factors exclude it (General theory).

Several aspects and the realised ecological niche must be included to determine a species' distribution precisely. First, it can be refined by including the species' propagule dispersal limitation (Moore and Elmendorf 2006; Jones et al. 2006). Historical and geographical barriers or the incapacity to disperse over long distances contribute to the inability to occupy all suitable habitat patches (Dambros et al. 2020). The species' success in suitable habitats must also be considered. Lack of physical space or stochastic events might compromise colonisation and induce a smaller overall distribution than the fundamental niche would predict (Shoemaker et al. 2020). Finally, the species' phenology and potential metapopulation dynamics with long periods of invisible vegetative state, extinction, or population expansion at the local time and space scale might bias the species' distribution compared to the realised ecological niche. (Naujokaitis-Lewis et al. 2013; Franklin et al. 2016; Munoz, Cheptou, and Kjellberg 2007). The following schematic resumes this ecological niche separation in a two-dimensional space (Figure 2).

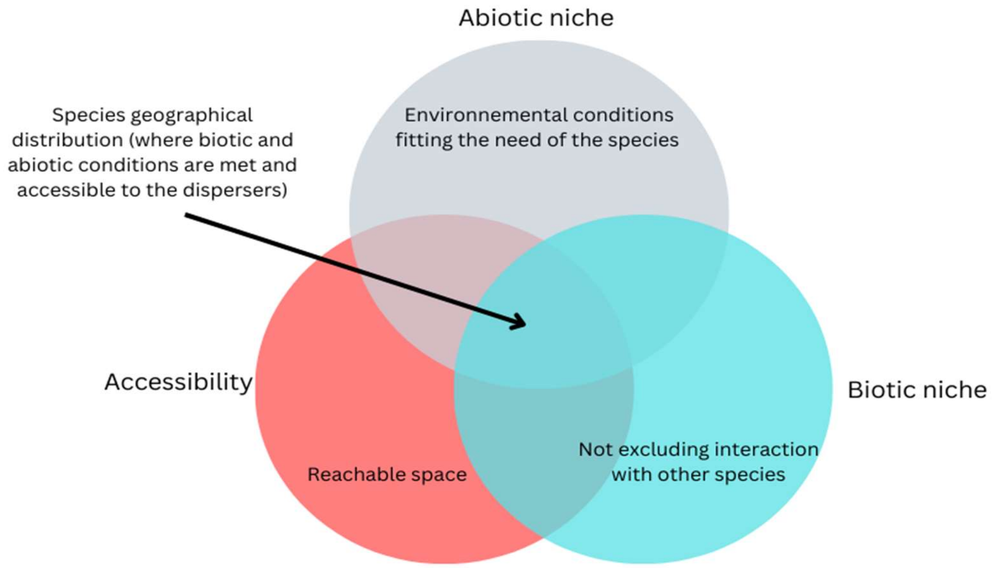


Figure 2: BAM diagram representing the components of the species distribution. The abiotic niche is the fundamental niche, and the union between the abiotic and biotic niche is the realised niche defined by Hutchinson. To complete this notion, accessibility or movement is added to obtain the species' spatial distribution.

Studying the ecological niche helps infer species distribution and understand its relation to its environment, but it also can shed light on its evolutionary history. Application of the ecological niche concept is essential to understanding species distribution patterns, as this theory explains how species are scattered across different habitats and how complex communities are distributed according to abiotic gradients. While it is common understanding that the diversity decreases with increasing latitude (Kessler 2010), Regional and smaller-scale distribution patterns of diversity are more challenging to characterise, especially in complex and highly diverse tropical ecosystems and the Amazonia region (Tuomisto, Poulsen, and Moran 1998; Zuquim et al. 2009; Tuomisto, Zuquim, and Cárdenas 2014; Moulatlet 2024). Focusing on characterising species distribution, forest type, and ecological niche in this part of the world is essential to understanding species diversity and contributing to global knowledge of the ecological and evolutionary processes that contribute to it. (ter Steege et al. 2013; Luize et al. 2024). For example, in Amazonia, different species have evolved to occupy specific ecological niches within the complex web of interactions by acquiring distinct functional traits. (Tilman 1994).

Amazonia encompasses 10% of the global diversity of vascular plants, and studies suggested that 3.500 to 4.000 species of ferns and lycophytes would be nested in the

Neotropics, making this region a biodiversity hotspot for richness and endemism for these groups (Tryon 1986; Tuomisto 1998; Moran 2008). However, this area is so broad that for time and budget constraints or sometimes accessibility matters, scientists had to devise ways to produce reliable ecological data to characterise it. By defining the ecological niche of species with narrow tolerance across a gradient (i.e. specific behaviour) or by understanding the distribution (abundance)-gradient relationship, some species (Indicator species) could be used as a proxy for the biotic and abiotic conditions and enable to state the condition of the environment. Ferns have great potential as indicators species as several studies in Amazonia established that they present a strong correlation between their geographic distribution and their environment (Ruokolainen, Linna, and Tuomisto 1997; Tuomisto, Poulsen, et al. 2003; Tuomisto and Ruokolainen 2006; Nervo et al. 2019; Suissa, Sundue, and Testo 2021; Della 2022). Ferns distribution patterns have been used all over Amazonia at different scales to infer floristic and edaphic patterns (Tuomisto et al. 2003; Zuquim et al. 2012; Ruokolainen et al. 2007; Zuquim et al. 2014; 2023).

More fern indicator species and species-specific knowledge are valuable for enhancing and perfecting our understanding of the ecological processes that shape the Amazonian forest. (Tuomisto et al. 2024). The details of the ecological data of ferns distribution and ecological niche are essential to infer some ecological questions, such as how fast the ecological niche of some species are evolving in high density and highly diverse environments (Niche evolution theory, (Page 2002; Laurance et al. 2011) Or how groups closely related rapidly diversify to be adapted to a specific range of gradients (Adaptive radiation and niche partitioning theory; (Bazzaz and Catovsky 2001; Chao et al. 2024). Going into the details of these processes will help understand how Amazonia became one the most significant biodiversity hotspots of the planet, where species coexist and are specialised to the microhabitat scale. Furthermore, complementary studies on ferns and spotting new indicator species will help to have a more supporting and refined understanding and modelling of the ecological environment to fasten and improve the characterisation of the extensively diverse Amazonian habitats. Moreover, using such indicator species can fasten and reduce the cost of environmental data collection and ecosystem integrity (Tuomisto 1998; Carignan and Villard 2002; Butler et al. 2012; Park, Byeon, and Cheon 2019); while providing accurate range data on the drivers impacting the studied communities.

1.2 Ecological niche modelling

Ecological niche modelling relies on the correlation between a species' observation and the environment in which it is occurring to assess its potential range (Peterson, Papeş, and Soberón 2015; Simoes et al. 2020). Several tools have been developed in ecology to characterise niche and species distribution. We can distinguish two approaches in this field: Correlative species distribution modelling, which relies on the observed distribution as a function of the environment, and Mechanistic species distribution modelling, which relies on the species' physiology to establish the optimal environmental conditions and tolerance. Environmental variables must be extensively examined in both cases, requiring intensive lab and fieldwork. On the other hand, Correlative models are less data-greedy. Even if they cannot untangle the effects of abiotic drivers, biotics drivers and accessibility of some areas, they provide a relatively good approximation of the realised ecological niche (Barve 2014; Peterson, Papeş, and Soberón 2015; Kearney, Wintle, and Porter 2010). For this reason, correlative models have been widely used in several studies of ecological niches to understand global diversity patterns from the spatial distribution of species (Vangansbeke et al. 2021; Sporbert et al. 2020; Dolci and Peruzzi 2022; Moser et al. 2005) and several previous works assessing fern distribution in Neotropics (Tuomisto, Ruokolainen, et al. 2003; Tuomisto, Ruokolainen, and Yli-Halla 2003; Costa 2003; Jones 2013; Moulatlet 2014; 2024). Two data collections are needed to create a reliable ecological niche model based on the correlative methods: response and predictor data.

The response data represents the observation of the species (i.e. abundance, cover estimate across an area). In the case of species counting, comparative studies suggest that abundance data might provide a more accurate characterisation by using Cohen’s kappa, which measures the degree of agreement between observers using different techniques to assess the same phenomenon. Species distribution models trained on presence-absence seem to have a slight fit according to Cohen’s kappa, while these same models trained with abundance data tend to show better performance (Newbold et al. 2012; Howard et al. 2014). Though Cohen’s kappa indices might be strict to interpret, they tend to show that the abundance data is more reliable when modelling species distribution in the case of these two publications. However, abundant data is more complex and time-consuming to collect as it is a more refined observation.

The predictor values correspond to environmental data that can characterise the conditions the organism is living in. Depending on the study organism, these variables will change, as each species has specific requirements regarding its performance. Several gradients can be implied in constructing the realised ecological niche, such as temperature, soil nutrient content, rainfall, etc. Several studies tend to underline the role of edaphic conditions as one of the main drivers of the plant community (Tuomisto and Poulsen 1996; Tuomisto, Poulsen, and Moran 1998; Tuomisto, Poulsen, et al. 2003; Phillips et al. 2003; ter Steege et al. 2013; Jones 2013).

Niche modelling is anchored in ecology as it aims to answer questions about how species are distributed. As part of the Neotropics, Amazonia presents an important diversity of forest types where species are not randomly distributed and, as mentioned earlier, encompasses almost 10% of the global biodiversity. However, this region's environmental characteristics and diversity pattern are poorly identified and understood, and very little exact information is available for the regions. Obvious reasons, such as complex geological and environmental dynamics (i.e., seasonally inundated, permanently waterlogged, high drainage), inaccessibility, and extensive diversity, are delaying its global and local scale comprehension. While distribution theory and their weight in the species observation and niche are still under debate (environmental filtering or stochasticity and propagule limitation), fern distribution has been established to rely consistently on the environmental conditions (Tuomisto and Poulsen 1996; Tuomisto 1998; Tuomisto, Ruokolainen, and Yli-Halla 2003; Tuomisto 2006; Costa, Magnusson, and Luizao 2005; Ruokolainen et al. 2007; Jones 2013; Moulatlet 2014)These two different regimes could be understood under the prism of the propagule limitation, to which ferns are not subject as much as vascular plants. An individual could produce thousands to millions of wind-dispersed spores in its lifetime. (Kramer 1995; Ponce 2021). Meanwhile, edaphic conditions have been established through several studies to shape the species composition of fern communities of neotropics. (Toledo et al. 2012; Zuquim et al. 2014; Araújo et al. 2017)As Pteridophytes can exhibit responses to their soil conditions, it has been hypothesised that partitioning diversity along the edaphic gradient has been one of the mechanisms leading to speciation and spatial coexistence of ferns' high diversity in the Neotropics. (Tuomisto, Zuquim, and Cárdenas 2014; Zuquim et al. 2014; Moulatlet 2024).

Ferns have been ecologically modelled to test this idea, establish their distribution, and understand the species richness distribution across the environmental gradient. (Zuquim et al. 2012, 200; Tuomisto et al. 2024)Concurrently, these studies established indicator species that are extensively specific to environmental conditions and valuable for easing and speeding up the assessment of habitat conditions. With their astonishing diversity, Ferns in the American tropics are worth studying.

1.3 Niche & evolution

While niche models offer a framework to understand present-day diversity patterns, they also serve as valuable tools for exploring the historical processes that shaped biodiversity. By integrating niche models with evolutionary theories such as niche conservatism and niche partitioning, scientists can trace the emergence and diversification of species within a region (Soberon and Peterson 2005; Holt 2009; Losos 2008; Wiens 2010; Peterson 2011). How do Neotropics, and especially the Amazonia region, encompass such diversity? This long-standing question is rooted in two alternative main hypotheses: sympatric or allopatric speciation. While the first one consists of the speciation process occurring within the same population, allopatric speciation is due to the geographical separation of two populations. Research in the hyper-diverse American tropics has aimed to untangle its intricate evolutionary history while understanding the ecological processes driving this extensive richness (Simpson and Haffer 1978; Haffer 2008; Lehtonen et al. 2021)Functional trait data, such as edaphic specialisation and paleoclimate information, can often reconstruct colonisation histories in time and space, linking diversification events to key environmental or geological changes (Gentry 1988; Pennington, Lavin, and Oliveira-Filho 2009; Hoorn et al. 2010). Understanding the evolutionary trajectories of specific clades thus contributes significantly to our comprehension of the global biodiversity patterns shaping species distributions today(Toledo et al. 2012; Lehtonen 2021).

Amazonian paleoclimatic conditions are quite under-studied. Some known significant events, such as the uplift of the Andes, the formation of the drainage basin and the aridification of East Brazil, are key events that significantly impacted the speciation in Amazonian (Hoorn et al. 2010; Antonelli 2011; 2021). With an abundant number of edaphic specialist trees (ter Steege et al. 2013) and understory vascular plants (Tuomisto and Poulsen 1996; Tuomisto 2006; Ruokolainen et al. 2007), Amazonia provides an extensive amount of potential vascular plants study organism. To some extent, looking at ecological and phylogenetic data is necessary to understand the biogeographical patterns underlying one species' distribution fully. Investigating the link between phylogenetic history and the evolution of functional traits is essential to understanding the ecological processes that led to the current state and infer the outcoming events. While studies on the phylogeny along these environmental gradients are pretty sparse, signals of such specialisation can be investigated to glimpse the evolution of habitat specialisation (Lehtonen et al. 2015). Ferns have shown a relatively strong correlation to soil conditions, and the edaphic niche can be seen as a continuous trait. Knowing the geological complex history of Amazonia (Kubitzki 1989) and sampling different signals from different life groups, the complex diversification history of the Neotropics can be elucidated.

Ecological niche characterisation primarily expands our tools to status on assessing environmental data and habitats. Identifying extensively specific species with a small tolerance range enables us to infer environmental drivers acting in ecosystems without extensive field or laboratory work based on these indicator species' presence or abundance. These species can be extensively relevant to characterise soil compositions, such as soil nutrient concentration. (Hulshof and Spasojevic 2020). Finally, determining ecological niches has several other outcomes in diverse biological fields. Under climate change and biodiversity loss, conservation in biology has been of growing interest. (Mendenhall, Daily, and Ehrlich 2012; Cardinale et al. 2012)Ecological niche modelling can more effectively characterise the potential habitats of endangered species, enabling the establishment of conservation policies and endangered status. (Wiens 2011; Zhu et al. 2013)Using long-term environmental data, we can recreate the distribution map and predict how this distribution will be affected in diverse future scenarios. These are key to preserving ecosystem architects' species and reducing biodiversity loss.

1.4 The *Polybotrya* fern genus

The *Polybotrya* genus is found exclusively in neotropical regions and belongs to the Dryopteridaceae family. Most species within this genus are root climbers capable of scaling trees while maintaining connectivity to the forest floor, although some remain fully terrestrial. This morphological diversity and local ecological significance render the genus noteworthy. (Canestraro and Labiak 2018). With a well-resolved taxonomy and a relatively abundant and widespread genus across the American tropics, implying sufficient ecological data, the genus is a potential candidate for investigating edaphic specialisation and evolution insight into the history of the American tropics.

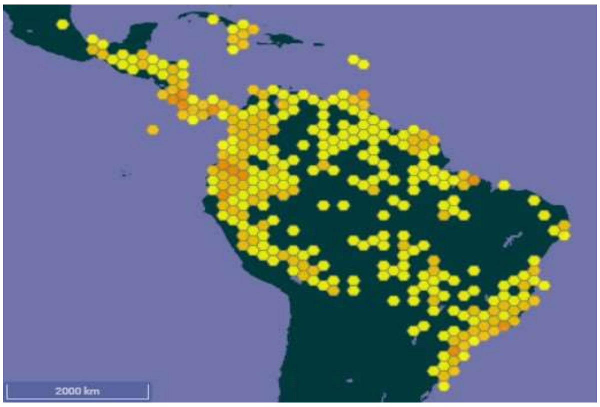


Figure 3: Distribution of the ***Polybotrya*** genus across South and Central America. Data was extracted from the GIBF database, with an overall of 2.888 georeferenced (extracted on 17th of March 2024)

Tuomisto published a previous study on the ecological soil specialisation of the *Polybotrya* genus (Tuomisto 2006). It included north-western Amazonian basin transects and focused on seven species of *Polybotrya*. The optimum for the species along the soil gradient was calculated using the weighted abundance mean of each quantitative soil variable across this study. Tuomisto established that some *Polybotrya* species show a rather specific distribution across soil characteristics (cations concentration, soil texture and inundation), which implies that the soil characteristics (such as Sum of base, drainage, soil texture) could specifically define the ecological niche of these species. It was shown showed that species from the *Polybotrya* genus present bias distribution across the edaphic gradient, with species presenting preferences for poorer soil (i.e. *P. sessilisora* or *P.glandulosa*), while some other species of this group showed more generalist behaviour (Tuomisto and Poulsen 1996; Tuomisto, Ruokolainen, and Yli-Halla 2003; Tuomisto 2006).

