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**PATTERNS OF ABUNDANCE AND FUNCTIONAL TRAITS OF
WOODY PLANTS COMMUNITIES IN IN ANDEAN ELEVATION
GRADIENTS**



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Tesis doctoral

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PORTADA: Paisajes de bosques montanos del Ecuador.
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Doctorado en Ecología Terrestre

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PATTERNS OF ABUNDANCE AND FUNCTIONAL TRAITS OF WOODY PLANT COMMUNITIES IN ANDEAN ELEVATION GRADIENTS

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ABSTRACT

Tropical Andean forests harbor a suite of biotic and abiotic characteristics that promote structural diversity and a higher accumulation of biomass. The representativeness of woody species that coexist in their various habitats presents different patterns of distribution, which could vary in relation with environmental factors that change between montane forests located at different elevations. The structural components of the species from mountain communities, such as abundance and frequency, as well as their functional characteristics, can be differentiated according to the scale at which they are evaluated, either local or at the landscape level. The evaluation of functional diversity, based on the characteristics of the species, sheds light on the structure and functioning of the ecosystems.

In chapter 2, I analyze the relationships between the biomass of woody arboreal plants of Andean montane forests and the dominance patterns within local communities and also at the regional scale, considering the effect of elevation and precipitation. Trees ≥ 2.5 cm DBH were assessed within plots established between 260–4350 m elevation from the Bolivian Amazon to the Andes. Data analyses were based on the calculation of: the Simpson's evenness index for all species (to determine abundances) and the biomass of each species within plots; and measurement of the frequency of each species from all plots at each plot's elevation. Linear models were used to evaluate the relationships between variables. We found that biomass is negatively related with elevation, and positively related with precipitation. Also, we found that biomass was negatively related to the Simpson's equity index, indicating that species abundance contributes to the increase in biomass along the elevation gradient. On the other hand, the negative relationship between the frequency of species and biomass indicates that the less frequent species contribute with greater biomass at the landscape scale. Finally, these relationships are stronger in the lowlands and decrease towards higher elevations.

The third chapter, evaluates the patterns of functional traits in relation to abundant species in local plots along elevational gradients. Woody species ≥ 2.5 cm DBH were analyzed within plots established along two elevation gradients, in Bombuscaro (Ecuador) and Río Abiseo (Peru). The following functional traits were considered: wood density, specific leaf area, leaf thickness, and plant height. For the analysis, the "Community Assembly by

Trait Selection" (CATS) model was used, considering the abundance of species within each plot as the response variable and the four functional traits, along with elevation, as the predictor variables. We found that abundance is significantly related to functional traits along the elevation gradient. At lower elevations, in Bombuscaro, the abundant species had lower values for wood density, and greater for height; while in Abiseo, the abundant species had higher individuals greater wood density. In both sites, at high elevations, the abundant species had greater values of leaf thickness. Lower values of specific leaf area were related to abundant species only in Abiseo. In conclusion, the thickness of the leaf, the density of the wood and the height of the individuals were mostly related to abundances of woody species in the Andean montane forests.

Chapter 4 analyzes the functional diversity of communities in relation to biomass at the plot level along the two elevation gradients, Bombuscaro (Ecuador) and Abiseo (Peru). The weighted average of the community and the functional variation index of wood density, specific leaf area, leaf thickness and plant height were analyzed in order to determine whether species with acquisitive or those with conservative strategies are the ones prevailing in communities from the elevation gradients studied. Functional diversity varies according to changes in species abundance along the elevation gradient. Species with acquisitive characteristics were found at low elevations, while in communities established at high elevations, the conservative traits prevail. The functional diversity showed variation between Bombuscaro and Abiseo. Possibly, this may be related to local limitations related to the environmental, structural and functional characteristics of the communities. High biomass values were found in communities dominated by species with acquisitive strategy.

RESUMEN

Los bosques andinos tropicales poseen un conjunto de características bióticas y abióticas que promueven diversidad estructural y gran acumulación de biomasa. La representatividad de especies leñosas que coexisten en sus variados hábitats presenta diferentes patrones de distribución, los cuales podrían variar conforme cambian los factores ambientales en bosque montanos ubicados a diferentes elevaciones. Los componentes estructurales de las especies que conforman las comunidades en montañas, como abundancia y frecuencia, así como sus características funcionales, pueden diferenciarse según la escala a la cual se evalúa, ya sea local o de paisaje. La evaluación de la diversidad funcional, basadas en las características de las especies, informará sobre la estructura y funcionamiento de los ecosistemas.

En el capítulo 2 se analizan las relaciones entre la biomasa de plantas leñosas arbóreas de bosques montanos andinos y los patrones de dominancia dentro de comunidades locales y a escala regional, considerando el efecto de la elevación y la precipitación. Se analizaron árboles ≥ 2.5 cm de DAP, procedentes de parcelas establecidas entre los 260–4350 m de elevación entre la Amazonía y los Andes de Bolivia. Los análisis de datos se basaron en cálculo del índice de equidad de Simpson para todas las especies (para determinar abundancias) y de la biomasa de cada especie, dentro de cada parcela; y la medida de la frecuencia de cada especie del total de parcelas a cada elevación. Se usaron modelos lineales para evaluar las relaciones entre variables. Encontramos que la biomasa está relacionada negativamente con la elevación y positivamente con la precipitación. También, encontramos que la biomasa estuvo negativamente relacionada con el índice de equidad de Simpson, indicando que la abundancia de las especies contribuye al aumento de la biomasa a lo largo del gradiente de elevación. Por otro lado, la relación negativa entre frecuencia de especies y biomasa, indica que las especies menos frecuentes aportan en su conjunto con mayor biomasa a escala de paisaje. Por último, estas relaciones son más fuertes en tierras bajas y decrecen hacia mayores elevaciones.

El tercer capítulo evalúa los patrones de rasgos funcionales en relación con especies abundantes en parcelas locales a lo largo de gradientes de elevación. Se analizaron especies leñosas ≥ 2.5 cm de DAP, dentro de parcelas establecidas en dos gradientes de elevación en Bosbuscaro (Ecuador) y Río Abiseo (Perú). Se consideraron los siguientes

rasgos funcionales: densidad de la madera, área foliar específica, grosor de la hoja, y altura de la planta. Para los análisis se utilizó el modelo “*Community Assembly by Trait Selection*” (CATS), considerando la abundancia de especies dentro de cada parcela como la variable respuesta y los cuatro rasgos funcionales, junto con la elevación, como variables predictoras. Encontramos que la abundancia está significativamente relacionada con los rasgos funcionales a lo largo del gradiente de elevación. En bajas elevaciones, las especies abundantes tuvieron bajos valores de densidad de la madera y un mayor porte (altura) en Bombuscaro, mientras que en Abiseo las especies abundantes presentaban una mayor altura de sus individuos, pero con valores de densidad de la madera mayores. En ambos sitios, para altas elevaciones, las especies abundantes presentaron valores altos de grosor de la hoja. Los valores bajos de área específica de la hoja estuvieron relacionados con las especies abundantes solamente en Abiseo. En conclusión, el grosor de la hoja, la densidad de la madera y la altura de los individuos, estuvieron principalmente relacionadas con las abundancias de especies leñosas en los bosques montanos andinos.

En el capítulo 4 se analiza la diversidad funcional de las comunidades en relación con la biomasa a nivel de parcela en los dos gradientes de elevación, Bombuscaro (Ecuador) y Abiseo (Perú). Se analizó la media ponderada de la comunidad y el índice de variación funcional de: densidad de la madera, área foliar específica, grosor de la hoja y altura de la planta, con la finalidad de determinar si en las comunidades estudiadas en el gradiente de altitud prevalecían especies con estrategia de tipo adquisitivo o conservativo. La diversidad funcional varía de acuerdo a los cambios en la abundancia de las especies a lo largo del gradiente de elevación. Se encontraron especies con características adquisitivas en bajas elevaciones; mientras que en comunidades establecidas en altas elevaciones prevalecen los rasgos conservativos. La diversidad funcional mostró variación entre Bombuscaro y Abiseo, potencialmente esto está relacionado con las limitaciones locales en relación con las características ambientales, estructurales y funcionales de las comunidades. Se encontraron altos valores de biomasa en comunidades dominadas por especies con síndrome adquisitivo.

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Capítulo 1

1. INTRODUCCIÓN GENERAL

1.1 Estado del arte acerca de las características generales de los bosques tropicales

Los bosques tropicales albergan gran riqueza de especies y hábitats en comparación con otras zonas del planeta (Gentry, 1988). Su ingente diversidad local y regional (Wright, 2002; Kraft et al., 2011; Sabatini et al., 2022) está directamente relacionada con el clima tropical estable, húmedo y cálido, que proporciona disponibilidad de energía, facilita las interacciones ecológicas y promueve procesos de adaptación de los organismos a dichas condiciones ambientales (MacArthur, 1972; Brown, 2014).

Los bosques tropicales son un componente clave en los ciclos globales hidrológicos y del carbono (Ciais et al., 2013). Contienen una gran biomasa aérea y diversidad estructural proporcionada por los diferentes estratos que coexisten, desde hierbas, plántulas, árboles juveniles, arbustos del sotobosque, árboles de dosel y emergentes (Myster, 2009). Además, presentan una importante variabilidad en la disponibilidad de nutrientes en el suelo, los cuales, a grandes rasgos, suelen ser poco profundos, ácidos, arcillosos-limosos, ricos en materia orgánica sólo en sus capas superficiales, donde se afianzan los árboles con sus raíces poco profundas (Myster, 2009).

La gran diversidad de árboles que alberga el bosque tropical lluvioso, tanto a escala local como regional (Wright, 2002), se corresponde con comunidades con composición de especies arbóreas muy variable (Gentry, 1988; Pitman et al., 2001; Myster, 2009; Pitman et al., 2012; Fauset et al., 2015). Debido a su alta diversidad, en estos bosques se pueden encontrar especies abundantes que cabe esperar contribuyen en gran medida a la biomasa aérea de estos ecosistemas, los cuales son considerados los más productivos del planeta (Lewis, 2006). Por otro lado, los patrones de abundancia de las especies son relevantes porque, a pesar de que los procesos que controlan el ensamble y el funcionamiento de las comunidades ecológicas son variados y complejos (Chase and Leibold 2003), la

competencia limita la diversidad ya que las especies que son mejores competidoras contribuyen a la exclusión de otras especies a escala local (Wright, 2002).

1.2 Componentes abióticos que determinan la distribución de especies en bosques montañosos andinos

Los bosques montañosos son reconocidos como puntos calientes de la biodiversidad global, ya que albergan gran número de especies endémicas y organismos altamente especializados (Myers et al., 2000; Körner et al., 2006). Se encuentran expuestos a gran variación de factores ambientales en distancias geográficas relativamente cortas, las cuales afectan a la biomasa de las especies y por ende al almacenaje de carbono (Clark and Clark, 2000; Alves et al., 2010; Girardin et al., 2013; Álvarez-Dávila et al., 2017). El crecimiento de las plantas en estos sitios está limitado por variables ambientales relacionadas con la elevación, tales como la precipitación y la temperatura. Aunque estas tienden a disminuir con el incremento de la elevación, la reducción general de la humedad con la elevación a menudo se ve interrumpida por un pico de precipitación a elevaciones medias (Körner, 1999; Körner et al., 2006). Por lo tanto, estos factores ambientales relacionados con la variación de la elevación son generalmente buenos predictores de la composición y estructura de la vegetación a escala regional.

Los ambientes extremos, como los cinturones montañosos alpinos y nivales, preferentemente están habitados por especies altamente especializadas que, obviamente, se adaptan a esas condiciones ambientales locales adversas (Cheviron and Brumfeld, 2012). En altas elevaciones, el ambiente se caracteriza comúnmente por presentar una temperatura media baja, vientos fuertes, radiación solar intensa y baja presión parcial de oxígeno, juntamente a una alta variabilidad temporal y espacial (Körner, 1999; Unger et al., 2012; Girardin et al., 2013; Strinella et al., 2020). En estas drásticas condiciones ambientales, los organismos deben presentar una alta flexibilidad fisiológica y de comportamiento para hacer frente a las difíciles condiciones abióticas, las cuales muchas veces presentan cambios repentinos en períodos de tiempo cortos (Strinella et al., 2020). Los organismos que se especializan en estos ambientes extremos pueden ser vulnerables a los cambios que se produzcan en sus hábitats ya que posiblemente vivan cerca del límite de su estrecho nicho ecológico y cualquier variación ambiental puede afectar a sus

poblaciones (Strinella et al., 2020). Es por eso que la mayoría de especies alpinas tienden a tener rangos de distribución estrechos (La Sorte et al., 2010).

Por todo lo expuesto, la variación del clima es el principal impulsor de la productividad primaria a lo largo de gradientes de elevación. Por un lado, el número de individuos que un área puede sustentar tiende a aumentar con la productividad primaria (Mittelblach, 2012). En los trópicos, el nivel más alto de productividad generalmente se encuentra en las tierras bajas y los bosques premontanos, con temperaturas más cálidas, que también contienen mayor diversidad de especies respecto a otras elevaciones (Benner et al., 2010; Mittelbach, 2012). Sin embargo, en bosques montanos de elevaciones medias se ha podido encontrar altos niveles de productividad debido a la complementariedad funcional entre especies que se daría en estas zonas de transición florística (Huaraca et al., 2013; Arellano et al., 2017). Por otro lado, los patrones de dominancia de especies arbóreas varían a lo largo del gradiente de elevación de las montañas. Esta dominancia se reflejaría en parámetros estructurales –como densidad de árboles, área basal, altura del dosel, biomasa–, y/o de composición florística (Richards, 1996; Guo and Rundel, 1997). Así, altas elevaciones contendrían menos árboles grandes, con la práctica desaparición de las lianas, mientras los arbustos se establecerían como la forma de crecimiento predominante (Janzen, 1975).

Una de las cadenas montañosas más extensas del mundo es la Cordillera de los Andes, de la región occidental de América del Sur, con una longitud de más de 8000 km, y elevaciones que superan los 7 000 m s.n.m. La Cordillera se subdivide en tres sectores: Andes del Norte, Centrales y del Sur (Ramos, 1999). Además, los bosques montanos de la Cordillera de los Andes también están sujetos a variaciones drásticas de factores ambientales a corta distancia.

Estos factores afectarían a la productividad y al almacenamiento de biomasa y de carbono de sus especies (Girardin et al., 2013), con repercusión en sus patrones de abundancia estructural a escala local y regional. Así, la biomasa de comunidades establecidas en elevaciones altas de la Cordillera de los Andes disminuiría debido a las bajas temperaturas, las pendientes pronunciadas, el régimen de precipitaciones, la velocidad del viento o el aumento de la nubosidad (Girardin et al., 2013). En elevaciones más bajas, algunos taxa que son abundantes a escala espacial local (por ejemplo, en una parcela de estudio dada) también son ubicuos y frecuentes a escala regional, coincidiendo con la

mayor riqueza de especies de árboles propia de los bosques de tierras bajas (Pitman et al., 2001; Macía and Svenning, 2005; Arellano, 2013). Este patrón de dominancia también está relacionado con una mayor similitud en las características ambientales en áreas que son homogéneas –por ejemplo, en hábitats de tierras bajas, donde el suelo y, especialmente, las variables climáticas cambian relativamente poco con la distancia–. Por el contrario, cuando las condiciones ambientales son heterogéneas y el filtrado ambiental más estricto, este patrón de dominancia de especies aparece como más débil (Pitman et al., 2001, 2012; Arellano et al., 2016).

1.3 Diversidad vegetal de los bosques montanos andinos en el gradiente de elevación

Los bosques andinos albergan gran diversidad vegetal –dentro de este ecosistema han sido identificadas 45 000 especies de plantas vasculares, 20 000 de las cuales son especies endémicas para la región–, siendo esta una de las razones por las que son considerados puntos calientes de la biodiversidad (Myers et al., 2000). En estos ecosistemas el gradiente de elevación genera una variabilidad de condiciones ambientales que contribuyen a la formación de microhábitats, los cuales promueven la diversidad de especies vegetales (Smethrust, 2000; Körner, 2006). El gradiente de elevación andino comprende desde ecosistemas típicos de altas elevaciones, como son los páramos, hasta bosques montanos y vegetación de tierras bajas (Sierra, 1999). En los Andes existe una importante variabilidad de la relación entre la elevación y la riqueza de especies o las características estructurales de los bosques, probablemente como consecuencia de las cambiantes condiciones ambientales que actuarían como filtro abiótico. Por ejemplo, en la sección tropical de los Andes, el área basal de los rodales de bosque puede aumentar con la elevación hasta elevaciones medias y luego disminuir o permanecer constante (Homeier et al., 2010; Unger et al., 2012). Por otro lado, se ha reportado un patrón de diversidad de plantas con un aumento de la riqueza en zonas de elevación intermedia (Balslev, 1988; Malizia et al., 2020). Muchas especies arbóreas muestran un patrón de distribución en los Andes tropicales de Ecuador, con un máximo en elevaciones por encima de los 1800 m s.n.m., que acaba disminuyendo con el aumento de la elevación (Homeier et al., 2010; Malizia et al., 2020).

Estos patrones pueden deberse al efecto del estrés físico existente en las zonas altas de las montañas con las interacciones entre especies. Por ejemplo, al disminuir el estrés ambiental en bajas elevaciones, las interacciones negativas –v.g., competencia– se incrementan, mientras que la menor rigurosidad climática en bajas elevaciones favorecería mayor riqueza de especies (Körner 2004; Malizia et al., 2020). El balance entre estos factores explicaría el pico de riqueza de especies en elevaciones intermedias.

En las zonas intermedias del gradiente de elevación andino se mantiene un alto nivel de humedad, un bajo estrés térmico (temperaturas moderadas) y, por tanto, una alta productividad, los cuales determinan la coexistencia de taxa. Así, el punto máximo de diversidad se da en un nivel intermedio del gradiente de elevación, correspondiendo con la zona donde los factores ambientales tienden a ser óptimos, y las interacciones entre especies permiten o incluso promueven la coexistencia de muchas especies (Lomolino, 2001).

La diversidad de familias taxonómicas también disminuye con la elevación, aunque de manera menos pronunciada que la riqueza de especies, y sólo por encima de los 2000 m. Así, los bosques de mayor elevación tienen menos familias, pero también presentan menor número de especies por familia, comparado con los bosques de elevaciones más bajas. Sin embargo, entre los 1000 y 1500 m, puede haber una mayor riqueza de familias, por el solapamiento de taxa propios de tierras bajas y los de altas elevaciones (Gentry, 1988). Por encima de los 1500 m, a elevaciones intermedias y también en cotas altas, de 2500 a 2900 m, los bosques son más distintos florísticamente, presentando familias diferentes de las encontradas en bosques premontanos o de tierras bajas (Gentry, 1988).

1.4 Abundancia y dominancia de especies en bosques montanos andinos

Los patrones de dominancia de especies vegetales en la Cordillera de los Andes, desde las tierras bajas a las altas elevaciones, varían en términos de estructura y composición florística, entre otros parámetros (Richards, 1996; Guo and Rundel, 1997). En concreto, los patrones de distribución y abundancia en comunidades de árboles en la Amazonía han sido explorados a escala local y regional (Pitman et al., 2001; Pitman et al., 2012; ter Stege et al., 2013). Uno de los patrones que más llama la atención es que frecuentemente unas determinadas especies presentan gran abundancia a escala local, repitiéndose este

patrón a escala de paisaje (Pitman et al., 2001; ter Stege et al, 2013). Es decir, existen especies que pueden presentar un patrón de elevada abundancia y además amplios rangos de distribución geográfica, a las que se ha denominado como “hiperdominantes” (ter Stege et al. 2013). Así, ter Steege et al. (2013) encontraron que solamente el 1.4 % de las especies de la Amazonía representaban el 50% del total de individuos de la región. Estas especies incluyen tanto taxa de etapas avanzadas de la sucesión (tolerantes a la sombra, con semillas grandes y con alta densidad de madera), como taxa pioneros (intolerantes a la sombra/helófilos, de semillas pequeñas y con baja densidad de madera). Estas especies pueden ser muy resistentes a patógenos, herbívoros especialistas y otros factores de mortalidad dependientes de la densidad (ter Stege et al, 2013). Este patrón se complementaría con el que presentan una pequeña proporción de especies arbóreas amazónicas, denominadas “oligarcas”, que son comunes a lo largo del paisaje (alta frecuencia regional) y que dominan las comunidades vegetales a escala local (Pitman et al., 2001; Pitman et al., 2012; Arellano and Macia, 2014), es decir, se presentan en altas densidades tanto localmente (abundantes), y a su vez presentan altas frecuencias regionales (comunes), formando un patrón que se repite en áreas extensas (Figura 1, Pitman et al., 2001). El resultado es que se pueden construir matrices con estas especies, que permitan establecer una distribución predecible en vastas áreas (al menos varios miles de kilómetros cuadrados) en cada región (Pitman et al., 2001; Arellano et al., 2016).

