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TESIS DOCTORAL

Determinants of taxonomic, functional and phylogenetic diversity that explain the distribution of woody plants in tropical Andean montane forests along altitudinal gradients

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A mi madre.

A mi padre.

A mi hermano.

A mis abuelos.

A Julissa.

“Entre todo lo que el hombre mortal puede obtener en esta vida efímera por concesión divina, lo más importante es que, disipada la tenebrosa oscuridad de la ignorancia mediante el estudio continuo, logre alcanzar el tesoro de la ciencia, por el cual se muestra el camino hacia la vida buena y dichosa, se conoce la verdad, se practica la justicia, y se iluminan las restantes virtudes […].”

Fragmento de la carta bulada que el Papa Alejandro VI envió al cardenal Cisneros en 1499 autorizándole a crear una Universidad en Alcalá de Henares

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1 | SUMMARY

Understanding the evolutionary and/or ecological mechanisms (including biotic, abiotic and stochastic factors) determining community assembly –*i.e.*, the composition, structure and distribution of biological communities on an ecosystem– remains a central theme in ecology. Beyond the classical taxonomic scope, functional and phylogenetic approaches have certainly improved our knowledge about the mechanisms generating biodiversity patterns within the last decades. However, many discrepancies still exist about which is the relative extent of those mechanisms and under which circumstances they exert their influence. In this sense, contradictory conclusions about what processes drive community assembly seem to be caused by different spatial scale considerations, hampering and embroiling the understanding of this topic. To incorporate this perspective, a hierarchical community assembly model has been proposed, which postulates that different community assembly mechanisms operate sequentially, at increasingly finer spatial scales, to render the observed biodiversity distribution patterns. This model comprises from evolutionary processes such as historical patterns of speciation, extinction or migration, that mostly act at large spatial scales, to abiotic and biotic processes, like environmental filtering or competitive exclusion, mainly performing at smaller scales.

We here propose a multi- spatial scale approach aiming to validate some of the hierarchical model postulates and to clarify which assembly mechanisms drive species occurrence in biological communities. To achieve this goal, we use the tropical montane forests (TMFs) in the Andes as model system. Mountain ranges provide an excellent natural laboratory to investigate how ecological and evolutionary mechanisms influence community assembly along their slopes. Besides, Andean TMFs foster an enormous biodiversity and their large geographical extent enables the replication of large altitudinal gradients over different latitudes, in areas with different climates, topographies and biogeographic and evolutionary histories. The replication of gradients is particularly important for the sake of the generalisation of conclusions beyond the singular contingencies of each studied site. Hence, in this doctoral thesis I study woody plant biodiversity patterns in Andean TMFs along altitudinal gradients to accomplish the following goals:

1) To investigate taxonomic, functional and phylogenetic diversity patterns along Andean TMFs altitudinal gradients and explore some of the mechanisms responsible for community assembly (Chapter I). This is a fundamental step for a later sound exploration of such mechanisms.

2) To test the postulate that ecological mechanisms responsible for community assembly –namely environmental filtering and competitive exclusion– operate at different spatial scales –small and large, respectively– (Chapter II).

3) To address how different environmental filters affect spatial variation of a specific functional trait –namely compound leaves– by quantifying changes in this trait patterns along altitudinal gradients and linking them to underlying potential ecological drivers –drought, light availability and wind– (Chapter III).

To accomplish these goals, we considered 114 (Chapter I), 60 (Chapter II) and 390 plots (Chapter III) scattered along 4, 2 and 11 altitudinal gradients in Andean TMFs, respectively. Plots' bioclimatic features were retrieved from world climatic databases. In all cases, all occurring woody individuals were surveyed. Individuals were identified taxonomically and the resulting taxa characterized functionally. In addition, we built a phylogenetic tree (Chapters I and III). That information was summarized using different metrics and analysed using statistical techniques, such as null models or generalized linear mixed effects models (GLMMs).

We found in Chapter I that taxonomic, functional and phylogenetic diversity monotonically decrease along altitude. This decrease is positively correlated with a decrease in temperature and gives clues about the importance of ecological processes shaping community assembly. The functional and phylogenetic diversity decrease suggests that the increasingly colder temperatures, as we move upslope, operate as an environmental filter (abiotic mechanism) that selects only for those species capable to adapt and survive. Those species, which historically migrated towards highlands and succeeded belong to few closely related clades originated in tropical warm lowlands (evolutive mechanism), in agreement with the Tropical Niche Conservatism hypothesis. The importance of environmental filtering for community assembly and the spatial extent of its effect was evidenced in Chapter II by showing that a functional traits clustering pattern only appears at large spatial scales (between plots at different altitudinal belts) that embrace stark environmental differences. Moreover, the effect of environmental filtering was confirmed by demonstrating that its fingerprint goes beyond the observed pattern, since along the altitudinal gradient plant species exhibit strong climatic preferences and their abundances dramatically shift. However, competitive exclusion was not found to act in this ecosystem, nor even at small spatial scales (within subplots) where plant species effectively compete for limited resources, at least by mediating a functional divergence among co-occurring species. Finally, in Chapter III, we reported a decrease on species bearing compound leaves –richness and abundance– from lower to upper altitudes, consistent across the Andean mountain range, but we found no evidence that this trend was caused by the environmental conditions hypothesized to favor this type of leaf in lower TMFs. Finally, we explored whether compound leaves altitudinal pattern could be the potential result of TMFs evolutionary history, but we found either support for this potential explanation.

In summary, by addressing functional and phylogenetic diversity in addition to the taxonomic one, we can obtain a much more complete understanding of the mechanisms responsible of community assembly that ultimately lead to the observed biodiversity patterns. Phylogenetic diversity offers us a window to the past that permits to infer the evolutionary mechanisms and events that explain the historical plant colonization of the Andean slopes. Our results suggest that few closely related lineages migrated from tropical warm lowlands towards the highlands. Functional diversity reveals how the species cope with their surrounding environment and shows that environmental filter is the overriding ecological mechanism determining the differential distribution of species along altitude. However, environmental filters seem not to shape the altitudinal trends of compound leaves, and thus, considering also that the evidences in this sense found in other studies are weak, we cannot advocate for the usage of compound leaf as an easily measurable, qualitative functional trait. The fact that our results are consistent among different study sites highlights the robustness of our conclusions and permits to generalize them in the Andean TMFs and beyond, in other tropical mountain ranges.

English: Bombuscaro river at Podocarpus National Park (Zamora-Chinchipe, Ecuador), one of the areas studied within this thesis. This area encompasses an altitudinal gradient ranging from 900 to 3600 masl. In 30 0.1 ha. plots we inventoried 9366 tree individuals belonging to 734 taxa.

Español: Río Bombuscaro en el Parque Nacional Podocarpus (Zamora-Chinchipe, Ecuador), una de las áreas estudiadas en esta tesis. Esta área abarca un gradiente altitudinal que se extiende desde los 900 a los 3600 msnm. En 30 parcelas de 0.01 ha. censamos 9366 árboles pertenecientes a 734 taxones.

2 | RESUMEN

Entender los mecanismos evolutivos y/o ecológicos (incluyendo los factores bióticos, abióticos y estocásticos) que rigen el ensamblaje de las comunidades –es decir, la composición, estructura y la distribución de las comunidades biológicas en un ecosistema– sigue siendo una cuestión fundamental en ecología. Más allá de la perspectiva taxonómica clásica, las aproximaciones funcional y filogenética han impulsado nuestro conocimiento sobre los mecanismos que determinan los patrones de biodiversidad durante las últimas décadas. Sin embargo, todavía existen muchas discrepancias sobre cuál es el alcance relativo de dichos mecanismos y bajo qué circunstancias ejercen su influencia. En este sentido, parece que la existencia de conclusiones contradictorias que afectan y enmarañan la comprensión de los procesos que determinan el ensamblaje de las comunidades pueda deberse a diferentes consideraciones relacionadas con la escala espacial. Para incorporar esta perspectiva se ha propuesto un modelo jerárquico de ensamblaje de comunidades que postula que los distintos mecanismos de ensamblaje operan de manera secuencial, a escalas cada vez más pequeñas, para generar los patrones de la distribución de la biodiversidad que observamos. Este modelo comprende desde procesos evolutivos e históricos tales como la especiación, la extinción o la migración, que operan a mayormente a escalas grandes, hasta procesos como el filtrado ambiental o la exclusión competitiva, que fundamentalmente operan a escalas más pequeñas.

Nosotros proponemos una aproximación a múltiples escalas para validar algunos de los postulados del modelo jerárquico y para esclarecer qué mecanismos de ensamblaje determinan la ocurrencia de especies en las comunidades biológicas. Para lograr este objetivo utilizamos los bosques tropicales montanos (TMFs) de los Andes como sistema de estudio. Las montañas proporcionan un excelente laboratorio natural para investigar cómo los mecanismos evolutivos y ecológicos influyen en el ensamblaje de las comunidades a lo largo de sus laderas. Además, los TMFs andinos atesoran una biodiversidad enorme y su gran extensión geográfica permite replicar latitudinalmente amplios gradientes altitudinales, a través de áreas con diferentes climas, topografías e historias biogeográficas y evolutivas. La replicación de estos gradientes es especialmente importante para poder generalizar las conclusiones más allá de las particularidades de cada lugar estudiado. Así pues, en esta tesis doctoral, yo estudio los patrones de biodiversidad de plantas leñosas en los TMFs andinos a lo largo de gradientes altitudinales con los siguientes objetivos:

1) Investigar los patrones de diversidad taxonómica, funcional y filogenética a lo largo de gradientes altitudinales en TMF andinos y explorar algunos de los mecanismos responsables del ensamblaje de comunidades (Capítulo I). Esto constituye un paso fundamental para una posterior exploración robusta de dichos mecanismos.