The Polybotroids class phylogeny has been untangled with previous work aligned with understanding the diversity (Moran, Labiak, and Ree 2015). By sequencing four different plastid DNA markers, the study could infer, with maximum likelihood and Bayesian inference methods, the phylogeny of this group (Moran, Labiak, and Ree 2015; Canestraro and Labiak 2018)This study has then been updated, and the time-calibrated phylogeny is now open-access to “the Constantly updated Ferns Tree of Life” (https://fernphy.github.io/) thanks to the research of the FTOL working group (2022).In this study, this phylogeny, along with the species distribution extracted from the KEW plant of the World website, will be used to infer the diversification of the clade (POWO 2025).

New data from ***Polybotrya*** species from Panama, the Brazilian Atlantic rainforest, Costa Rica and the Amazon basin have been collected since the previous publication on the genus (Tuomisto 2006). Meanwhile, a complete phylogeny of the clade has been published, enabling further analysis of this genus's ecological niche and diversification history. Across the different expeditions, eleven species' abundance data was collected among the different Neotropics' study sites. From the current data over the Neotropics, one species has been observed in several geographical areas: *Polybotrya osmundacea* Humb. & Bonpl. ex Willd (Amazonian basin & Mesoamerica). While the six species that have been reported from the Amazonian basin transects are *Polybotrya caudata* Kunze, *Polybotrya crassirhizoma* Lellinger, *Polybotrya fractiserialis* (Baker) J.Sm., *Polybotrya glandulosa* Kuhn., *Polybotrya pubens* Mart., and *Polybotrya sessilisora* R.C.Moran. Finally, three species were reported from the East Atlantic Coast of Brazil: *Polybotrya cylindrica* Kaulf., *Polybotrya semipinnata* Fée, and *Polybotrya tomentosa (speciosa)* Brade.
Numerous taxonomists consider *Polybotrya caudata* and *Polybotrya villosula* synonymous, but Panama, Costa Rica, and Amazonia descriptors suggest they are different species. In the University of Turku's herbarium, they are considered separate. Consequently, this study will consider this distinction and consider them separate species.

Figure 4: Pictures of some of the ***Polybotrya*** species from the East Atlantic Forest: A. Polybotrya semipinnata Fée, sterile and fertile leaves; B.Polybotrya tomentosa, Brade, sterile and fertile leaves; C. Polybotrya cylindrica Kaulf., sterile and fertile leaves (Canestraro and Labiak 2018).

This research will utilise floristic and edaphic data gathered from diverse expeditions across the American tropics to characterise the specific soil requirements of *Polybotrya*. These datasets will be used to determine the soil optima and tolerances for 10 species reported across the study transects. By linking their ecological specialisation (Weighted average analysis results), lineage and current spatial distribution, this study will try to shed light on their evolutionary trajectory and potential diversification pattern. Furthermore, for the species with sufficient data, a model of their response curves along the edaphic gradient will be performed and used to map their potential realised edaphic niche across the Amazonian basin.

2 Materials and Methods

2.1 Fieldwork: Data collection

The data used in this study compiled different expeditions realised for various research projects between the 1990s and 2010s, including both soil and floristic data from several study sites across South America. The persons responsible for data collecting were for Costa Rica and Panama: Mirkka Jones, the Amazonia: Hanna Tuomisto, Mark Higgins, Anders Sirén, Patrick Weigelt and Glenda Cárdenas, and Coastal Brazil: Samuli Lehtonen and Maarten Christenhusz.

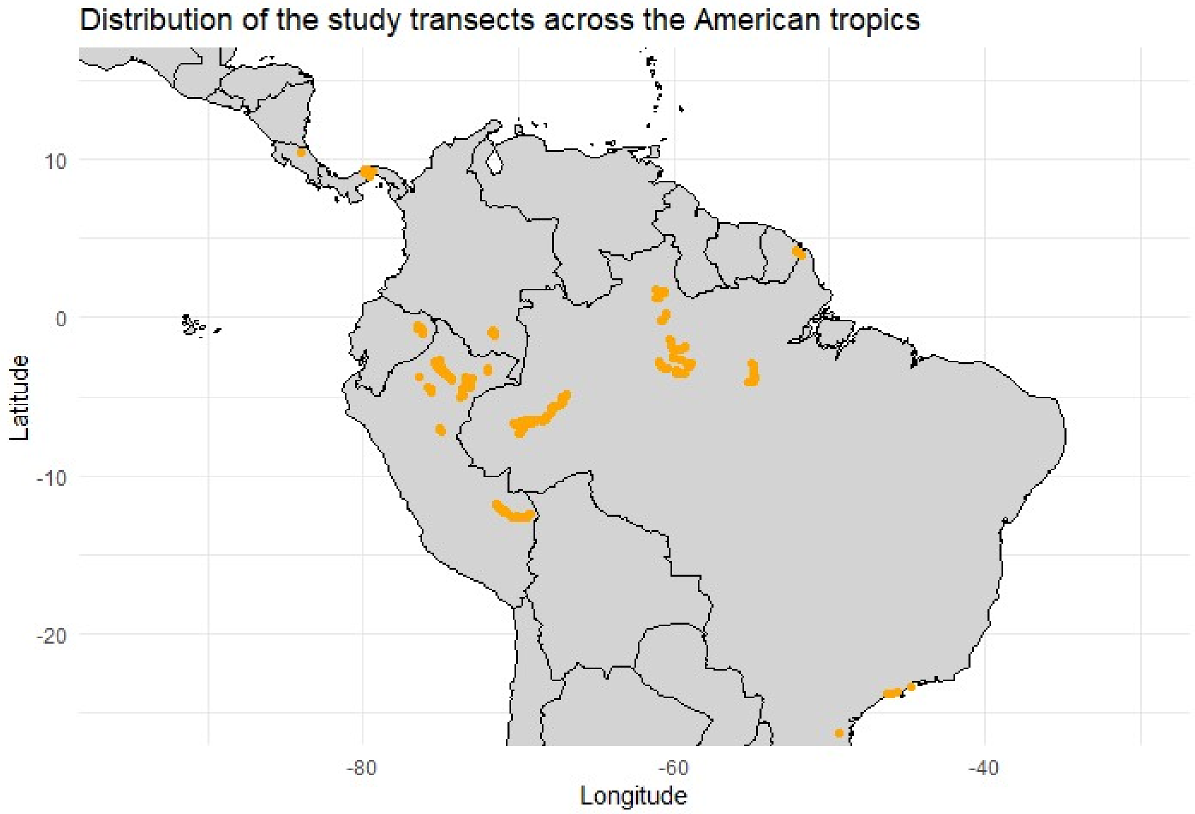


Figure 5: Distribution of the study transect (abundance or absence data available) across the American tropics (orange dots). These transects are the ones used in the following analysis and fitting the transect selection (complete soil data, 0-30cm deep core sampling and abundance data (number of individuals per transect).

Amazon Basin Data

Amazonian basin transects have various lengths, from several expeditions from the 1990s until the 2010s aiming for different goals. For floristic data collection, transects were 5 meters wide, and their length would mostly be 500 meters. Researchers picked transect starting points and directions based on satellite imagery. Specimens reported had over 10 cm long leaves and were not higher than 2 m from the ground. All ferns, when possible, were identified at the species level. For a 500-meter-long transect, three composite soil samples were assembled to represent the transect's topographic variation. When the transect was hilly, two samples were generally taken on hilltops and one in a valley. Each composite sample consisted of five subsamples collected within a few meters of each other and merged to obtain a soil value for each location. Soil samples were taken from the top of the mineral soil (after removal of the leaf litter layer) to a depth of 5 or 10 cm. After being dried and sieved, the soil samples were analysed according to basic soil geological methods described in detail by Suominen et al., 2013 and referred to the Van Reeuwijk protocol published in 1993.

Brazilian East Coast Data

East Brazilian coastal plots were originally sampled to document which fern species grow together with *Danaea* or *Lindsaea* species. The sample unit was a circle of 100 square meters centred on the focal species, and abundance data were recorded for all encountered ferns. One composite soil sample was collected per plot. In total, 19 plots were sampled. Soil samples were analysed using the same protocol as the Amazonian transects.

Costa Rica Data

The Costa Rican data was collected across 5 km2 of old-growth rainforest at La Selva Biological Station of the Organization for Tropical Studies (OTS). A grid covering the whole area was arranged by 100 * 50 meters, and at each crossing, a permanent sampling plot of 100 m^2 was sampled. In 2001 and 2002, fern prospection was conducted along three transects of different lengths (1750 m, 1940 m and 2150 m) and 5-meter wide. The long-term soil monitoring in the area provides the soil chemical dataset. For each plot of the La Selva grid occurring within the transect, a composite soil sample (8–10 pooled subsamples) was analysed according to König & Fortmann (1996). Each subsample was taken to a depth of 10 cm and was collected within a 1-m radius of the grid post.

Panama Data

Panama data was collected in tropical forests around the Panama Canal over 3000 km². All the sites were under 300 metres in elevation. The abundance data for pteridophytes was surveyed between January and November 2008. Each plot was composed of two parallel transects 100 m long and 5 m wide, resulting in a sample area of 0.1 ha. The separation of the two transects in each plot was usually 35 m. All individuals (or ramets, in clonal species) with green fronds bigger than 10 cm and growing within 2 m of the ground were recorded, including low-trunk epiphytes and climbers. Soil samples are 10 cm deep and were taken after removing the leaf litter layer to expose the soil surface. Spacing between samples was at least 5 m and usually above 10 m. Twenty cores from the highest and 20 from the lowest areas were pooled together, resulting in two soil samples per plot. The soil nutrient analysis was performed at the STRI soil laboratory.

As established, these expeditions provide soil and floristic data for each transect in the different locations, though they all presented different data formats. Each transect or plot used in this study is treated as a sampling unit. As a means of standardisation, abundance was calculated for a defined surface of 2500m² (5*500 meters in most cases) for every transect present in Amazonia, Panama and Costa Rica, as these countries share some species. For Amazonian transects longer than the standardised length, a subunit of 500 meters was artificially made, and the sum of individuals present in this subunit was calculated to obtain the subunit abundance. The soil nutrient content was not available for each subunit. Consequently, the soil characteristic was average per transect and then attributed to each subunit of the transect (if the length was higher than 500). The same treatment was applied to Costa Rican data. The 500-meter-long subunit was disjointed for each transect and treated as a new sample unit. The sum of the individuals across the subunit was calculated. As the soil data was available for every 50 meters along the transect, it was possible to reconstruct each subunit's average soil value. In both cases, when the last subunit was not equal to 500 meters long, they were taken out of the analysis as a means of standardisation. For Panama, which has an abundance of 1000 m² (200*5), a theoretical abundance of 2500m² was calculated by multiplying the observed abundance by 2.5. Finally, as the species from the East Atlantic Forest are not occurring anywhere else and the sampling protocol was quite different, the abundance was kept to the initial condition (for 100m²).

Soil sample variables measured are the calcium (Ca), potassium (K), magnesium (Mg), and aluminium (Al) contents as mg/kg or cmol(+)/kg (or equivalent) and pH values. Before any analysis, the soil data in mg/kg were converted to cmol(+)/kg by being divided by their molar mass with three decimals. They multiplied their charge (applied for Ca2+, K+, and Mg2+ respectively 40.078, 39.098 and 24.305) before being multiplied by 100 (mol to cmol)); see the following equation.

$$n(cmol(+)/kg) = m(g/kg)/M(g/mol) * 100Nc \tag{1}$$

n the quantity of mole in centimoles,
m the observed weight in grammes,
M the molar masse of the element,
Moreover, Nc is the number of charges for this element.

The exchangeable base cation sum was calculated as the Ca, K and Mg sum. Soil nutrient values were then log-transformed under a base of 10. Even if other ion concentrations or soil characteristics were available for some transects (I.e. Sodium (Na) or Manganese (Ma) available for Panama), these actions were not taken in the analysis in a mean of avoiding the difference induced by the data availability and not ecological characteristic of the species. The soil chemical property dataset also extracted pH and Aluminium (converted in cmol(+)/kg and log-transformed). Any transects with missing values for the soil measurements were removed to avoid aberration, even if the other soil components were measured. The final dataset compiles 490 sample units from Amazonia, Costa Rica, Panama and Mata Atlantica forests. A principal component analysis (PCA) was performed with the soil cations (Ca, K, and Mg) and the soil's pH and Al content to represent the soil variability available for this study.

2.2 Ecological analysis

2.2.1 Weighted averaging calibration (WA)

The weighted averaging (WA) analysis estimates the species optimum along an environmental gradient. When applying WA analysis based on species abundance, each environmental value at a site is weighted by the number of individuals observed. This means that sites with higher abundance contribute more heavily to the averaged ecological value and the niche. The environmental value average is calculated and interpreted as the species' optimum value (Equation 2). The species' tolerance is seen as the variance of the weighted environmental values (Equation 3). This indicates how the weighted values are distributed around the optimum of one species.

$$\frac{(S1 \cdot NumInd(1) + S2 \cdot NumInd(2) + \cdots + Sn \cdot NumInd(n))}{Totalnumberofindividuals} = Optima \tag{2}$$

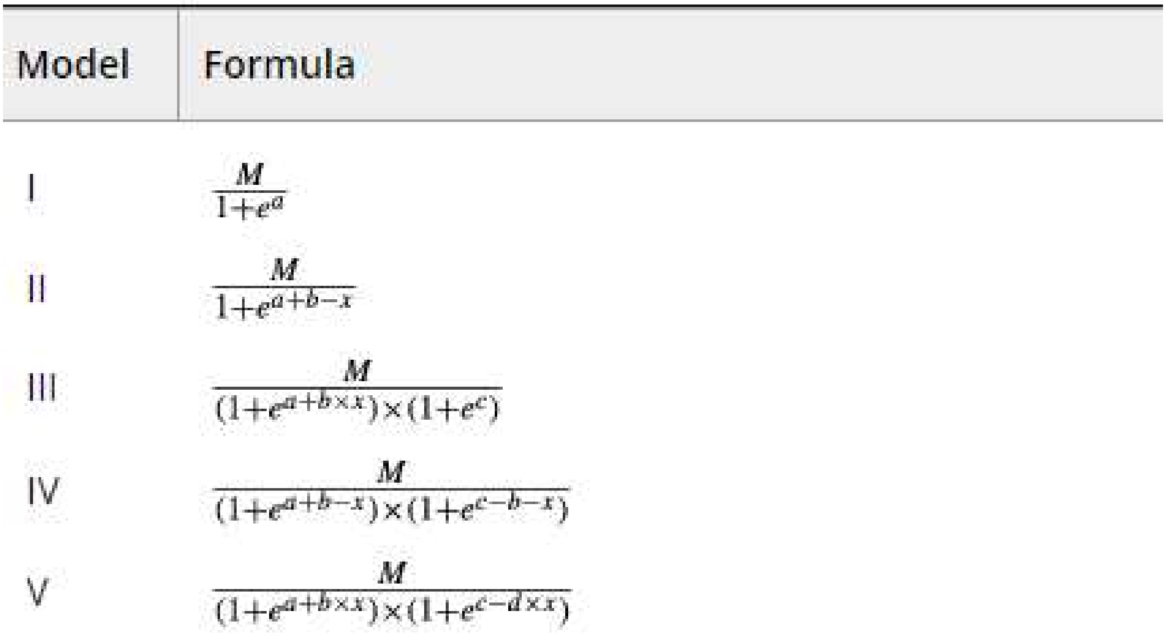
$$\frac{\left(S1 \cdot (NumInd(1) - A \qquad)^2 + \cdots + Sn \cdot (NumInd(n) - AveInd)^2\right)}{Totalnumberofindividuals} = Tolerance \tag{3}$$

Equations 2 & 3:

- *S(n)* represents the environmental characteristic (soil nutrient, etc.),
- *NumInd(n)* represent the number of individuals for the location n,
- *AveInd* corresponds to the mean number of individuals observed per location.