Ambos patrones de hiperdominancia y oligarquía se darían particularmente en áreas con una alta homogeneidad ambiental, evidentemente, lo que facilita que las especies comunes tengan una buena capacidad para movilizar recursos y asimilar energía de forma más eficiente que el resto de especies (Hall et al., 1992). A escala regional, estas especies dominantes podrían estar utilizando ampliamente los recursos a lo largo del paisaje (Condit et al., 2000). Si el ambiente se vuelve más heterogéneo, similar a lo que ocurre al aumentar la elevación, este patrón de dominancia disminuye o se debilita (Pitman et al., 2001, Pitman et al., 2012; Trujillo et al., 2019).

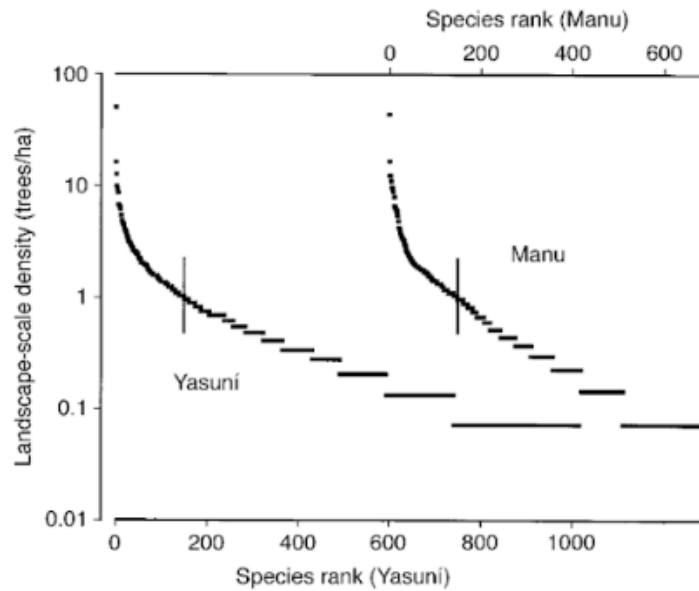


Figura 1.- Distribución de densidades a escala de paisaje de todos los árboles registrados en inventarios de Ecuador (Yasuní) y Perú (Manu). La línea vertical que intercepta cada distribución, marca el límite de densidad de 1 individuo por hectárea (especies comunes). Los dos lugares de estudio presentan similar número de especies comunes (fuente: Pitman et al., 2001).

1.5 Relación entre dominancia y distribución de la biomasa de especies de plantas en bosques montanos andinos

Los bosques tropicales son muy importantes para la regulación del ciclo global del carbono, ya que tienen el potencial de acumular más biomasa que cualquier otro tipo de bosque (Pan et al., 2011; Malizia et al., 2020). En estos bosques, cabe esperar que los patrones de distribución caracterizados por especies con abundancias locales repetidas a lo largo del paisaje tengan un impacto sobre la biomasa aérea de estos bosques. Estas especies dominantes contribuyen a la biomasa de distintas formas: la dominancia a escala local indica una adaptación a asimilar grandes cantidades de energía, por ejemplo, al poseer un mayor número de tallos, que a su vez aportan más biomasa (Hall et al., 1992; Condit et al., 2000). La mayor frecuencia a escala regional indicaría una capacidad para explotar una gama más amplia de recursos y hacerlo en áreas más extensas, aportando una mayor biomasa a escala de paisaje (Higgins and Richardson, 1999).

Los bosques montanos tropicales son sistemas de estudio particularmente apropiados para comprender mejor las relaciones entre los parámetros ambientales y la estructura de los ecosistemas (Malhi et al., 2006). Los factores abióticos afectan a la biomasa a lo largo del gradiente de elevación (Malhi et al., 2006), mientras que la contribución relativa de la abundancia y frecuencia de las especies a la biomasa presentaría una cierta consistencia, aunque con importantes matices, a lo largo del gradiente. En regiones con mayor homogeneidad ambiental existen taxa que muestran un patrón de dominancia, en términos de abundancia y frecuencia, como los explicados anteriormente. Conforme incrementa la elevación, aparecen condiciones más heterogéneas, y un filtrado ambiental más estricto, provocando que el patrón de dominancia de especies no sea constante a lo largo del gradiente de elevación (Pitman et al., 2001, 2012; Trujillo et al., 2019). Así, a baja elevación, la mayor cantidad de biomasa se encuentra concentrada sobre todo en especies y géneros frecuentes a escala regional. En altas elevaciones, la mayor biomasa se encuentra en unas pocas especies con muchos tallos que logran su dominancia al haber menos riqueza taxonómica.

La relación entre las variables climáticas y la producción primaria se evidencia en el cambio gradual de la estructura del bosque a medida que aumenta la elevación, dándose paralelamente una disminución en la riqueza de especies leñosas y en la biomasa (Körner, 1999; Girardin et al., 2013; Reich et al., 2014; Álvarez-Dávila et al., 2017) al aumentar la elevación, mientras que en las zonas bajas del gradiente las altas temperaturas y precipitación explican una mayor biomasa y productividad (De la Cruz-Amo, et al., 2020). Así, la mayor cantidad de árboles grandes, y por ende mayor biomasa, se encuentra en comunidades de tierras bajas y zonas medias del gradiente de elevación. Los individuos grandes pueden ser parte del grupo de especies dominantes a escala de paisaje. Estos poseen una buena facilidad para dispersarse a grandes distancias (Condit et al., 2000). Tienen además mayor área total de hojas que les permite captar más radiación y mayor asimilación, lo que les permite crecer más rápidamente y aumentar su biomasa, contribuyendo significativamente a la productividad en la región (Stephenson et al., 2014). Asimismo, las especies frecuentes, con grandes individuos, serán superiores competidores capaces de prevalecer exitosamente en toda la región (Guadet and Keddy, 1988). Alternativamente, dicha frecuencia puede también explicarse por quedar sus requisitos ecológicos, incluidos factores edáficos y climáticos, satisfechos de forma

similar a lo largo del rango de distribución de la especie en el territorio (Brown, 1984; Pitman et al., 2001; ter Steege et al., 2013).

1.6 Rasgos funcionales y diversidad funcional en relación a patrones de dominancia de plantas en bosque montanos andinos

El éxito de las diferentes especies a lo largo de los gradientes ambientales está relacionado con la adecuación de sus rasgos funcionales a las condiciones que se dan en dicho gradiente (Westoby and Wright, 2006). A su vez, las diferencias entre especies en estos rasgos, determinan que éstas no son equivalentes ecológicamente y cumplan diferentes roles en el funcionamiento del ecosistema. Ejemplos de esos rasgos son la altura de los individuos, el área específica foliar, el tamaño y grosor de las hojas, la concentración de nitrógeno foliar, la densidad de la madera o la profundidad de las raíces. Estos rasgos funcionales son características inherentes a una determinada especie que afectan el crecimiento, la supervivencia y la reproducción de individuos y en última instancia determinan el *fitness* de las poblaciones de la especie (Violle et al., 2007; Pérez-Harguindeguy et al., 2013).

Por tanto, los rasgos funcionales son útiles para comprender mejor los procesos ecológicos y evolutivos dentro de las poblaciones, las comunidades y los ecosistemas (Shipley et al., 2012; Sonnier et al., 2012; Warton, et al., 2015), considerando diferentes escalas ambientales. Por ejemplo, los rasgos funcionales varían ampliamente en los gradientes de elevación de los trópicos (Asner et al., 2014). Sin embargo, la relación entre los rasgos funcionales de las especies y los patrones y procesos relacionados con la estructura de los bosques son menos conocidos, sobre todo por la dificultad en el acceso y toma de medidas en lugares remotos y difíciles de acceder, como son los bosques montanos y submontanos andinos. Sin embargo, podemos esperar que las especies frecuentes a lo largo del paisaje, potencialmente generalistas, compartan con las especies dominantes a escala local rasgos funcionales que les permiten el uso de una gama más amplia de recursos a través de gradientes ambientales (Condit et al., 2000). Estas especies numéricamente abundantes aportarán más a la biomasa dentro de un bosque. Por otro lado, las especies frecuentes, presumiblemente con eficiente capacidad de dispersión en

el paisaje, tendrían rasgos funcionales que les permitiría explotar recursos en áreas más extensas.

Así pues, cabe esperar que los rasgos funcionales de las especies vegetales que estructuran las comunidades y su funcionamiento (Violle et al., 2007; Shipley et al. 2012), estén implicados en los patrones de distribución de especies dominantes y su efecto en la biomasa del bosque (Warton et al., 2015; Strahan et al, 2018). Algunos rasgos funcionales como el área específica de la hoja, el grosor de la hoja, la altura del individuo y la densidad de la madera pueden estar correlacionados con el patrón de dominancia local y regional de las especies a lo largo del gradiente de elevación andino, desde los bosques premontanos hasta los de mayor elevación, atendiendo al impacto que las condiciones cambiantes a lo largo del gradiente tienen en el filtrado de rasgos funcionales (Cornwell and Ackerly, 2010; Lisner et al., 2021), como se evaluará en el Capítulo 3. Así mismo, los rasgos foliares permiten comprender los procesos de asimilación de carbono, obtención de agua y balance energético (Cunningham et al. 1999; Fonseca et al. 2000; Ackerly, et al. 2002), los cuales, a su vez, pueden relacionarse con la abundancia de especies a escala local (Cornwell and Ackerly, 2010; Warton et al., 2015; Lisner et al. 2021). Todo ello facilitaría el entendimiento del ensamble de comunidades en el gradiente de elevación, según las diferentes respuestas adaptativas de las especies conforme a las condiciones ambientales de temperatura, exposición al viento y disponibilidad de nutrientes y humedad del suelo que varían con el gradiente de elevación (Körner, et al. 1986; Körner, 2012; Pandey et al., 2021). Así, en bajas elevaciones existen especies abundantes con individuos que presentan mayores alturas que las especies establecidas en cotas altas, reflejando el efecto de la elevación en el crecimiento de los árboles (Coomes and Allen, 2007). Por otro lado, valores bajos de densidad de madera pueden existir en especies abundantes de bajas elevaciones como resultado de mayor presencia de especies pioneras (Gartner and Meinzer, 2005; Wright et al. 2010). Por último, las especies dominantes ubicadas en bajas elevaciones tienden a presentar hojas de menor grosor y mayor área (Körner, 2012). En conjunto, estos rasgos funcionales de las especies dominantes sugieren una estrategia ecológica adquisitiva. Sin embargo, estas inferencias de las relaciones entre patrones de abundancia y rasgos funcionales en el gradiente de elevación deberían verificarse mediante estudios específicos, como el que se desarrolla en el Capítulo 3.

La diversidad funcional generalmente aumenta con la riqueza de especies dentro de las comunidades; sin embargo, esta relación puede cambiar según la escala y el tipo de bosque (Tilman, 2001, Chiang et al., 2016; Fotis et al., 2018; Andrew et al., 2021), y muy en particular con los gradientes ambientales. En general, existen patrones de diversidad funcional a nivel de comunidad que responden al gradiente de elevación en las montañas andinas. Conforme aumenta la elevación, el filtro ambiental tienden a promover la coexistencia de especies con valores similares en los rasgos funcionales que responden a los correspondientes gradientes abióticos (Swenson et al., 2012).

Así pues, la diversidad funcional, descrita como la medida de los rasgos funcionales presentes dentro de una comunidad, de acuerdo a su presencia o abundancia, (Tilman, 2001; Hatfield et al., 2018), es de gran interés para comprender las propiedades de los ecosistemas en relación a la variabilidad ambiental a la que están expuestos. Por ejemplo, la variación de la diversidad funcional está asociada a la existencia de especies que tienden a adquirir recursos de forma rápida, es decir de forma adquisitiva, y que cabe esperar se establezcan a bajas elevaciones, en hábitats con alta disponibilidad de recursos, y/o a especies con síndrome asociado a la conservación de recursos, que muestran una alta tolerancia al estrés, y probablemente tengan éxito en hábitats con baja disponibilidad de recursos (Díaz et al., 2004; Porter et al., 2010; Sterck et al., 2011). El análisis del papel de la diversidad funcional y de los rasgos asociados en los patrones de dominancia debe basarse en la relación entre los valores predominantes de los rasgos funcionales y la biomasa de las comunidades a lo largo del gradiente de elevación.

1.7 Objetivos de la tesis

- 1.** Investigar las relaciones entre la biomasa de plantas leñosas arbóreas de bosques andinos y los patrones de dominancia a escala local y regional, considerando el efecto de la elevación.
- 2.** Evaluar los patrones de distribución de rasgos funcionales de especies leñosas arbóreas en relación con su abundancia, y la elevación, en comunidades forestales establecidas en los Andes.
- 3.** Analizar patrones de diversidad funcional de especies leñosas arbóreas en gradientes de elevación de bosques montanos andinos.

1.8 Estructura de la tesis

La presente tesis se estructura de la siguiente forma: Capítulo 1, que corresponde a la introducción general del trabajo. Capítulo 2, que contiene el artículo publicado, “*Contribution of species abundance and frequency to aboveground forest biomass along an Andean elevation gradient*”, correspondiente al objetivo 1. Capítulo 3, titulado “*Functional traits explain the species abundance in plant communities of Andean tropical montane forests*”, correspondiente al objetivo 2. Capítulo 4, titulado “*Patterns of forest functional diversity through a tropical Andean elevation gradient*”, correspondiente al objetivo 3. Capítulo 5, que corresponde a la discusión general. Capítulo 6 que considera las conclusiones generales del presente estudio.

Capítulo 2

2. CONTRIBUTION OF SPECIES ABUNDANCE AND FREQUENCY TO ABOVEGROUND FOREST BIOMASS ALONG AN ANDEAN ELEVATION GRADIENT

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2.1 Summary

Aims

To determine whether species that contribute most to a plot's biomass are the most abundant (high local abundance at plot scale) or the most frequent (occur the most across plots at landscape scale), or both. In the tropical Andes, these patterns may change with elevation. This study assesses the contribution to plot's above-ground biomass (AGB) of the plant community abundance pattern –the prevalence of within-plot dominant species– and the over-occurrence of regionally frequent species, in an elevation gradient.

Methods

We considered all trees ≥ 2.5 cm DBH from 446 0.1 ha plots in an Amazonia-Andes 260–4350 m elevation cline in N Bolivia. Plot AGB was calculated as the sum of AGBs for all stems contained. We grouped plots into four bins segregated by elevation and ran a bootstrap analysis over subsets of 58 random plots per bin with 100 iterations. Simpson evenness index (E_D) for all species in each plot was used as a measure for its species abundance. Values for each plot's species frequency was calculated as the mean of all species' in the plot mean frequencies across the bin (i.e. the fraction of plots where each species occurs). We used linear models to correlate plot AGB with (1) elevation and mean annual precipitation (MAP), and (2) E_D , plot species frequency and elevation. We performed all analyses at the species, genus and family levels.

Results

Plot AGB was related negatively with elevation, and thus positively with MAP, and also negatively with plot E_D and plot species frequency, all significant. Plot species abundance therefore contributes positively to explain the relationship with AGB along elevational gradients, while plot species frequency does so negatively (i.e. less frequent species contribute more to a plot's AGB across elevation). AGB, for both generic and familial levels was also significantly and negatively correlated with E_D , but not related with plot species frequency biomass at these taxonomic levels.

Conclusions

Plot AGB was mainly associated with elevation and floristic composition where species, genera and families tended to be abundant at the local (plot) scale. Species that were less frequent at the regional scale contributed with more AGB regionally, while frequency at generic and familial scales did little to explain AGB patterns. This association seems stronger at lower elevations for all taxonomic levels while decreases toward higher elevation. Our study reveals a relationship between plot structural features like C stocks –influenced by species local abundances– and the distribution of taxa across the landscape.

2.2 Introduction

Most carbon sequestration in the Neotropics takes place in tropical rain forests. These ecosystems are estimated to account for ~60% of global forest biomass and ~50% of terrestrial biomass (Houghton et al., 2009). Given the ecological importance of these forests, it is relevant to assess the contribution of species abundance patterns to a plot's above-ground biomass (AGB), hereafter referred to as an attribute of an entire plot, including all individuals within.

Montane forests in the Andes are subject to great variation in environmental factors at relatively short geographic distances, which could affect their AGB and carbon storage (Clark and Clark, 2000; Alves et al., 2010; Girardin et al., 2013; Álvarez-Dávila et al., 2017). In mountainous regions, growth is mainly constrained by physical characteristics, related to elevation such as temperature and precipitation. Both rainfall and temperature tend to diminish with elevation, although the overall reduction in rainfall with elevation is usually discontinuous due to a precipitation peak at middle elevation (Körner, 1999). In general, these climatic variables are good predictors of the variation in species composition, diversity, structure, and primary productivity along the elevation gradient (Poorter et al., 2017); mainly, high precipitation and seasonal water availability are strongly related with an increase of biomass in Neotropical forest (Álvarez-Dávila et al., 2017; Poorter et al., 2017). In turn, the number of individuals that an area can support tends to increase with primary productivity (Mittelbach, 2012).

In tropical rain forests, high scale of productivity is usually found in lowland and premontane forest, which also contain the richest species diversity likely due to warmer temperatures, and high water availability (Benner et al., 2010; Mittelbach, 2012; Álvarez-Dávila et al., 2017; Poorter et al., 2017); although in mid-elevation tropical montane forests have also been found high scales of productivity (Huaraca et al., 2013; Arellano et al., 2017). At the same time, patterns of tree species dominance vary across the elevation gradient in terms of structure (i.e. tree density, basal area, canopy height, and biomass), floristic composition, or both (Richards, 1996; Guo and Rundel, 1997). Accordingly, very large trees and lianas practically disappear at the highest elevations, where shrubs become the prevalent growth form (Janzen, 1975). In addition to lower temperatures and less precipitation, other potential environmental factors that change with elevation are steeper slopes, greater wind speed, more intense UV radiation, more cloudiness, and poorer soils with lower pH (Körner, 1999; Unger et al., 2012; Girardin et al., 2013).