2) Verificar el postulado de que los mecanismos ecológicos responsables del ensamblaje de comunidades –a saber, filtrado ambiental y exclusión competitiva– operan a diferentes escalas espaciales –pequeña y grande, respectivamente– (Capítulo II).

3) Abordar cómo diferentes filtros ambientales afectan a la variación especial de un rasgo funcional específico –a saber, hojas compuestas– cuantificando cambios en los patrones de dicho rasgo a lo largo de gradientes altitudinales y relacionándolos con posibles causas ecológicas –sequía, disponibilidad lumínica y viento– (Capítulo III).

Para cumplir con dichos objetivos, fueron consideradas 114 (Capítulo I), 60 (Capítulo II) y 390 parcelas (Capítulo III) distribuidas a lo largo de 4, 2 y 11 gradientes altitudinales en TMFs andinos, respectivamente. Las características bioclimáticas de las parcelas fueron obtenidas de bases de datos climáticos mundiales. En todos los casos, todos los individuos leñosos fueron censados. Los individuos fueron identificados taxonómicamente y los taxones resultantes caracterizados funcionalmente. Además, construimos un árbol filogenético (Capítulos I y III). Esa información fue resumida usando diferentes métricas y analizada empleando técnicas estadísticas tales como modelos nulos o modelos lineales generalizados mixtos (GLMMs).

En el Capítulo I nosotros encontramos que la diversidad taxonómica, funcional y filogenética disminuyen de forma monotónica con la altitud. Esta disminución está correlacionada positivamente con un descenso de la temperatura y nos da pistas a cerca de la importancia de los procesos ecológicos para el ensamblaje de las comunidades. La disminución en la diversidad funcional y filogenética sugiere que, conforme nos movemos hacia arriba en la ladera de la montaña, las temperaturas cada vez más frías funcionan como un filtro ambiental (mecanismo abiótico) que selecciona únicamente a aquellas especies capaces de adaptarse y sobrevivir. Esas especies que históricamente migraron hacia las partes altas y allí tuvieron éxito pertenecen a unos pocos géneros estrechamente relacionados que se originaron en las tierras bajas cálidas tropicales (mecanismo evolutivo), de acuerdo con la hipótesis del conservadurismo del nicho tropical. La importancia del filtrado ambiental para el ensamblaje de comunidades y el alcance espacial de su efecto quedó demostrada en el Capítulo II al encontrar que un patrón de convergencia en los rasgos funcionales solo aparece a escalas espaciales grandes (entre parcelas a diferentes altitudes) que abarcan fuertes diferencias ambientales. Además, el efecto del filtrado ambiental fue confirmado al demostrar que su efecto va más allá del patrón observado, ya que a lo largo del gradiente altitudinal las especies vegetales exhiben preferencias climáticas marcadas y sus abundancias oscilan radicalmente. Sin embargo, no se detectó el efecto de la exclusión competitiva en este ecosistema, ni siquiera a escalas espaciales pequeñas (dentro de las subparcelas), donde las especies vegetales compiten de manera efectiva por recursos limitados, al menos mediante un patrón funcional divergente entre las especies que coexisten. Finalmente, en el Capítulo III, demostramos que tanto la riqueza como la abundancia de especies de hojas compuestas disminuyen de las partes bajas a las partes altas de la montaña de manera consistente en Los Andes, pero no encontramos ninguna evidencia de que este patrón esté demostrado por alguna de las condiciones ambientales que hipotéticamente podrían favorecer la presencia de este tipo de hojas en las partes bajas de los TMFs. Por último, exploramos si el patrón altitudinal de hojas compuestas pudiera ser consecuencia de la historia evolutiva de los TMFs andinos, pero tampoco encontramos evidencias a favor de esta potencial explicación.

En resumen, considerar la diversidad funcional y filogenética además de la taxonómica permite obtener una comprensión mucho más profunda sobre los mecanismos responsables del ensamblaje de comunidades que en última instancia producen los patrones de biodiversidad observados. La diversidad filogenética ofrece una ventana al pasado que permite inferir los mecanismos y eventos evolutivos que explican la historia de la colonización vegetal de las laderas de los Andes. Nuestros resultados sugieren que unos pocos linajes estrechamente emparentados emigraron de las zonas tropicales bajas y cálidas a las tierras altas. La diversidad funcional revela como las especies lidian con el ambiente que las rodea y muestra que el filtrado ambiental es el mecanismo ecológico dominante que determina la distribución diferencial de las especies a lo largo de la altitud. Sin embargo, los filtros ambientales no parecen determinar los patrones altitudinales en hojas compuestas y, por consiguiente y considerando también que las evidencias en este sentido encontradas por otros estudios son débiles, nosotros no recomendamos el uso de la hoja compuesta como un rasgo funcional cualitativo fácilmente medible. El hecho de que nuestros resultados sean consistentes entre diferentes zonas de estudio destaca la robustez de nuestras conclusiones y nos permite generalizarlas en los bosques tropicales de los Andes y en otros sistemas montañosos tropicales.

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English: cloud forest in Río Abiseo National Park (San Martín, Peru), another area studied in this thesis. This area encompasses from 350 to 4200 masl. 8905 trees from 526 taxa were found.

Español: bosque nuboso en el Parque Nacional Río Abiseo (San Martín, Perú), otra área estudiada en esta tesis. Este área abarca de los 350 a los 4200 msnm. 8905 árboles de 526 taxones fueron encontrados.

3 | GENERAL INTRODUCTION

3.1 | Setting the stage

During their expeditions in the XIX century, naturalists as Humboldt, Darwin or Wallace become enthralled by the vast biological diversity existing on Earth and started wondering how it was generated and which factors determined its different patterns. Their observations and cogitations on this topic set the ground for the inception of community ecology. This discipline pursues to understand the principles and rules determining the assembly of biological communities, this is, the processes and mechanisms shaping the composition, structure and distribution of biological communities across different ecosystems. Within the XX century scholars broadly addressed this theme and, although very valuable discoveries and theories have contributed to move forward our understanding in the topic, the discussion still flames and remains being a priority for modern ecology (Pavoine and Bonsall 2011, Sutherland et al. 2013).

In the quest for mechanisms that explain the assemblage of biological communities in nature, academics have proposed a long list of hypotheses –Palmer (1994) identified at least 120–. However, attending to their causal nature, they can be boiled down into deterministic and stochastic ones. The former considers that a community is the result of deterministic, understandable underlying rules that determine its structure and composition, whereas the latter posits that communities are merely a stochastic and intractable compilation of organisms (Swenson 2012).

3.2 | The historical inception of some of the most broadly embraced assembly rules

On the one hand, on his theory of evolution, Darwin (1859) suggested that the competition among living organisms –a competition that becomes stronger the more similar the species are– is key on the struggle for existence and the basis of natural selection. On the other hand, on his investigations about the distribution of plants, Humboldt noticed how the physical environment frames the distribution of species across the landscape (Humboldt and Bonpland 1805). Hence, although some of the most pervasive ideas in the study of biological communities can be traced back to the XIX century, the development of those concepts within the framework of community ecology deeps its roots in the 1970's.

Diamond (1975), that was who introduced the idea of "assembly" and "assembly rules" in the context of community ecology, explored the role of competition. By investigating the co-occurrence patterns of bird communities in New Guinea's islands, Diamond considered that coexisting species compete for the resources until one excludes the other and, therefore, the lesser two species compete the more likely they are to coexist. As consequence of this competitive exclusion principle, he argued that competition is the main mechanism behind community assembly.

Another now well-established core idea in the field of community assembly is the concept of "filter", which was firstly introduced by Nobel & Slatyer (1977) on their studies about succession following fire disturbance in Mediterranean ecosystems. They envisioned the idea that certain environmental factors act as a selective filter or barrier that only allows that species with certain features can establish and survive, whereas those lacking the features required to cope with particular environmental conditions are culled. In this regard, environmental filtering would constitute a paramount force fuelling the assembly of communities.

Alternatively to the concepts of competition and filter, which belong to the category of deterministic rules, another authors suggested precisely the opposite, *i.e.*, that community assembly is mainly ruled by non-deterministic factors. The consideration of the large spatial and successional variability in plant community composition, lead Gleason (1939) to invoke randomness as the cause of species distribution in opposition to the predictability of communities given, for instance, local environmental factors (Clements 1916). However, Gleason' ideas remained largely ignored until other authors as Connell (1978) or Fagerström (1988) revisited and highlighted the fundamental role that stochasticity plays in shaping species distribution.

3.3 | Current state of the knowledge: The hierarchical community assembly model

Within the last decades community assembly research has kept going on, leading somehow to a polarization on which stochastic and deterministic mechanisms are presented as opposing, mutually-excluding stark choices (Lortie et al. 2004, Gaston and Chown 2005, Leibold and McPeek 2006, Vergnon et al. 2009). This has ultimately led to the current scenario where two main coexistence theories prevail: the niche theory and the neutral theory.

Niche theory considers that distinct species have different ecological strategies –*i.e.*, abiotic and biotic requirements and limitations– that determine the niche that they can occupy and therefore, when the niches of several species overlap, one specie will exclude all or most others (Hutchinson 1959, MacArthur and Levins 1967). Hence, the coexistence within a community requires that its species exploit different niches, which could ultimately be predicted by defining their ecological strategies (Chase and Leibold 2003, Silvertown 2004).

In opposition, neutral theory (Hubbell 2001) assumes that species are ecologically equivalent and interchangeable –*i.e.* the potential interspecific advantages or disadvantages are in fact irrelevant or neutral to their performance and fitness–. Therefore, species distribution would be merely the result of dispersal limitation events and stochastic demographic processes such as ecological drift or individuals births and deaths (Bell 2000, Chave 2004).