2.2.2 Huisman-Olff-Fresco (HOF) modelling

Huisman-Olff-Fresco models (HOF, (Huisman et al., 1993)) were introduced in the late 20th century as Hierarchical logistic regression models, offering an effective tool for univariate species response modelling. Mainly used with climatic and soil data, this modelling method has been proven to perform better than other methods, such as generalised linear models (GLM) or beta functions. (Oksanen et al., 2002; Lawesson et al., 2003)HOF models compile the abundance data distribution across the environmental variable, fit one of the five ecological responses models, and select the most recurrent models and parameters according to the observed distribution: I) flat, II) monotone, III) plateau, IV) unimodal symmetric, and V) unimodal skewed (Figures 6 & 7).



Model	Formula
I	$\frac{M}{1+e^{a}}$
II	$\frac{M}{1+e^{a+b-x}}$
III	$\frac{M}{(1+e^{a+b\times x})\times(1+e^{c})}$
IV	$\frac{M}{(1+e^{a+b-x})\times(1+e^{c-b-x})}$
V	$\frac{M}{(1+e^{a+b\times x})\times(1+e^{c-d\times x})}$

Figure 6: Equation behind the five ecological meaningful models of Huisman-Olff-Fresco (HOF). In these equations, x is the variable modelling the species response, M is the maximum value (in case of abundance, the highest abundance observed), and a, b, c and d, are parameters to be estimated (Extracted from the publication of (Jansen et al., 2013)).

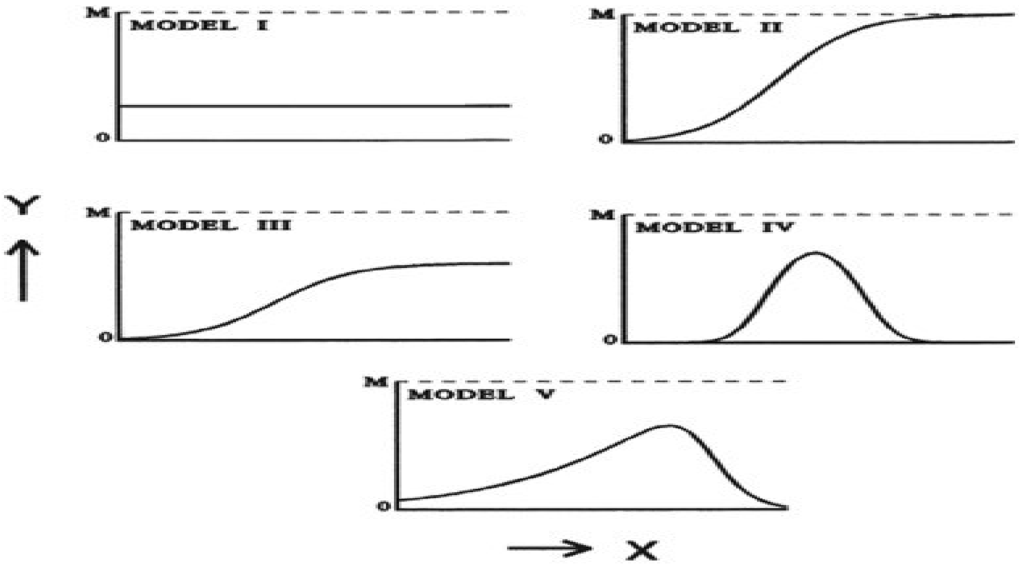


Figure 7: Model response curves for y the response variable and x the explanatory variable according to the different HOF models chosen. Model 1 shows a non-significant trend, Model 2 infers an increasing or decreasing trend reaching the maximum M, Model 3 infers an increasing or decreasing trend but not reaching the maximum M, and Model 4 infers a symmetrical response curve with the same increase and decreasing rate (~Gaussian response), and Model 5 infer on a skewed response curve implying increasing and decreasing rate different.

Extended Huisman-Olff-Fresco models (eHOF) also include bimodal symmetric and skewed response curves (respectively, model VI and VII). These models present two optima. These models are more complex as they involve another equation type (Equation 4):

$$y = M\frac{1}{1+e^{a+bx+cx^2}} \text{ where } c > 0. \tag{4}$$

eHof modelling is a strong ecological tool for analysing ecological data for several reasons. 1. Assess the skewness of ecological data underlining the distributional characteristics of the data (for example, if a bias is present), which may impact the statistical model choices. 2. Provide various curves of attributes (by determining the different parameters (a, b, c or d) that can be derived from the data and be valuable for further analyses and ecological distributions. 3. Analyse niche widths of species along environmental gradients, aka the tolerance of one species, shedding light on how species respond to changes in environmental conditions (not necessarily with a bell-shaped response curve). 4. It can be bootstrapped, improving the reliability of model choices and parameter value, particularly in situations with unbalanced samples or rare species. 5. Include bimodal regression shapes, which allow a more accurate representation of the species' responses.

However, this study doesn’t consider models VI and VII as they would be challenging to interpret. Indeed, capturing a bimodal response would be most useful when studying several gradients. Given the available data (only soil-based cations), assessing the inference of other environmental conditions would be tricky.

In this study, HOF models were performed to obtain an expected abundance across the soil exchangeable base cations (Marked as Sum of bases or nutrient) content using the abundance data and the log-transformed soil base cations concentration. Using the eHOF package on R (Jansen & Oksanen 2013), these models were selected based on the corrected Akaike Information Criterion (AICc). A bootstrap approach (of 999 permutations) was used to ensure the model's performance and the best estimations of the model parameters. Species with less than 10 transect occurrences (*Polybotrya glandulosa* (8 transects)*, Polybotrya cylindrica* (4 transects)*, Polybotrya semmipinnata* (2 transects) and *Polybotrya tomentosa* (1 transect)) had to be excluded from the HOF modelling. Models used the Poisson family functions (some of Panama's transect abundance values had to be rounded as the original values were transformed to a density per 2.500 m^2.)

2.2.3 Realised edaphic niche spatial distribution

Based on the HOF models inflexion points and the occurrence data from the species occurring in Amazonia, maps predicting the highest density of occurrence within the Amazonian Basin were produced for the following species: *Polybotrya caudata*, *Polybotrya crassirhizoma, Polybotrya osmundacea, Polybotrya pubens, Polybotrya fractiserialis* and *Polybotrya sessilisora.* These maps were made by extracting the inflexion point of the species

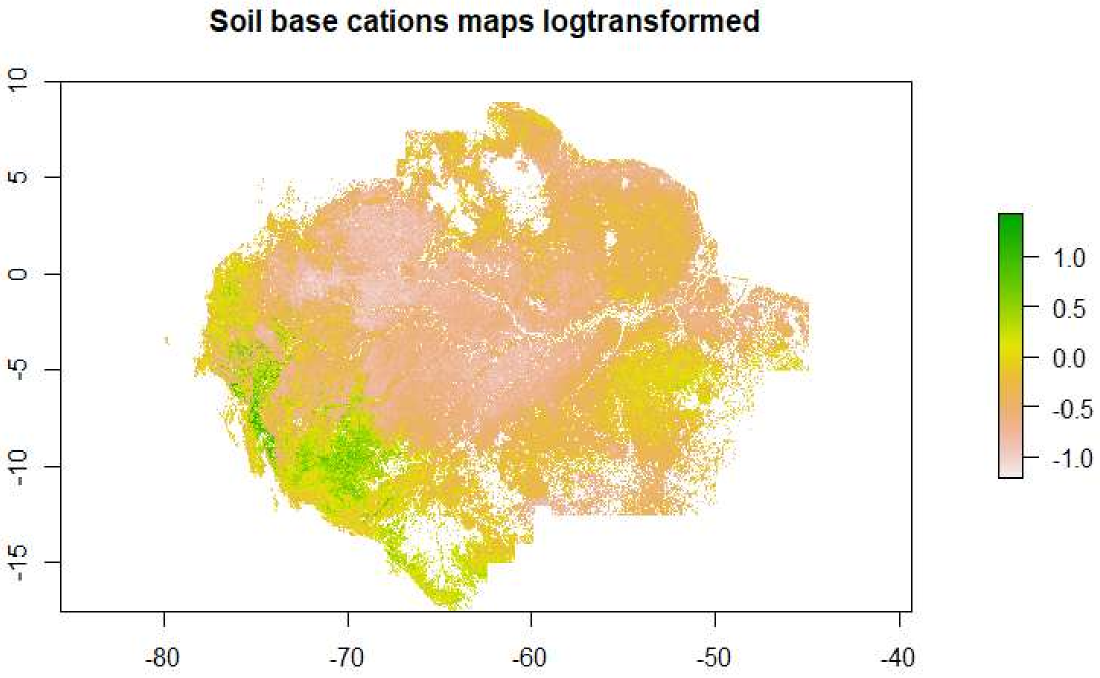


Figure 8: Log10-transformed base cation (sum of Mg, Ca, and K elements) in cmol(+)/kg modelled with environmental data and indicator species. This soil map of Amazonia was extracted from the publication of Zuquim 2023 and the Fairdata database.

responses modelled by HOF and then colour the pixel between their value on the Soil base cations map produced and published by G. Zuquim (*Zuquim et al., 2023; Figure 7*).

2.2.4 Lineage exploration

Lineage exploration will infer the potential evolution history of the genus; this study will rely on the data from the online publication A Constantly Updated Fern Tree of Life research group. From this website (https://fernphy.github.io/), a phylogenetic tree of species from the ***Polybotrya*** genus was isolated and extracted using Phytools package on R. Among those species, ten occur in the dataset and would be looked upon regarding their edaphic condition specialisation established through the ecological analysis of this study. Some divergence and patterns of diversification will be hypothesised regarding the species' distribution along with the Neotropics' paleo-climatic events. In the case of *P. caudata*, as samples in the phylogeny only come from Panama and Costa Rica, it was replaced in the phylogenetic tree as *P. villosula*. Including this differentiation, nineteen species are missing ecological characterisation due to the dataset's lack of data and sampling bias.

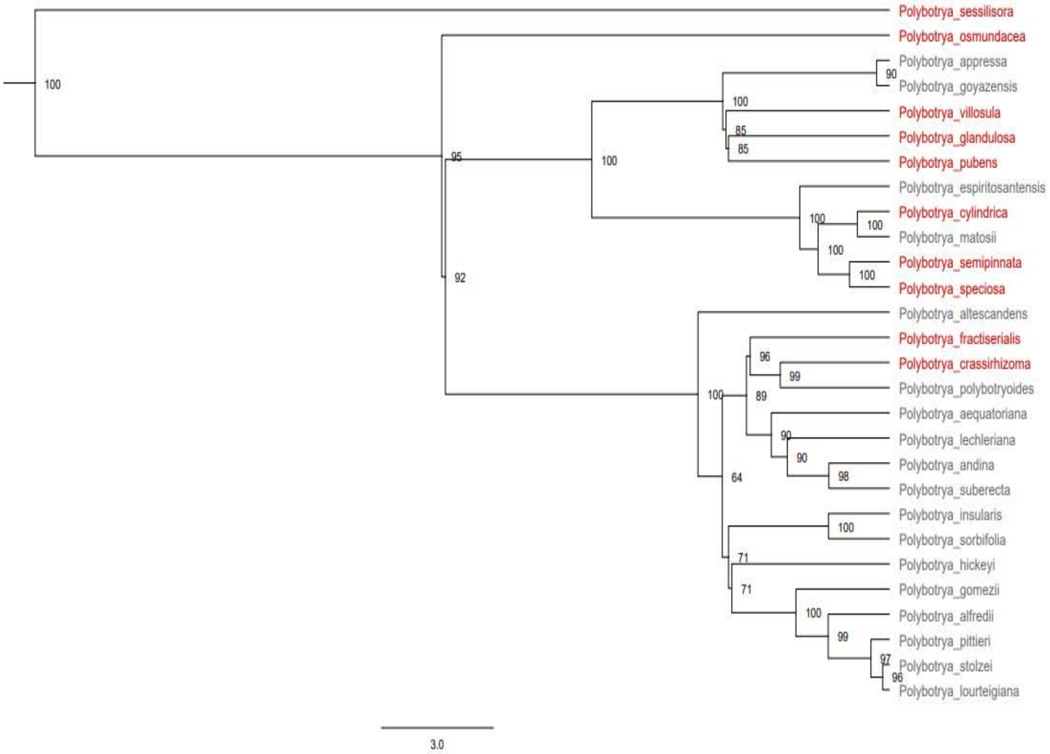


Figure 8: Timed calibrated tree extracted from the Constantly updated Ferns Tree of Life (https://fernphy.github.io/) focusing on the American tropic's genus **Polybotrya**. The scale is in millions of years (and backwards), and the node value corresponds to the support value of the branch. Species were highlighted in red if ecological data was available and in dull grey when missing ecological data. In the phylogeny, *P. speciosa* and *P. tomentosa* are synonymous.

3 Results

3.1 Data overview

This study compiles **490** transects across the Amazonian Basin, Mesoamerica and East Atlantic Brazil (**403**, **68** and **19**). **59,497** fern individuals of the ***Polybotrya*** genus were reported within all sample units. The Amazonian Basin is the dataset's most diverse and abundant region, with seven species out of the 11 observed and an overall 54.672 individuals. The East Atlantic was the area with the least sample unit and the smallest area, but it was pretty diverse as three endemic species were reported in this region (*Table 1*).

Table 1: Summary of the sample's unit across the different bio-geographical area

Geographical Area	Number of sample unit	Area of sample unit (m²)	Total number of reported individuals	Number of Species
Amazonian Basin	403	2.500	54.672	7
Mesoamerica	68	2.500	4.427	2
East Atlantic Brazial	19	100	398	3
Total	490		59.497	11

Across the **403** transects of Amazonia, **293** were reported with the presence of ***Polybotrya****; the others* are treated as absence data. Three of the seven species in Amazonia were the most abundant in the dataset, with more than **10,000** individuals (*P. caudata*, *P. pubens*, and *P. sessilisora*). While *P. caudata* and *P. pubens* relatively occurred in numerous transects (respectively **160** and **148**), *P. sessilisora* was only present in **52** transects but had a similar abundance, implying an extremely high abundance when occurring. In this regard, we can already suspect a difference in behaviour between those species with *P. caudata* and *P. pubens*, which have more generalist behaviour and *P. sessilisora*, which have more specialist behaviour. The rarest species of the Amazonian basin is *P. glandulosa,* which occurred in only **six** transects and an overall abundance of **55** individuals; *P. fractiserialis* was more common but still relatively rare and occurred in **27** transects for an entry of **664** individuals (*Table 2.a*). It is hard to hypothesise anything on that, as it might be more a pattern from the sampling than species' ecological patterns.

The two species reported from Mesoamerica were *P. villosula and P. osmudacea* (only in Costa Rica). Over the **68** transects, *P. villosula* occurred in **22** of them, with an overall count of 1.252 individuals in Panama and **2,487** individuals in Costa Rica. Interestingly, *P. osmudacea* observed in Costa Rica is also present in the Amazonian basin but not in Panama. The reference point of *P. osmudacea* from Costa Rica, **746** individuals were reported along the **11** transects from Costa Rica *(Table 2.b*).

The East Atlantic Brazilian coast included three endemic species to the region along its **19** plots. With an abundance of **240** individuals occurring in **4** plots, *P. cylindrica* is the most common species reported in that area. The second most abundant species is *P. semipinnata; it* happened in **2** plots with an overall abundance of **122** individuals. The rarest species, *P. tomentosa*, has only been reported in one plot but has a high abundance of **36** (Table 1).