In addition to environmental drivers, the diversity and composition of species may determine biomass in Neotropical rain forests (Poorter et al., 2017; Sullivan et al., 2017) on the basis of how dominant species are in a particular area. Any forest community taken at a regional scale includes a subset of species that are considerably more abundant locally, and at the same time may have a broad range of distribution, thus becoming considerably frequent across localities. These species have often been named as “common” (Brown, 1984; Pitman et al., 2001). This pattern has been supported by some studies showing that most abundant species (at the plot scale) often are also frequent at the landscape scale (Pitman et al., 2001; Pitman et al., 2012; Arellano and Macía, 2014). Thus, any species can be defined according to two components: abundance (local relative number of individuals) and frequency (occurrences across landscape). Although the reasons why a given species is abundant (“numerically”) are many and difficult to discern, some generalizations could be made: (1) numerically abundant species can be assumed to have a higher capacity to mobilize resources and assimilate energy (Hall et al., 1992), or (2) more resistance to pathogens, herbivores, or any source of frequency-dependent mortality (as pointed out by ter Steege et al., 2013), or (3) species density depends on its population long-term dynamics (balance between mortality and recruitment), for instance, by exhibiting low mortality rates (Lines et al., 2010). Regarding frequent species, they are assumed to be generalists, sharing with dominant species traits that allow

them the use of a broader range of resources across environmental gradients (Condit et al., 2000). These species-level properties could have an impact on forest-level AGB, given that local species compositions and their respective distributional patterns change: in some places “numerically abundant” species will prevail over “numerically scarce” species (or vice-versa), and/or species “frequent in the landscape” will prevail over those “infrequent in the landscape” (or vice-versa) (Pitman et al., 2001). Although in different ways, both components contribute to local plot scale AGB. Unless they exhibit very low wood density, numerically abundant species will obviously contribute more to AGB, while species that are frequent at the landscape scale are expected to have greater ability to exploit a wider range of resources (Higgins and Richardson, 1999), thus contributing to a more complete exploitation of resources within plots. The latter would increase plot productivity and AGB, an effect reinforced because frequent species are also expected to disperse more efficiently, reaching more plots. Moreover, this tendency ought to persist at the genera and family levels as well because those taxonomic groups with more abundant and/or frequent species would contribute to a biomass pattern that extrapolates to the landscape scale (ter Steege et al., 2013).

In tropical montane forests, abiotic environmental gradients that affect plot AGB are well summarized by elevation (Malhi et al., 2006), but the relative contribution of species abundance and frequency is often not discriminated when community biomass is considered as a whole. Amazonian lowland forests have very high species richness at the plot scale (alpha-diversity) (Gentry, 1988), and their pattern of dominance in terms of abundance and frequency is likely favored by environmental homogeneity (essentially soil and climate) across a rather flat landscape. When environmental filtering becomes more stringent in higher elevation forests, this pattern of species dominance turns out to be weaker (Pitman et al., 2001; Pitman et al., 2012; Trujillo et al., 2019). Therefore, species abundance and frequency could help to explain elevational patterns of AGB at the plot scale (i.e., low AGB at higher elevation) since their values decline with elevation largely due to the increase of environmental harshness and heterogeneity along the gradient (Stein et al., 2014). Despite the importance of Andean mountain forests in providing ecosystem services to the entire region (Körner, 1999), intimate knowledge of the biotic and abiotic factors determining biomass is scant (Gentry, 1988; Chave et al., 2003; Unger et al., 2012; Girardin et al., 2013; Álvarez-Dávila et al., 2017). Most studies have explored the relationship between biomass and structure of the tropical forest

focusing on lowland forests (Clark and Clark, 2000; DeWalt and Chave, 2006; Anderson et al., 2009), but there are fewer studies that consider the role of dominant species on biomass in tropical montane forests (Fauset et al., 2015), much less on this relationship across elevation gradients.

Here, we aim to investigate the relationship between AGB at the plot scale and the dominance patterns (abundance, frequency) of species, genera and families across an Amazon-Andes elevation gradient. We also analyzed data to taxonomic levels above species because dominance patterns have sometimes been assessed at the genus and family levels (ter Steege et al., 2013). AGB was calculated from allometric functions based on stem diameter, height and wood density (Kebede and Soromessa, 2018; Chave et al., 2015). We consider dominance value as a stand (plot) attribute, which is a function of its tree community assemblage. While plot AGB is expected to decrease with elevation, we hypothesize that the effect of elevation on AGB will be smaller in plots where dominance is higher.

Our specific hypotheses thus are: 1) stand AGB, estimated from trees contained in a plot, decreases as MAP decreases and elevation increases; 2) the two components of dominance —abundance and frequency, both considered as stand attributes— are positively correlated with AGB, which also makes elevation and AGB be negatively related; 3) the effect of both components of plot-scale dominance on AGB across elevation is consistent at different taxonomic levels: species, genus and family.

2.3. Methods

2.3.1. Study area

We analyzed plot data from Parque Nacional Madidi and surrounding areas, a region 18,854 km² in northern Departamento de La Paz, Bolivia. The study was carried out in this tropical region, between 14°33' 52"S, 67°40' 24"W and 14°36' 26"S, 69°08' 52"W, which includes large swaths of the Bolivian Amazonia and the Andes mountains, ranging from lowland rain forests and dry savannas below 200 m a.s.l., to cloud and mid to high elevation montane forests, to summits above 5000 m with subnival vegetation (Fuentes, 2005; Forrest et al., 2008) (Fig. 1).

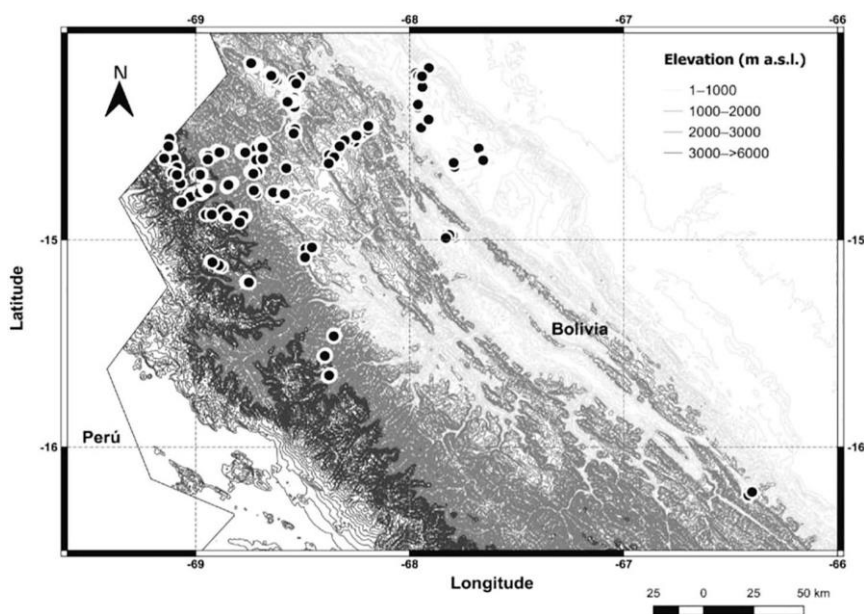


Fig. 1. Study area in the Madidi region, Bolivia. Points show study plots.

The Madidi region encompasses large physiographic units that include the Cordillera Oriental and the Subandino mountain systems, with rainy and dry bioclimates. Precipitation varies with elevation and topography, from the mean annual 2,335 mm of the Amazon lowlands (Navarro et al., 2004) to the broad 100–3,500 mm range of Andean uplands. Annual mean temperature ranges from 25 °C in the eastern lowlands to –2.5–0.5 °C near the summits (Fuentes, 2005).

Data was obtained from 446 inventories of 0.1 ha forest plots carried out by various researchers between 2001 and 2011 as part of the Madidi Project (<https://madidiproject.weebly.com/>). The location of plots ranged from the Amazonian lowlands ca. 260 m a.s.l. to the high elevation Andes up to 4,350 m, with most plots between 1,000 and 3,000 m. Inventory data consisted of tree height and diameter at breast height (DBH, 130 cm above ground) of all woody individuals (≥ 2.5 cm DBH), including palms, tree ferns and lignified Poaceae (Arellano et al., 2016), while lianas were excluded from the analyses. All stems of the multiple stemmed individuals were accounted only once for the analysis. The height of each stem, necessary to estimate biomass of individuals, was estimated visually, with some prior training or experience.

The dataset contained a total of 123,856 individuals belonging to 2,060 species (including morphospecies), 527 genera, and 126 families. Vouchers were deposited at the Herbario

Nacional de Bolivia in La Paz (LPB, with duplicates at the Missouri Botanical Garden, MO). Analyses were conducted separately at three levels of taxonomic resolution: species, genus and family.

The mean annual precipitation (MAP) was obtained from the WorldClim-Global Climate Data (version 2.0, Fick and Hijmans, 2017), at a spatial resolution of ca. 1 km².

2.3.2. Analyses

To estimate plot AGB we used allometric measures that include tree height, diameter and wood density, using the equation proposed by Chave et al. (2015):

$$AGB = 0.0673(\rho Di^2 H)^{0.976}$$

where ρ is wood density (g/cm³), Di is diameter (cm) and H is tree height (m). Di and H were measured for each individual within each plot, while data for wood density were obtained from the Global Wood Density Database (Zanne et al., 2009). Since measurement of wood density was not available for many species, we assigned those the mean wood density of congeners that have one. We then calculated plot AGB as the sum of all stems' biomass within the plot.

To determine the species abundance at the plot scale we estimated the prevalence of within-plot dominant species by calculating the Simpson Evenness index (E_D), applied to the number of stems of all species present in each plot (plot species evenness). A high value of the evenness index indicates that species are equally abundant (none dominates), while a low value indicates that a few species account for most of the stems (i.e., high co-dominance of those few). Plots whose community assemblage contain species with high abundance will have low E_D values. This indicator allows to relate AGB with the degree of occurrence of many individuals or stems of a few species, or alternatively with the degree of plot homogeneity in terms of species relative abundance.

To calculate E_D , we first estimated the Inverse Simpson index (D) as the inverse of the sum of the squared proportions of every taxon (p_i).

$$D = \frac{1}{\sum_{i=1}^S P_i^2}$$

E_D was calculated as the quotient between D and the maximum value of D , corresponding to species evenly distributed in the community, where S = species richness.

$$E_D = \frac{D}{D_{max}} = \frac{1}{\sum_{i=1}^S P_i^2} \times \frac{1}{S}$$

We used a bootstrap analysis using 100 iterations to determine plot species frequency variable in order to minimize the asymmetry between the very many plots from the dataset from lowland Amazonian forests and the very few from the uplands. We segregated the total 446 plots into four bins corresponding to four elevation bands: 260–1000 m, 1000–2100 m, 2100–3200 m and 3200–4400 m, where the bin with the least plots (those above 3200 m) contained 59 plots. So, subsets of 58 plots were randomly sampled for each elevational bin; then, 100 iterations of this procedure were conducted.

To determine plot species frequency, we estimated the prevalence of frequent species across plots within a bin by calculating the proportion of total plots (58 randomly sampled plots in each elevational bin) in which each species occurred. We then used the average value from all species present in the plot. A high value for plot species frequency means that such plot has many species that are frequent at the landscape scale. The same procedure was applied when estimating plot ED and plot taxon frequency at the genus and family levels by pooling the values for all species belonging to the same genus and to the same family, respectively.

To test the first hypothesis, which establishes that stand AGB decreases with the MAP associated with greater elevation, we used univariate linear models to explain the relationship between plot AGB with elevation and MAP separately. To test the second hypothesis, which relates the plot AGB with the patterns of species abundance and frequency at the plot scale, we used general linear models, with plot AGB as the response variable and plot elevation, ED (high local abundance) and plot species frequency (high occurrence of species on plots across landscape) as predictor variables. The same linear models were used for subsequent analyses at the genus and family levels in order to answer the third hypothesis.

The statistical linear models were assessed with the Akaike information criterion (AIC) for selecting the better fitting linear model (lower AIC). We also used the variance inflation factor (VIF) to detect multicollinearity between variables and then selected the linear models with lower VIF. AGB data were square-root-transformed to meet the assumptions of normality. All analyses were carried out in R (R Core Team, 2018).

2.4 Results

Among the 123,856 recorded individuals, 3,010 belonged to *Oxandra espintana*, 2,828 to *Polylepis pepeii*, 1,800 to *Hedyosmum racemosum*, and 1,700 to *Iriartea deltoidea*. The rest of species each had <1,500 individuals throughout the dataset. For genera, we registered 7,597 individuals belonging to the genus *Miconia*, 4,411 to *Polylepis*, 3,338 to *Weinmannia*, and 3,135 to *Trichilia*; the rest of genera had each fewer than 3,000 individuals. Melastomataceae was the family with most individuals (9,225), followed by Rubiaceae (7,834), Arecaceae (6,239) and Myrtaceae (6,117); the rest of families had each fewer than 6,000 individuals (Supplementary material, Table 1).

The species that occurred in the most plots were *Euterpe precatoria* (125 plots of the total 446), *Alchornea glandulosa* (120), *Tapirira guianensis* (115), *Iriartea deltoidea* (104), and *Guatteria punctata* (102); the rest were found in fewer than 100 plots. The genera present in most plots were *Miconia* (267 plots), *Ocotea* (234 plots), *Piper* (216 plots), *Inga* (214 plots), and *Myrcia* (202 plots); the rest were found in fewer than 200 plots. The families that occurred in most plots were Myrtaceae (336 plots), Lauraceae (329 plots), Rubiaceae (326 plots) and Fabaceae (308 plots); the rest occurred in fewer than 300 plots (Supplementary material, Table 1).

We found a total of 8542.211 Mg of AGB over all the plots. Plot AGB ranged between 0.16 and 76.14 Mg (mean = 19.15, SD = 11.3). The species that contributed the most to plot AGB, throughout the whole elevation gradient, were *Anadenanthera colubrina* (315.57 Mg), *Schinopsis brasiliensis* (147.91 Mg), *Pseudolmedia laevis* (105.12 Mg) and *Pouteria bilocularis* (103.89 Mg). The genera that contributed with the most AGB throughout were *Anadenanthera* (315.57 Mg), *Polylepis* (225.07 Mg), *Ocotea* (222.31 Mg) and *Pouteria* (216.94 Mg). We found Fabaceae (1044.97 Mg), Moraceae (676.49

Mg), Lauraceae (506.89 Mg) and Malvaceae (341.77 Mg) to be the families with greatest AGB.

2.4.1 Relationships between plot AGB, elevation and MAP

Plot AGB was significantly and negatively correlated with elevation ($R^2 = 0.39$, $P < 0.001$, Fig. 2). There were significantly positive linear relationships between plot AGB and MAP ($R^2 = 0.27$, $P < 0.001$). Also, we found a negative relationship between MAP and elevation ($R^2 = 0.85$, $P < 0.001$) (Supplementary material, Fig. 1).

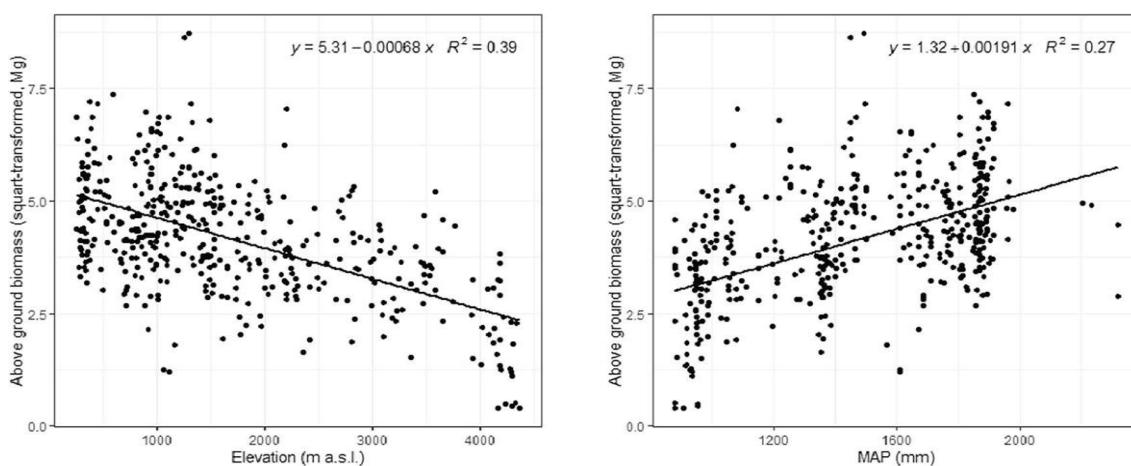


Fig. 2. Linear regressions relating plot AGB with elevation (a): $R^2 = 0.39$, $P < 0.001$, and MAP (b): $R^2 = 0.27$, $P < 0.001$.

2.4.2 Relationships between plot AGB, elevation and dominance

Various models were considered before determining that the model: elevation, E_D and frequency, made the best predictor. There was a significant negative linear relationship of plot AGB with elevation and with E_D at all three taxonomic levels: species, genus and family (Fig. 3a, b, c; Table 1). Thus, along the elevational gradient, plots with higher AGB contained few taxa contributing with the most individuals. The negative significant interaction between AGB and E_D indicates that plots with greater AGB tended to contain individuals from species, genera and families that were abundant. In other

words, there are some within-plot dominant taxa that contribute positively to the AGB. AGB was also negatively correlated with plot species frequency (Fig. 3d, Table 1). This means that there are plots with higher AGB that contain fewer species that occur frequently at the landscape scale, although this result is not consistent at the generic and familial levels.

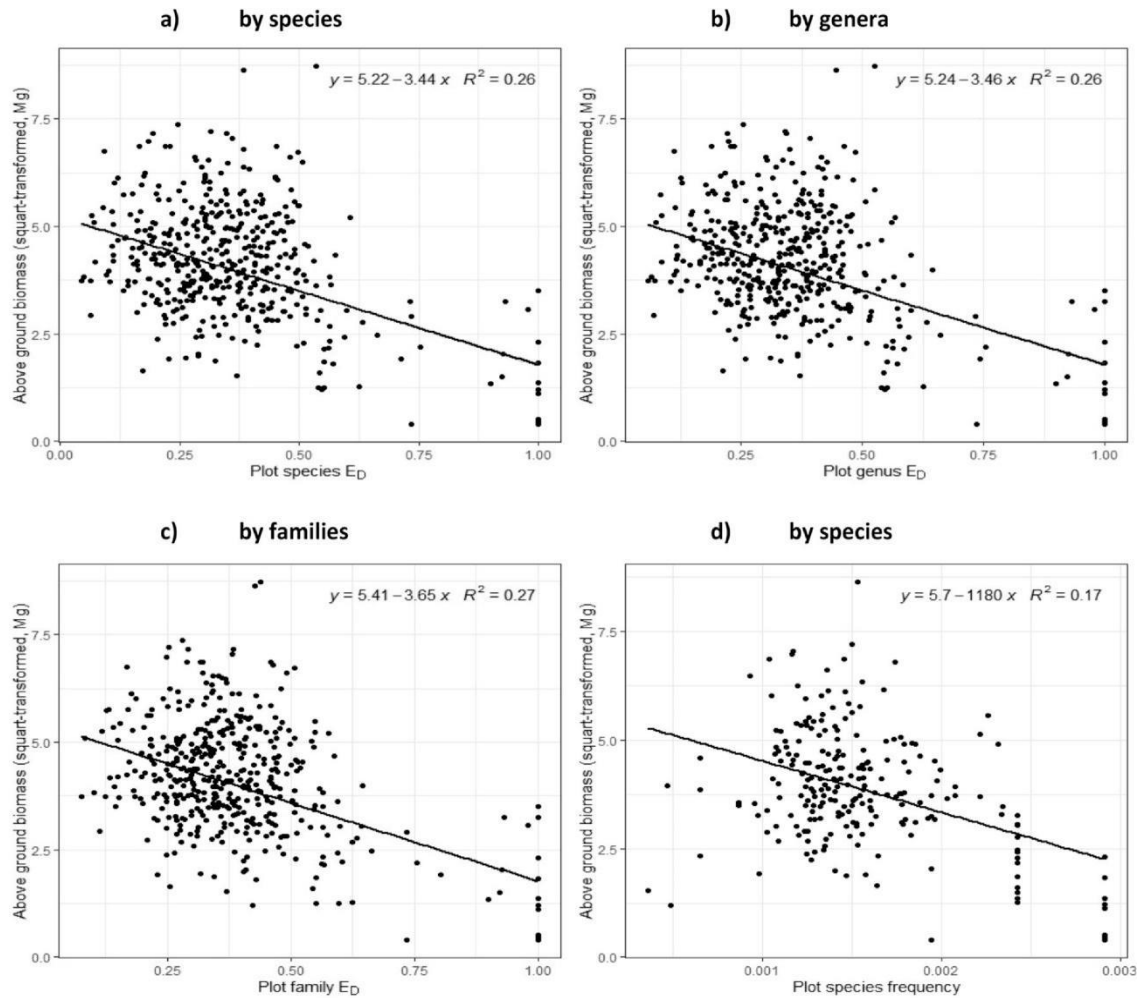


Fig. 3. Linear regressions relating the AGB with plot-scale species E_D at the a) species, b) genus, and c) family level; d) relationship of AGB with plot-scale species frequency.