Although it is undeniable that the inordinate amount of time and energy consumed by researchers has generated important advances in the understanding of community assembly, community ecologists are still far from solving the puzzle (Lortie et al. 2004, Götzenberger et al. 2012, Escudero and Valladares 2016). At this point, the current conceptual framework: i) posits, by conciliating elements from niche and neutral theories, that communities result from both non-mutually exclusive deterministic and stochastic processes (Adler et al. 2007, Valladares et al. 2015); and ii) considers that the relative importance of those processes shifts across different temporal and spatial scales (Wiens 1989, Levin 1992, Whittaker et al. 2001). The first statement is not surprising since, in most of the polarized issues with viewpoints at the opposing edges of a conceptual gradient, none of the perspectives themselves can explain the whole scenario (Perry 1994). The second observation, however, is more remarkable: despite accounting for spatial scale is of utmost importance in ecology (McGill 2010), sometimes a blatant disregard towards the consideration of its implications have led community assembly to a quagmire (Chase 2014, Viana and Chase 2018). For instance, rather than merely questioning about which assembly process is more relevant, the focus should be placed on how the explicit considerations imposed by the spatial scale determine our ability to detect their existence and extent. Thus, e.g., studies testing for the existence of competitive exclusion over vast spatial scales, by comparing individuals spaced long distances (Bycroft et al. 1993), or those investigating the existence of abiotic filters at fine spatial scales, at which the environmental conditions are essentially the same (Kraft and Ackerly 2014), have no possibilities to reach sound conclusions about the processes under study. It was precisely to overcome the dichotomy between niche versus neutral theories and to incorporate the spatial scale importance issue that a hierarchical community assembly model was developed.

The hierarchical community assembly model conciliates different community assembly processes and incorporates a spatial scale-explicit context by conceptually equating the processes to filters or sieves that operate sequentially and distinctly across different spatial and temporal scales (Colwell and Winkler 1984, Weiher and Keddy 1995a, Götzenberger et al. 2012, HilleRisLambers et al. 2012). This model encompasses from evolutive and biogeographic processes, such as historical patterns of speciation, migration or extinction at large–regional scales, to ecological processes like environmental filtering, competitive exclusion or demographic stochasticity at smaller–local scales. The former mechanisms define a regional pool of potential colonizer species over which the latter operate at increasingly finer scales, rendering the final subset of species that is capable to occurs within locally observed communities. The detailed investigation of current community assemblages can reveal signatures of those mechanisms that shape their structure and composition.

3.4 | Tools for community assembly study: strengths and limitations

Functional and phylogenetic diversity

Traditionally community assembly mechanisms have been explored by studying taxonomic diversity, *i.e.*, taxonomic patterns of species composition, abundances and dynamics. And although this approach has sometimes found non-random patterns for those attributes, the reality is that it is very low informative since it treats all species as ecologically equivalent and evolutionarily independent and hence yields little to no information about the underlying ecological strategies or evolutive histories of the species (Fukami et al. 2005, Swenson 2012, Gagic et al. 2015). For instance, two communities may not have any species in common (*i.e.*, high taxonomic beta diversity) but their species could be identical or distinct in terms of their ecological requirements and strategies (*i.e*., low or high functional beta diversity, respectively) or share a close or far evolutive history (*i.e*., low or high phylogenetic beta diversity, respectively). Therefore, if a naturalist only focuses on taxonomic diversity but ignores the functional and phylogenetic facets, no speculations about assembly mechanisms other than dispersal limitation events or stochastic demographic processes can be formulated.

Functional diversity has proven to be a more powerful and suitable tool than classical taxonomic approaches for the study of ecological assembly rules. While the latter merely scrutinize non ecologically informative taxonomic indexes based on Linnaean binomials, functional diversity analyzes species functional traits –any morphological, physiological, phenological or behavioral feature of the species potentially related to their growth rate, survival probability or reproductive performance– that can describe their abiotic and biotic functioning within a community (McGill et al. 2006, Petchey and Gaston 2006, Violle et al. 2007). In other words, functional diversity allows to truly characterize and even predict where species can thrive, how they interact or how they contribute to ecosystem function and therefore to have an insight into the underlying community assembly mechanisms (Shipley et al. 2006, Mason and De Bello 2013, Violle et al. 2014).

Within the last years the trait-based ecology has made significant progresses identifying highly informative functional traits across different taxa, such as animals (Pedley & Dolman, 2014; Brousseau *et al.*, 2018), plants (Westoby & Wright, 2006; Funk *et al.*, 2017) or microorganisms (Litchman *et al.*, 2007; Fierer *et al.*, 2014). By scaling up those trait data to community level, processes as competitive exclusion or environmental filtering have been invoked as key mechanisms shaping community assembly across different ecosystems (e.g., rockfishes in the Pacific ocean [Ingram & Shurin, 2009], trees in the Amazon [Kraft et al. 2008, Baraloto et al. 2012], grasses in Scandinavia [de Bello *et al.*, 2013], lichens in Europe [Hurtado *et al.*, 2019] or soil bacteria in the Tibetan plateau [Song *et al.*, 2019]). However, measuring certain traits is time consuming and resource demanding (Cornelissen et al. 2003) and therefore the identification of new easily measurable, qualitative functional traits is highly desirable (Pérez-Harguindeguy et al. 2013, Garnier et al. 2015).

Under the functional ecology framework, environmental filtering is seen as to favor the coexistence of species that are similar in the ecological strategies enabling them to overcome the sieve imposed by the abiotic environment and to stablish and survive. Thus, a functional trait convergence/ clustering is predicted to characterize a community that has suffered this process (Keddy 1992, Lavorel and Garnier 2002, Cornwell et al. 2006). Conversely, under competitive exclusion a community functional trait divergence/ overdispersion is hypothesized, as the coexistence of species should be facilitated if they deploy different ecological strategies (Tilman 1982, Watkins and Wilson 2003, Silvertown 2004). Nevertheless, within last years some studies have challenged this dichotomy claiming that a community clustering pattern can also arise from competition and other biotic processes (Uriarte 2000, Grime 2006, Mayfield and Levine 2010). In this regard, additional evidences beyond community functional dispersion patterns can certainly contribute to detect the signature of a given mechanism. For instance, different functional traits have been demonstrated to respond to environmental constraints (*i.e.*, light, water or nutrient availability in the specific case of plants). Hence, the spatial patterns of a given functional trait can confirm the effect of different environmental filters in as much as spatial variation on the firsts can be linked with changes in environmental conditions (Cadotte and Tucker 2017).

In addition to functional diversity, phylogenetic diversity has demonstrated to be a very valuable resource to understand community assembly rules beyond the consideration of species abiotic and biotic interactions. By considering the phylogenetic relationships between coexisting species –quantifying their degree of relatedness– the phylogenetic approach reveals how historical and evolutionary processes have shaped species distribution (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2009). Therefore, this approach is particularly suitable for investigating evolutive assembly rules. For instance, it permits to trace back the historical speciation, migration and extinction events that have generated the current regional species pool from which species are withdrawn in the local assemblages. In addition, phylogenetic approach has also been used for addressing abiotic and biotic ecological assembly rules under the assumption that the more closely related two species are the more ecological similarities share in terms of functional traits and niche occupation (Webb 2000, Vamosi et al. 2009). In this sense, environmental filtering and competitive exclusion are expected to cause on co-occurring individuals phylogenetic dispersion patterns –clustered or overdispersed– equivalent to the functional ones (Swenson 2013). However, this affirmation must be taken with caution, since the phylogenetic signal of functional traits has proven not to be as common as originally hypothesized (Losos 2008, Cahill et al. 2008, Gerhold et al. 2015).

<u>*Null models*</u>

The importance of null models in ecology sparkled 40 years ago, when Connor & Simberloff (1979) questioned the methodology and results of Diamond's work (1975). Since then, null models have become the most broadly used methodological approach to confirm the existence of community assembly rules (Colwell and Winkler 1984, Gotelli and Graves 1996).

Null models are based upon the comparison of the observed distribution of any community feature, e.g. functional diversity or phylogenetic relatedness, against its random distribution generated by breaking down the real community structure into a null stochastic one (Gotelli and Graves 1996). Departures on the observed distribution from the null expectation would suggest the existence of deterministic community assembly processes, such as environmental filtering or competitive exclusion. However, for the results to make full ecological sense, it is crucial that null models are generated including certain design restrictions and premises that enable them to detect the presence or absence of solely a given ecological process at a time (Gotelli 2000, Götzenberger et al. 2012). Consequently, randomizations algorithms must be adapted to detect only the hypothesized mechanism while excluding the rest. This is especially relevant under the current framework, since the number of parameters that can be manipulated –*e.g.*, species richness or species abundances– and the amount of randomization procedures available –*e.g.*, randomizing the community information, the functional information or both– can certainly complicate the selection of a suitable null model for detecting the fingerprint of a specific ecological process (Götzenberger et al. 2016). Spatial scale consideration illustrates this fact: it is not possible to identify whether a certain assembly mechanism operates at certain spatial scale if the null model does not incorporate constraints and assumptions based on the spatial scales at which it is expected to occur, thus guaranteeing the full ecological significance of the results. However, that rarely occurs and since the usage of a unique null model for testing different hypotheses is broadly extended, the reliability of the results is compromised and the truthfulness of the discoveries limited (Wilson et al. 1987, Peres-Neto et al. 2011, Baraloto et al. 2012).

3.5 | Study system: Altitudinal gradients in Andean tropical montane forests (TMFs)

Biogeographers have broadly studied latitudinal gradients pursuing to understand the causes of spatial variation in species diversity (Mittelbach et al. 2007). However, altitudinal gradients –*i.e.* mountains– have proven to be even more suitable for this endeavour (Rahbek 1995, Sanders and Rahbek 2012). On one side, mountains capture a broad, heterogeneous array of ecological and environmental variations over shorter geographic distances than latitudinal gradients (Körner 2007, Rahbek et al. 2019b): they encompass different climate types, bear high topographic complexity and experiment a large mosaic of physical parameters variation and environmental oscillations (e.g, seasonality). On the other side, mountains' biodiversity fosters the fingerprint of deep-time evolutionary and historical processes such as speciation, adaptation, migration and extinction driven by the effect of climatic and geological events (Antonelli et al. 2018, Rahbek et al. 2019a). In addition and caused by the previous facts, mountains are unusually biodiverse given their relative small area and host an extraordinary amount of endemism (Myers et al. 2000). All those considerations make mountains an exceptional natural laboratory to investigate how evolutive and ecological mechanisms shape diversity patterns and to evaluate the validity of some of the postulates of the hierarchical community assembly model (Körner 2004). In this sense, the tropical forests of the Andes mountain range (Andean TMFs) stand out as a particularly unparalleled system (Malhi et al. 2010).