Table 2.a: Presentation of the species from the Amazonian Basin; overall abundance represents the sum of all individuals across all transects or plots; the average density is the mean of the individual per occurring transect, and the maximum observed is the highest density observed on a sample unit.

Species Amazonian Basin **a.**	Overall abundance (individuals)	Average density per occurring transects (individuals/2500 m2)	Maximum observed density (individuals/2500 m2)
P. caudata	12.270	77	607
P. crassirhizoma	9.105	86	420
P. fractiserialis	664	25	227
P. glandulosa	55	9	39
P. osmudacea	7.945	86	444
P. pubens	10.852	78	651
P. sessilisora	13.781	265	1.767

Table 2.b: Presentation of the species from the Meso-America and East Atlantic Brazil; overall abundance represents the sum of all individuals across all transects or plots; the average density is the mean of the individual per occurring transect, and the maximum observed is the highest density observed on a sample unit.

b. Species Mesoamerica (Panama & Costa Rica)	Overall abundance (individuals)	Average density per occurring transects (individuals/2500 m2)	Maximum observed density (individuals/2500 m2)
P. villosula	3.739	170	1.767
P. osmundacea	688	76	353

c. Species East Atlantic Brazil	Overall abundance (individual)	Average density per occurring transects (individuals/100 m2)	Maximum observed density (individuals/100 m2)
P. cylindrica	240	60	117
P. semipinnata	122	61	99
P. tomentosa	36	36	36

A PCA based on the soil base cations (Ca, K, and Mg), pH and Al content was performed for each biogeographical region to complete the data presentation and see if there are already some specialisation signals. The distribution of the species across the dataset follows some trends along the edaphic conditions. Species occurrence points are grouped in most cases, and the first dimension of the PCA is explained by the base cation soil content (Ca, K, Mg). The species likely show polarised distribution along the two axes. Furthermore, the PCA was quite strongly informed about the overall soil diversity. For example, the soil in Panama and Costa Rica are plotted quite far from each other, implying that they have substantial dissimilarities. However, when looking at the overall dataset, there is not any segregated group, meaning there is a continuum in the gradient.

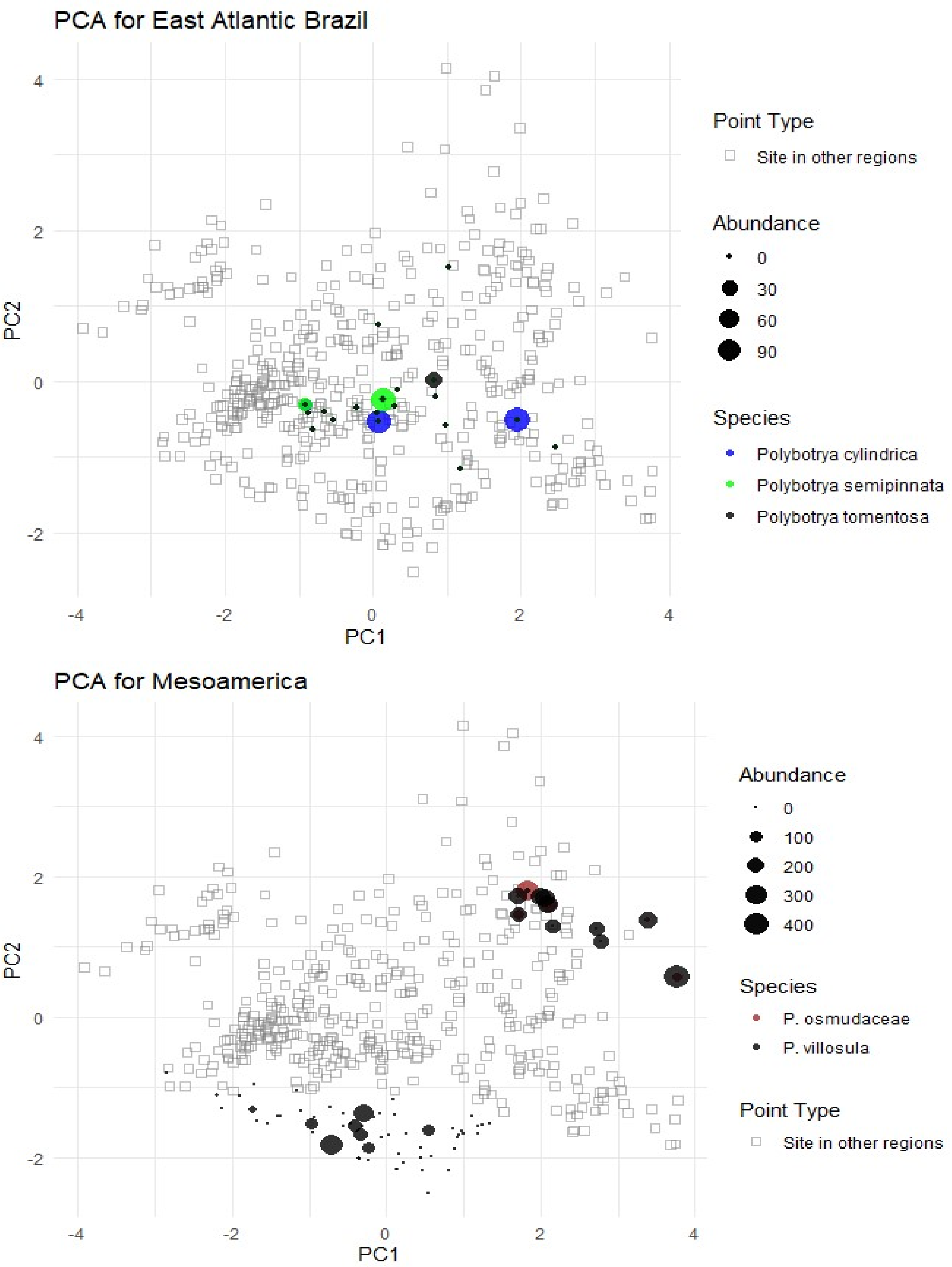


Figure 9.a: Principal component analysis of East Atlantic Brazil and Meso-America data. The PCA is based on the soil base cations (Ca, K, Mg) and the other soil parameters (Al, pH). The PCA explain 78% of the data variance (PC1: 53%; PC2: 25%). The principal elements of PC1 are Ca, K and Mg, while for PC2, the principal elements are Al and K.

On each graph, all the data points are present; full dots are the points from one region, and the empty dot is from another region. Each species is represented by a coloured dot, and the abundance observed of this species on the datapoint scales the size of the dot.

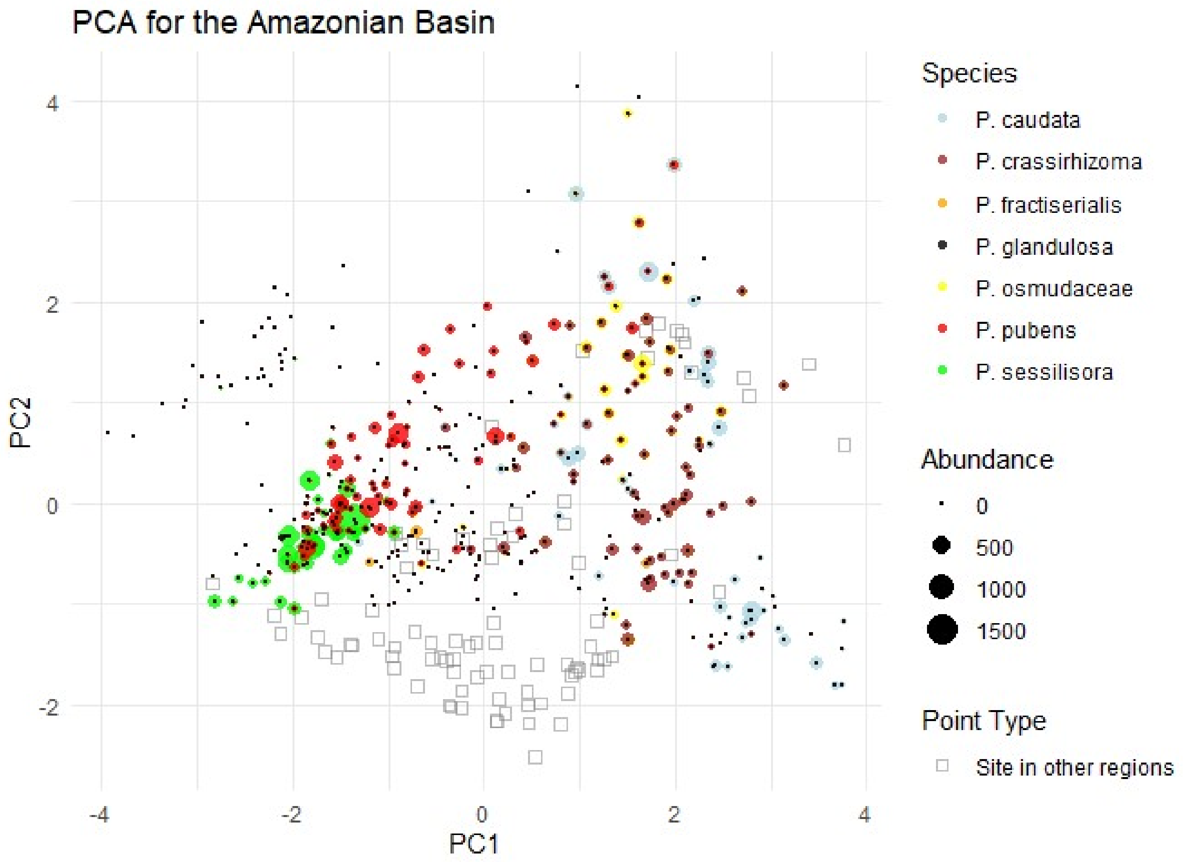


Figure 9.b: Principal component analysis of Amazonian Basin data. The PCA is based on the soil base cations (Ca, K, Mg) and the other soil parameters (Al, pH). The PCA explain 78% of the data variance (PC1: 53%; PC2: 25%). The principal elements of PC1 are Ca, K and Mg, while for PC2, the principal elements are Al and K.

All the data points are present on the graph. Full dots are the points from the region, and empty dots are from another region. A coloured dot represents each species, and the abundance observed of this species on the data point scales the size of the dot.

3.2 Edaphic realised ecological niche:

3.2.1 Weighted average analysis

Overall, each species of the *Polybotrya* genus presents a specific niche across the different edaphic gradients *(Table 3, Figure 10)*. The most interesting response for the edaphic niche is the species distribution across the sum of the base cation gradient, as this informs the soil richness preference for each species.

The species response patterns appear to be quite different from one to another, confirming the niche diversification and partitioning from the poorest to the wealthiest side of the exchangeable base cations' gradient. *P. sessilisora* and *P. glandulosa* appear to be very poor soil specialist species with optima values for exchangeable base cations, respectively **-0,83** and **-0,91**. Similarly, but to a lesser extent, *P. tomentosa and P. pubens* show poor soil optimum but with a more generalist behaviour with optimal values comprising about **-0,48** and a wider tolerance range *(Table 3, Figure 10)*. East Atlantic Brazil species optima are seen as intermediate species along the exchangeable base cation gradient, while *P. tomentosa* doesn't appear that specific, *P. cylindrica* and *P. semipinnata* present a relatively narrow tolerance and an optimum for slightly richer soil than their sister species (respectively **-0,22** and **-0,28** as optima and about **0,19** of tolerance range). *P. osmudacea and P. villosula* follow up as the concentration of the exchangeable base cations increases; they present mid-rich soil optima **0,55** and **0,34** *(Table 3, Figure 10)*. Finally, species standing out for showing rich soil optima response are *P. crassirhizoma* and *P. caudata*, with optimum values for exchangeable base cations, respectively **0,77** and **0,75**.

While the sum of exchangeable base cations is the sum of calcium, potassium, and magnesium, the species' response to each element was investigated, and there are some noticeable changes across the species' behaviour cations-wise. The WA shows the species as more magnesium variation-dependent than the calcium variation. Species present more or less superior tolerance for the Ca than the Mg, which is accentuated as they cover a smaller gradient range for the Mg (-1.8 to 0.6 for Ca and -1.5 to 0 for Mg). Nonetheless, the species' similar pattern and distribution were observed across the Calcium and Magnesium gradient.

P. caudata and *P. crassirhizoma* show a rather specific occurrence to very rich Ca and Mg content soil, confirming their overall preference for the rich soil. However*, P. caudata is* showing a preference for richer Mg than *P. crassirhizoma*. Similarly, *P. glandulosa* and *P. sessilisora* maintain their spot in poor soil optima for Ca and Mg. However, the first one tends to show a preference for richer Ca soil than the second and vice versa for the Mg response. While *P. semipinnata*, *P. cylindrica, and P. tomentosa (speciosa)* occupy the same part of the gradient, *P. tomentosa(speciosa)* present the strongest response for poor Ca soil. *P. pubens* response is closer to the East Atlantic species for the Ca, while it is closer to the poorest soil species for the Mg. Finally, *P. fractiserialis* is still present between the East Atlantic and rich soil species. Its optima are closer to the East Atlantic Brazil species for the Ca and closer to the rich soil species for the Mg.

P. crassirhizoma is seen to be slightly more specific than *P. caudata*. These two species are not so highly separated from the other rich calcium soil species (*P. villosula* and *P. osmudacea).* First, their optima and tolerance range overlap with each other. Nonetheless, combining these species can refine the determination of the environment Mg and Ca. Results also indicate that these two species are pretty specific as their tolerance range is low, and similar deduction can be made for *P. cylindrica* and *P. semipinnata*. On the other hand, *P. pubens* and *P. tomentosa* can be seen as much less specific as their tolerance range may overlap with the species with low Ca optima *(Table 2, Figure 10)*.

Even though there mainly were similarities between the exchangeable base cations, Calcium and Magnesium, their response to potassium is quite different. The analysis shows a strong preference for Potassium in very poor soil. Overall, the optima encompass between (-1.3 and -0.2), making most of the species overlap. *P. tomentosa* and *P. villosula* stand out by their wide tolerance range. Furthermore, there is some change in the species distribution across the gradient. *P. pubens* preferred rich K soil over the East Atlantic species, always on the rich part of the gradient than *P. pubens* for the other element. *P. villosula,* P. *osmundacea* and *P. caudata* present higher optima values than the *P. crassirhizoma,* which was not the case for the previous element, and *P. villosula* optima is noticeably higher than the other rich K species. *P. sessilisora* and *P. glandulosa* are keeping their inferior side of the potassium gradient (**-1,18** and **-1,27**).

Overall, an interesting pattern within the tolerance range of this species emerges, showing a rather specific and relatively narrow not exceeding **0,33** units long along the edaphic potassium gradient for most species. A pattern is not present in *P. tomentosa and P. villosula* as they present a tolerance range of about **1** unit along the potassium gradient.

The weighted average analysis also studied aluminium soil content (Al). Still, this element is not considered a plant nutrient, and while Ca, Mg, and K increase the soil pH, Al tends to reduce it and make it more acidic. Its analysis and results show a somewhat different species distribution along its gradient than the previously observed. Groups of species emerge from the study: *P. tomentosa (speciosa)*, *P. cylindrinca*, *P. semipinnata,* and *P. fractiserialis* represent the very poor aluminium-specific soil species as they show some similar optima values relatively low, respectively **2,10**; **1,88**; **1,91** and **2,41** (Table 3, Fig 5). Evenwith their important tolerance, they do not cover the full range of the gradient (from 0.2 to 7). Among them, *P. fractiserialis* emerges as a strong generalist, while the others are extensively specific. *P. sessilisora* and *P. glandulosa* also show a trend toward the aluminium-poorish soil (**2,71** and **2,97**) and present a narrow tolerance for this elemen**t**. *P. pubens* with a poorer soil preference until then have a distinctive response and a strong preference for mid-rich Al soil. Its wide tolerance range covers a big part of the gradient, overlapping with some poor Al species and rich Al species. Similarly, *P. villosula* has a distinctive behaviour for Al compared to the other elements. With a preference for poor Al soil, this species gets a strong separation from the other species with which it was sharing the ecological space before (i.e. *P. crassirhizoma*, *P. caudata* and *P. osmundacea).* These three species stand out as mid-rich and rich, strong generalist patterns. Their aluminium tolerance covers an extensive part of the gradient but mainly on the richer part.