Table 1.- Statistical summary of the general linear model results for plot AGB and elevation, plot species evenness (E_D) and plot species frequency (Frequency) as predictors. The models were also applied to the genus and family levels. Statistically significant in bold ($P < 0.05^*$; $P < 0.01^{}$; $P < 0.001^{***}$). E: regression coefficient.**

Sqrt Biomass (Mg)		
	E	P
Species		
Elevation	-0.0005	0.000***
ED	-1.048	0.053*
Frequency	-445.278	0.039*
R ² (adjusted) = 0.44		
Genus		
Elevation	-0.001	0.000***
ED	-1.389	0.005**
Frequency	66.414	0.216
R ² (adjusted) = 0.42		
Family		
Elevation	-0.001	0.000***
ED	-1.749	0.000***
Frequency	58.874	0.07
R ² (adjusted) = 0.43		

2.5 Discussion

In this study we show that above-ground biomass, one of the most important structural properties of tropical forests, is negatively correlated to elevation and, as expected, is greater where precipitation (MAP) is higher, (i.e., plots in the rainier Amazonian lowland forests had greater ABG than plots from montane forests). The Andean elevational gradient exhibits the common pattern of a gradual change in forest structure as elevation increases, paralleled with a general decline in AGB and woody species richness (Girardin et al., 2013; Álvarez-Dávila et al., 2017), although often hump-shaped (Trujillo et al., 2019; de la Cruz-Amo et al., 2020). The relationship between climate variables and forest primary production (Körner, 1999; Reich et al., 2014; Álvarez-Dávila et al., 2017) is largely determined by water availability, one of the variables most responsible in

determining forest structure and carbon stocks (Álvarez-Dávila et al., 2017; de la Cruz-Amo et al., 2020). Unsurprisingly, we found the greatest number of stems –and the highest values of plot AGB– in the rainier lowlands. According to the second hypothesis, the two components of dominance —abundance and frequency— were significantly correlated with AGB, which makes them relevant to elucidate the pattern of AGB, in our case along the elevation gradient. The significant negative relationship of AGB with E_D , for all taxonomic levels, showed that plots whose woody plant assemblage contains some species that are locally abundant, contribute more to the AGB and productivity of an area (Fauset et al. 2015). AGB is also negatively correlated with plot species frequency (presence of species with high occurrence across an elevational band), meaning that to landscape scale few species contributed with greater biomass. This negative effect of frequency on AGB, however, is present only at the species but not at the generic and familial levels.

In this study we show that plots with less frequent species attain more AGB than plots containing species that are widely distributed. That could mean that species with larger stem sizes –one may argue– are perhaps less frequent, –specifically in the lowlands– but still, due to their large size may be contributing disproportionately to those few plots where they are present. According to Fauset et al., 2015, both, abundance of species and their maximum stem size are the principal predictors of species contribution to regional biomass and productivity (Fauset et al., 2015).

As our study shows, the presence of plots dominated by abundant species –mainly those in low-elevation forests–, with higher AGB, is likely the result of relative environmental homogeneity (Pitman et al., 2001; ter Steege et al., 2013; Fauset et al., 2015). In low-elevation tropical forest a few abundant species have been found to account for most of the biomass to these forests, contributing to their dominance in the landscape in the same way that frequent species do (Pitman et al., 2001; ter Steege et al., 2013; Fauset et al., 2015). We hypothesize that many of these species are distributed according to similar ecological requirements, including edaphic and climatic factors (Brown, 1984; Pitman et al., 2001; ter Steege et al., 2013). We found few studies that assessed the contribution of common taxa to community biomass at regional or plot scales. Fauset et al. (2015) showed that few species account for most biomass regionally, this is mainly because they are more common, and they only contribute to high AGB in plots if they are common regionally and/or have high wood density. There is evidence that the stem density

increases toward high elevations (Culmsee et al., 2010), however the biomass decreases in these areas. Then, according to Moser et al. (2008) it is likely that the highest biomass contribution does not depend on abundance but also on structural attributes such as wood density, basal area or plant height. Then, commonness in plots could also lead to dominance in the landscape (ter Steege et al., 2013).

The greater AGB at low elevations may be explained not only by the general trend of tropical lowlands harboring species that are more common, but also by those with large individuals (Pitman et al., 2001; Ghazoul and Sheil, 2014; Mittelbach, 2012; DeWalt and Chave, 2006). The gentle topography of the lowlands favors the establishment of large trees (Valencia et al., 2009), less present in the steep slopes of mountains. Nutrient limitation due to limited soil microbial activity, low sunlight, reduced transpiration and strong winds result in the smaller but multiple-stem trees of highland forests that may end up containing greater biomass (Leuschner et al., 2007; Ghazoul and Sheil, 2014). The overall association between common species and AGB could therefore be better explained by the existence of species by the number of individuals representing them locally than for the widely distribution that they may have at the landscape scale, overall in lowlands; while, the highlands AGB is most dependent on small-sized multi-stemmed trees and shrubs (Janzen, 1975). We found that the observed negative relationships between plot taxon frequency and plot AGB did not carry over at the genus and family taxonomic levels, probably because there are many genera represented by few common species, or families represented by few common genera. Palms are represented by several abundant species in Madidi and most Amazonian forests, but with few genera, as the *Arecaceae* that contribute greatly to the number of stems in a given plot, or *Iriartea* that is one of the genus found most predictably in any plot of *terra firma* forest in Amazonia (Pitman et al., 2001; Fauset et al., 2015), probably *Arecaceae* is one of the families with the most overall biomass.

It is noteworthy that two palm species from those forests, *Iriartea deltoidea* and *Euterpe precatoria*, were mostly responsible for the family pattern we observed due to their broad distribution and total AGB (90.78 Mg and 26.54 Mg, respectively).

One explanation for this taxonomic pattern in relationship to their contribution to AGB is that for certain families with a low speciation rate, the few extant species would tend to have broad distributional ranges (Domínguez-Lozano and Schwartz, 2005). In tropical

rainforests, although high tree diversity implies a low relative density of individuals for most species (Huston, 1979; Condit et al, 2000), some genera and families may dominate in number of individuals, so there will be genera and families with more specificity for a particular environment and thus show higher local abundance.

At the genus level, we found ubiquitous genera such as *Ocotea* (222.31 Mg), *Pouteria* (216.94 Mg), *Pseudolmedia* (185.14 Mg), *Miconia* (166.79 Mg) and *Tetragastris* (98.88 Mg), that accumulated large AGB, mainly because of their many large-sized individuals. In the uppermost Andean highlands, on the other hand, many plots are strongly dominated by any number of species of *Polylepis* (Gareca et al., 2010), each contributing greatly to plot AGB with their many stems.

It is also likely that AGB of tropical forests may be determined by species traits and shifts in the structure and composition on species with elevation (Culmsee et al., 2010), because there may be structural features that can be phylogenetically conserved (Moser et al., 2008). Then will be interesting to assess the traits of the taxa in relation with community proprieties in elevational gradients.

As a conclusion, we found that in the Madidi region AGB values, as expected, decreased towards higher elevations, thus increasing with the higher MAP of low elevations. The more favorable climatic conditions of wet low elevations facilitate spatial patterns of density distribution of taxa that are very different from montane forests. These biotic and abiotic conditions allow for low elevation forests to be most productive. From our results we found AGB—a rough proxy for productivity—to be associated with species that occur most abundantly within plots, particularly at low elevations. Thus, a few species with many individuals at the local scale and with narrow distribution along elevational gradients could contribute the most to total forest biomass and productivity. The pattern is particularly important for lowland forests, which accumulate the largest aboveground reserves of carbon (Ghazoul and Sheil, 2014; Chave et al., 2015; Esquivel-Muelbert et al., 2018). To Fauset et al. (2015), half of the carbon stock and half of the woody plant productivity in Amazonia are the contribution of just 1% of all species. In terms of biomass, these few common species at the local and few at the landscape scale provide a large proportion of ecosystem services to the region, such as regulation of regional and global climate by sequestering CO₂, by microclimate regulation of moisture and temperature, and by providing shade and shelter (Gaston, 2010; Daba and Dejene, 2018).

2.6 Acknowledgements

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Capítulo 3

3. FUNCTIONAL TRAITS EXPLAIN THE SPECIES ABUNDANCE IN PLANT COMMUNITIES OF ANDEAN TROPICAL MONTANE FORESTS

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3.1 Summary

Species functional traits may be involved in the community assembly of montane forest by determining species dominance. We assessed whether tree species functional trait values are related to species abundance in plots distributed along two elevational gradients in the tropical Andes (the Bombuscaro, Ecuador and Río Abiseo, Peru locations). We analysed a total of 60 inventories of woody species > 2.5 cm DBH from 0.1 ha plots sampled in those gradients. Species were characterized by in situ measures of wood density (WD), specific leaf area (SLA), leaf thickness (LT) and height (H). We used a Community Assembly by Trait Selection (CATS) model for each elevational gradient, considering species' abundance (mean number of stems per plot for each species in each plot) as response variable, and elevation and the four functional traits as predictor variables. Interactions between predictor variables were also considered.

Species abundance was significantly related with functional traits along both elevational gradients. The most abundant species exhibited lower WD and occurred at lower elevations in Bombuscaro, while the opposite was observed in Abiseo. Species abundance in the uplands of both sites was related to higher LT. Taller species were more abundant at lower elevations in Bombuscaro, while in Abiseo abundance was also higher among species with small trees at low elevations. Lower values of SLA were significantly related to greater species abundance only in Abiseo.

Mainly LT, H and WD are driving patterns of relative abundance of tree species within communities of Andean forest, and this effect varies from premontane to higher elevation forests in the elevational gradient. The important PFTs to determine species abundance pattern, could be those associated with leaves as LT and SLA (only in Abiseo), and stem as WD and H. Last, the PFTs contribute to the co-dominance of species in terms of biomass and this supports the hypothesis of trait-based niche assembly.

3.2 Introduction

Plant functional traits (PFTs) are characteristics inherent to a given species that presumably affect the growth, survival and reproduction of individuals and species (Violle et al., 2007; Pérez-Harguindeguy et al., 2013). PFTs are useful to better

understand the ecological and evolutionary processes within populations, communities and ecosystem (Shipley et al., 2012; Sonnier et al., 2012; Warton, et al., 2015) at different environmental scales. For instance, the variability of PFTs between species to some extent drives community assemblage (Shipley et al., 2006; Shipley et al., 2012; Sonnier et al., 2012; Strahan et al., 2018), as well as ecological processes related to resource use, and the subsequent ecosystem services (Kattge et al, 2011; Pérez- Harguindeguy et al., 2013).

Differential species abundance is a major feature of plant communities, which may eventually result in the dominance of some species. Two inherent components of species dominance are their local abundance and frequency across the landscape. In tropical rain forests, a pattern of dominance, named “co-dominance” (Pitman et al., 2001), has been recognized in both, lowland (Pitman et al., 2001; ter Steege et al., 2013) and higher elevation (Macía and Svenning, 2005; Arellano and Macía, 2014; Sandoya et al., 2021) forests. This co-dominance pattern implies that there are species that are, at the same time, abundant at the small spatial scale (i.e., plot) and frequent at the landscape scale. This pattern should be particularly present in regions that are relatively homogenous in environmental conditions, particularly regarding soils (Pitman et al. 2012). Although the causal factors for this pattern occurring at plot and landscape scales have not yet been fully identified, PFTs have the potential to be a contributing factor (Violle et al., 2007; Shipley et al. 2012). Although PFTs have been widely used to assess species ecology (f.e. Westoby et al., 2002), their ability for assessing species dominance patterns has not been fully explored (Pitman et al. 2001).

Trait-based models have been proposed to explain community assembly, especially in relation to species dominance, by assessing those biological attributes that could influence their fitness in a given environment (Warton et al., 2015; Strahan et al, 2018). Therefore, some PFTs can be identified as predictors for community assembly (Violle et al., 2007). Certain key PFTs may be particularly informative to explain ecological strategies and abundance patterns of plant species (Shipley et al., 2012; Warton, et al., 2015). Leaf traits such as specific leaf area (SLA) and leaf thickness (LT) relate to photosynthetic efficiency and resource requirements through species' life history, thus can be associated with species distribution and abundance (Aranda et al., 2004; Hoffmann et al., 2005). Wood density (WD) relates to resource allocation to structural support of plants, and ultimately to the stem carbon content. Plant height (H) relates mainly to the competitive ability for

light, and is also a proxy of plant size, which informs of the plant's ability to capture and store resources (Hoffmann et al., 2005; Richardson et al., 2013).

Accordingly, within communities, dominant species are expected to share similarities in their key PFTs relative to other species, provided these traits are responsible for a species success in dealing with resource availability and other conditions. Therefore, the adoption of distinct PFT values by a species could explain its distribution and persistence in a given environment (Maracahipes et al., 2018). So, these characteristics in a dominant species may act as potential indicators of its ability to successfully establish and spread widely (Shipley et al., 2006; Shipley et al., 2012; Warton, et al., 2015). Indeed, variation in the distribution of the biomass of dominant species across the elevation gradient (Sandoya et al., 2021) may be related to their PFTs. In turn, there may also exist modifications in PFT values when communities change their composition along environmental gradients. Not surprisingly, correlations between PFTs and environmental variables have been extensively explored with the aim of describing and interpreting plant strategies – in terms of plant fitness (Wright et al., 2004) –, in response to specific environmental filtering. For example, leaf size and SLA decline along gradients of decreasing moisture and/or nutrient availability (Cunningham et al., 1999; Ackerly et al., 2002), or SLA, LT and WD increase as temperatures increase (Bañares-de-Dios et al., 2020).

Andean tropical montane forests are subject to great variations in environmental factors at short distances, which could affect the distribution of species and the values of plot PFTs along elevation gradients. In these areas, dominant species could also have broader distribution at different elevations because they exhibit suitable trait values. Nevertheless, up to now the relationship between PFTs and species abundance has been seldom investigated in Andean wet forests. The main goal of this research is to assess the relationship between the values of WD, SLA, LT and tree height [H] and the plot-level abundance of species within forests across Andean elevational gradients. For such purpose, we used the mathematical model CATS (Community Assembly by Trait Selection) that reveals *how* and *why* species may differ in their distribution, based on their PFTs (Shipley et al 2006; Warton et al., 2015).

We address the following questions: 1.- Is there a relationship between tree species PFT values and their abundance? Specifically, we hypothesize that WD, SLA, LT and H may be relevant traits determining abundance of plant species in tropical montane forests.

2.- Are PFTs associated to abundance changes across the elevational gradient? We hypothesize that the environmental gradient acts as a filter for PFT values in abundant species, specifically namely, that elevation is a determinant in the distributional range of abundant species and PFTs.

3.3 Methods

3.3.1 Study area

The study was conducted using data from 60 plots from two sites in the Andes region. Plots were distributed along two elevational gradients: one located in the Río Bombuscaro basin within the Parque Nacional Podocarpus (Bombuscaro, hereafter) in the Andean Cordillera Real of southern Ecuador; the other one in the Parque Nacional Río Abiseo (Abiseo, hereafter), in the Eastern slope of the Andes of northern Peru (Figure 1). The forests from these localities have different structure relative to elevation; for instance, the treeline in Bombuscaro is lower than in Río Abiseo (Young and Leon, 1988; Bañares-de-Dios, per. com., 2021). Both, Abiseo and Bombuscaro have similar average temperatures that range from 12 to 18 °C, and annual precipitation from 1000 to 5000 mm (Young and León. 1988; Sierra, 1999).

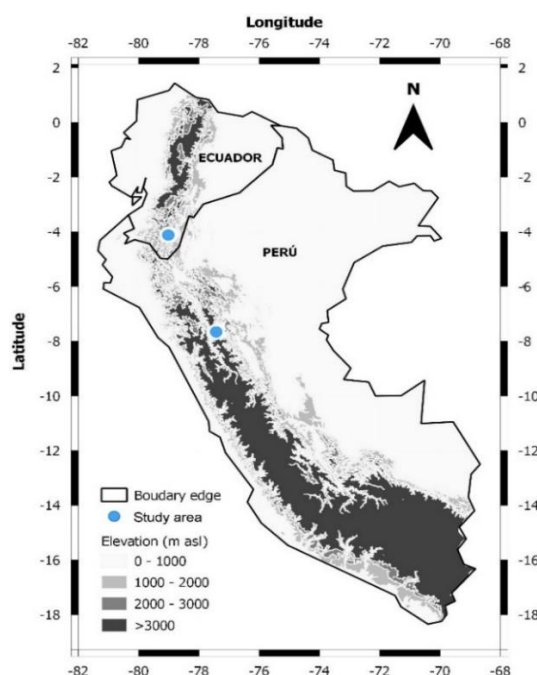


Figure 1.- Study area. Blue dots indicate the location of Podocarpus National Park: Bombuscaro (Ecuador) and Río Abiseo National Park (Peru).

3.3.2 *Sampling design*

We used a dataset from the BOTROPANDES project, consisting of 60 inventories of woody species (plants > 2.5 cm DBH) from 0.1 ha (50x20 m) plots surveyed along two elevational gradients (30 plots in each site: Bombuscaro, Ecuador, and Abiseo, Peru), in which three elevational belts were recognized at each site: 745-1245 m, 1800-2200 and 2674-2980 m a.s.l. (Bañares-de-Dios et al., 2020). The dataset included in Bombuscaro a total of 10838 stems belonging to 840 species (including morphospecies), 338 genera and 87 families, and in Abiseo a total of 11600 stems belonging to 544 species (including morphospecies), 286 genera and 101 families. Only those morphospecies with functional trait data were used in the analysis.

For each species, we considered the mean values of WD, SLA, LT and H. Branch wood density was used as a proxy for WD. Measurements were obtained from segments of branches ca. 10 cm long (as cylindrical as possible), whose diameter (after stripping the cortex) and length were measured in the field with a calliper to determine the fresh volume. Branch wood density was calculated dividing fresh volume by dry mass after drying the samples at 80°C for 48–72 h (Bañares-de-Dios et al., 2020). SLA was calculated from five leaves as the ratio of leaf area (measured with a portable laser leaf area meter CI-202, CID Bio-Science, Camas, Washington, USA) to leaf dry mass (after drying at 80°C for 48 h). LT was measured in the field with a digital caliper, in three leaves of the same tree than SLA. H (height of sampled individual) was estimated visually (Bañares-de-Dios et al., 2020). These mean measures of PFTs were obtained averaging values from one, three or four individuals from each species.

3.3.3 *Analyses*

For each site we calculated the mean number of stems per plot for each species as an estimation of species' abundance. Then we used a Community Assembly by Trait Selection (CATS) model for each site (Bombuscaro and Abiseo) to assess the relationship between species' abundance and PFTs along the elevational gradients. This analysis is a General Linear Model that considers the maximum entropy (maximum likelihood) and a binomial regression (Warton, et al., 2015). In our case, the CATS analysis included in a single model the four PFTs (LT, SLA, WD and H) and elevation as predictor variables, and the mean number of stems of each species (as an estimation of species abundance) as

the response variable. The interactions between elevation and each functional trait were also included. We reapplied the model for each site. We ran this analysis with a negative binomial regression because it gave the lowest value according to a Bayesian Information Criterion (BIC) diagnostic test, showing a better fit for the model. Significance p-values were calculated using 1000 resampling iterations. All statistical calculations were performed in R (R Core Team, 2020); we used the “mvabund” package and “manyglm” function for the analyses, and the latticeExtra package with “levelplot” function for plotting the results.