A rich evolutive history and a plethora of climates, soils and topographies are key to understand the origin and maintenance of the high diversity of Andean TMFs, one of the hottest diversity hotspots (Brummitt and Lughadha 2003, Mittermeier et al. 2005). Among the most important historical events explaining the genesis of Andean biodiversity highlights the uprising of the Andes, which meant the creation of new and vast areas available for life colonization and the closure of Panamanian isthmus, which allowed a massive migration of taxa from North America to South America (Antonelli et al. 2009, Hoorn et al. 2010). Besides, the Andean slopes display a variety of climatic conditions –ranging from the hot and seasonally dry western side and the more humid and rainy oriental side to the frosted paramo– and soils (Cuesta et al. 2009, Pitman et al. 2013). Thus, the stark environmental gradients found in the Andes, together with its very complex topography in which valleys and mountains alternate, favours the isolation of populations, which ultimately leads to high speciation rates and small-ranged endemism (Antonelli and Sanmartín 2011, Rull 2011).

In addition to the previously described facts, the possibility of replicating altitudinal gradients over a large latitudinal extent and compare the similarities and differences between them makes from Andean TMFs even a more attractive study site to study diversity distribution (Malhi et al. 2010, Rahbek et al. 2019b).

English: Montecristo- Abiseo rivers basin in Río Abiseo National Park (Peru). Andean TMFs encompass are featured by the alternance of mountains, valleys and rivers generating high topographic complexity.

Español: Cuenca de los ríos Montecristo- Abiseo en el Parque Nacional Río Abiseo (Perú). Los TMFs andinos se caracterizan por la alternancia de montañas, valles y ríos que genera una gran complejidad topográfica.

4 | GOALS AND CHAPTERS

The general aim of this thesis is to use the functional and phylogenetic diversity framework to shed light into the processes and mechanisms that determine the distribution/community assembly of woody plants in Andean tropical montane forests along altitudinal and latitudinal gradients. To tackle this aim, the thesis is divided in three synthetic goals addressed within their respective chapters.

Goals

1) To describe taxonomic, functional and phylogenetic patterns of woody plants along Andean TMFs altitudinal gradients (Chapter I).
2) To test the postulate that ecological mechanisms behind the observed patterns operate at different spatial scales (Chapter II).
3) To report altitudinal patterns of compound leaves and to address whether different environmental filters are responsible of such patterns (Chapter III).

Chapters

Each one of the three chapters is structured according to the main sections of a per review research article: introduction, materials and methods, results, discussion, conclusions and supplementary information.

I. In the first chapter we describe patterns of the three facets of diversity –taxonomic, functional and phylogenetic–along altitude in four Andean TMFs altitudinal gradients. Besides, we test how those three facets of diversity are correlated. The mere description of the patterns suggests some clues about potential ecological and evolutive mechanisms behind the observed patterns and is key for later investigating those patterns more in detail. In this chapter we used Hill numbers to explore patterns, which allows to obtain some extra information by considering not only their richness but also their abundance and dominance.

II. In the second chapter we explore the existence of ecological assembly rules that determine the coexistence of woody plants in Andean TMFs. More specifically, we test in two Andean TMFs whether ecological mechanisms –environmental filtering and competitive exclusion– exert their influence at different spatial scales –small and large– to validate one of the most important postulates of community assembly hierarchical model. In this chapter we used functional traits dispersion patterns and null models to detect the signature of different community assembly rules at the spatial scales they are more likely to operate and sought further evidences to unambiguously link the observed patterns to the underlying assembly processes.

III. In the third chapter we investigate altitudinal trends in compound leaves species –richness and abundance– in 11 TMFs by using GLMMs. Then, we explore whether different environmental filters favour compound leaves at lower altitudes given the alleged ecological advantages of this type of leaf –drought tolerance, mechanical resistance against wind or rapid growth under low light availability–. In addition, we also explored whether those patterns could be the mere result of compound leaves evolutionary history.

5 | LIST OF MANUSCRIPTS

This thesis rests on three manuscripts published or intended to be published in international, per reviewed scientific journals. Title, information about the authors and publication state of each manuscript is available below.

- A comparison of woody plant biodiversity patterns along altitude in Andean tropical forests: ecological and evolutionary insights from a taxonomic, functional and phylogenetic perspective.

  Guillermo Bañares-de-Dios, Manuel J. Macía, Íñigo Granzow-de la Cerda, Itziar Arnelas, Julia Vega-Álvarez, Carlos I. Espinosa, Norma Salinas and Luis Cayuela.

  In preparation

- Linking patterns and processes of tree community assembly across spatial scales in tropical montane forests.

  Guillermo Bañares-de-Dios, Manuel J. Macía, Íñigo Granzow-de la Cerda, Itziar Arnelas, Gabriel Martins de Carvalho, Carlos I. Espinosa, Norma Salinas, Nathan G. Swenson and Luis Cayuela.

  Ecology (In Press)

- Altitudinal changes in compound leaf species in tropical Andean communities: Ecological advantages or evolutionary causes?

  Guillermo Bañares-de-Dios, Íñigo Granzow-de la Cerda, Manuel J. Macía, Esteban Álvarez-Dávila, Gabriel Arellano, Itziar Arnelas, Selene Baez, Marijn Bauters, Cecilia Blundo, Rudi Cruz, Miro Demol, Carlos I. Espinosa, William Farfán-Ríos, Jürgen Homeier, Lucio Malizia, Alex Nina, María Prieto, Norma Salinas, Miles Silman, Hans Verbeeck and Luis Cayuela.

  To be submitted to Global Ecology and Biogeography

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7 | CHAPTERS

- **Chapter I:** A comparison of woody plant biodiversity patterns along altitude in Andean tropical forests: ecological and evolutionary insights from a taxonomic, functional and phylogenetic perspective.

- **Chapter II:** Linking patterns and processes of tree community assembly across spatial scales in tropical montane forests.

- **Chapter III:** Altitudinal changes in compound leaf species in tropical Andean communities: Ecological advantages or evolutionary causes?

CHAPTER I

A comparison of woody plant biodiversity patterns along altitude in Andean tropical forests: ecological and evolutionary insights from a taxonomic, functional and phylogenetic perspective

Manuscript in preparation

Abstract

Given the rich mosaic of topographies and climates they encompass across relatively short geographical distances, altitudinal gradients are a very useful natural laboratory to explore biodiversity distribution patterns and to investigate their causes. In this sense, Andean tropical montane forests (TMFs) provide unparalleled experimental sites because their vast biodiversity and the possibility of replicating those gradients across latitudes. However, TMFs remain quite unknown compared to tropical lowland forests and no studies to date have investigated altitudinal taxonomic, functional and phylogenetic diversity patterns, simultaneously, along their latitudinal range. In this study we investigated these three facets of diversity for woody plants along four altitudinal transects (elevation ranges *ca.* 2000 m) that encompass 114 plots of 0.1 ha over a broad latitudinal gradient (*ca.* 1200 km). Our results indicate a monotonic decrease in taxonomic, functional and phylogenetic diversity along altitude that is consistent among transects. In agreement with previous studies, both taxonomic and functional diversity were expected to decline with altitude since, at increasingly colder temperatures and harsher conditions towards highlands, species proliferation would decrease and less functional strategies would permit survival. Phylogenetic diversity, on the other hand, was expected to increase towards the highlands due to the arrival of distantly related, extra-tropical lineages adapted to cold temperatures (Out of the Tropical Lowlands hypothesis). However, our results point towards the validity of the opposing hypothesis (Tropical Niche Conservatisms) that posits that, due to their strong niche conservatism, just few closely related tropical lowland clades have been able to adapt to cold temperatures and migrate uplands. Besides, a solid description of functional and phylogenetic diversity patterns is a key step for later understanding the ecological and evolutionary mechanisms behind the patterns and to stablish conservation policies that look beyond mere taxonomic richness in possibly the most hyper-diverse terrestrial hotspot.

Keywords: taxonomic diversity; functional diversity; phylogenetic diversity; altitudinal gradient; tropical montane forest; Tropical Niche Conservatism; Out of the Tropics Lowlands; Andes

1 | INTRODUCTION

Although biodiversity distribution patterns are one of the most pervasive issues explored since the early beginnings of natural history (Humboldt and Bonpland 1805), understanding their underlying causes remains a central theme for ecologists (Storch et al. 2005, Sutherland et al. 2013). In the quest for explanations, the study of mountains represents a cornerstone towards developing a general theory of species diversity (Lomolino 2001, Sanders and Rahbek 2012). On the one hand, over shorter geographic distances, altitudinal gradients encompass broader different climate types, foster higher topographic complexity and experience a larger mosaic of short and long-term environmental oscillations –e.g. seasonal or daily climate variation and historical climatic shifts– in comparison to the wider, traditionally addressed latitudinal gradients (Antonelli et al. 2018, Rahbek et al. 2019a). On the other hand, mountains contribute exceptionally to terrestrial biodiversity given their relatively small area (Myers et al. 2000). For instance, on merely 25% of world’s land mass, mountains harbour roughly 87% of terrestrial global biodiversity, of which a large amount is endemic of these regions (Rahbek et al. 2019b). Furthermore, the interest in mountains has increased since the turn of this century because they can be used as microcosms to investigate the effects of global warming on the distribution of biodiversity (Parmesan 2006). Therefore, altitudinal gradients represent excellent natural laboratories to investigate the ecological and evolutionary mechanisms shaping biodiversity (Körner 2004, 2007, Rahbek et al. 2019b). Yet, a solid understanding of the origin, maintenance and fate of biodiversity through the study of altitudinal gradients requires not only a statistically rigorous test of diversity trends along altitude, but also comparisons of these trends among mountain ranges (Lomolino 2001), something that has is seldom found in the literature to date (Chun and Lee 2017).