The soil in the Neotropics is quite acidic (ranging from **3,61** to **4,09**). All the species tolerance overlaps with each other for this soil parameter. Some species are on the extreme part of the gradient, and we can find P. *villosula* in the more basic soil and in the more acidic soil, *P. pubens* or *P. osmundacea*. They all also present a similar tolerance range except for *P. tomentosa (speciosa)* and *P. caudata*, with a tolerance of more than one unit on the pH gradient *(Table 3, Figure 10)*. All species overlap could be seen either as a highly conserved trait along the pH gradient or as the species occurring randomly and their distribution specifically representing the full range of the gradient. Consequently, there is no clear signal of specialist species along the pH gradient.

Overall, specific patterns emerged among the different *Polybotrya* species. The WA analysis spotted some signals among the study species. It established some poor soil specialist behaviour (*P. glandulosa* and *P. sessilisora*), some more poor generalist species (*P. pubens*), mid-poor specific and generalist species (East Atlantic Brazil species), some mid-rich more or less generalist species (*P. villosula, P. osmudacea* and *P. fractiserialis*) and finally some rich generalist species (*P. caudata* and *P. crassirhizoma*). Some potential specialisations across the genus have been identify across the genus.

Table 3: Results of the weighted Average analysis for all the studied species of ***Polybotrya*** genus in the Neotropics. The WA is based on the abundance of the species per an area of 100 m² under an “x ± y” format, where x represents the optimal value for the edaphic element and y is the species' tolerance in cmol(+)/kg. Ca, K, Mg and Exchangeable cations values are log-transformed here. Species highlighted in orange are species that occurred more than in 10 transects and which will have their response modelled by HOF.

Species	Ca_meq optima and tolerance	K_meq optima and tolerance	Mg_meq optima and tolerance	Sum cations optima and tolerance	Al_meq optima and tolerance	pH optima and tolerance
P. osmudacea	0,34 ± 0,56	-0,62 ± 0,33	-0,01 ± 0,39	0,55 ± 0,43	8,79 ± 4,27	3,61 ± 0,35
P. villosula	0,11 ± 0,46	-0,21 ± 0,98	-0,16 ± 0,45	0,34 ± 0,43	4,05± 2,83	4,09 ± 0,4
P. caudata	0,54 ± 0,65	-0,57 ± 0,21	0,17 ± 0,46	0,75 ± 0,53	6,46 ± 5,14	3,84 ± 0,93
P. crassirhizoma	0,61 ± 0,52	-0,69 ± 0,14	0,13 ± 0,13	0,77 ± 0,43	5,90 ± 3,8	3,83 ± 0,32
P. fractiserialis	-0,05 ± 0,85	-0,73 ± 0,19	-0,45 ± 0,76	0,21 ± 0,73	2,41 ± 2,96	3,80 ± 0,36
P. pubens	-1,23 ± 0,68	-0,96 ± 0,21	-0,89 ± 0,38	-0,48 ± 0,41	5,43 ± 3,42	3,61 ± 0,28
P. sessilisora	-1,83 ± 0,25	-1,18 ± 0,13	-1,20 ± 0,14	-0,83 ± 0,12	2,71 ± 1,11	3,88 ± 0,27
P. glandulosa	-1,63 ± 0,23	-1,27 ± 0,25	-1,37 ± 0,26	-0,91 ± 0,20	2,97± 0,56	3,70 ± 0,17
P. cylindrica	-0,65 ± 0,27	-0,98 ± 0,12	-0,59 ± 0,16	-0,22 ± 0,18	1,88 ± 0,23	3,84 ± 0,22
P. semipinnata	-0,75 ± 0,3	-1,01 ± 0,12	-0,6 ± 0,11	-0,28 ± 0,19	1,91 ± 0,07	3,84 ± 0,11
P. tomentosa	-1,33 ± 1	-1,06 ± 1	-0,68 ± 1	-0,47 ± 1	2,10 ± 1	3,78 ± 1

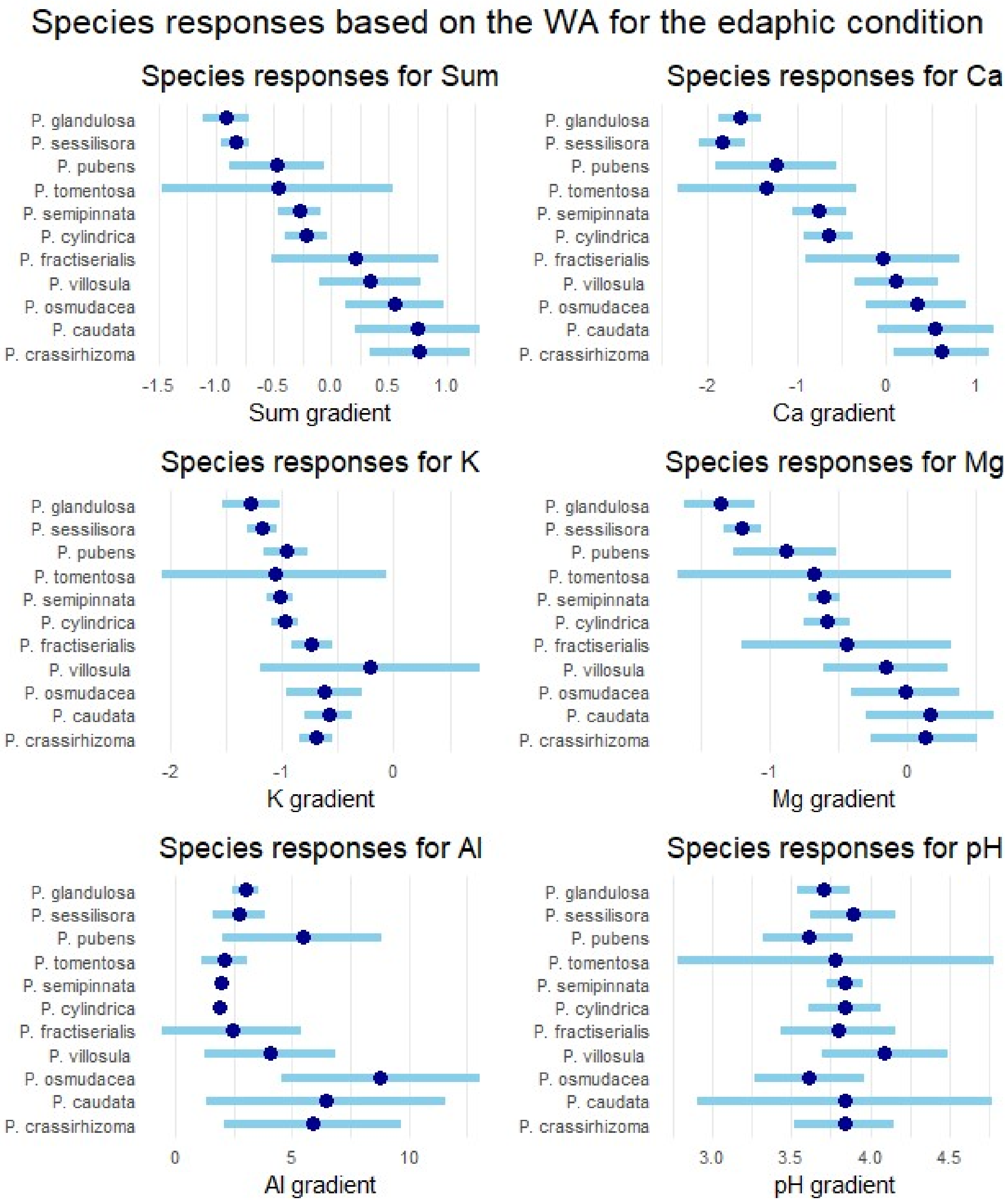


Figure 10: Ecological niche based on the Weighted average analysis. This figure encompasses the species response for the 6 edaphic conditions thanks to the horizontal bar plot. Optima (mean, the blue dots) and tolerance (variance, blue line) of the species along the edaphic gradient. Species were ordered for all plots from the smallest Sum optima to the highest. The weighted analysis is based on the species abundance data per 100m² (East Atlantic Brazil) and 2500m² (Amazonian Basin, Costa Rica and Panama).

3.2.2 HOF modelling

The HOF models, a significant tool in research, refine the species' distribution pattern across the gradient. *P. sessilisora* was identified as a poor soil specialist, and its HOF model shows a similar response. With a skewed unimodal (model V) response, a peak of expected abundance is around **-0,90** along the edaphic gradient (log10(cmol(+)/kg)). The curve also presents a small range (Figure 11.a). The expected abundance reaches its maximum at around **150** individuals per 2500m².

P. pubens presents an abundance peak in relatively poor soil, with a skewed Gaussian response curve. The expected abundance reaches a maximum on the gradient's poor side, reaching a value of around 100 individuals per 2500m². The right end of its response curve shows a rather important tolerance in the mid-rich as the expected abundance decreases steadily but still covers a big part of the gradient. Under these edaphic conditions, the species remain abundant. The HOF model's optimal value is around **-0,**90 and infers a wide tolerance, presenting *P. pubens'* variability for mid-poor to mid-rich soil but not for extremely poor soil. Among the species sufficiently abundant to be modelled, *P. fractiserialis* has the lowest occurrence (only **15** transects) and shows a flat skewed Gaussian response curve across the gradient (model V). The expected abundance predicted by the HOF model is relatively low, about 1 to 2 individuals per 2500m².

P. villosula has a slight trend of a specialist as its model (response curve V) shows a similar pattern with a narrow tolerance on one side of the gradient (poor side) and a more spread range on the richer side of the gradient. With an optimum located toward mid-rich like the WA), these species present a peak of the expected abundance of almost **50** individuals per **2500**m², reaching this maximum for nutrient **0,25** (*Figure 10).*

P. osmudacea shows its highest density for **0,6** values in the edaphic gradient, with a maximum abundance reaching about **70** individuals per 2500 m² for this value. The expected abundance follows an almost perfect bell-shaped curve around this optimum.

P. caudata, a particularly interesting species, has shown quite a unique outcome. Its response curve, with its plateau shape, indicates a broader distribution than the observed gradient in Amazonia. The species shows a vast distribution range, covering more than three gradient units. With a maximum reach on the rich side of the edaphic gradient and its vast tolerance, the maximum of the species is reached for around **100** individuals per 2500m², one of the highest densities observed among the species of the *Polybotrya* genus. *P. crassirhizoma* has quite similar behaviour to *P. pubens* but is on the other side of the gradient. Indeed, the HOF model again shows a skewed response curve, with a maximum of the expected abundance reached for soil values around 1 (Figure 11.b), reaching a density of about **80** individuals per **2500**m^2. The tolerance crosses almost **1** unit of the gradient on that side while it continues for **0,5** units toward the richer side with a more Gaussian shape. This species could be characterised as a generalist towards mid-rich and rich soil, as its expected abundance decreases slowly toward the mid-rich and poor soil and drops as we pass to very rich soil.

Most of the species show a strong specificity along the gradient. Across the gradient aa shift of dominance of several species covering a relatively wide part of it could be seen. They all present good potential as indicators of species to estimate the nutrient soil content with one exception: *P. caudata,* whose distribution overlaps with almost all the species (except *P. sessilisora*). Interestingly, *P.caudata* and *P. crassirhizoma* appeared under the HOF model predictions, with different responses to the edaphic gradient. Moreover, the HOF model never presented a perfect Gaussian curve, inferring a biased distribution of the species toward one edge of the gradient. This reveals more substantial details on the species preference.

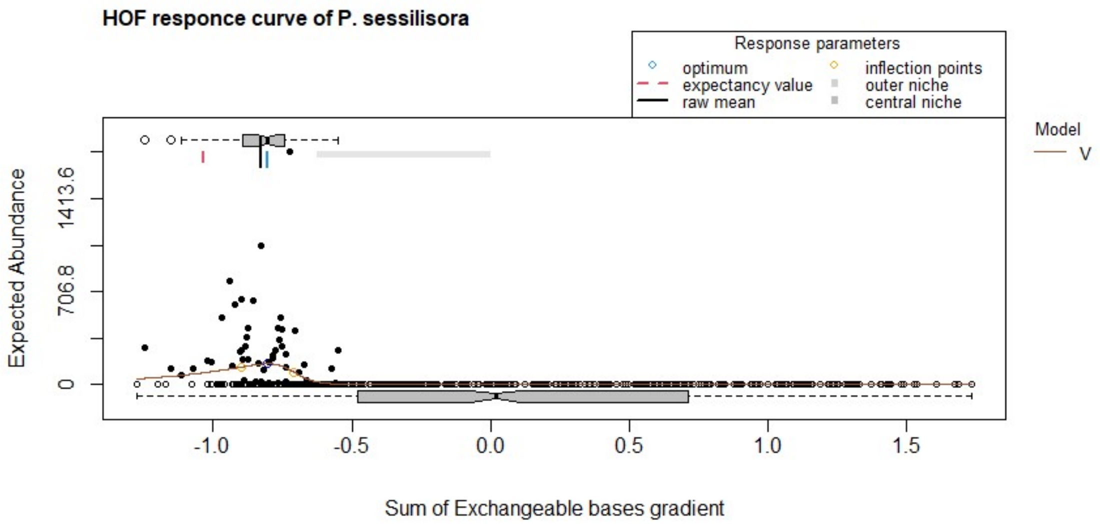
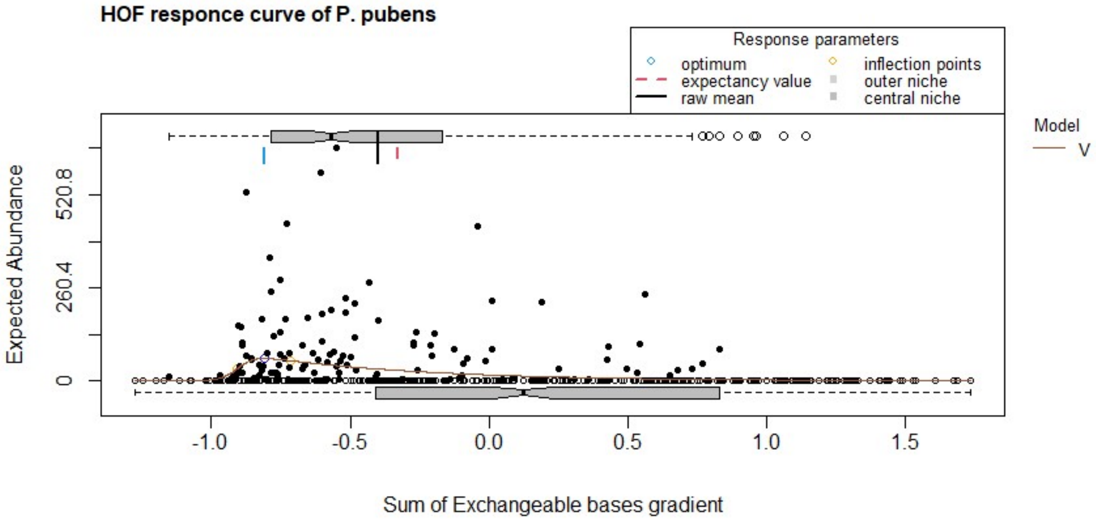


Figure 11.a: Response curve of the abundance of *P. sessilisora* across the log-transformed exchangeable cation present in the soil according to the HOF Models with abundance data and absence transect. The HOF models were realised with 999 bootstraps and with Gaussian function families.