3.4 Results

In Bombuscaro we obtained PFTs and abundance data for a total of 657 species, with the most abundant taxon being an unidentified MELASTO:Gen_ignot 1indet.sp. (209 stems), followed by *Weinmannia fagaroides* (199 stems), *Myrsine sodiroana* (193 stems), *Dacryodes peruviana* (169 stems) and *Ilex andicola* (154 stems). In Abiseo we obtained data for PFTs and abundance for a total of 484 species; the most abundant being: *Piper* sp. (948 stems), *Hedyosmum racemosum* (646 stems), *Piper crassinervium* (542 stems), *Piper areolatum* (352 stems) and *Palicourea perquadrangularis* (302 stems). The composition of the abundant species differed between lower (745-1245 m a.s.l.), middle (1800-2200 m a.s.l.) and higher elevations (2674-2980 m a.s.l.), for both sites (Supplementary material, Figures 1 and 2).

In both sites, the effect of WD, LT and H on species abundance was significant along the elevational gradient. Lower SLA was significantly related to greater species abundance only in Abiseo. Moreover, the interactions between WD, LT and H and elevation significantly explained species abundance in both Bombuscaro and Abiseo. The interaction between SLA and elevation was not significant for any site.

Species with low values of WD were more abundant in Bombuscaro, where the most abundant species occurred at lower elevations. In contrast, in Abiseo, species abundance was related with greater WD values, while the most abundant tended to be from higher elevation forests (Figure 2).

In both study sites, species with greater LT exhibited greater abundance, particularly in the uplands (Figure 3), and species abundance was greater when plants were taller at

lower elevations (Figure 4). In Abiseo, species abundance was also greater when smaller plants occurred at higher elevations (Figure 4).

Table 1.- Results of the CATS model for the Bombuscaro and Abiseo sites, showing the relationship between species abundance and PFTs (WD, SLA, LT and H) and elevation.

	BOMBUSCARO		ABISEO	
	<i>Coefficients</i>	<i>P-value</i>	<i>Coefficients</i>	<i>P-value</i>
Intercept	4.032	< 0.001	1.048	0.193
WD	-7.235	< 0.001	3.684	< 0.001
SLA	-0.035	0.424	-0.067	0.002
LT	-14.567	< 0.001	-13.811	< 0.001
H	0.354	< 0.001	0.153	< 0.001
Elevation	-0.002	< 0.001	0.001	0.067
WD:Elevation	0.004	< 0.001	-0.004	< 0.001
SLA:Elevation	0.00002	0.237	0.000003	0.761
LT:Elevation	0.007	< 0.001	0.008	< 0.001
H:Elevation	-0.0003	< 0.001	-0.0001	< 0.001

P-value calculated using 1000 resampling iterations.

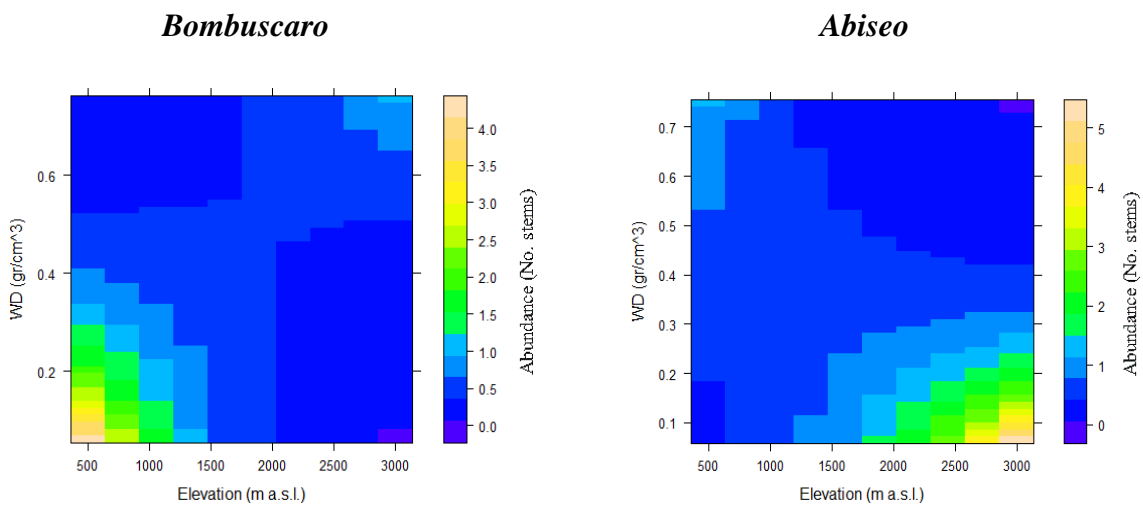


Figure 2.- Level plot graphics showing the species abundance (number of stems) in relation to WD along the elevational gradient in Bombuscaro and Abiseo.

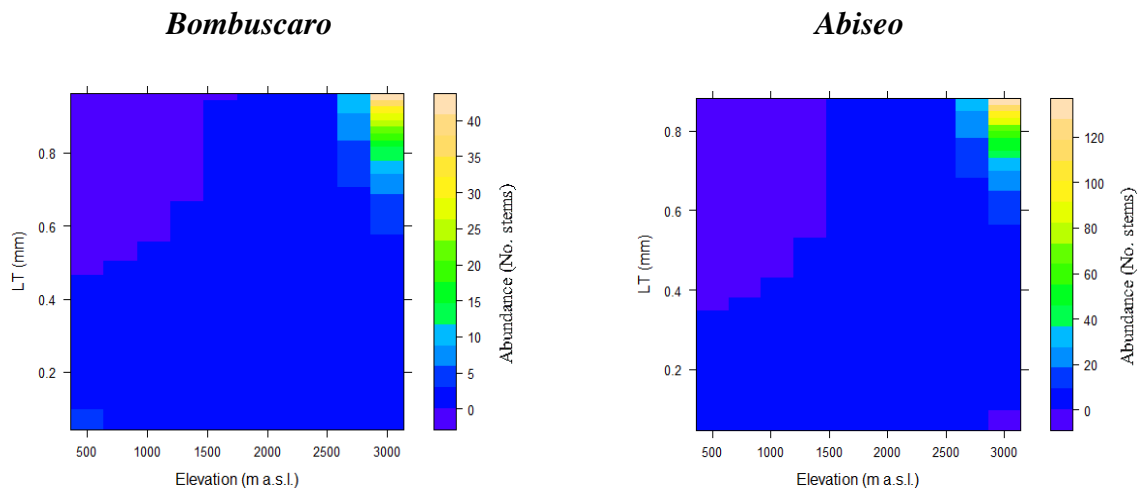


Figure 3.- Level plot graphics showing the species abundance (number of stems) in relation to LT along the elevational gradient in Bombuscaro and Abiseo.

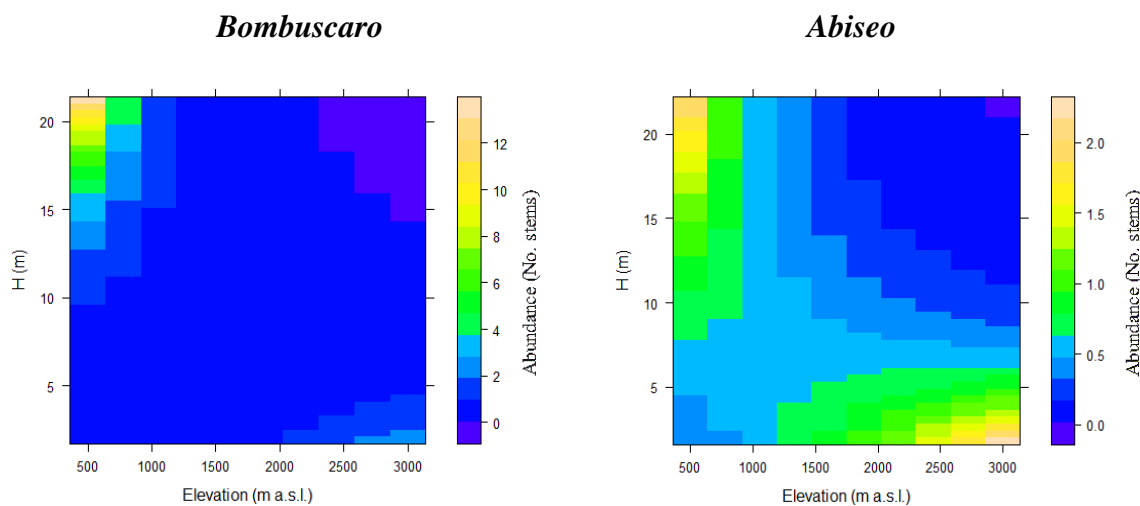


Figure 4.- Level plot graphics showing species abundance (number of stems) in relation to H along the elevational gradient in Bombuscaro and Abiseo.

3.5 Discussion

Our results showed that relevant PFTs, such as LT, H and WD, correlated with the distribution pattern of species abundance along the Andean elevational gradient, from premontane to higher elevation forests. The overall similar patterns found in the two studied sites suggest that community filtering associated to PFTs along elevational

gradients are consistent, despite local variations in floristic composition, diversity, treeline and successional stage.

Although the presence of species dominance could be the result of stochastic events, we show as the PFTs could explain the commonness patterns of species in montane forests. Similar results were found in Cornwell and Ackerly (2010) and Lisner et al. (2021), who evidenced that species abundance patterns are shaped by intraspecific trait variability, especially in relationship with H and SLA. In our research, we found that the important PFTs to determine species abundance pattern, could be those associated with leaves as LT and SLA (only in Abiseo), and stem as WD and H.

Leaf traits are key to understand the relations between carbon assimilation, water assimilation and energy balance (Cunningham et al. 1999; Fonseca et al. 2000; Ackerly, et al. 2002). Furthermore, the leaf PFTs have been found to relate with species abundance at the local scale (Cornwell and Ackerly, 2010; Warton et al., 2015; Lisner et al. 2021). In gradients of elevation, the leaves of trees tend to change their morphology, suggesting adaptive responses to different environmental conditions such as temperature, wind exposure, and nutrient and soil moisture availability (Körner, et al. 1986; Körner, 2012; Pandey et al. 2021). Thereby, we found a positive relationship between species abundance and LT, which increased with elevation in both studied localities. This pattern agrees with other studies in which the greater values of LT were related with decreasing leaf area and SLA values at high elevation. The leaves in species of higher elevations are exposed to harsh environmental conditions, higher radiation levels, lower temperatures, and strong winds (Körner, 2012). The higher values of LT correspond to greater mesophyll tissue thickness and to an increase in stomatal density; these morphological features may allow leaves to have relatively lower transpiration rates, enhanced internal temperature and water status, and improved photosynthetic capability (Körner et al, 1986; Liu et al., 2020). Also, LT could be related to long leaf survival, nutrient retention, and protection from desiccation, which may be advantageous at higher elevations. All these plant conservative features, likely allow abundant species to be more successful in the face of stressful environments at higher elevations.

For SLA, we only found a significant negative relationship with the distribution of species abundance in Abiseo, but it was not correlated with elevation. SLA is an important PFT because it affects many aspects of plant performance. This trait generally increases in

leaves that grow under low radiation conditions; alternatively, it often diminishes with decreasing water or nutrient availability, corresponding to those favored by evergreen species (Cunningham et al., 1999; Fonseca et al., 2000; Ackerly et al., 2002). Lower SLA concurs with long leaf survival, nutrient retention, and protection from desiccation (Ackerly et al., 2002), because a small leaf size helps maintain favorable leaf temperatures and photosynthetic activity under conditions of high solar radiation but low water availability. This strategy, involving the association of low SLA and higher H with retaining resources for longer periods of time, is also associated with the late successional species (Cornwell and Ackerly, 2010). Our observations in Abiseo agree with studies that show that lower SLA values and higher H values are prevalent among abundant species (Cornwell and Ackerly, 2010; Lisner et al., 2021), thus suggesting that greater abundance was positively related with this conservative strategy in regards to SLA. Moreover, PFTs often show a strong phylogenetic signal, thus highlighting the genetic proximity of abundant species that share similar SLA values (Shipley, 2010).

It is well-known that, plant height decreases with increasing elevation in mountain areas (Körner, 2012). Accordingly, we found, in both sites, that abundant species exhibit greater height in forest from the lowest elevations. That reflects the effect of elevation on tree growth (Coomes and Allen, 2007), which, is expected, to be greater at lower elevations. Also, the greater values of H in abundant species found in lower elevation forest, likely reflects the short-term dominance of pioneer species with a better colonizing ability (Cornelissen et al., 2003; Wright et al., 2007). In addition, at higher elevations in Abiseo, abundant species exhibited low tree height. They likely correspond to small-tree species able to survive in the harsh high-elevation environments of low temperatures and strong winds by minimizing tissue damage (Körner, 2012).

Low values of WD were found in abundant species from both localities. In Bombuscaro these species were located at the lowest elevations, while in Abiseo they mostly were in high elevation forests. In the former, this may be the result of a strong presence of pioneer species, characterized by being short-lived, fast-growing, a strong photosynthetic investment and low WD values (Gartner and Meinzer, 2005; Wright et al. 2010). In Bombuscaro, we also found abundant species with large values for H at low elevations, reinforcing that early successional species, usually fast-growing, and light-demanding (Enquist et al., 1999) are abundant at lower elevations. In Abiseo, instead, the low values of WD could be related to abundant tree species that grow under the lower temperatures

of higher elevations, where the water is more viscous, and the plants need a lower density wood to maintain water flow (Gartner and Meinzer, 2005). Along with this, in this site we found species abundance to be related to lower H at higher elevations. Thus, not surprisingly, WD appears to be related with H, since both traits are associated with growth rate (Enquist et al., 1999).

Our research evidence that functional traits, such as LT, H and WD, and elevational gradient interact to determine species abundances in montane tropical forests, thus contributing to co-dominance patterns in terms of biomass (Sandoya et al., 2021). It also supports the hypothesis of trait-based niche assembly (Cornwell and Ackerly, 2010; Lisner et al., 2021). Understanding the ecology and distribution of dominant species is essential because these abundant species are key to ecosystem processes such as carbon storage. Future studies should expand the assessment of distribution patterns of species and PFTs in montane tropical forest in order to shine light on those plant traits that are influencing ecosystem functioning and the ecosystem services provided by these montane forests.

3.6 Acknowledgements

The first author was able to conduct her research thanks to the invaluable support of Secretaría de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT) from Ecuador. Field campaigns and data acquisition and management were funded by BOTROPANDES Project (grant from the Spanish Ministry of Economy and Competitiveness (MINECO; CGL2013- 45634-P, CGL2016-75414-P).

Supplementary Material

Capítulo 3

3.7 Supplementary material

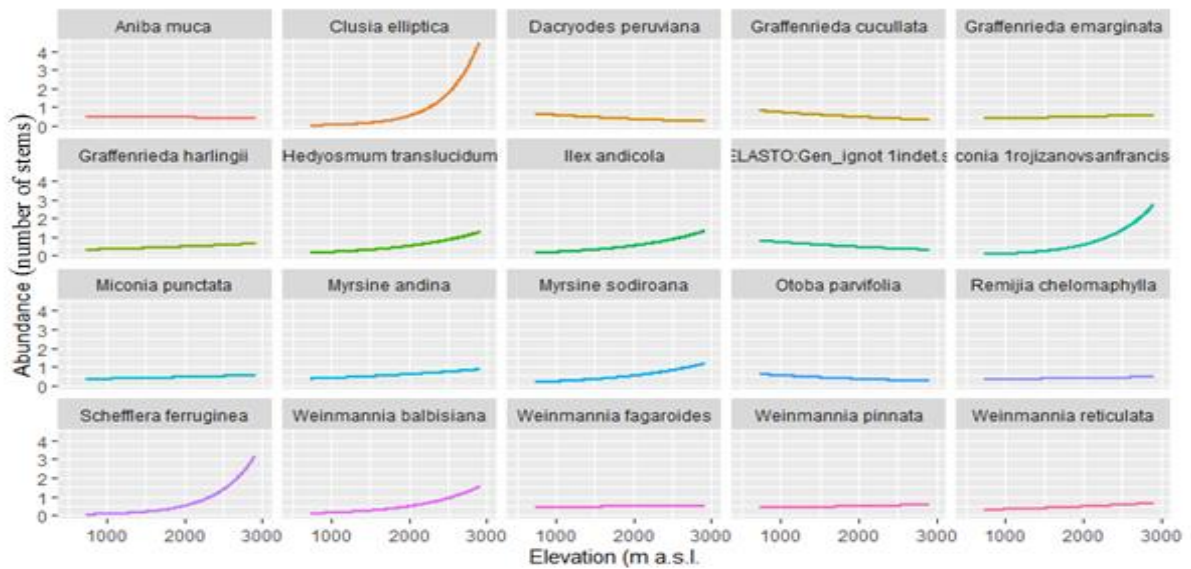


Figure 1.- Distribution along the elevational gradient of the most abundant (number of stems) species, in Bombuscaro.

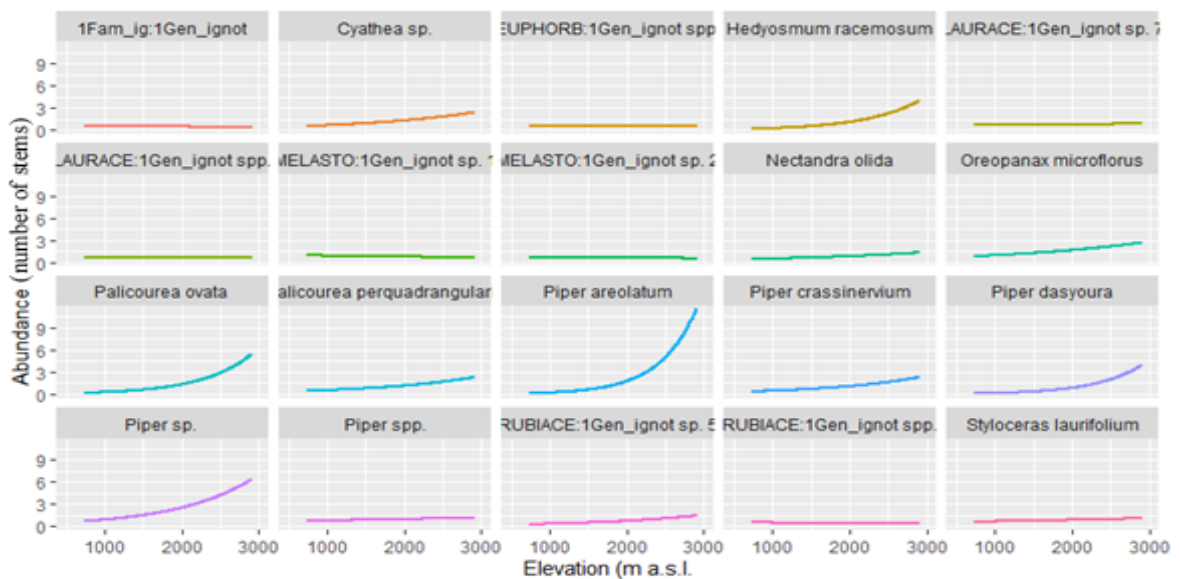


Figure 2.- Distribution along the elevational gradient of the most abundant (number of stems) species, in Abiseo.

Capítulo 4

4. PATTERNS OF FOREST FUNCTIONAL DIVERSITY THROUGH A TROPICAL ANDEAN ELEVATION GRADIENT

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4.1 Summary

Plant functional diversity (FD) of a community' may determine ecosystem structure and functioning, and what is more, patterns of FD through relevant environmental gradients, such as elevation, are expected to be associated to community biomass. We assessed whether FD correlate with plot-level biomass in two elevational gradients in montane Andean forests (Bombuscaro, Ecuador and Río Abiseo, Peru). We used community weighted mean (CWM) and functional variation (FDvar) of selected traits, reflecting acquisitive *vs* conservative strategies. Source of data were 60 inventories of woody species that were characterized by measuring wood density (WD), specific leaf area (SLA), leaf thickness (LT) and height (H).