Tropical mountains harbour different ecosystems that rank among the richest on Earth in terms of species (Myers et al. 2000, Rahbek et al. 2019b). This is the case with Andean tropical montane forests (TMFs), probably the world`s species richest one (Brummitt and Lughadha 2003, Hughes and Eastwood 2006), which is estimated to host one-sixth of all plant species in less of 1% of Earth’s terrestrial surface and to foster an inordinate 44% of endemicity (Myers et al. 2000). Moreover, TMFs perform functions such as carbon storage, nutrient retention, water provisioning, pollination and pest control, which provide essential services to human societies and economies from local to global scales (Josse et al. 2009, Sundqvist et al. 2013). All things considered, it is not surprising that Andean TMFs represent one of the most important biodiversity hotspots for conservation priorities (Myers et al. 2000, Mittermeier et al. 2005). Therefore, their vast biodiversity, their rich mosaic of topographies and climates and the chance to replicate broad altitudinal gradients within the same region, make Andean TMFs a particularly unparalleled scenario to investigate altitudinal biodiversity patterns (Malhi et al. 2010).

Biodiversity has traditionally been explored in terms of taxonomic diversity, i.e., through the analysis of alpha and/or beta species richness and abundances (Mangurran 1988). Today, this framework has demonstrated to be relatively simplistic, since indexes based on species binomials treat all of them as ecologically equivalent and evolutionary independent. Such approach renders scarce information about their ecological strategies or biogeographic history, which are the ultimate factors responsible for species observed distributions (McGill et al. 2006, Pavoine and Bonsall 2011, Swenson 2011). A more accurate depiction of diversity must therefore incorporate its three main dimensions ¬–taxonomic, functional and phylogenetic– in order to describe comprehensive patterns of biodiversity and understand the mechanisms responsible for such patterns. On the one hand, functional diversity rests on the use of species functional traits ¬–any physical, behavioural or phenological feature of species potentially related to their performance or fitness¬ as much more informative tools in describing and even predicting where species can thrive, how they interact or how they contribute to ecosystem function (Petchey and Gaston 2006, Violle et al. 2007, Cadotte et al. 2011, Reich 2014). On the other hand, phylogenetic diversity considers phylogenetic origins of taxa and their distances to address how historical and evolutionary processes generate species and shape their distribution and co-occurrence patterns (Ricklefs 2006, Cavender-Bares et al. 2009, Srivastava et al. 2012). These three dimensions of diversity are intrinsically related ¬–e.g., phylogenetic diversity has been widely used to infer functional diversity under the assumption that closely related species share functional traits (Webb et al. 2002, Moles et al. 2005)–. Nonetheless, their responses to environment may not always be positively correlated and can show differential trends (Devictor et al. 2010, Zupan et al. 2014). In this regard, investigations that account simultaneously for patterns in the three facets of diversity under variable environmental conditions (Meynard et al. 2011, Purschke et al. 2013, Arnan et al. 2016, Hurtado et al. 2019), especially along altitudinal gradients (Dehling et al. 2014, Chun and Lee 2017), are very informative but also rare.

Studies conducted across different biomes and for different taxonomic groups have revealed that for i) taxonomic diversity, the most prevalent pattern consists of an overall decrease in species richness with altitude (Figure 1a), although a hump shaped trend in which diversity peaks at middle elevations (ca. 1500 m) has often been described (Rahbek 1995, McCain 2005). Similarly, for ii) functional diversity, the most broadly reported trend also consists of a decrease in the functional strategies as one moves upslope (Figure 1b), where conditions are harsher (Swenson et al. 2011, de Bello et al. 2013, Thakur and Chawla 2019). In the case of iii) phylogenetic diversity, the patterns along altitude are inherently specific to the biogeographic history of the study site (Faith 1992, Ricklefs and Schluter 1993).

Focusing on phylogenetic diversity and for the particular case of TMFs, two hypotheses have been proposed to explain contrasting trends (Qian and Ricklefs 2016): the ‘Tropical Niche Conservatism’ (TNC) and the ‘Out of the Tropic Lowlands’ (OTL). TNC was originally conceived to explain the latitudinal pattern of decreasing species diversity (Latham and Ricklefs 1993). According to this hypothesis, tropical clades were originated under warm conditions (e.g., tropical lowlands). Since tropical species exhibit a strong niche conservatism –*i.e.*, they mostly retain their ancestral climatic niches– and have narrow thermal tolerances (Janzen 1967), the acquisition of the adaptations required to survive and thrive in colder latitudes was quite infrequent (Wiens and Donoghue 2004, Wiens and Graham 2005, Ricklefs 2006). Therefore, just a few, closely related lineages succeeded to adapt and thus phylogenetic clustering sensu Webb et al. (2002) would increase from the Equator towards the poles (Donoghue 2008, Graham et al. 2009). Because the altitudinal trend of decreasing temperature within a warm and humid tropical region mirrors the latitudinal trend (MacArthur 1972, Stevens 1992), TNC could also explain how a subset of phylogenetically related clades from the lowlands expanded upwards in elevation by adapting to colder conditions (Kerkhoff et al. 2014). If this were the case, the species assemblages in the highlands would be mere clustered and impoverished phylogenetic subsets of their respective lowland floras (Figure 1c) which would have migrated across environmental filters, where those clades would have subsequently radiated (Graham et al. 2009). In contrast to TNC, OTL hypothesis is based on the idea of convergent evolution. OTL was formulated by Qian and Ricklefs (2016) after the 'Out of The Tropics' hypothesis (Jablonski et al. 2006), which posits that although most of the clades were certainly originated in tropical lowlands, several of these managed to quickly expand towards cooler latitudes as their enabling adaptations would be the result of evolutionary convergence –thus minimizing the importance of niche conservatism–. Therefore under OTL, conversely to TNC, neither would lineages be necessarily more closely related, nor would the phylogenetic clustering increase towards extratropical regions. In the context of tropical altitudinal gradients, the OTL hypothesis poses that, in addition to a relatively frequent migration and adaptation of tropical lowland clades towards tropical highlands, extra-tropical cold-tolerant lineages might have also colonized the highlands through a latitudinal migration that used the coolness of high altitudes as a corridor. Those events would be translated into a phylogenetic overdispersion pattern –rather than clustering– pattern along the altitudinal gradient. Empirical data generally support the validity of the TNC hypothesis to explain latitudinal phylogenetic gradients (Hawkins et al. 2012, Kerkhoff et al. 2014). However, within tropical mountain regions (e.g., the Andes, [Qian 2014] or Mount Kinabalu in Borneo [Culmsee and Leuschner 2013]), the observed phylogenetic patterns for woody plants give greater support to the OTL than to the TNC hypothesis. In the case of the Andes, the explanation would be as follows: during early angiosperm radiation several lowland Amazonian primitive clades, not necessarily related, acquired features –niche convergence– enabling them to dwell along the increasingly cooler altitudes during the Andes uplift. In addition, Andean highland local floras became afterwards enriched by trans-Andean elements that migrated from higher latitudes along a cold high-altitude corridor. Therefore, the phylogenetic clustering ought to decrease and phylogenetic alpha diversity increase with altitude (Figure 1 d) (González-Caro et al. 2014, Qian 2014, Ramírez et al. 2019).

The present study is the first one to our knowledge that considers the altitudinal trends of the three facets of diversity –taxonomic, functional and phylogenetic– in the Andes by investigating across a broad latitudinal gradient that encompasses four elevation gradients of Andean TMFs in Ecuador, Peru and Bolivia. The comparison of trends among different transects will provide interesting insights for a better understanding of the ecological and evolutionary mechanisms generating woody plants altitudinal biodiversity trends and to endorse conservation initiatives in a hyper-diverse hotspot that still is poorly known in comparison to tropical lowlands (Bubb et al. 2004) and that faces the threats of human destruction and global warming (Vuille et al. 2003, Sommer et al. 2010).

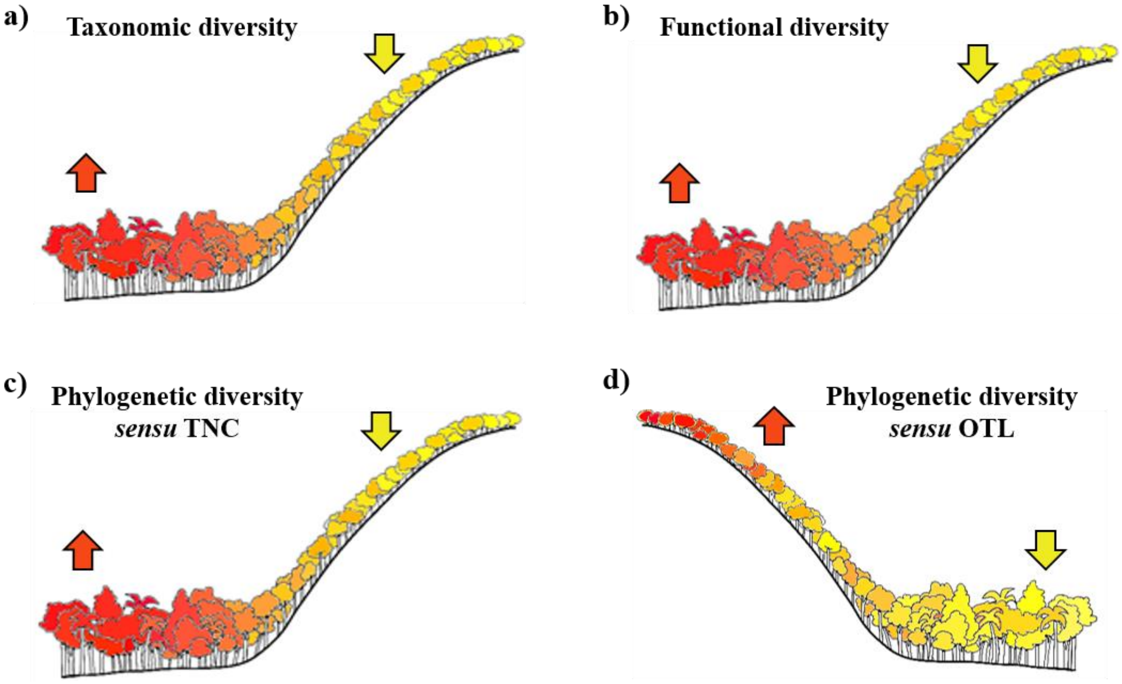

FIGURE 1. Schematic representation of the expected alpha diversity values along altitudinal gradients for different facets of diversity according to the broadest reported patterns in literature. a) Taxonomic diversity, b) Functional diversity and Phylogenetic diversity (contrasting patterns proposed in Andean TMFs according to TNC [c)] and OTL [d)] hypotheses). Reddish colours represent high values and yellowish low values.