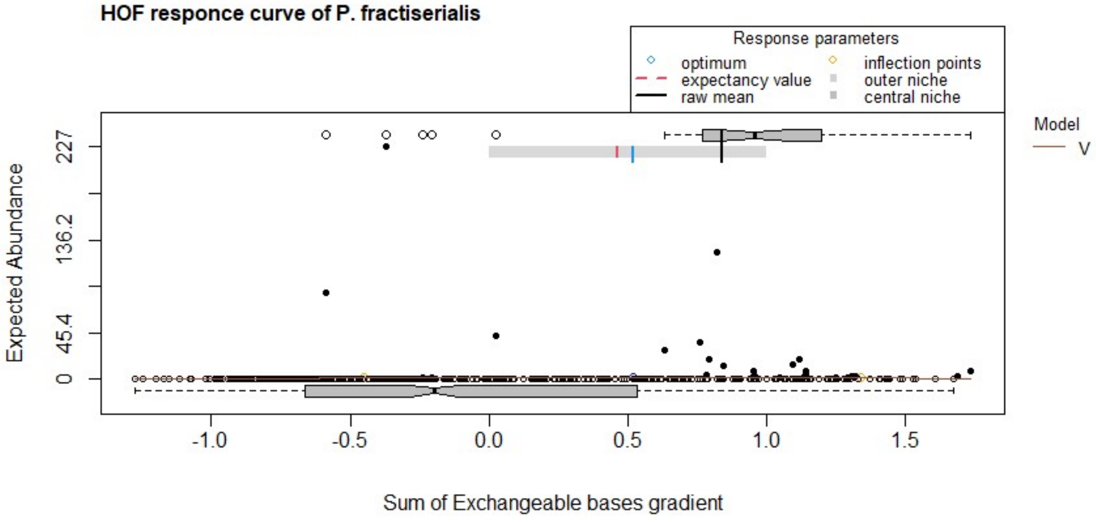
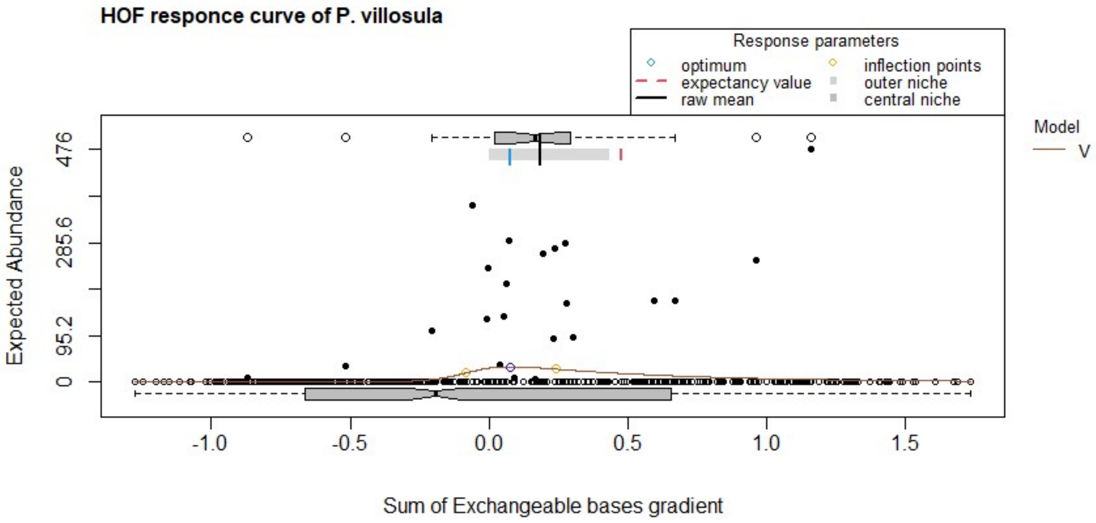


Figure 11.b: Response curve of the abundance of P. pubens and P. fractiserialis species across the log-transformed exchangeable cation present in the soil according to the HOF Models with abundance data and absence transect. The HOF models were realised with 999 bootstraps and with Gaussian function families.



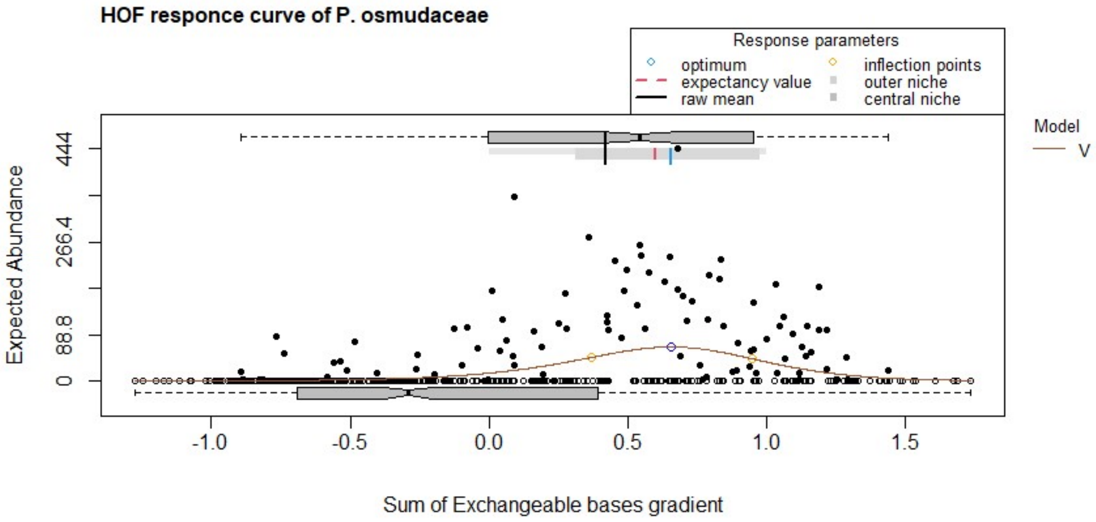
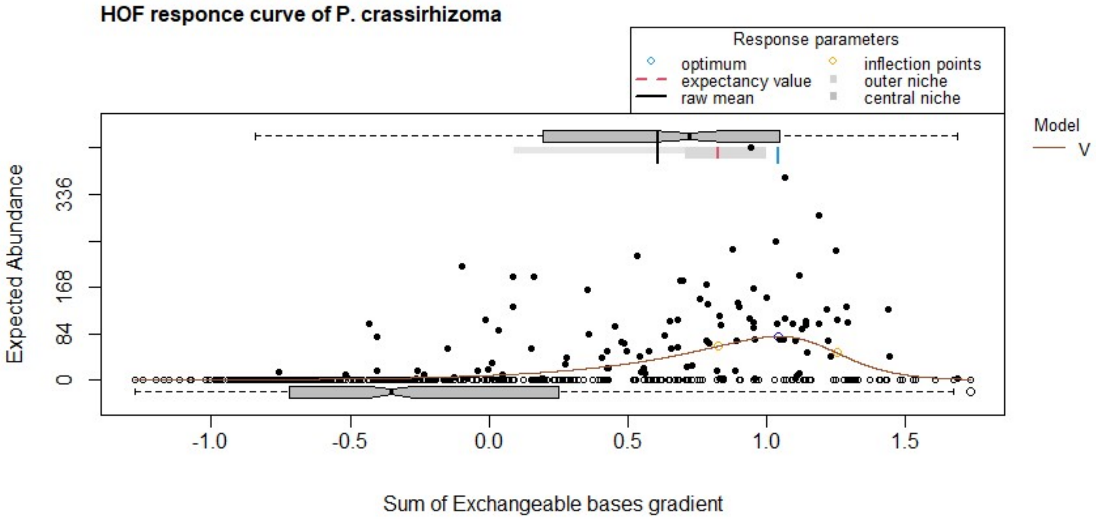


Figure 11.c: Response curve of the abundance of P. villosula and P. osmudacea species across the log-transformed exchangeable cation present in the soil according to the HOF Models with abundance data and absence transect. The HOF models were realised with 999 bootstraps and with Gaussian function families.



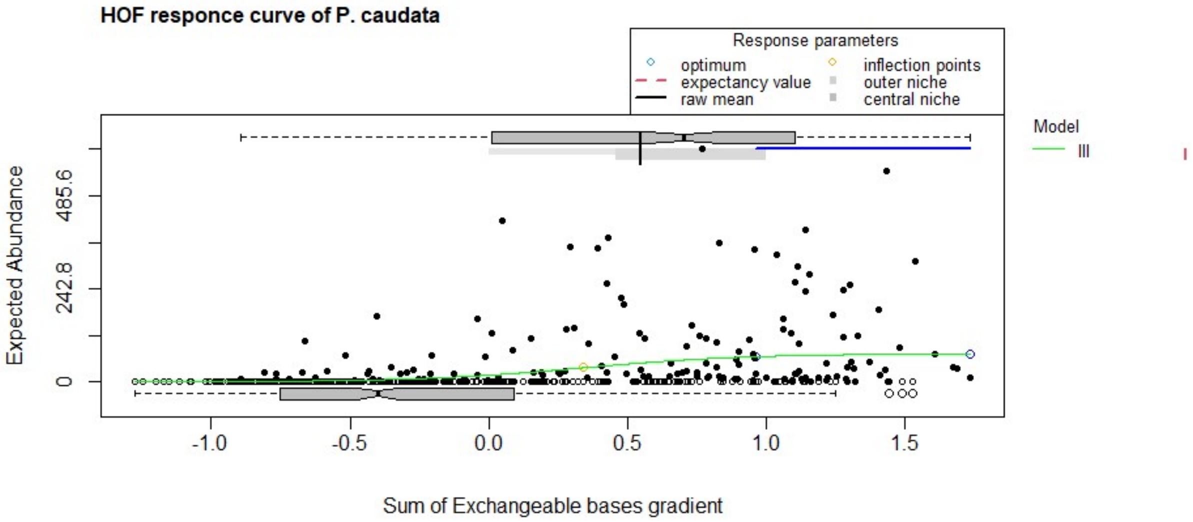


Figure 11.d: Response curve of the abundance of the species of *P. crassirhizoma* and *P. caudata* across the log-transformed exchangeable cation present in the soil according to the HOF Models with abundance data and absence transect. The HOF models were realised with 999 bootstraps and with Gaussian function families.

3.3 Distribution of the realised edaphic niche across the Amazonian Basin:

The two parameters corresponding to the inflexion points were extracted from the HOF model. These inflexion points represent the range across the gradient where the species are expected to reach their highest abundance. For the following species (*P.crassirhizoma*, *P.caudata, P.osmundacea, P.pubens* and *P. sessilisora),* the range between the inflexions point was colour in dark green. To compare it to the species' observed range and spot some high-interest areas, the maximum and minimum values of the Exchangeable base cations of the observed species niche were extracted. This observed range was light green on the Amazonian soil maps from Zuquim et al. 2023 and available in the Fairdata database.

From the soil base cation map, several areas of interest can be characterised:
(1) The southwestern part of the map shows the beginning of the Andes and the transition to the lowland plains that condense mid-rich and rich soil. This area condenses erosion residuals from the Andes, where nutrients are accumulating. This area goes from the North of Bolivia to the South of the Columbia in the Northern part. (2) The Amazonian drainage basin that covers the Amazonian River, the central and central Eastern parts of the map, has extremely poor and poor soil. (3) The Guyana shield in the Northeast has poorish to average soil; some nutrients are accumulating there due to the erosion of the midland and the Guianan hills. (4) the Brazilian shield with poor to mid-rich soil *(Figure 12)*.

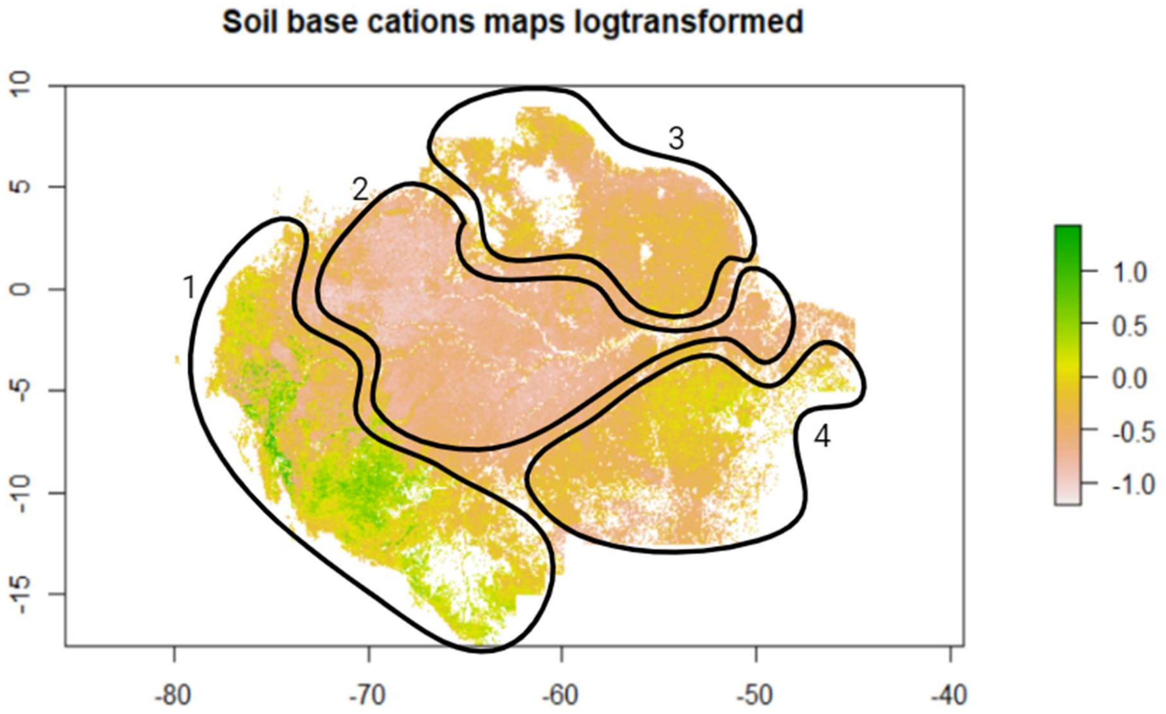
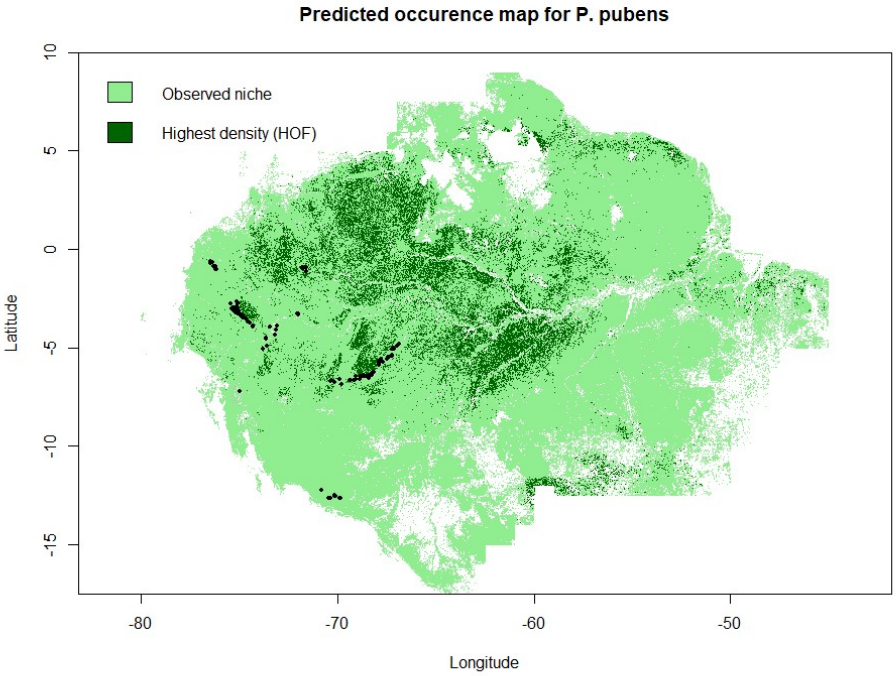


Figure 12: Log10-transformed base cation (sum of Mg, Ca, and K elements) in cmol(+)/L modelled with environmental data and indicator species. This soil map of Amazonia was extracted from the publication of Zuquim 2023 and the Fairdata database. In this figure, the geographical region has been delimited: the transition Andes Lowland (1), the central Amazonian sediment plains (2), the Guyana Shield (3) and the Brazilian Shield (4).