CWM of traits exhibited contrasting patterns: LT increased with elevation in both sites, WD was negatively related with elevation in Abiseo and positively in Bombuscaro, H was negatively related with the elevation in Bombuscaro, while non-significant in Abiseo, and SLA was not significantly related with elevation in any of the two study sites. FDvar of traits also varied between localities: H was negatively related with elevation in Abiseo and Bombuscaro, FDvar of LT and WD were negatively related with elevation in Bombuscaro, while SLA increased as elevation increased. The FDvar relationships of LT, WD and SLA with elevation were not significant in Abiseo. AGB was positively related with CWM of SLA and negatively so with CWM of LT and with FDvar of SLA in Bombuscaro, while in Abiseo AGB was positively related only with FDvar of SLA.

Our results show that in tropical Andean forest functional diversity in terms of CWM and FDvar vary with elevation. This variation corresponds to changes in the abundance of species, which corresponds to a prevalence of acquisitive traits in lower elevations, while conservative traits are prevalent in the highlands. according to the availability of resources along the elevational gradient. There is an important variability in FD patterns between sites across the elevational gradient, reflecting local constraints in the structural and functional features of communities, presumably because local environmental factors foster this variation. The relationship between biomass and FD diversity is revealed by higher AGB in communities dominated by species with acquisitive syndrome, especially in Bombuscaro. Overall, our results support the biomass-ratio hypothesis, which states that the prevalent value of plant functional traits would be a major determinant of ecosystem carbon stock.

4.2 Introduction

Tropical rain forests harbour enormous biological diversity and may contain species, especially trees, that are widely distributed, from the local to the landscape scales (Pitman et al., 2001). These distribution patterns are associated to a large diversity in structure, physiognomy and habitats (Ghazoul and Sheil, 2010), which is particularly enhanced across elevational gradients.

In Andean mountain regions, the variation of species distributions along the elevational gradient maintain forest communities that are exposed to sharp environmental changes as elevation increases (Körner, 2012). Indeed, elevation influence in the patterns of species distribution and abundance can be a determinant of community above ground biomass (AGB) and number of plants (Sandoya et al., 2021). So, species abundance may contribute to the distribution of AGB in tropical elevational gradients (Lisner et al., 2021; Sandoya et al., 2021): sites where some species attain high abundance may exhibit greater stand AGB, although the derived pattern of species abundance could represent less species diversity. These patterns may be related with the community response to changes in environmental conditions induced by elevation, involving both intrinsic properties of the species and interactions between organisms.

Functional diversity (FD) is a measure of range, distribution, and relative abundance of the adaptative functional traits of organisms, in this case plants, thus playing a major role in determining ecosystem functioning (Tilman, 2001; Hatfield et al., 2018). The variation in ecosystem function is explained by the functional characteristics of dominant species in the community, which can be estimated using the community weighted mean of functional trait values (Chiang et al., 2016). FD generally increases with species richness within communities; however, this relation may change according to scale and the type of forest (Tilman, 2001; Chiang et al., 2016; Fotis et al., 2018; Andrew et al., 2021).

Overall, traits can follow a spectrum ranging from a syndrome corresponding to fast acquisition of resources, with high specific leaf area (SLA), low leaf thickness (LT), low wood density (WD) and fast-growth, to a syndrome associated to conservation of resources, with inverse values for SLA, LT and WD and slow-growing species (Díaz et al., 2004; Porter et al., 2010). Thus, acquisitive species are expected to be successful in high-resource habitats, while conservative species –showing high stress tolerance– are likely successful in low-resource habitats (Sterck et al., 2011). These strategies are

expected to correspond to the leaf economics spectrum (Wright et al., 2004). That is, species with acquisitive strategy tend to have short-lived leaves, while conservative species invest more resources into thick and durable leaves (Read et al., 2013).

Leaf traits are key to understand relations between carbon assimilation, water assimilation and energy balance (Fonseca et al., 2000; Ackerly et al., 2002). The ecological hypothesis of biomass-ratio effect has been proposed to explain the relationship between FD and AGB in forests (Chiang et al., 2016). The hypothesis proposes that ecosystem processes are driven by the traits of the most abundant species in the community, so the most dominant values of plant functional traits would be major determinant factors of the ecosystem carbon stock (Grime, 1998; Díaz et al., 2009). In general, higher biomass productivity could be expected in communities dominated by species exhibiting the acquisitive syndrome, rapid growth and higher specific leaf area that favor light capture, photosynthetic rates and net carbon gain (Poorter and Bongers, 2006). In dry forest, however, highest biomass growth has also been reported for communities dominated by low SLA species (conservative species) because these species have an improved water balance due to reduced transpiration (Sterck et al., 2011; Prado-Junior et al., 2016).

The distribution of plant functional traits, particularly those related to leaf morphology (Körner et al., 1986; Körner, 2012), is expected to respond to elevational gradients of the kind found in tropical regions. The environmental filter resulting from constraints induced by elevation may permit preferential selection of species with specific functional traits within of the communities (Kraft et al., 2015). Therefore, different patterns of forest community assemblages may be established along elevational gradients. Particularly, a trend is expected toward communities whose species present conservative resource use strategy traits at higher elevations (Read et al., 2013; Homeier et al., 2021). Communities at higher elevations have species with higher values of LT, which is related to greater leaf longevity (Liu et al., 2020). LT is likely associated to protection from desiccation, and should be advantageous for tolerating higher radiation levels and lower temperature toward high elevation (Körner, 2012). Indeed, species from higher elevations may have relatively lower transpiration rates, enhanced internal temperature and water status, and improved photosynthetic capability (Körner et al., 1986; Liu et al., 2020). Thus, at these sites more abundant species are expected to exhibit these traits. SLA is generally greater in leaves growing under low radiation conditions, and it often decreases with decreasing water or nutrient availability (Fonseca et al., 2000; Ackerly et al., 2002). In turn, plant

height (H) decreases with increasing elevation in tree communities of mountain areas (Coomes and Allen, 2007; Körner, 2012). Also, low SLA and large height (H) values are associated with a conservative strategy of late successional species (Cornwell and Ackerly, 2010). The presence of abundant species with greater H values in lower elevation Andean forest, thus could be the results of the short-term dominance of pioneer species with a better colonizing ability (Cornelissen et al., 2003; Wright et al., 2007). In addition, low values of WD are found among abundant species from both communities in the lowest and highest elevation edges (see Chapter III).

Although there is not a simple, satisfactory or standardized measure of community FD, this can be quantified with two relevant measurable components: community weighted means (CWM) –which expresses the dominant trait value of each community–, and functional divergence (FDvar), which expresses the variance of a single trait within a community weighted by relative abundances of each specie, this index is of ecological importance because it is the component of diversity that influences ecosystem dynamics, stability, productivity, nutrient balance, and other aspects of ecosystem functioning (Mason et al., 2003; Mouillot et al., 2005; Villéger et al., 2008).

The distribution patterns of plant species and their biomass in communities affected by different environmental factors along elevational gradients and their association with plant functional diversity are poorly known. Particularly so in Andean montane forest. The aim of this research is to study the functional diversity of these forest communities, represented by their CWM and FDvar indices, as well as their relation with the biomass of communities along elevational gradients of Andean forests. Specifically, we hypothesized that:

- 1.- Functional diversity varies with elevation. Environmental conditions allow the occurrence of a greater number of species with an acquisitive strategy in communities from low elevations. That is, communities living at lower elevations would show significantly higher CWM values of SLA and H and significantly lower CWM values of LT, while lower CWM values of WD are expected in lower elevations.
- 2.- Functional divergence (FDvar) varies with elevation. At higher elevation, communities exhibit significantly lower FDvar values of SLA, LT, H and WD. The opposite occurs at lower elevations, where functional variability increases due to the presence of greater habitat and taxonomic diversity.

3.- Functional attributes, CWM and FDvar of leaf traits, have an important role in predicting biomass of communities along the elevational gradient. Communities with species showing conservative strategy (with lower CWM values of SLA, higher CWM values of LT, and lower FDvar values of SLA) could contribute to increase biomass along the elevational gradient.

4.3 Methods

4.3.1 Study area

The study was conducted using data from two elevational gradients in the Andes region: one in the Río Bombuscaro basin within the Parque Nacional Podocarpus (Bombuscaro, hereafter) in the Andean Cordillera Real of southern Ecuador, the second one in the Parque Nacional Río Abiseo (Abiseo, hereafter) in the Eastern slope of the Andes of northern Peru (Figure 1). Both, Abiseo and Bombuscaro elevational gradients show average temperatures that range from 12 to 18 °C, and annual precipitation from 1000 to 5000 mm. (Young and León. 1988; Sierra, 1999). However, the forests of these localities have differences according to elevation, since the treeline in Bombuscaro is lower than in Abiseo (Young and Leon, 1988).

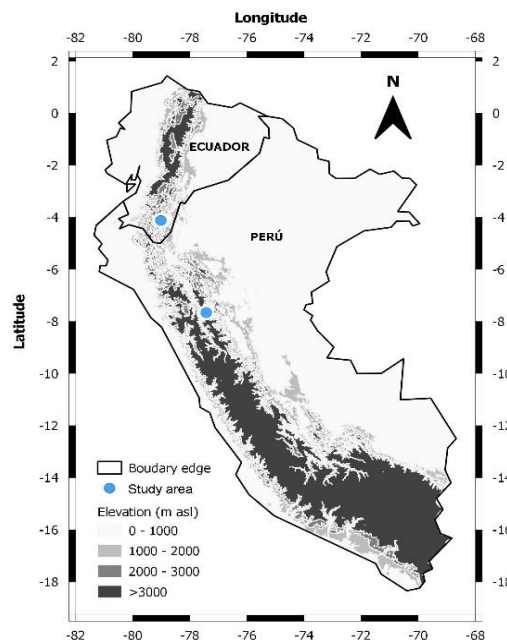


Figure 1.- Study area. Blue dots indicate the location of Podocarpus National Park in Río Bombuscaro (Ecuador) and Río Abiseo National Park (Peru).

4.3.2 Sampling design

We used a dataset from the BOTROPANDES project, consisting of 60 inventories of woody species > 2.5 cm DBH from 0.1 ha (50x20 m) plots from the two elevational gradients (30 plots from each, Bombuscaro, Ecuador and Río Abiseo, Peru) in which three elevational belts were recognized at each site: 745-1245 m, 1800-2200 and 2674-2980 m a.s.l. (Bañares-de-Dios et al., 2020). The dataset included in Bombuscaro a total of 10838 stems belonging to 840 species (including morphospecies), 338 genera and 87 families, and in Abiseo a total of 11600 stems belonging to 544 species (including morphospecies), 286 genera and 101 families. Only those morphospecies with functional trait data were used in the analysis.

4.3.3 Functional trait estimation

For each species, we considered the mean values of WD, SLA, LT and H. Branch wood density was used as a proxy for WD. Measurements were obtained from segments of branches ca. 10 cm long (as cylindrical as possible), whose diameter (after stripping the cortex) and length were measured in the field with a calliper to determine the fresh volume. Branch wood density was calculated dividing fresh volume by dry mass after drying the samples at 80°C for 48–72 h. SLA was calculated from five leaves as the ratio of leaf area (measured with a portable laser leaf area meter CI- 202, CID Bio-Science, Camas, Washington, USA) to leaf dry mass (after drying at 80°C for 48 h). LT was measured in the field with a digital caliper, in three leaves of the same tree that for SLA. H (height of sampled individual) was estimated visually (Bañares-de-Dios et al., 2020). Mean measures of plant functional traits were obtained from the mean of one, three or four individuals for each species (Repository: <https://github.com/vsandoya/Species-datatraits.git>).

4.3.4 Functional diversity indexes

We used CWM and FDvar indices to analyse the FD within each plot. We selected these indices because they incorporate relative abundance.

CWM, which expresses the dominant trait value within each plot, was calculated from the community-weighted means of WD, SLA, LT and H considering the density of each species for each plot:

$$\text{CWM}(\text{trait}_x) = \sum p_i x_i$$

Where p_i is the relative abundance, in terms of number of stems of the i -th species in the community, and x_i is the mean trait value of the i -th species (Conti and Díaz, 2013; Zuo et al., 2016).

FDvar index (Mason *et al.*, 2003), that express the single-trait divergence for a community, turnover or variance of single trait, was calculate for the variance in trait values weighted by the abundance in terms of number of stems of each species in the community:

$$\text{FDvar} = \frac{2}{\pi} \arctan(5V)$$

$$V = \sum_{i=1}^N w_i (\ln x - \overline{\ln x})^2$$

Where x is the trait value for the species i and w_i is the relative abundance of the species i in the community, that is: $w_i = a_i / \sum_{j=1}^N a_j$; where a_i is the abundance of species i and a_j is the abundance of all species. Finally, $\overline{\ln x}$, is the weighted logarithmic mean of the character:

$$\overline{\ln x} = \sum_{i=1}^N w_i (\ln_i)$$

4.3.5 Biomass estimation

AGB was estimated by using allometric measures that include tree height, diameter and wood density, using the equation (Chave et al., 2015):

$$\text{AGB} = 0.0673 (\rho \text{ Di}^2 \text{ H})^{0.976}$$

Where ρ is wood density (g/cm³), D_i is tree diameter (cm) and H is tree height (m). D_i and H were measured for each stem within each plot. The AGB was calculated considering the density of each species within of each plot and then the AGB values of all species were added for each plot.

4.3.6 Data analysis

All data were analyzed at plot level, along the elevational gradient, considering each plot as one replicate of community. Separate analyses were performed for the Abiseo and Bombuscaro elevational gradients.

We used linear models to explain the different hypothesis. For the first hypothesis we used CWM of each trait (H, SLA, LT, WD) as the response variables and elevation as the predictor variable. For the second hypothesis, we used FDvar values for each as the response variables (FDvar of H, SLA, LT, WD) and the elevation as predictor variable. To test the third hypothesis, we used biomass (AGB) as the response variable and CWM and FDvar of each leaf trait (SLA, LT) as the predictor variables. Moreover, we assessed the same model (AGB in relation with variable CWM and FDvar of each leaf trait) with elevation, but the results were better explained without elevation.

The analyses were carried out in R statistical software (version 4.1.1) using the package “tidyverse” to perform linear models and calculate the CWM and FDvar indexes.

4.4 Results

In Abiseo, the plots with highest number of stems were at 2222 m of elevation (649 stems in 0.1 ha) and 2821 m (589 stems). In Bombuscaro, the plots with higher number of stems were at 2851 m (676 stems) and at 2703 m (645 stems). In terms of AGB, in Abiseo the plots with highest mean biomass were at 2767 m with 36.86 Mg and at 819 m with 33.2 Mg; while in Bombuscaro the plots with highest biomass were at 1860 m with 47.5 Mg and at 1851 m with 38.2 Mg.

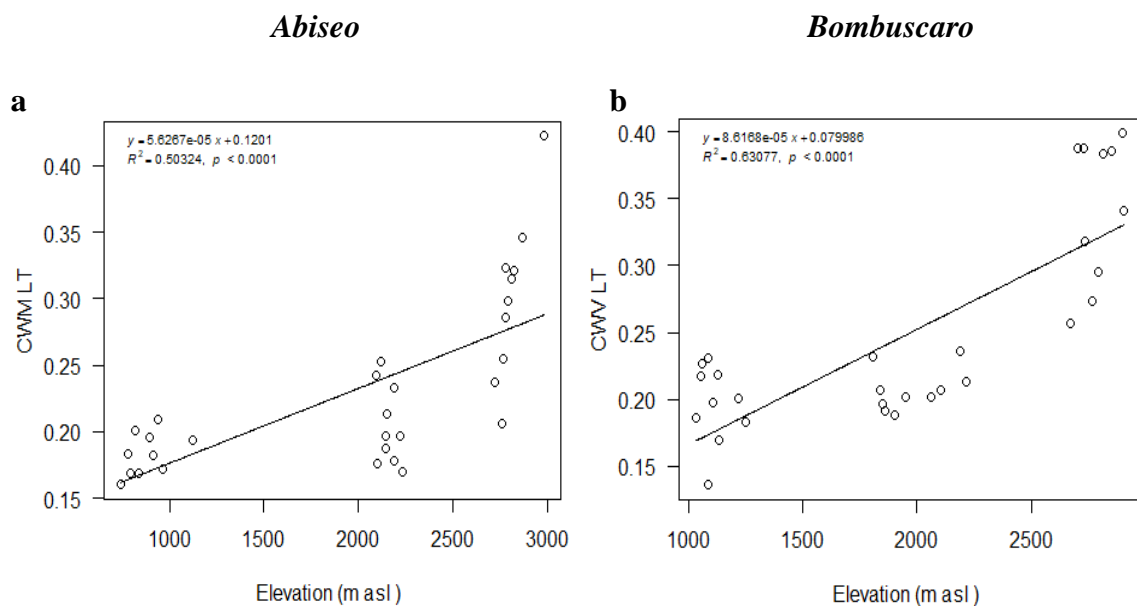
In Bombuscaro we obtained data for functional traits and abundance for a total of 657 species, with the most abundant taxa being *Melastome* sp. (209 stems), followed by

Weinmannia fagaroides (199 stems), *Myrsine sodiroana* (193 stems), *Dacryodes peruviana* (169 stems) and *Ilex andicola* (154 stems). In Abiseo we obtained data for functional traits and abundance for a total of 484 species; the most abundant taxa were: *Piper* sp. (948 stems), *Hedyosmum racemosum* (646 stems), *Piper crassinervium* (542 stems), *Piper areolatum* (352 stems) and *Palicourea perquadrangularis* (302 stems).

4.4.1 Community weighed mean of functional traits across elevational gradient

In both sites, for the LT and WD traits, CWM varied significantly with elevation (Table 1). In Abiseo and Bombuscaro the CWM of LT was significantly greater at higher elevations (Abiseo: $p < 0.001$, Figure 2a; Bombuscaro: $p < 0.001$, Figure 2b). Regarding WD in Abiseo, CWM was significantly higher at lower elevations (Abiseo: $p < 0.001$, Figure 2c), while the opposite pattern was observed in Bombuscaro ($p < 0.001$, Figure 2d).

For the H trait, the CWM in Bombuscaro was significantly negatively related with elevation ($p < 0.001$, Figure 2e), while in Abiseo this relationship was not significant. SLA did not show any significant relation with elevation in either study site.