2 | MATERIALS AND METHODS

2.1 | Study area and climatic characterization

The study was carried out along four broad elevational gradients (traversing *ca*. 2000 m) of Andean TMFs (Figure 2) located in remote and largely inaccessible regions (hereinafter referred to as “sites” or “transects”): one in Podocarpus National Park (Ecuador), one in Río Abiseo National Park (Peru), one in Madidi National Park (Bolivia) and one close to Pilón- Lajas Biosphere Reserve (Bolivia). Exact location can be found in Bañares-de-Dios et al. (in press) for sites in Ecuador and Peru and in Arellano and Macía (2014) for those in Bolivia. Three altitudinal belts were defined at each site (lower, 750-1200 m; intermediate, 1800-2250 m; upper, 2700-3100 m) and, on each belt, nine or ten 0.1 ha (50 × 20 m) plots were stablished following Arellano et al. (2016), accounting for a total of 114 plots (Table 1). At each belt, plots were spaced at least 300 m apart and set in mature forest areas with no signs of human perturbations or natural disturbances. On each plot, all woody plant individuals ≥ 2.5 cm in diameter at breast height (DBH;

measured at 1,3 m above the ground) rooted within the plot limit were inventoried and their height estimated. At least one voucher from every taxon was collected for identification. Overall, 37,869 individuals were inventoried (Tables 1).

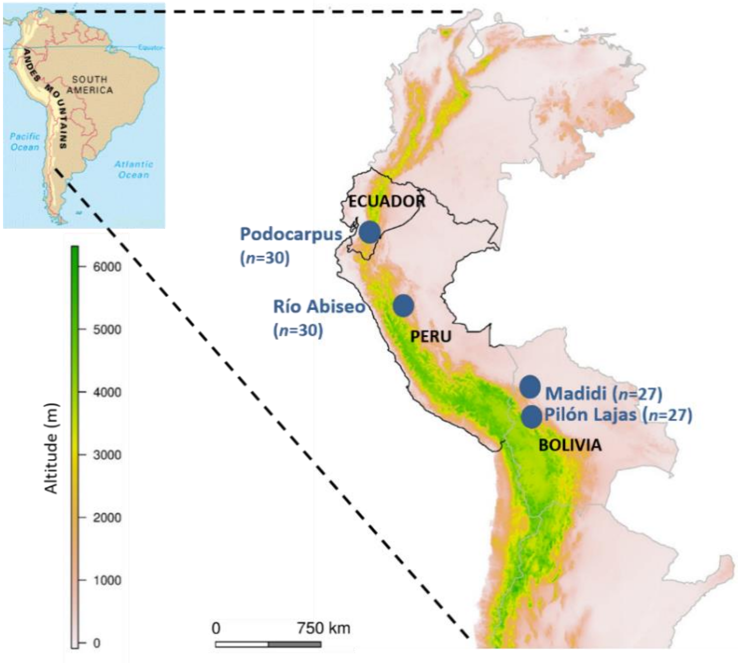

FIGURE 2. Map with the location of the four Andean tropical montane forest altitudinal gradients (blue dots), scattered across Ecuador, Peru and Bolivia. In total n=114 plots, 0.1 ha were stablished.

TABLE 1. Altitudinal gradients and plots individuals and taxonomic data.

Site (*n*_plots)	Belt	Mean altitude (masl)	Range altitude (masl)	*n*_ind.	*n*_taxa	*n*_taxa res. specie	*n*_taxa res. genera	*n*_taxa res above genera
Podocarpus (30)	Lower	1114	1033 - 1249	3153	452	268	98	86
	Interm.	1978	1806 - 2217	2917	389	265	85	39
	Upper	2788	2674 - 2906	3840	187	147	21	19
Altitude gradient: 1873 m			1033 - 2906	9910	832	517 (62 %)	186 (22 %)	129 (16 %)
Río Abiseo (30)	Lower	881	745 - 1122	2770	355	154	138	63
	Interm.	2158	2093 - 2233	3339	230	54	77	99
	Upper	2807	2721 - 2980	3099	148	50	30	68
Altitude gradient: 2235 m			745 - 2980	9208	585	211 (36 %)	205 (35 %)	169 (29 %)
Madidi (27)	Lower	1345	1166 - 1496	2892	275	230	38	7
	Interm.	2214	2139 - 2281	2751	156	140	15	1
	Upper	2892	2789 - 3061	2944	119	99	18	2
Altitude gradient: 1895 m			1166 - 3061	8587	462	399 (86 %)	54 (11 %)	9 (3 %)
Pilón Lajas (27)	Lower	1375	1224 - 1531	3111	269	230	35	4
	Interm.	2168	2019 - 2203	2219	205	167	32	6
	Upper	2988	2801 - 3106	4832	88	75	13	0
Altitude gradient: 1882 m			1224 - 3106	10162	466	397 (85 %)	60 (13 %)	9 (2 %)

Environmental characterization of the plots was conducted using bioclimatic variables from CHELSA climatological dataset (Karger et al. 2017). Mean annual temperature is the most representative variable for studies along altitudinal gradients since it represents the fundamental climatic change associated with altitude (Körner 2007).

Small changes in mean annual temperature are expected to have a major influence on biodiversity distributions, especially in the tropics where species have narrow thermal tolerances (Janzen 1967). In our study sites, mean annual temperature exhibits high correlation with altitude (r>0.98). Altitudinal thermal ranges span 12º C in Podocarpus, 9º C in Río Abiseo and 10º C both in Madidi and Pilón Lajas. Alternative climatic variables related with precipitation are not as relevant for our study since moist TMFs, characterized by persistent fog throughout most of the year, are not subjected to relevant hydric stress.

2.2 | Taxonomic characterization

Voucher specimens were identified at different herbaria from Ecuador (HUTPL, LOJA, QCA), Peru (HAO, HUT, MOL, USM) and Bolivia (LPB), acronyms according to Thiers (2019). Overall, average per plot species richness ranged from 51 taxa (Madidi) to 76 (Podocarpus) considering transects and from 332 taxa (lower) to 245 (intermediate) and 135 (upper) considering altitudinal belts (see Table 1 for taxonomic information regarding individuals and taxa and the taxonomic resolution at each site and altitudinal belt). Standardization of taxonomic species names was conducted using the R package ‘Taxonstand’ (Cayuela et al. 2012, 2017). It is important to notice that taxonomic resolution achieved was substantially lower for Río Abiseo than for the rest of sites (Table 1).

2.3 | Functional characterization

Functional characterization was conducted only for Podocarpus National Park (Ecuador) and Río Abiseo National Park (Peru). For each taxon, the following functional traits were measured: specific leaf area (SLA), leaf thickness (LT), and wood density (WD). These are widely used functional traits that address key woody plants functional strategy axes (Wright et al. 2004, Chave et al. 2009). SLA was calculated from five leaves as the ratio of leaf surface area measured with a portable laser leaf area meter (CI- 202, CID Bio-Science, WA, USA) to leaf dry mass measured after drying at 80 °C for 48 h. LT was measured using a digital caliper. Branch wood density was used as a proxy for WD, since both are strongly and positively correlated (Swenson and Enquist 2008). Sections of branches ca. 10 cm, as cylindrical as possible, were stripped of bark and their fresh volume determined geometrically using a caliper to measure their diameter and length. Density of the branch section was calculated dividing its fresh volume by its dry mass measured after drying at 80 °C for 48-72 h. Mean trait values were calculated for each taxon. All these protocols were based on Cornelissen et al. (2003). Functional data for the three functional traits were available for 649 taxa in Podocarpus (78 % of the total), encompassing 8936 individuals (90 % of the total) and for 497 taxa in Río Abiseo (85 % of the total), representing 8723 individuals (95 % of the total inventoried).

2.4 | Phylogenetic tree generation

We generated a phylogenetic tree (Text S1) using the ‘V.PhyloMaker’ R package (Jin and Qian 2019). This package allows to prune our species list from a mega-tree that currently represents the largest dated phylogeny for vascular plants (based on Smith and Brown [2018] for seed plants and on Zanne et al. [2014] for pteridophytes), encompassing 10587 genera and 74533 species. The phylogenetic tree was constructed using the function phylo.maker with the parameters nodes=nodes.info.1 and scenarios=S3. For phylogenetic diversity calculations we only considered taxa taxonomically resolved at species level or morphospecies at genus level, excluding those morphospecies above genera level. Accordingly, phylogenetic characterization represented 703 taxa in Podocarpus (88 % of the total), 416 taxa in Río Abiseo (71 % of the total), 453 taxa in Madidi (97 % of the total) and 457 taxa in Pilón Lajas (98 % of the total).