The produced maps differ for each species (Figure 13 a, b, and c). *P. sessilisora* presents a map quite different from the other species. Indeed, the dark green and the light green areas almost entirely overlap. This underlines the edaphic specialisation of the species for the poor soil. The species expected to have the highest abundance are the central Amazonian sedimentary plains, where the poorest soil of Amazonia is located. Even though the *P. pubens* map presents a similar distribution of the highest expected abundance to *P. sessilisora* (nested mainly in the central Amazonian sediment plains, the species range from the observed dataset covered most of the Amazonian Basin (Figure 13.a). For *P. crassirhizoma*, the map presents a relatively small range where the species reaches a maximum abundance in the Amazonian basin, more specifically in the transition zone with the Andes and the Lowlands, which concentrate the richer soil of Amazonia, and even though the green colouring is covering almost the whole part of the Amazonian basin (exclusion of the Amazonian river system). For *P. osmudacea* and *P. caudata*, a similar pattern can be seen on their maps, as their occurrence range does not include central Amazonian sediment plains (Figure 13 b and c). However, their highest density predicted area is much larger, and they cover most of the transition of the Andes Lowlands zone. They also present some spots of high density in the Guianian shiel and Brazilian shield. These areas present some of the intermediate and rich soil of the Amazonian Basin. *P. fractiserialis* follows a similar pattern to the previously described species, with the highest density for the transition Andes and Lowland and an exclusion for central Amazonian sediment plains (Figure 13b)



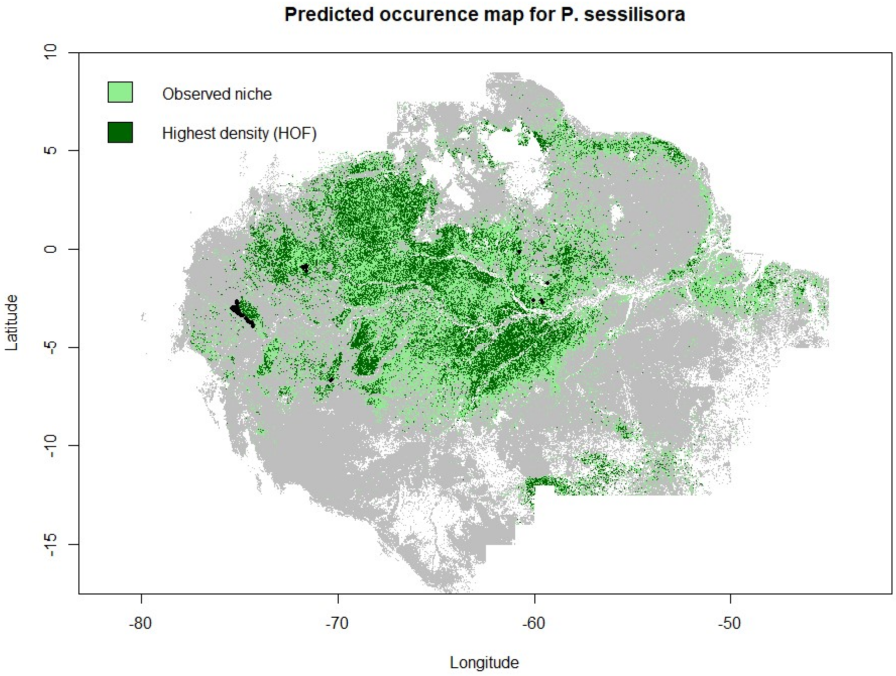
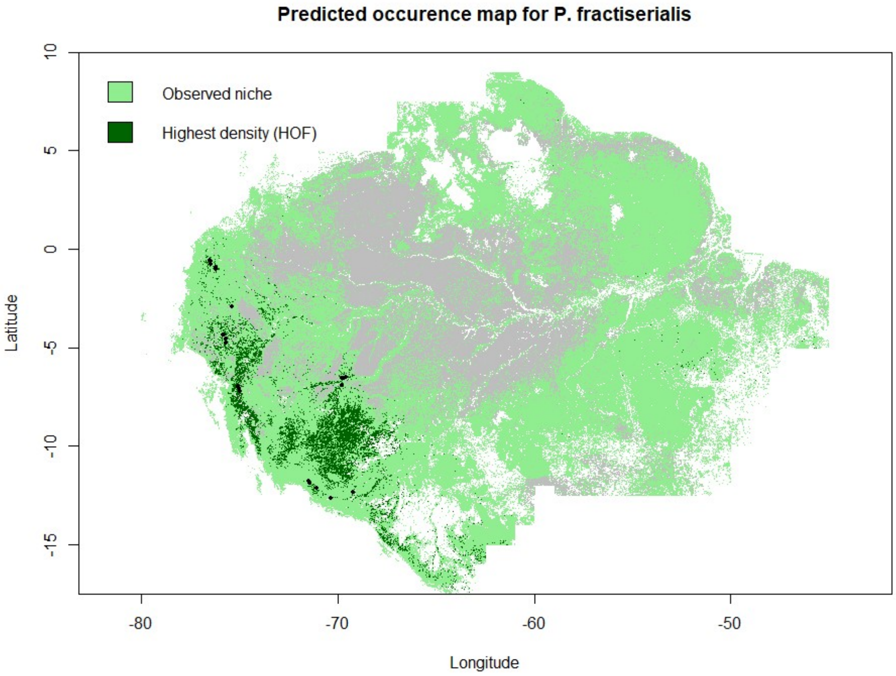


Figure 13.a: Qualitative expected distribution maps based on the top soil exchangeable base cation and HOF model inflexion point for *P. pubens* and *P. sessilisora*. The dark green area represents high expected abundance, based on the range between the inflexion point of the HOF model, and the light green area represents the potential range, based on the edaphic range in which the species occurred. Black dots correspond to the transect where the species occurred.



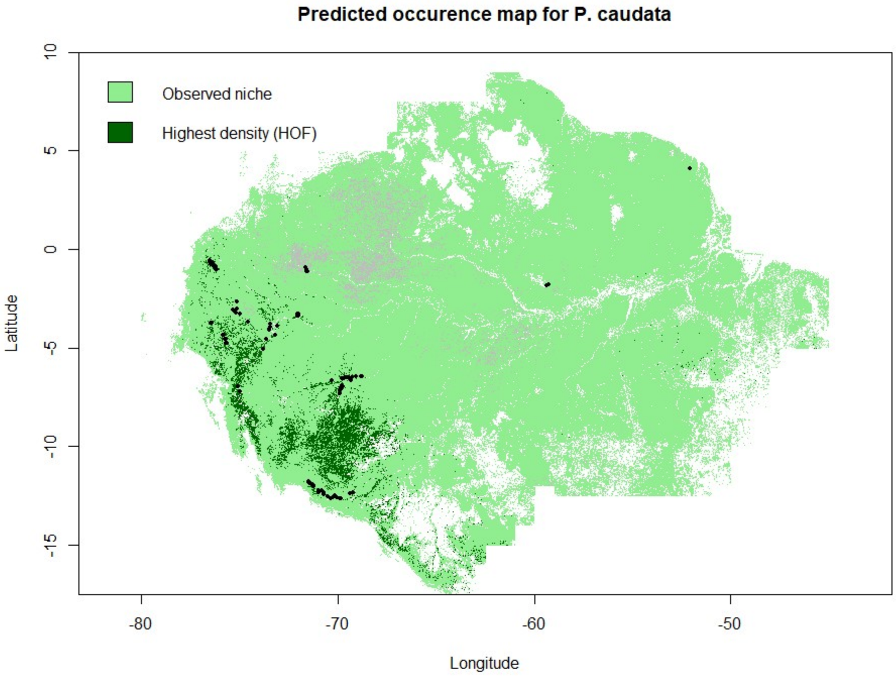
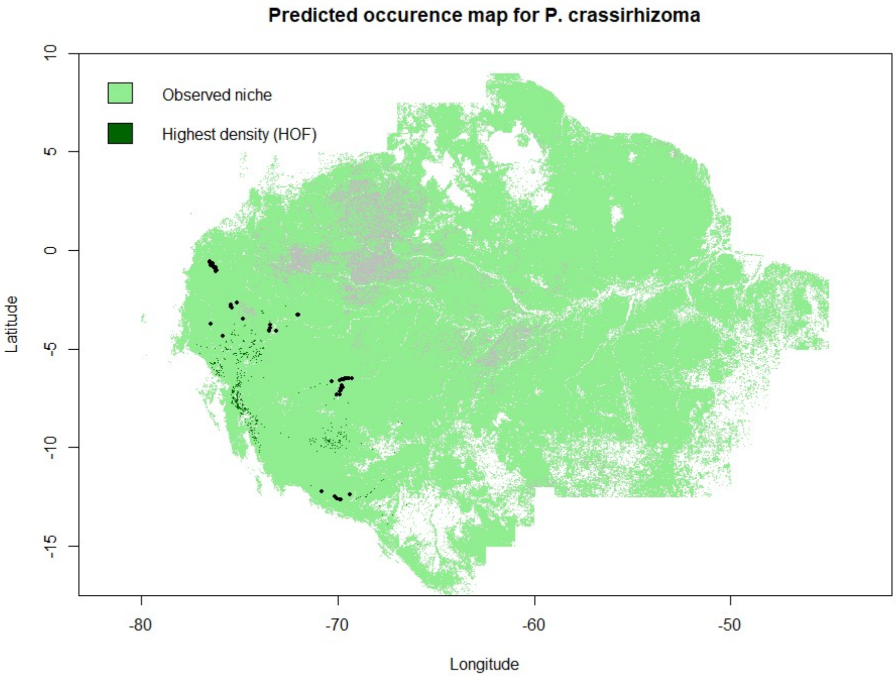


Figure 13.b: Qualitative expected distribution maps based on the top soil exchangeable base cation and HOF model inflexion point for *P. fractiserialis* and *P. caudata*. The dark green area represents high expected abundance, based on the range between the inflexion point of the HOF model, and the light green area represents the potential range, based on the edaphic range in which the species occurred. Black dots correspond to the transect where the species occurred.


Predicted occurence map for P. crassirhizoma

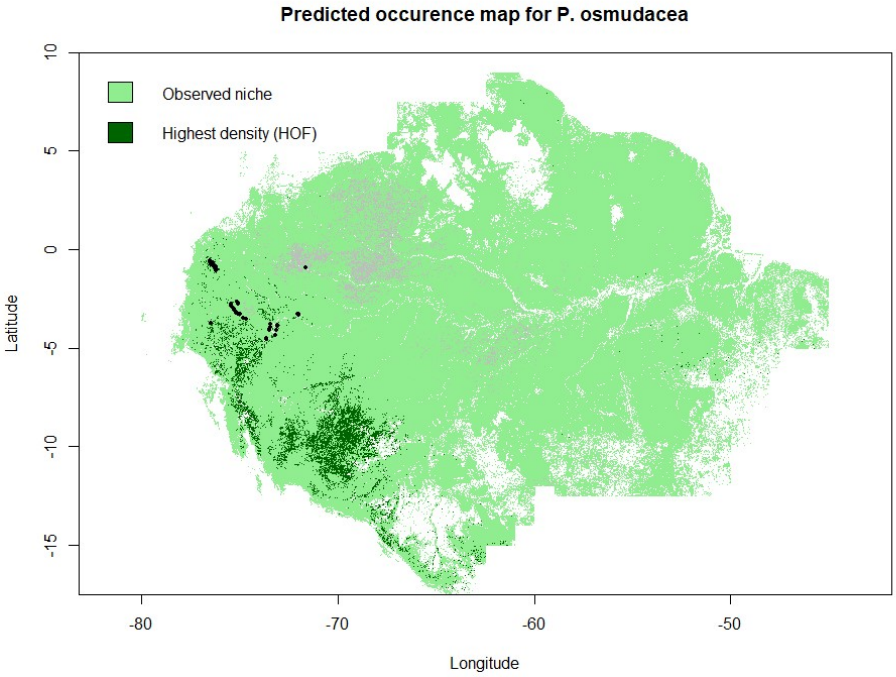

Predicted occurence map for P. osmudacea

Figure 13.c: Qualitative expected distribution maps based on the top soil exchangeable base cation and HOF model inflexion point for *P. crassirhizoma* and *P. osmudacea*. The dark green area represents high expected abundance, based on the range between the inflexion point of the HOF model, and the light green area represents the potential range, based on the edaphic range in which the species occurred. Black dots correspond to the transect where the species occurred.

3.4 Phylogenetic and functional trait

When looking at the genus's biogeography, some clades show a wide distribution range, and some are restricted to a specific area. For example, the East Atlantic Brazil species are all part of a monophyletic clade. On the other hand, the clade composed of *P. pubens*, *P. glandulosa* and *P. villosula* is spread across two bioregions (Amazonian Basin and Meso-America). Furthermore, when the phylogenetic and the taxa are studied aside from each other (Figure 14 and Table 4), some clades present species with uniform edaphic preferences; for example, the East Atlantic Brazilian clade only involves species with edaphic optima for poor soil. At the same time, some other clades, such as the one previously mentioned, involve species with poor soil optima (*P. glandulosa*) and species with rich soil optima (*P. villosula*). Finally, out of the 28 species of the *Polybotrya*, 18 species are missing ecological data

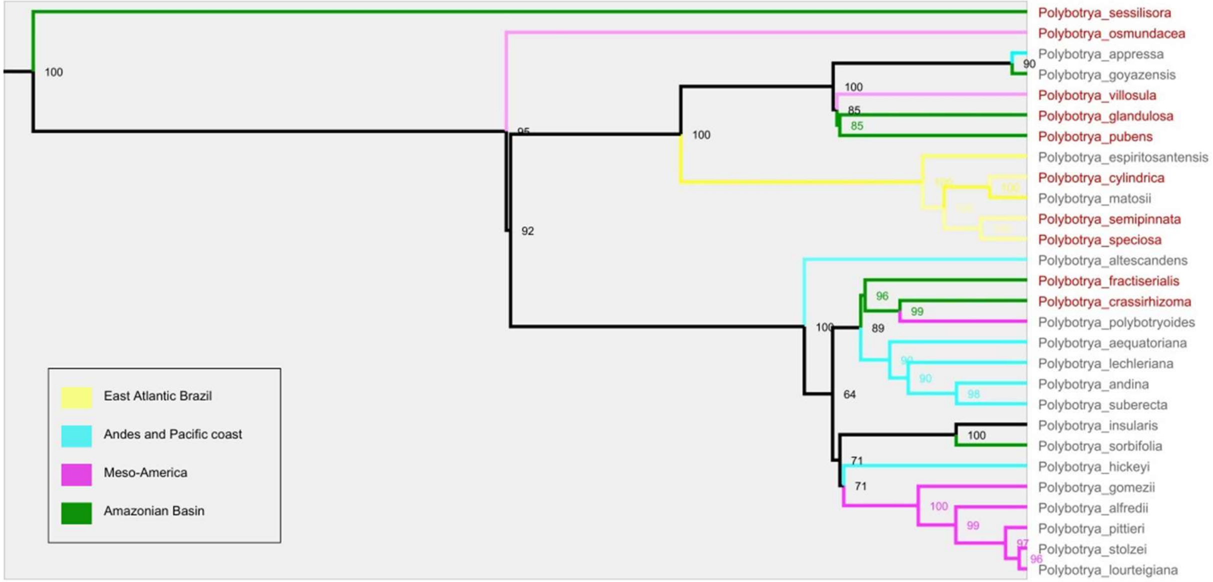


Figure 14: Time-calibrated phylogenetic tree of the Polybotrya species. The nod values represent the support values of the node. Each branch was coloured according to the bioregions in which the species occurs (Yellow for East Atlantic Brazil, Blue for the Andes and Coastal Pacific, Pink for Meso America and Green for the Amazonian Basin). The taxa names are highlighted in red if ecological data and analysis were performed in this study. Here, P. tomentosa and P. speciosa are synonymous.

Table 4: Results of the Weighted average analysis for the studied species from the Amazonian basin, Panama, and East Atlantic Brazil transects. According to the weighted average analysis results, this table summarises the soil species' preferences and behaviour along the gradient. This table is based on the species abundance data per 100m² for the East Atlantic Species and 2500m² for the Amazonian and Mesoamerican species. Categories were made by separating the gradient by 0.5 for the soil preference (-1 to -0.5: impoverished soil, -0.5 to 0 poor soil; 0 to 0.5 average soil, 0.5 to 1 rich soil; 1 to 1.5 very rich soil), by classing the tolerance range (0 to 0.25 specialist, 0.25 to 0.5 intermediate, above 0.5 generalists). The geographical information for each species was extracted from the KWE Plant of the World website. In the phylogeny, *P. speciosa* and *P. tomentosa* are synonymous.