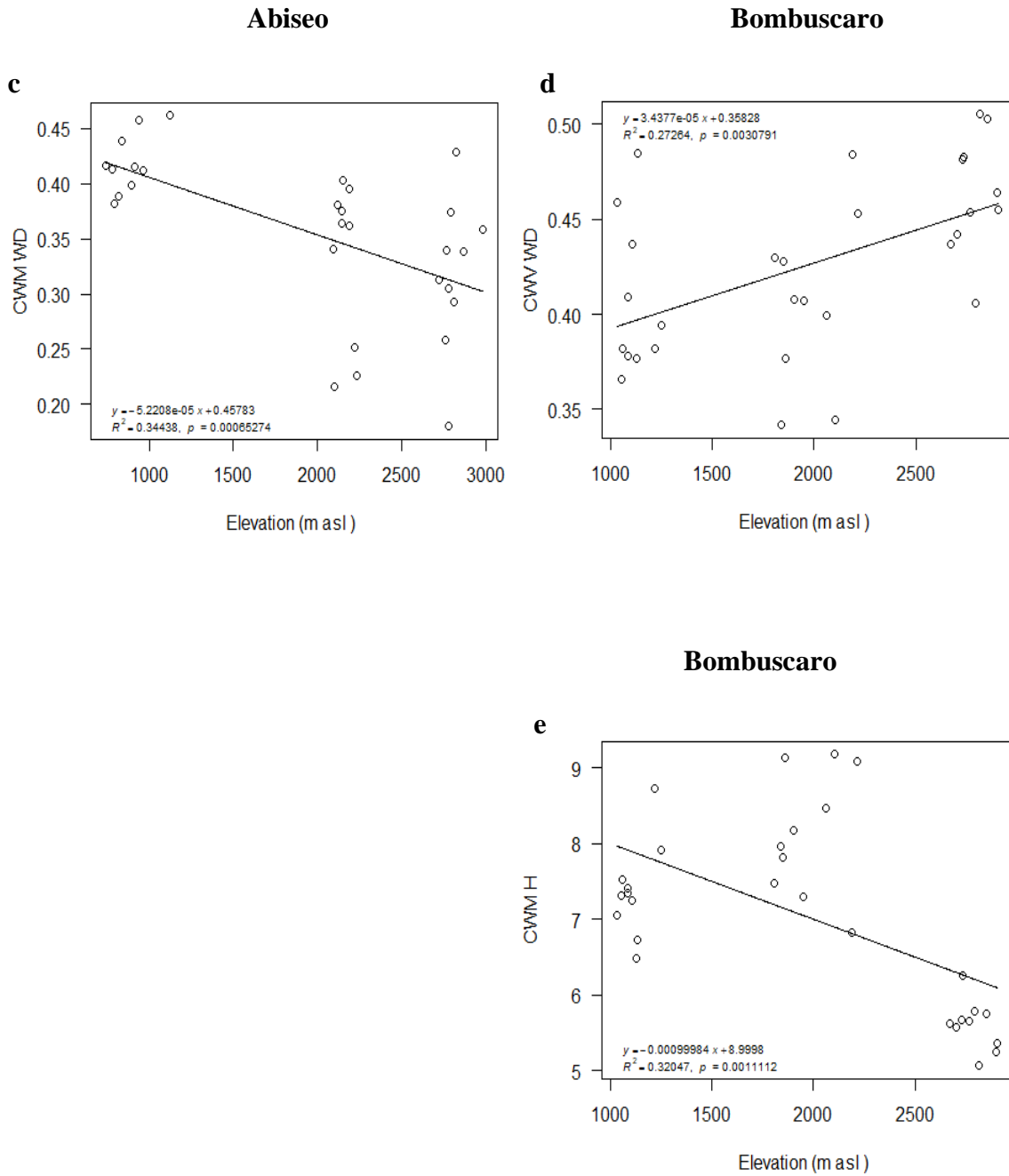


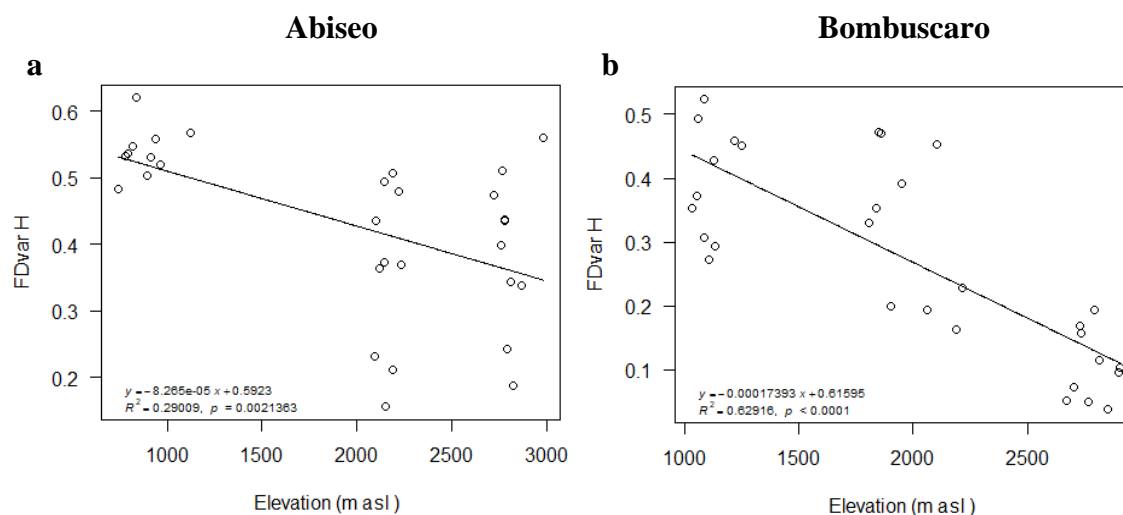
Figure 2.- Linear regressions relating CWM of LT (a) and WD (c) with elevation in the Abiseo elevational gradient and CWM of LT (b), WD (d) and H (e) with elevation in the Bombuscaro elevational gradient.

Table 1.- Statistical summary of linear model for CWM of LT, SLA, WD and H traits in relation with elevation, from plots in the Abiseo and Bombuscaro elevation gradients. Statistically significance in bold.

ABISEO	R ²	Estimate	Std. Error	t value	P value
Elevation					
CWM LT	0.503	<0.001	<0.001	5.326	<0.001***
CWM SLA	0.1	-0.001	0.001	-1.486	0.148
CWM WD	0.344	<-0.001	<0.001	-3.841	0.001***
CWM H	0.121	-0.001	<0.001	-1.97	0.059
BOMBUSCARO					
Elevation					
CWM LT	0.631	<0.001	<0.001	6.916	<0.001***
CWM SLA	0.1	-0.001	<0.001	-1.636	0.113
CWM WD	0.273	<0.001	<0.001	3.24	0.003**
CWM H	0.32	<-0.001	<0.001	-3.634	0.001***

4.4.2 Functional divergence of functional traits across the elevational gradient

In both Abiseo and Bombuscaro, the FDvar of H was negative and significantly related with elevation (Abiseo: $p = 0.002$, Figure 3a; Bombuscaro: $p < 0.001$, Figure 3b) (Table 2). In Abiseo, the FDvar of LT, SLA and WD were not statistically related with the elevational gradient (Table 2). In Bombuscaro, however, these traits showed significant relationships with elevation (Table 2): the FDvar of LT and WD was negative and significantly related with elevation (LT: $p = 0.04$, Figure 3c; WD: $p = 0.001$, Figure 3d), while the FDvar of SLA was positive and significantly related with elevation ($p = 0.034$, Figure 3e).



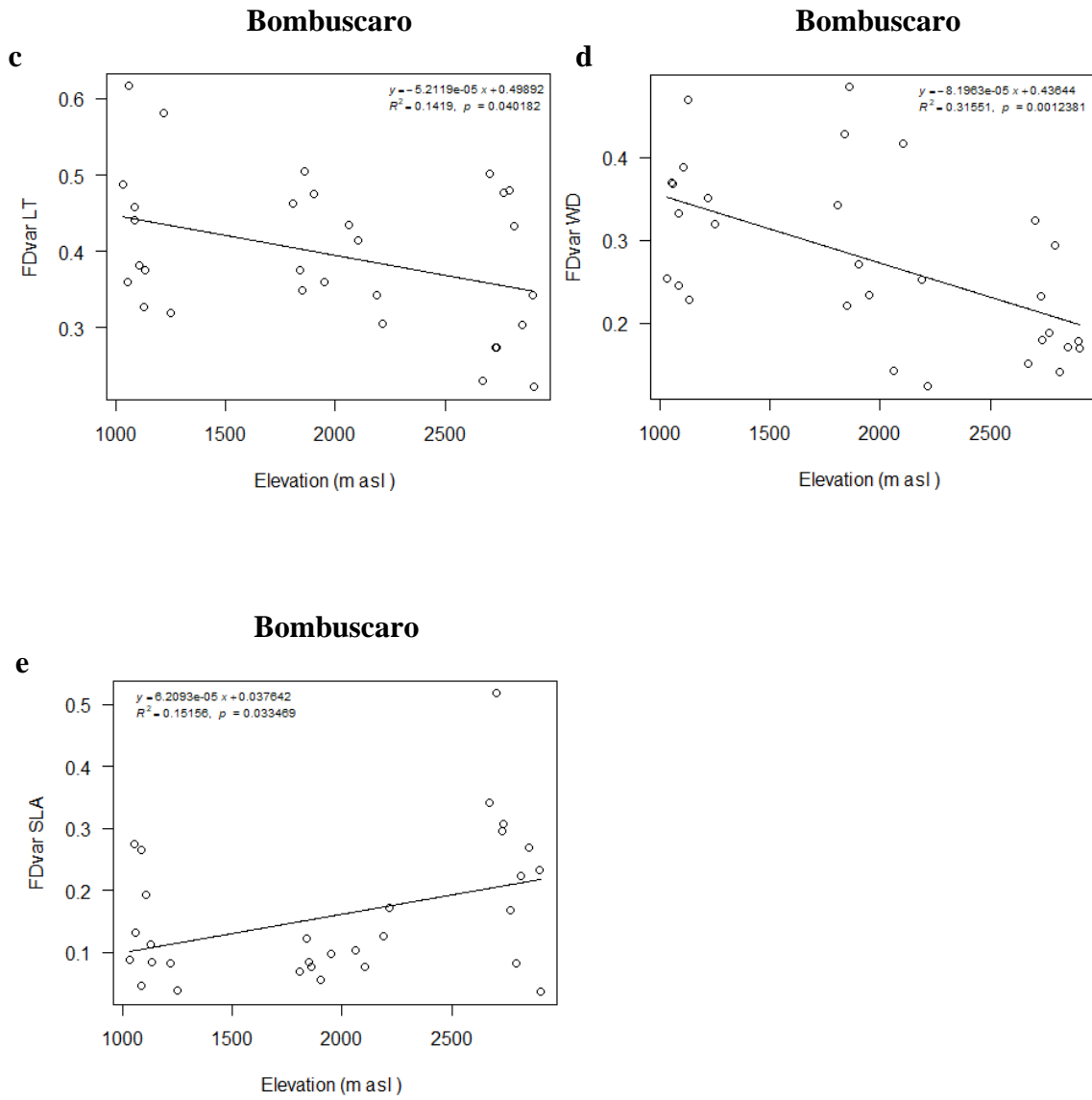


Figure 3.- Linear regressions relating FDvar of H with elevation in Bombuscaro (a) and Abiseo (b) elevations gradients. FDvar of LT (b), FDvar of WD (c) and FDvar of SLA (d) with elevation in the Bombuscaro elevational gradient.

Table 2.- Statistical summary of linear model for FDvar of LT, SLA, WD and H traits in relation with elevation, from plots in the Abiseo and Bombuscaro elevational gradients. Statistically significance in bold.

ABISEO	R²	Estimate	Std. Error	t value	P value
Elevation					
FDvar LT	0.01	<-0.001	<0.001	-0.363	0.719
FDvar SLA	0.002	<0.001	<0.001	0.260	0.797
FDvar WD	0.05	<0.001	<0.001	1.149	0.261
FDvar H	0.3	<-0.001	<0.001	-3.383	0.002 **
BOMBUSCARO					
Elevation					
FDvar LT	0.14	<-0.001	<0.001	-2.152	0.04 *
FDvar SLA	0.2	<0.001	<0.001	2.236	0.034 *
FDvar WD	0.32	<-0.001	<0.001	-3.593	0.001 **
FDvar H	0.63	<-0.001	<0.001	-6.892	< 0.001***

4.4.3 Functional diversity in relation to biomass (AGB)

In Abiseo, the relation between AGB and FDvar of SLA was significant and positive (Table 3, Figure 4a). In Bombuscaro, AGB was significantly and negatively related with FDvar of SLA (Table 3, Figure 4b); while, AGB was significantly and negatively related with CWM of LT (Table 3, Figure 4c) and significantly and positively related with CWM of SLA (Table 3, Figure 4d). Finally, in both Abiseo and Bombuscaro, there were not significant interactions between FD indexes and elevation.

Table 3.- Statistical summary of linear models for AGB in relation to CWM and FDvar of leaf traits (LT, SLA) in plots along the Abiseo and Bombuscaro elevational gradients. Statistically significance in bold.

ABISEO	R²	Estimate	Std.	t value	P value
AGB					
CWV SLA	0.01	-0.033	1.861	-0.4	0.692
CWV LT	0.001	<0.001	0.002	0.203	0.841
FDvar SLA	0.18	0.007	0.003	2.505	0.018 *
FDvar LT	0.001	<-0.001	0.002	-0.159	0.875
BOMBUSCARO					
AGB					
CWV SLA	0.176	0.054	0.022	2.447	0.021*
CWV LT	0.4	-0.005	0.001	-4.4	0.0001***
FDvar SLA	0.33	-0.006	0.002	-3.670	0.001 **
FDvar LT	0.08	0.005	0.002	1.542	0.134

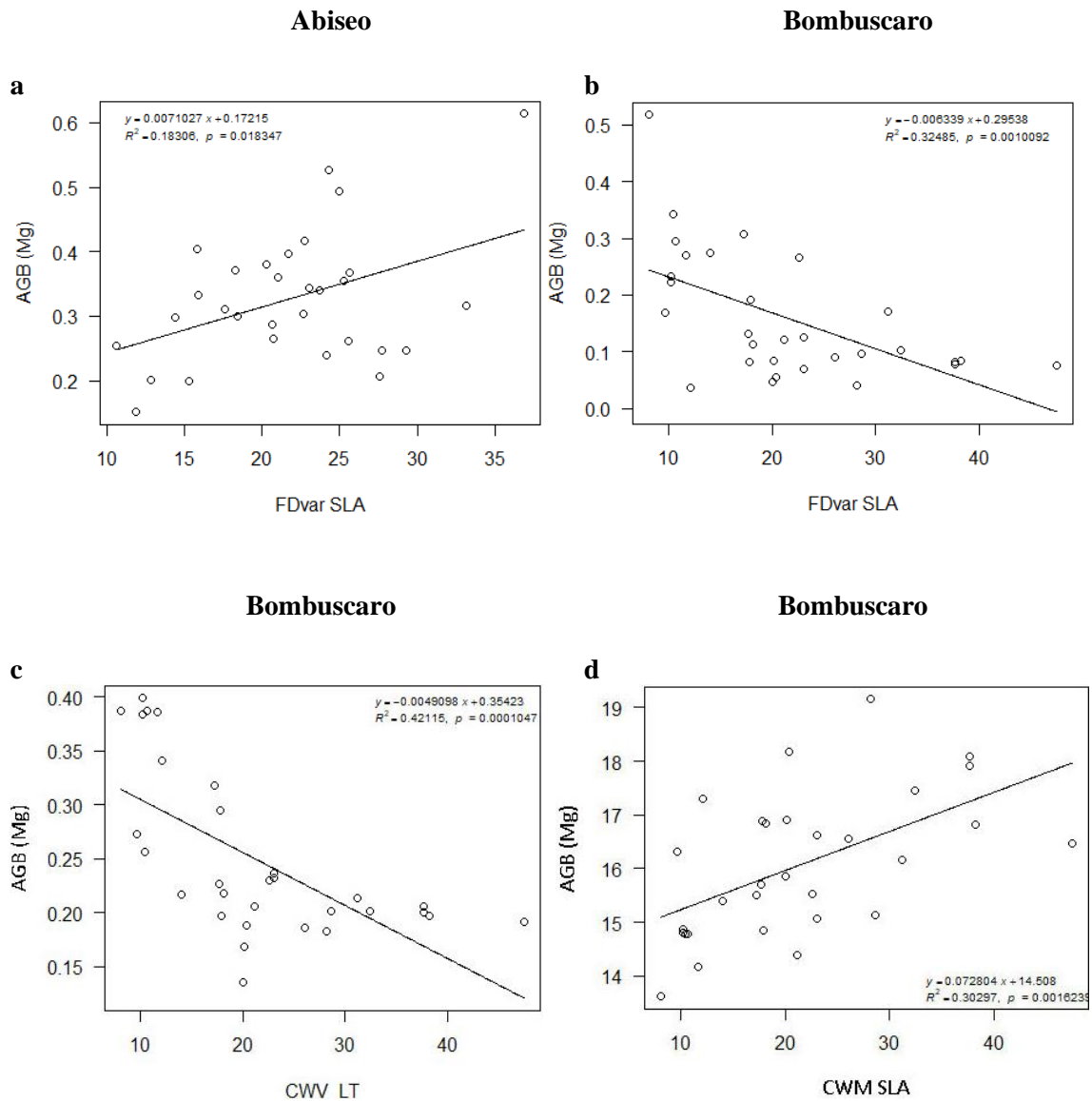


Figure 4.- Linear regressions relating AGB with FDvar of SLA in the Abiseo (a) and Bombuscaro (b); and AGB with CWM of LT (c) and CWM of SLA (d) in Bombuscaro elevational gradient.

4.5 Discussion

Our study reveals that patterns of functional diversity at community level respond to the elevational gradient in the Andean mountains. While for some traits, such as LT, these patterns are consistent between sites and obey to the expected environmental constraints associated to an elevational gradient, other, such as WD or SLA, show contrasting

responses among sites. This reveals the importance of local drivers in configuring tree assemblages in these forests. Interestingly, this response of FT to the elevational gradient not only affects the mean values of traits (CWM), but also the divergence among values (FDvar) for some traits such as H, LT, SLA, and WD within the community. This response of FT to the elevational gradient –at least for some traits, such as LT and SLA– eventually appears associated to patterns of plot biomass (AGB).

The communities in Bombuscaro showed patterns that agrees with our hypothesis, since acquisitive traits – lower values of CWM of LT and WD, and higher values of CWM of H – tend to appear more in lower elevations, where more abundant resources would favor acquisitive species (Poorter et al., 2008).

Some studies have shown that CWM of SLA decreased at higher elevation with increasing stress conditions, while the opposite occurs in habitats that are rich in resources (Poorter et al., 2008; Ding et al., 2019). Communities with species with lower values of SLA have an improved water balance since they transpire less (Poorter and Bongers 2006; Sterck et al. 2011). The higher values of LT correspond to greater mesophyll tissue thickness and to an increase in stomatal density (Liu et al., 2020). These morphological features may allow leaves to have relatively higher rates of carbon assimilation and photosynthetic performance per unit area (Körner et al., 1986; Hovenden and Brodribb, 2000; Liu et al., 2020). This is expected for leaves of species from higher elevations since their exposure to harsh environmental conditions such as higher radiation, lower temperatures and stronger winds (Körner, 2012). Moreover, species from communities at higher elevations are smaller (van der Sande et al., 2021), as we found in Bombuscaro. The observed higher values of CWM of H in lower elevations reinforce the role of acquisitive, fast-growing species (Enquist et al., 1999).

Poorter and Markesteijn (2008) found that evergreen species in tropical forests follow a conservative strategy by increasing their physiological tolerance with high wood density. While environmental filtering tends to select species with conservative strategies at high elevations, this strategy may also appear in part at lower elevations (Ding et al., 2019). In Abiseo we found a similar pattern than in Bombuscaro for LT, but their communities in lower elevations showed higher values of CWM of WD, in contrast with our expectation. This suggests higher abundance or number of conservative species in lower elevations in Abiseo.- In Bombuscaro, as expected the communities at lower elevations showed lower

values of CMW of WD, likely due to the abundance of acquisitive species, characterized by being fast-growing and short-lived.

This study also shows that FDvar respond, overall, to elevation, particularly in communities from Bombuscaro. This index explains the variation of a single trait within the community (Mason et al., 2003; Mouillot et al., 2005; Villéger et al., 2008). FD in general increases with species richness within of communities and it is expected to be higher in less extreme environments, where a broader range of functional strategies can persist; therefore, the elevational gradient is expected to have a relevant effect in the functional variation of the community (Andrew et al., 2021). We found that FDvar values of LT, H and WD were overall higher in lower elevations, where functional variability increases due to the presence of more habitats and higher taxonomic diversity. In Abiseo, however, FDvar values of SLA were higher in high elevations. In gradients of elevation, the leaves tend to change their morphology, as an adaptive response to different environmental conditions (as temperature, wind exposure, soil moisture availability) (Körner et al., 1986; Körner, 2012). Thus, the higher functional divergence of SLA at higher elevations may be the result to the variation in the taxonomic composition or life-form categories dominant in highlands (Venn et al., 2014; Zhang et al., 2020).