2.5 | Diversity measurements

Attribute diversity consists of a unified framework for assessing biodiversity that integrates its three facets –taxonomic, functional and phylogenetic–, each one measured in different units or entities (Chao et al. 2014). For taxonomic diversity the attribute value is unity for each taxa, so all taxa (taxonomic entities) are treated as being taxonomically equally distinct. For functional diversity, the attribute value is the functional distance between each pair of taxa, so all taxa pairs with a unit of pairwise distance (functional entities) are treated as functionally equally distinct. For phylogenetic diversity, the attribute value is the length of each branch segment, so all unit-length branches (phylogenetic entities) are treated as phylogenetically equally distinct. The most interesting advantages of this approach are that the three facets of diversity 1) can be boiled down as Hill numbers and 2) can be virtually compared between each other by transforming them into the same currency or unit (termed effective number of species). Hill numbers were originally aimed to quantify abundance-based taxonomic diversity by using an index, q, that under different scenarios is more or less sensitive to common species and dependent on rare ones (Hill 1973, Jost 2006). For q=0, taxa abundances are not considered, and its value equates taxa richness. For q=1, all taxa are weighted by their abundance, equating Shannon`s diversity. Lastly, for q=2, dominant taxa are more heavily considered while rare ones are irrelevant, equating the inverse of Simpson’s concentration. Attribute diversity framework extended the usage of Hill numbers beyond taxonomic diversity to functional and phylogenetic ones by weighing each entity by its relative abundance (see Chiu and Chao 2014 for functional and Chao et al. 2010 for phylogenetic diversity). Recent applications of this approach to characterize biodiversity from an integrated perspective can be found in, e.g., Vega-Álvarez et al. (2019) or Coudrain et al. (2016).

We calculated all attribute diversity indexes for Hill numbers at plot level using the R package 'hillR' (Daijang 2018). However, it is important to notice that given that the input is different for the three facets of diversity –as are limited both functional characterization and taxonomic resolution, we neither had functional traits values available for all taxa nor could identify all morphospecies to a taxonomic level suitable for being incorporated in the mega-tree), an integrated comparison among the three facets of diversity in terms of effective number of species can not strictly be conducted.

2.6 | Statistical analyses

We first explored correlations among distinct facets of diversity –taxonomic, functional and phylogenetic– for different Hill numbers –q=0, q=1 and q=2– using Pearson's correlation and a significance level of α=0.05. Note that comparisons for functional diversity were conducted only for Podocarpus and Río Abiseo, since functional data for Madidi and Pilón Lajas were not available

Then, we used generalized linear models (GLMs) to investigate the altitudinal changes of the distinct facets of diversity for different Hill numbers. Overall, for each diversity facet and Hill number, we fitted five models that included all possible combinations of effects: 1) null (i.e., no effect), 2) only altitude, 3) only site, 4) similar effect of altitude across sites (i.e., additive model with parallel slopes) and 5) differential effect of altitude among sites (i.e., interaction model with different slopes. A negative binomial error distribution was used to account for overdispersion. We compared alternative models based on the Akaike Information Criterion corrected for small sample sizes (AICc). Models with a difference in AICc > 2 suggest that the worst model had virtually no support and was omitted. Deviance (D2) was calculated for the best, most complex model. Analyses were conducted using the R packages 'MASS' (Venables and Ripley 2002) and 'MuMIn' (Barton 2018). Finally, when the best fitted model included the interaction between elevation and site, we performed post-hoc tests to evaluate whether the slopes significatively varied among sites utilizing the R package 'phia' (de Rosario- Martínez 2015) and a significance level of α=0.05.

3 | RESULTS

When analysing all sites together, taxonomic and functional diversities were always significantly and positively correlated for q=0, q=1 and q=2 (Figure 3 and Table S1). However, taxonomic and phylogenetic and functional and phylogenetic were solely significantly and positively correlated for q=0 and q=1. When analyzing sites independently, taxonomic and functional diversities were always significantly and positively correlated for q=0, q=1 and q=2. Nevertheless, taxonomic and phylogenetic diversities were only significantly and positively correlated for q=0 and q=1 (except in Podocarpus for q=1, where the correlation was not significant), while for q=2 correlations were idiosyncratic at different sites (positively significant and non-significantly positive or negative correlated). Functional and phylogenetic diversities were only significantly and positively correlated for q=0 and q=1 (except in Podocarpus for q=1, where the correlation was not significant) while all correlations for q=2 were non-significant.

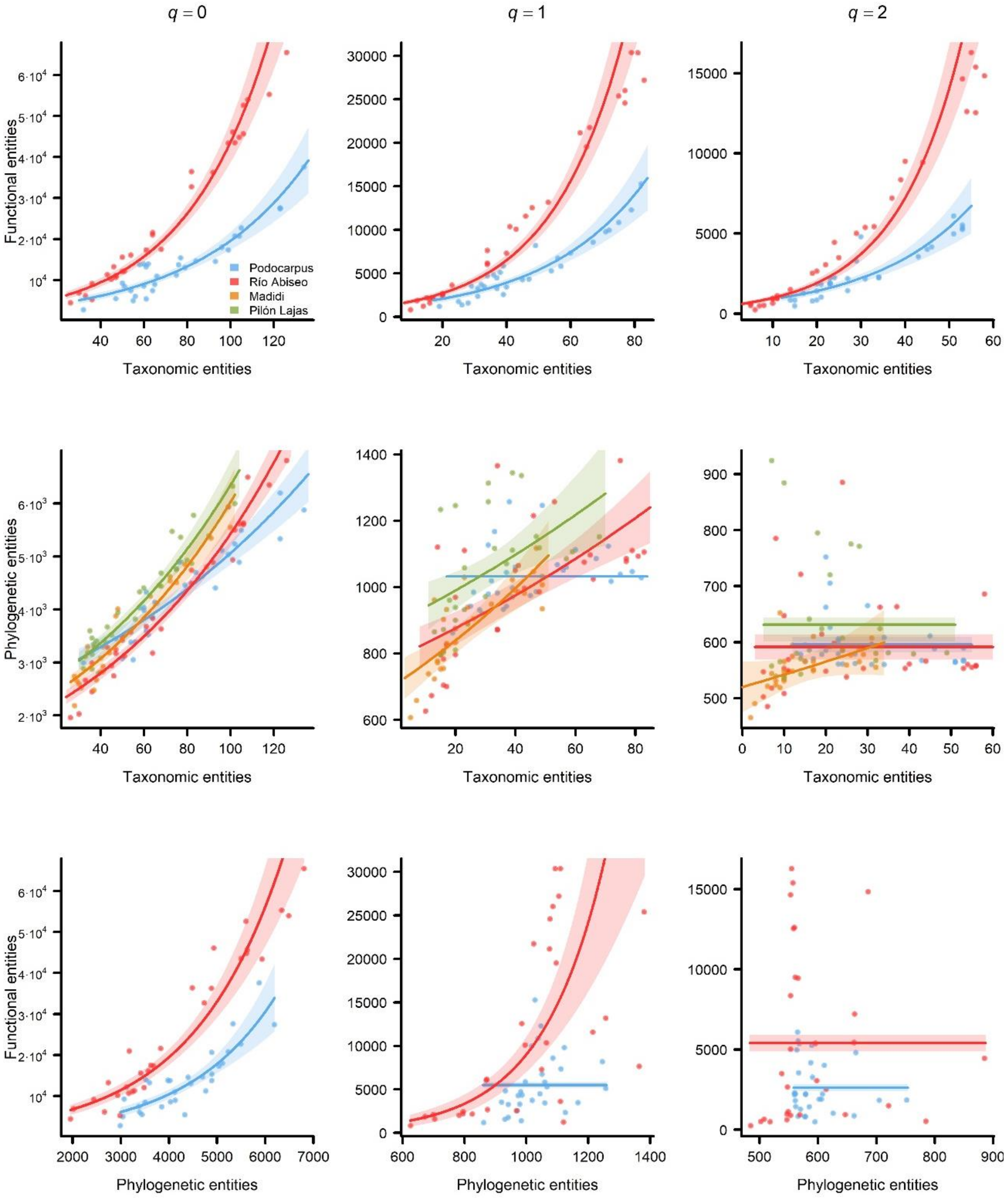

FIGURE 3 Pairwise diversity facets comparison for different sites. Functional versus taxonomic (upper charts), phylogenetic versus taxonomic (medium charts) and functional versus phylogenetic (lower charts) values of attribute diversity indexes for Hill numbers *q*=0 (left column), *q*=1 (central column) and *q*=2 (right column) were compared.

All three facets of diversity decreased along altitude for q=0, q=1 and q=2 (Figure 4). This decrease was consistently stronger and absolute values of different diversity facets consistently higher for q=0 than for q=1 and for q=1 than for q=2. This decrease was especially marked for phylogenetic diversity. Model predictions indicated that diversity values for all facets of diversity were higher at lower altitudes and best fit models always included both altitude and site (additive and/or interaction models) as predictors (Table 2). Results for post-hoc tests to evaluate how the changes in diversity varied among sites are included in Table S2.