Species	***Exchangeable Cation's soil preference***	***Bioregions of occurrence***
P. sessilisora	very poor soil	Amazonian basin
P. glandulosa	very poor soil	Amazonian basin
P. tomentosa (speciosa)	poor soil	East Atlantic Forest
P. pubens	poor soil	Amazonian basin
P. semipinnata	poor soil	East Atlantic Forest
P. cylindrica	poor soil	East Atlantic Forest
P. fractiserialis	average soil	Amazonian basin
P. osmudacea	rich soil	Amazonian basin & Mesoamerica
P. villosula	rich soil	Mesoamerica
P. caudata	very rich soil	Amazonian basin
P. crassirhizoma	Very rich soil	Amazonian basin

4 Discussion

4.1 Polybotrya’s realised edaphic niche and interpretation

Polybotrya ferns have a biased distribution about the edaphic conditions (Table 5). Each species shows a clear ecological niche for each study element (Sum of exchangeable base cations, Ca, Mg, K and Al) and pH. This is visible thanks to the WA analysis, HOF models and maps produced in this study. Coupled with the previous work on this genus, the study results corroborate and refine the knowledge about the niche specialisation along the edaphic gradient. This was observed in many studies on ferns and, to some extent, on *Polybotrya* (Tuomisto and Poulsen 2000; Tuomisto et al. 2002; Tuomisto, Ruokolainen, et al. 2003; Tuomisto 2006; Cárdenas and Halme y Hanna Tuomisto 2007). While the WA analysis provided some intel on the species' behaviour across the gradient, the HOF response curves refined it. They predicted the species' abundance regarding the sum of these elements. The ecology of these species can be summarised in the following table.

Table 5: Summary table of the edaphic behaviour of the species according to the WA and HOF results

Species	*Exchangeable Cation's soil preference*	*Specificity*	*Niche skewness (based on HOF response)*
P. sessilisora	very poor soil	specialist	Poor soil
P. glandulosa	very poor soil	specialist	Unknown
P. tomentosa (speciosa)	poor soil	generalist	Unknown
P. pubens	poor soil	intermediate	rich soil
P. semipinnata	poor soil	specialist	Unknown
P. cylindrica	poor soil	specialist	Unknown
P. fractiserialis	average soil	generalist	Unknown
P. osmudacea	rich soil	intermediate	Almost not skewed
P. villosula	rich soil	intermediate	Rich soil
P. caudata	very rich soil	generalist	Rich soil
P. crassirhizoma	very rich soil	intermediate	Poor soil

HOF quantitative response presented in this study increases the value of the *Polybotrya* species as indicator species for future and past work as the species' local abundance could provide a reliable estimation of the edaphic conditions. More particularly, the species response curves providing an expected abundance regarding the edaphic conditions are extremely interesting as they offer the first quantitative way of the genus response to nutrient availability. By compiling several well-defined species' responses from different genera, scientists can consistently and reliably infer the edaphic conditions of an area from the abundance, which seems more precise than just the presence or absence of the species. This study also highlights the potential uses of the HOF model in ecology by mapping potential distribution thanks to the edaphic realised ecological niche, which has rarely been done. Even though it was tried, this study could not provide quantitative maps of species distribution from the HOF equations, which involve some improvement of the package (equation parameters extraction and responses curves centred on undetermined parameters); the species responses curve is quite informative itself and provides a more refined value of the edaphic thanks to the observed abundance. The produced maps inferring the highest density from the HOF model are extensively crucial for further work in Amazonia. These maps present further areas for prospection. For example, the North of Bolivia was presented as a hotspot for average and rich species. It is an interesting place to prospect as the biome differs strongly from the Amazonian tropical rain forest, as it is a palm forest, riverine forest and wetlands (Killeen et al. 2007). The Guianan and Brazilian shields are also spotted as having a high density for these species. While the Andes provide nutrient-rich sediment, these areas lack poor sediment and provide a mosaic of relatively poor soil, which could encompass the edge niche of the rich species tolerant to nutrient deprivation (Nishizawa and Uitto 1995). For the poor species, *P. pubens* and *P. sessilisora* seem to have their expected highest density within the Amazonian River area (the poorest part of the Amazonian basin). Not much data was available for that area. For the other species, several regions of interest can be noticed. Indeed, *P. osmudacea, P. caudata, P. fractiserialis* and *P. crassirhizoma* all present one shared cluster at the edge of Peru and the beginning of the Andes. This North-South corridor is a good prospect for further ecological work on these species and model testing. Another part of the transition Andes lowlands could be of potential interest for species with rich and average soil base cations: the north of Bolivia. Finally, some species (*P. osmudacea* and *P. caudata*) harbour dots in the Guiana Shield and Brazilian Shield. These areas are worth prospecting for further ecological data on the *Polybotrya* species as they match average and rich soil and encompass new biomes that could further define the species' ecological niche. In the previous studies on the *Polybotrya* groups, the tolerance range was seldom estimated, nor was the overall response across the gradient, and they only presented optimum values. This study grants further understanding of the *Polybotrya* genus. Nonetheless, it provides a tolerance range for the species. It offered potential details on the skewness of the species' responses toward one edge of the gradient, which is relatively new for this genus (Tuomisto and Poulsen 1996; Tuomisto, Ruokolainen, et al. 2003; Tuomisto 2006). Each species' response can be used to infer the species' behaviour. Some species are pretty specialist species with a relatively small tolerance range (*P. sessilisora*), some are more tolerant (*P. osmudacea*), and some harbour an assertive generalist behaviour (*P. caudata*). Compiling several modelling and methods is necessary to support the behaviour of the species. In this study, while the optimum values and the tolerance range might differ, both methods classify the species toward a similar edge of the gradient and support and complete each other, refining the overall understanding of the species' response to edaphic conditions.

Moreover, the study shows some dissimilarity when comparing the WA and HOF results for the tolerance range and the optimum values. For example, the optimal values of *P. pubens* or *P. crassirhizoma* are quite different from those of Wa or HOF. In the first case, the HOF value is much lower (about -0.8 instead of -0.4), and in the second case, the HOF value is much higher (about 1.1 instead of 0.8). A similar assertion can be made for the tolerance range of the species. A good example is the skewed response of *P. pubens*, which is strongly asymmetrical, with a wide tolerance for rich soil but none for poor soil. Similarly, the plateau response of *P. caudata* is highly inferring on the capacity of the species to thrive in the richest soil, extending the tolerance range predicted by the WA by half a unit of the gradient. Almost every studied species presented a skewed Gaussian curve towards one side of the gradient (HOF model V). The HOF model helps refine the species response curves and intercept specialisation and niche differentiation signals. This model further explained the species' distribution along edaphic conditions and showed how species that would have shared most of their niche in WA present significantly different distributions. The WA predicted an overlapping of their niche for the species leaning toward rich conditions. However, with the HOF modelled, species responses are much more informative, and each species is polarised. *P. oscmudacea* and *P. crassirhizoma* WA inferred that most of their niches overlap. However, the HOF model shows that *P. osmudacea* is much more lenient towards poorer soil and *P.crassirhizoma* towards richer soil (Figure 11). Their response curves present a minimum of overlap while their optima are relatively close. Similar patterns can be observed in *P. pubens* and *P. sessilisora*. Along with their marked distribution across the gradient, the results of this study support the partition of the species across the edaphic gradient and the ecological theory behind the Neotropics' high diversity.

4.2 Speciation

With this study's results, the phylogeny can be approached from a more ecological point of view. According to the phylogeny and the ecology of the genus, it is likely that the genus diversifies from poor soil to richer soil (Figure 8), as the oldest node implies the emergence of *P. sessilisora* from the common ancestor. However, investigating the sister group of *Polybotrya*, the *Cyclodium* genus, must confirm this hypothesis. Further in time, *P. osmundacea* differentiation could be linked to the beginning of the geological formation of the Andes 12 million years ago. With the formation of the mountain chain, erosion would have created a new nutrient input from the Andes to the Amazonian basin, creating a niche with intermediate to rich soil. (Almeida-Silva and Matheus Servino 2024). Furthermore, this uplift dramatically affected the climate, creating wetlands of shallow lakes and swamps in Western Amazonia and increasing the number of potential ecological niches available on a gradient other than the edaphic one. For example, in her study in 2006, Tuomisto mentioned that the specificity of *P. caudata* and *P. glandulosa* tended to prefer mainly inundated and waterlogged areas. The potential diversification leading to these species might result in creating those ecological niches across amazonian geological context.

Regarding understanding the diversification in Neotropics, several interesting clades arise. *P. villosula*, *P. glandulosa*, and *P. pubens* present different edaphic optima and behaviours while they diverge from a common ancestor relatively at the same time about 6 million years ago. And while *P. pubens* and *P. glandulosa* share the same geographical area. P. *villosula* occurs only in Meso-America. Consequently, it is likely to assume that the first two species could be an example of sympatric diversification in the Amazonian Basin. In contrast, their sister species could have derived from allopatric speciation, as they do not occur in the same bioregion. A dry corridor currently separates the East Atlantic Brazilian Forest and the Amazonian forests, known as the “diagonal of open formations” (Pereira 2022), began to emerge during the Oligocene and across expansion and contraction 8 million years (10M-2M years ago) (Werneck et al. 2012; Antonelli 2021; Meseguer and Michel 2022). The East Atlantic Brazilian common ancestor emerged about 10 million years ago, separating from the Amazonian species clade; it is legitimate to suspect that their diversification is an analogue to a vicariance pattern. The fact that only this branch of the tree occurs in East Atlantic Brazil corroborates this hypothesis.

Overall, there is some sign that the diversification history of this genus is linked with the geographical and climatic history of the Neotropics, as other studies show for different species (Carneiro et al. 2018; Almeida-Silva and Matheus Servino 2024; Luize et al. 2024)Further work is needed to improve the global ecological knowledge of the Polybotrya group, which will make the hypothesis regarding the group's diversification more reliable and supported. With a well-supported phylogeny, further work to understand the ecological pattern of the missing species of this genus can help to understand the evolutionary history of this species group.

4.3 Limitations and Further Works

In this study, few species occurred in less than 10 study sites, which can result in biased edaphic ecological niche estimation (WA results). A concrete example is the East Atlantic Brazil species present in a few plots (4, 2 and 1). In order to produce a species distribution model, response data and predictor data are both necessary. To support an efficient and reliable model, a large sample size of records is needed (Coudun and Gégout 2006; Naujokaitis-Lewis et al. 2013). This study's sampling density is quite heterogeneous across the Neotropics (Sampling following some rivers, etc…). More and more scientists are addressing these problems regarding the species distribution models and how to correct them by including a detection rate and a probability of occurrence (Occupancy Estimation and Modelling, 2006). Compared to the study's previous work on the genus, more than 100 new transects and almost 15,000 individuals and new species were added. This study also includes three new bioregions in the Neotropics: Panama, Costa Rica and the East Atlantic Brazilian Coast. While this study's results are biased toward western Amazonian soil, it is essential to underline that they are also based on the most complete dataset of this genus. In that sense, the results presented are the most confident regarding establishing the edaphic niche of the *Polybotrya* species.

Soil composition and its variation at broad and local scales are complex in the Amazonian Basin's geological context. With the formation of the Andes, nutrients are coming out from the mountain on a poor base soil layer ((Herrera, Jordan, and Medina 1978; Jordan and Herrera 1981). Yearly flooded forests and ravines are accumulating nutrients. Data production in this part of the world is highly costly and time-consuming for accessibility reasons. The studied transects, data collection and analysis limit the ability to glimpse the small-scale characteristics. The dataset and how it was treated by averaging the edaphic condition to one transect (pooled soil sample then mixed) imply that the small-scale variation and distribution patterns along the transects are lost. Consequently, analysing the transect as homogeneous in edaphic conditions and species composition is not an optimal solution. However, using indicator species and their floristic data can fasten and increase soil determination and improve research in this part of the world that is difficult to access. The soil map used and previous work on fern indicator species align with this characterisation of Ferns niche with the global aim of understanding the Neotropics soil and diversity (Zuquim et al. 2023; Tuomisto et al. 2024). This study's results align with the intention to use floristic data by spotting suitable indicator species to establish environmental values (Table 5 & Figure 11.a, b and c).

Finally, the astonishing diversity of tropical rainforests in the Neotropics has always triggered scientists to investigate the possibility of species coexistence. While niche differentiation and the ecosystem resources partitioning might play a role in the overall diversity at the local scale by the presence of several microhabitats, species usually show a trade-off between a higher density when the condition gets closer to their optima and a smaller population along their tolerance range. Because of that, one cannot say that a species outcompetes one another and that competition exclusion is to be mitigated, as this driving force is not that decisive regarding the species density and the small-time scale it happens. Species may show some specific pattern by claiming the first microhabitat from each other due to their phenology or stochastic events. Furthermore, limiting competition to just within a genus would be quite an underestimation of the ongoing biotic interaction. As shown in *(Figure 12)*, the expected density from the HOF modelling of the *Polybotrya* rarely exceeds 100 individuals/ 2500 m^2, and it is also likely that species are not in direct contact with each other *(Figure 12)* at the local scale. When one looks at the total density of herbaceous plants in the understory, density can rise to more than 140 individuals/ 100m^2 (Tuomisto 2006; Tuomisto, Zuquim, and Cárdenas 2014). Consequently, it is logical to assume that *Polybotrya*'s close neighbours are not species from the same genus, and competition is more likely to happen with another genus or plant group. In order to further understand this ecological interaction and species dynamics that led to species diversity in the regions, more research on species' ecological niche is needed, and by crossing results, the ecological mechanism of diversification would be more well characterised (Tuomisto and Poulsen 2000; Hoorn et al. 2010; Antonelli 2021; Meseguer and Michel 2022; Luize et al. 2024).

Conclusion

This study contributes to Polybotrya's ecological dynamics and evolutionary background across the Neotropics. By mapping the edaphic niches of several species and examining their specialisation along soil nutrient gradients, this study underscores the complex interplay between environmental factors and species distribution patterns. Using a new model and tool such as HOF, the ecological response can be better comprehended as the ecological value of indicator species and showing species tendencies towards certain edges of the gradient. This degree of refining of ecological niche is necessary to comprehend and understand species distribution and niche differentiation. Furthermore, these abundance-based response curves are much more efficient in characterising the environmental data from indicator species. By compiling several species response curves, scientists can fasten the characterisation of the edaphic conditions in the Neotropics and avoid using costly and disruptive techniques such as soil sampling by only relying on abundance observation and floristic data.

Studying species niche variations is essential for understanding how biodiversity is structured in the Neotropics. Characterising these variations and species distribution can retrace speciation processes and adaptive radiations in response to environmental heterogeneity. Finally, this thesis reaffirms the significance of integrating ecological niche theory with evolutionary perspectives to decode the origins and sustainability of biodiversity in the Neotropics. This study's results enrich our understanding of this genus, tropical fern ecology, and species-environment interactions.

5 Acknowledgement

I want to extend my gratitude to everyone who made this work possible.
To Mirkka Jones, who provided valuable data from Costa Rica and Panama to Hanna Tuomisto, Mark Higgins, Anders Sirén, Patrick Weigelt, and Glenda Cárdenas, who generously shared their expertise and data from Amazonia and to Samuli Lehtonen and Maarten Christenhusz for their contributions from coastal Brazil data.

I would also like to express my gratitude to the many field workers and Indigenous communities who enabled these expeditions with their deep knowledge and collaboration with the researchers. I am also profoundly grateful to the foundations that funded these research programs in Amazonia and Neotropics, enabling us to pursue essential ecological insights.

My supervisors, Hanna Tuomisto and Samuli Lehtonen, have guided forces throughout, offering their expertise and support at every stage, and I would be eternally grateful for that. I'd also like to thank my Amazonian team—Venni and Gabriela—for their dedication and help in pursuing this research.

I am immensely grateful to my friends Marie and the Glamazons group, whose help with the literature suggestions, advice and proofreading has been valuable. Their keen eye for detail and unwavering support helped refine and strengthen this work.

Finally, I am thankful to the University of Turku for fostering an environment of research that made this thesis possible.

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