We found that FD of traits was associated with AGB of communities from both elevational gradients, although the relationship with specific traits varied between sites. In Bombuscaro, AGB was positively related with CWM of LT and negatively to CWM and FDvar of SLA; while in Abiseo it was positively related with FDvar of SLA. The relationships between plant functional traits and AGB has been previously explored across of different forests (Wang and Ali, 2021). For instance, SLA is related to plant growth rate and to strategies of resource use (acquisitive or conservative), thus to the response to gradients of nutrients and water availability (Díaz et al., 2004; Wright et al., 2004). In turn, FD is influenced by climate and soil, so that in general, environmental filtering in stressful environments reduces the range of trait values, thus promoting functional convergence (Kraft and Ackerly, 2010). In particular, our results support the hypothesis of biomass-ratio, explaining ecosystem functioning (Finegan et al., 2015) since the most dominant values of plant functional traits would be major determinants of the ecosystem carbon stock (Grime, 1998; Díaz et al., 2009). Overall, leaf traits corresponding to the plant's leaf economic spectrum are expected to correlate with the aboveground C storage (Wang et al., 2020). Therefore, higher AGB and biomass

productivity are expected in communities dominated by species that exhibit acquisitive syndrome (Ali et al., 2017). This is, in communities with higher values of CWM of SLA and lower values of CWM of LT (Díaz et al., 2004; Porter et al., 2010; Read et al., 2013), which is what we found in Bombuscaro.

The opposite relationship between AGB and FDvar of SLA in Abiseo and Bombuscaro elevational gradients may be interpreted according to the niche complementarity hypothesis, which indicates that FD, estimated as the FDvar that reflects species diversity, could increase the efficiency of resource utilization, and hence increase C storage (Díaz et al., 2009). In Abiseo, the positive relationship between AGB and FDvar of SLA is likely related to a high number of species with acquisitive strategy in the study plots. In Bombuscaro, the negative association between AGB and FDvar of SLA does not support the niche complementarity hypothesis (Ali et al., 2017), and it may be explained by AGB being mostly determined by dominant old trees belonging to species with conservative strategy, as found by other studies (Wang et al., 2020). In fact, in dry forest, the highest biomass growth has been reported from communities dominated by conservative species, likely because these have an improved water balance due to less water loss by evapotranspiration (Sterck et al., 2011; Prado-Junior et al., 2016). Finally, the lack of a significant relationship between AGB and elevation indicates the importance of local factors, such as successional stage and local environmental conditions, in determining plot biomass. In Andean mountains, the height and growth of trees commonly decrease with increasing elevation due to climatic factors such as temperature, drought periods, radiation, wetness, wind speed or to less developed soils (Moser et al., 2011).

This study provides insight about forest FD at plot level across Andean elevational gradients and how its variation is related with AGB. Traits associated with the acquisitive vs conservative spectrum contribute to explain plot AGB values. This FD, thus, should likely play an important role in climate change mitigation strategies. Ultimately, the observed variability between locations indicates the need to further research on the relationship between FD and structural and functional features of forests for a better understanding of the ecological mechanisms that underlay the functioning of Andean montane forests.

4.6 Acknowledgements

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Capítulo 5

5. DISCUSIÓN GENERAL

5.1 Biomasa y biovolumen en especies dominantes en relación con la elevación y la precipitación

El presente estudio muestra que en bosques andinos la biomasa aérea, disminuye al incrementar la elevación y aumenta donde la precipitación es mayor. Es conocido que en los bosques tropicales la altura y las tasas de crecimiento de los árboles disminuyen a mayor elevación (Körner, 1999). Las condiciones climáticas, como precipitación y temperatura, o factores edáficos relacionados con las propiedades del suelo son muy relevantes a la hora de interpretar este patrón. La producción primaria de los bosques está determinada principalmente por la disponibilidad de agua (precipitación) que varía con la elevación (Körner, 1999; Reich et al., 2014; Álvarez-Dávila et al., 2017). En bajas elevaciones, donde la precipitación es mayor y las condiciones ambientales son más homogéneas (Pitman et al., 2001; ter Steege et al., 2013; Fauset et al., 2015), existen árboles altos, los cuales aportan valores altos de biomasa y biovolumen a la región, contrario a lo que ocurre en altas elevaciones. Hay que destacar que los bosques montanos tropicales mantienen una amplia gama de condiciones ambientales climáticas que resultan de cambios en la elevación (Janzen, 1975), a diferencia de las tierras bajas, donde el clima es más homogéneo. En consecuencia, los Andes presentan un cambio gradual de la estructura del bosque con el incremento de la elevación, con declinación de la riqueza de especies leñosas y por ende de la biomasa.

En este estudio se muestra que la biomasa aérea de estos bosques se correlaciona positivamente con la abundancia de las especies forestales a escala de rodal. Encontramos parcelas conformadas por ciertas especies leñosas dominantes que presentan un patrón de mayor abundancia local. Estas contribuyen con mayor biomasa a la del conjunto del rodal, y previsiblemente a su productividad (Fauset et al., 2015). Este hecho se ve apoyado por la relación negativa entre la biomasa y el índice de equidad de Simpson de las parcelas, para todos los rangos taxonómicos, cuyos valores bajos se darían en parcelas con un

destacado papel de dichas especies dominantes. El aporte local en biomasa y por parte de individuos de gran tamaño dentro de las parcelas se replica para la región.

Sin embargo, nuestros resultados no muestran que las especies más frecuentes a escala de paisaje contribuyan significativamente más a la biomasa de la parcela, sino todo lo contrario. El gradiente de elevación juega un papel relevante a la hora de interpretar estos patrones. Así, en la zona amazónica la gran contribución a la biomasa de la parcela por parte de individuos de gran tamaño –cuyas especies no serían tan frecuentes debido a la alta beta diversidad propia de comunidades de pluvisilva– ayudaría a entender este patrón. Por otro lado, en altas elevaciones -cuyos bosques presentan menor biomasa- unas pocas especies con muchos tallos tienden a aportar altos valores de biomasa y biovolumen que contribuyen particularmente a la biomasa de los rodales; en estas altas elevaciones existen menos especies y su frecuencia es más alta, lo que en conjunto favorece al dominio -en términos de abundancia y frecuencia- de ciertos taxa en comparación con bajas elevaciones (Girardin et al., 2013).

Por tanto, nuestro estudio muestra, por un lado, la importancia de los taxa abundantes en los rodales a la hora de determinar la biomasa de los bosques andinos a escala local, y por otro lado, la correspondencia de esa abundancia local con la frecuencia a escala de paisaje; esta correspondencia variaría a lo largo del gradiente de elevación. Sin embargo, nuestros resultados no corroboran que las especies comunes regionalmente (frecuentes) en zonas bajas –donde las condiciones climáticas y topográficas son favorables para su establecimiento (Valencia et al., 2009)– contribuyan más a la biomasa a escala de rodal (Fauset et al., 2015). Este patrón va cambiando conforme incrementa la elevación, de modo que, en cotas altas, donde la limitación de nutrientes, la baja actividad microbiana y la reducida transpiración, dan como resultado la presencia de árboles de pequeño tamaño (Leuschner, 2007; Ghazoul and Sheil, 2014). Sin embargo, esos árboles pequeños presentarían un patrón de distribución y de dominancia a escala de rodal que les permite aportar una mayor biomasa a escala regional.

5.2 Rasgos funcionales y patrones de abundancia local en gradientes de elevación

Los resultados obtenidos en esta tesis evidencian que los rasgos funcionales están correlacionados con los patrones de abundancia de las especies de bosques montanos

andinos. Esta relación proporciona evidencia importante sobre los mecanismos que estructuran estas comunidades ecológicas a escala local.

Aun cuando la presencia de especies dominantes puede ser el resultado de otros factores estocásticos, existen importantes rasgos funcionales, como el grosor y el área específica de la hoja y la altura de la planta, los cuales emergen como importantes para comprender la dominancia de ciertas especies en el gradiente de elevación: desde los bosques premontanos hasta los de grandes elevaciones. Nuestros resultados concuerdan con otros estudios que demuestran patrones de abundancia de especies en relación con rasgos funcionales (Cornwell and Ackerly, 2010; Warton et al., 2015; Lisner et al., 2021). Esta representatividad de rasgos intraespecíficos en relación con la dominancia variaría según la elevación a la que se encuentre el bosque montano evaluado.

Los rasgos funcionales de la hoja proporcionan información sobre las capacidades de las plantas en relación con la asimilación de carbono, la asimilación de agua y el balance energético (Cunningham et al., 1999; Fonseca et al., 2000; Ackerly et al., 2002). Al relacionar los rasgos foliares en especies establecidas en los gradientes de elevación estudiados, podemos determinar que estos tienden a cambiar como resultado de respuestas adaptativas a las condiciones de estrés que se presentan al incrementar la elevación (temperatura, exposición al viento, disponibilidad de nutrientes, humedad del suelo) (Körner et al., 1986; Körner, 2012; Pandey et al., 2021). En este estudio se muestra una relación positiva entre la abundancia de especies a escala de rodal y el grosor de la hoja, la cual aumentó con la elevación. Las hojas de las especies que se encuentran a mayores elevaciones están expuestas a condiciones ambientales adversas, con tasas de radiación incidente más altas, temperaturas más bajas y vientos fuertes (Körner, 2012). Por tal razón, un aumento en el grosor de la hoja proporciona un mayor espesor del tejido mesófilo y una densidad estomática más baja, lo cual facilita a las hojas menores tasas de transpiración, a la vez que se mantiene una temperatura interna más adecuada, mayor cantidad de agua y mejor capacidad fotosintética (Körner et al., 1986; Liu et al., 2020). Estas características conservativas, permitirían a las especies abundantes superar el filtrado ambiental y establecerse y crecer con éxito en cotas altas.

Por otro lado, el área específica de la hoja, otro rasgo foliar importante, generalmente aumenta en las hojas que crecen en condiciones de baja radiación y disminuye con una menor disponibilidad de agua o nutrientes (Cunningham et al., 1999; Fonseca et al., 2000;

Ackerly et al., 2002). En nuestro estudio, este carácter estuvo correlacionado con especies abundantes de gran porte - altura -, en uno de los sitios de estudio. Estas especies presentan valores bajos de área específica de la hoja, reflejando una estrategia conservativa en el uso de recursos, en concordancia con otros estudios (Cornwell and Ackerly, 2010; Lisner et al., 2021). Bajos valores de este rasgo foliar se corresponden con una mayor supervivencia de la hoja, retención de nutrientes y protección contra la desecación (Ackerly et al., 2002), y están asociados a especies de sucesión avanzada (Cornwell and Ackerly, 2010).

La abundancia local de las especies también presentó relación con la altura de sus individuos en los sitios estudiados, aunque con importantes diferencias a lo largo del gradiente de elevación. En zonas premontanas, las especies abundantes exhibieron mayor altura, probablemente reflejando la dominancia a corto plazo de especies pioneras con una mejor capacidad de colonización (Cornelissen et al., 2003; Wright et al., 2007) y de alcanzar rápidamente el dosel. Mientras que, en elevaciones más altas, las especies abundantes estuvieron representadas por árboles de baja estatura, capaces de tolerar ambientes adversos con bajas temperaturas y fuertes vientos (Körner, 2012), reflejan el efecto de la elevación sobre el crecimiento de los árboles (Coomes and Allen, 2007).

A su vez, la relación entre abundancia y densidad de la madera también se ve modulada por el gradiente de elevación, con diferencias entre localidades. Así, en la localidad de Bombuscaro las especies abundantes en cotas bajas presentaron valores bajos de densidad de la madera, lo cual puede ser el resultado de la dominancia de especies pioneras propias de las fases tempranas de la sucesión que se caracterizan por su vida corta, rápido crecimiento, alta exigencia de luz y por una fuerte inversión fotosintética (Gartner and Meinzer, 2005; Wright et al., 2010; Enquist et al., 1999). En la localidad de Abiseo, las especies abundantes a cotas altas presentan una densidad de madera baja que probablemente facilita el flujo de agua en condiciones de baja temperatura (Gartner and Meinzer, 2005).

5.3 Patrones de diversidad funcional de especies dominantes arbóreas en gradientes de elevación

Esta tesis proporciona evidencia empírica de la variación de la diversidad funcional de especies forestales leñosas de los bosques montanos andinos en el gradiente de elevación. Dicha diversidad depende del rasgo funcional considerado, el cual responderá a las condiciones ambientales asociadas con la elevación (Ding et al., 2019) así como a las condiciones bióticas y abióticas locales propias de las comunidades evaluadas, tal como se ha observado en los dos gradientes de elevación estudiados. La diversidad funcional determina el funcionamiento de los ecosistemas y refleja los patrones de presencia y dominancia de especies, a su vez resultado de las interacciones ecológicas que definen el ensamblaje de las comunidades (Kraft et al., 2008; Cornwell and Ackerly, 2010). En nuestro estudio, la diversidad funcional evaluada a escala de comunidad se ha basado en el cálculo de la media ponderada de la comunidad (CWM) de los valores de los rasgos funcionales considerados -altura de la planta, densidad de la madera, grosor de las hojas, área específica de la hoja y en el de la divergencia entre rasgos (FDvar). En las tierras bajas se encontraron comunidades con valores bajos de CWM para grosor de la hoja y densidad de la madera y valores altos de CWM para altura de los individuos, lo que indica que son abundantes las especies con estrategias adquisitivas, capaces de aprovechar de forma exitosa los ricos recursos existentes a bajas elevaciones (Poorter et al., 2008). No obstante, aparecen algunas diferencias entre las zonas de estudio, ya que mientras que en Bombuscaro a baja elevación se encontraron comunidades con bajos de CWM para densidad de la madera –evidenciando abundancia de especies adquisitivas–, en Abiseo a elevaciones más bajas se encontró mayor abundancia de especies conservadoras. En las comunidades forestales de cotas altas se observó una disminución del área específica de la hoja, adaptación para mantener un mejor balance hídrico por una menor transpiración (Poorter and Bongers 2006; Sterck et al., 2011). Por otro lado, el CWM para el grosor de la hoja aumenta en comunidades de altas elevaciones, asociado a un mayor grosor del tejido mesófilo y a un aumento de la densidad estomática (Liu et al., 2020), características importantes para tolerar las condiciones ambientales adversas a las que las hojas están expuestas en esos ambientes (Körner, 2012). Así mismo, las comunidades establecidas en las elevaciones bajas de los gradientes evaluados, presentaron altos valores de CWM para la altura de los individuos, confirmando la abundancia de especies con estrategia adquisitiva en estos lugares (Enquist et al., 1999).

Los resultados de FDvar para altura de los individuos, densidad de la madera y grosor de la hoja, presentaron valores más altos en elevaciones más bajas, donde la variabilidad funcional aumenta debido a la presencia de más hábitats y una mayor diversidad taxonómica. En general, esta medida de diversidad funcional aumenta con la riqueza de especies y se espera que sea mayor en ambientes menos restrictivos, donde puede persistir una gama más amplia de estrategias funcionales (Andrew et al., 2021). Sin embargo, estos patrones no fueron idénticos en las diferentes zonas de estudio, ya que en Abiseo los valores de FDvar para el área específica de la hoja fueron mayores en elevaciones altas. Esta mayor divergencia funcional puede ser el resultado de la variación en la composición taxonómica o en las formas de vida dominantes en las tierras altas (Venn et al., 2014; Zhang et al., 2020).

Por último, la diversidad funcional, específicamente para los rasgos funcionales de grosor y área específica de la hoja estuvo asociada con los patrones de biomasa -y por tanto con los estocs de carbono- de las comunidades evaluadas en ambos gradientes de elevación, la cual presenta valores más bajos en cotas altas. Las condiciones ambientales y edáficas que se dan en altas elevaciones producirían filtrado ambiental que reduciría el rango de valores de los rasgos funcionales, promoviendo la convergencia funcional (Kraft and Ackerly, 2010). Los rasgos funcionales para los que se ha observado una relación con la biomasa estarían asociados a una mayor productividad y corresponderían a especies que presentan estrategias adquisitivas (Grime, 1998; Díaz et al., 2009; Ali et al., 2017; Wang et al., 2020). Sin embargo, de nuevo aparecen ciertas diferencias entre las zonas de estudio. En Abiseo, la relación positiva entre biomasa y FDvar de área específica de la hoja probablemente esté relacionada con un alto número de especies con estrategia adquisitiva, mientras que en Bombuscaro la asociación negativa entre las mismas variables podría indicar que la biomasa está principalmente contenida en árboles con estrategia conservadora (Wang, et al., 2020).

Capítulo 6

6. CONCLUSIONES

6.1 Capítulo 2

- En las localidades estudiadas, los valores de biomasa y biovolumen son menores en los bosques más altos del gradiente de elevación. Es decir, los valores de ambos parámetros son mayores en lugares que presentan mayor precipitación y altas temperaturas, propios de *tierras bajas*.
- Las localidades de bosque tierras bajas tienen condiciones climáticas favorables que facilitan una mayor diversidad y patrones espaciales de distribución de la densidad de especies, géneros y familias, en relación con su abundancia local o frecuencia a escala regional.
- La biomasa y el biovolumen son indicadores que permiten evidenciar diferencias en la productividad de los bosques a lo largo del gradiente de elevación. Los bosques de tierras bajas, que mantienen condiciones ambientales homogéneas, contienen mayor productividad en relación con bosques de altas elevaciones.
- La frecuente presencia de ciertos taxa, a escala regional, contribuye con mayores cantidades de biomasa y productividad, particularmente a bajas elevaciones, donde se acumulan las mayores reservas de carbono aéreas.
- Los taxa frecuentes a escala regional aportan mayor biomasa a nivel de especie y género, mientras que el aporte de biovolumen está mayormente representado a nivel de género y familia; este patrón tiende a ser más evidente en bajas elevaciones.
- En altas elevaciones, las comunidades dominadas por pocas especies aportan mayor biomasa y biovolumen.
- Existen relaciones entre las características estructurales de las parcelas – relacionadas con la biomasa y ocupación del espacio– y la composición de la comunidad, que está determinada por las abundancias locales de especies y su distribución a escalas más amplias de paisaje.

6.2 Capítulo 3

- En los bosques montanos andinos estudiados se ha observado que los rasgos funcionales de grosor de la hoja, altura de los individuos y densidad de la madera están asociados a la abundancia relativa de las especies de árboles.
- En los gradientes estudiados, el efecto de la influencia de los rasgos funcionales sobre la abundancia de las especies varía a lo largo del gradiente de elevación, desde los bosques premontanos hasta las mayores elevaciones.
- En Abiseo, rasgos funcionales foliares como el grosor y el área específica de las hojas estuvieron asociados a la abundancia de los árboles, mientras que en Bombuscaro lo fueron rasgos foliares relacionados con el tronco como la densidad de la madera y la altura del individuo.
- Los rasgos funcionales y la elevación interactúan para determinar la abundancia de especies en los bosques montanos, contribuyendo así a los patrones de codominancia en términos de biomasa.

6.3 Capítulo 4

- En los bosques tropicales andinos la diversidad funcional en términos de CWM y FDvar varía con la elevación.
- La variación de la diversidad funcional evaluada a escala de comunidad mediante el CWM y la FDvar está relacionada con cambios en la abundancia de especies dominantes, las cuales presentan características de estrategia adquisitiva en bajas elevaciones y rasgos conservadores en altas elevaciones.
- Las diferencias en los patrones de diversidad funcional entre los gradientes de elevación estudiados podrían estar relacionados con las limitaciones locales que afectan a las características estructurales y funcionales de las comunidades, resultantes de las condiciones ambientales existentes en cada sitio.
- La biomasa tiende a ser mayor en comunidades dominadas por especies con estrategia adquisitiva.

- Es importante realizar estudios futuros relacionados con la variabilidad de la diversidad funcional entre sitios para comprender mejor los procesos de ensamblaje de comunidades y funcionamiento de los ecosistemas en bosques montanos andinos.

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