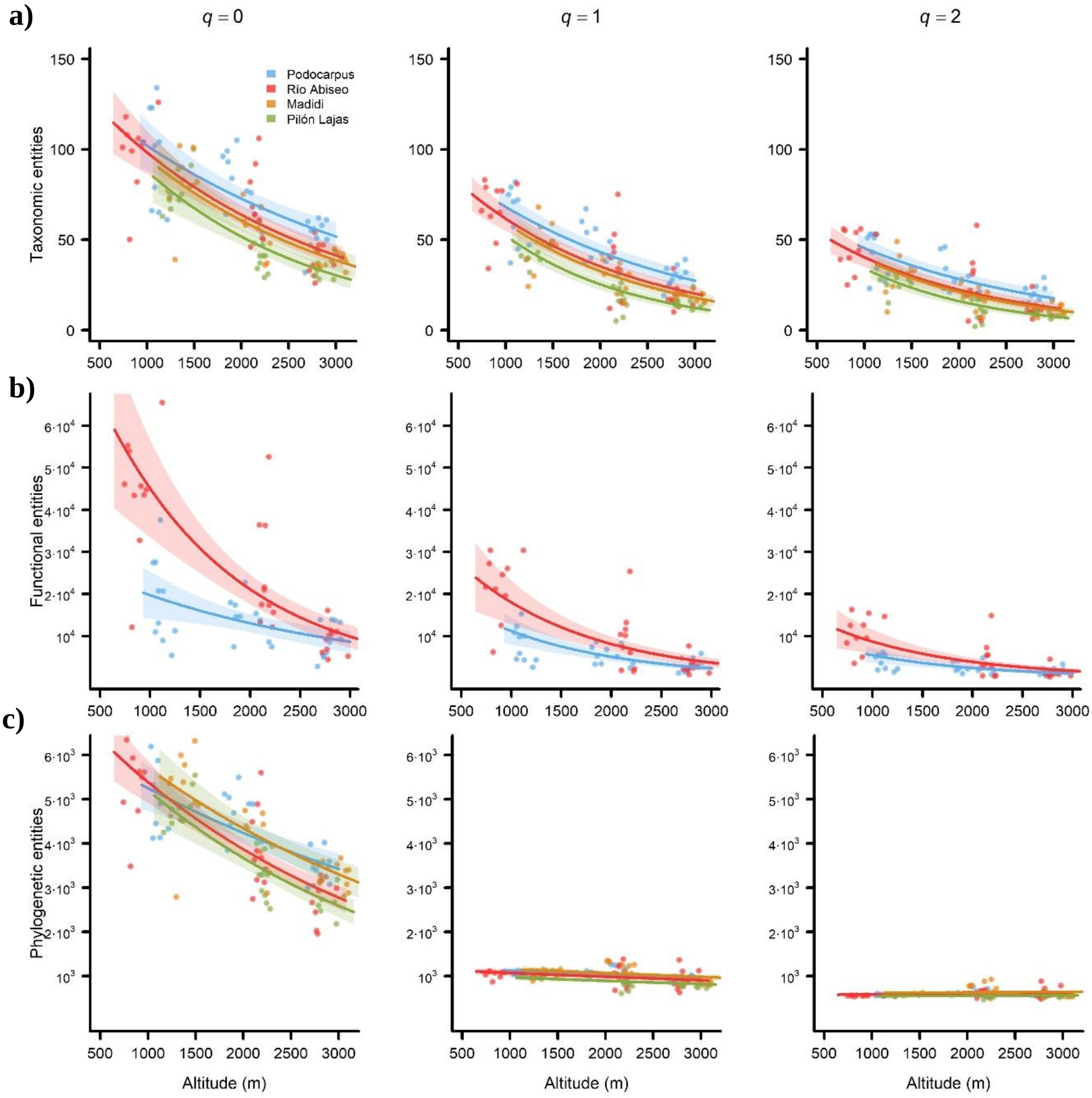

FIGURE 4 Patterns of CL along altitude for different sites. Taxonomic (upper charts), functional (medium charts) and phylogenetic (lower charts) diversity patterns along altitude for Hill numbers *q*=0 (left column), *q*=1 (central column) and *q*=2 (right column).

TABLE 2. AICc values for generalized linear models (GLMs) on the taxonomic, functional and phylogenetic diversity values calculated for different Hill numbers in relation to distinct predictors. Explained deviance D^2 was calculated only for the best, more complex model (in the case that here were two best models, differences between the most complex and the less complex in terms of deviance would be minimal).

	AICc			**D^2**		
Taxonomic diversity	**$q = 0$**	**$q = 1$**	**$q = 2$**	**$q = 0$**	**$q = 1$**	**$q = 2$**
-	1059.49	988.25	908.37	**-**	**-**	**-**
Altitude	959.23	895.57	830.82	**-**	**-**	**-**
Site	1048.93	973.07	894.85	**-**	**-**	**-**
Altitude + Site	**939.53**	868.04	**810.33**	**0.68**	**-**	**-**
Altitude : Site	942.22	**864.05**	**808.73**	**-**	**0.68**	**0.60**
Functional diversity	**$q = 0$**	**$q = 1$**	**$q = 2$**	**$q = 0$**	**$q = 1$**	**$q = 2$**
-	1297.02	1204.95	1119.08	**-**	**-**	**-**
Altitude	1262.95	1164.07	1084.03	**-**	**-**	**-**
Site	1286.12	1196.45	1111.83	**-**	**-**	**-**
Altitude + Site	**1251.23**	**1157.86**	**1079.89**	**-**	**0.55**	**0.48**
Altitude : Site	**1249.44**	1162.64	1083.67	**0.58**	-	-
Phylogenetic diversity	**$q = 0$**	**$q = 1$**	**$q = 2$**	**$q = 0$**	**$q = 1$**	**$q = 2$**
-	1919.31	1489.19	1303.35	**-**	**-**	**-**
Altitude	1823.22	1475.77	1304.43	**-**	**-**	**-**
Site	1917.71	1475.89	**1294.10**	**-**	**-**	**-**
Altitude + Site	**1810.94**	**1460.23**	**1295.25**	**-**	**-**	**-**
Altitude : Site	**1811.94**	**1460.02**	**1295.56**	**0.65**	**0.28**	**0.14**

4 | DISCUSSION

In this study we explored altitudinal patterns of the three facets of alpha diversity – taxonomic, functional and phylogenetic– in Andean TMFs along four different transects spanning over a broad latitudinal gradient (*ca*. 1740 km in distance and *ca*. 1200 km in latitude). Overall, our results showed an altitudinal monotonic decrease in the three facets of diversity consistently across all transects. While taxonomic and functional diversity decreases were expected, phylogenetic diversity was not, challenging the validity of the OTL hypothesis for explaining diversity along tropical altitudinal gradients.

In TMFs, the three facets of diversity were positively correlated for q=0 and q=1 while only taxonomic and phylogenetic diversity were so also for q=2 (Figure 3 and Table S1), thus meaning that the three components of diversity respond similarly to altitude. Such a positive correlation could *a priori* be regarded as expected simply by chance, as the more species present the more functional traits and lineages present would be (Losos 2008). However, this is not always necessarily true: two ecosystems with equal number of species could greatly differ in the function and services that perform or in their evolutionary history and composition (Safi et al. 2011, Tucker et al. 2012). In fact, in the particular case of TMFs, the TNC and OTL hypotheses imply opposing relations between PD and TD or FD along the altitudinal gradient: while TNC implies a positive one (phylogenetically impoverished uplands communities have less species with less functional strategies –trait conservatism– than lowland ones) the OTL implies a negative one (uplands communities are phylogenetically more diverse than lowlands ones despite fostering less species with less functional strategies –trait convergence–). In any case, the relations between the three facets of diversity indicate that in Andean TMFs by preserving taxonomic diversity functional and phylogenetic ones are also indirectly preserved, that their role as a hotspot for conservation is not limited to species diversity and that on those biomes, different facets of diversity (can be used interchangeably as they) are surrogates of each other.

4.1 |Taxonomic diversity

Our results show a monotonic decrease in taxonomic diversity (i.e., taxa richness) along altitude across all the study transects (Figure 4 a). Besides, this decrease is consistent for different Hill numbers, indicating that such a decrease occurs regardless whether or not taxa are weighted by their abundance (q=1 or q=0, respectively) or by their dominance (q=2). Traditionally, a monotonic decline in taxonomic diversity with altitude has been one of the most widely accepted biogeographic patterns (Rahbek 1995) in as much as higher temperatures at lower elevations lead to increased energy availability and productivity, that would ultimately result in higher proliferation of species (Hutchinson 1959, Allen et al. 2002). But on a meta-analysis, Rahbek (1995) questioned the universality and generalization of this pattern, highlighting that instead a hump-shaped curve with the greatest richness at intermediate altitudes was more common (Rahbek 2005). Indeed, such pattern has been widely reported for woody plants (Gentry 1988, Lieberman et al. 1996, Vázquez and Givnish 1998, Girardin et al. 2014, Ramírez et al. 2019, Veintimilla et al. 2019), non woody plants (Wolf and Flamenco 2003, Krömer et al. 2005, Kessler et al. 2011) and small mammals (McCain 2005), and also –although to a lesser extent– for birds (McCain 2009) and invertebrates (Olson 1994, García-López et al. 2012, da Silva et al. 2018). The existence of this hump in taxonomic diversity with altitude could be expected since, albeit temperature declines with elevation, stable water supply increases. Most altitudinal gradients are featured by a relatively stable condensation zone (cloud belt) at mid elevations, particularly distinguishable in the tropics, which renders the most favourable conditions for the majority of organisms' groups. The more diversity in certain groups (e.g., epiphytes) can beget and favour the more diversity in other groups (e.g., invertebrates) by providing more variety of habitat and resources (Rahbek 1995). Further, the net primary productivity decline with altitude sharply increases where the cloud immersion zone begins in TMFs (Girardin et al. 2010, Malhi et al. 2017), which would coincide with an important loss in the availability of resources from middle altitudes upwards. All considered it is not surprising that in mountain regions, and specifically in TMFs, taxonomic diversity typically peaks at middle altitudes (ca. 1500 m) and this pattern is driven mostly by climatic and productivity factors (Gentry 1995, Field et al. 2009, Girardin et al. 2014, Huaraca Huasco et al. 2014).

In the present study, we detected a consistent monotonic decrease of taxonomic diversity with altitude across all sites. Those results are well in agreement with former studies on TMFs albeit we did not find a hump-shaped pattern since, despite comprising large enough altitudinal gradients (on average ca. 2000 m), our transects neither 1) embrace low enough altitudes (< 1000 m) to capture a decrease in richness left of the hump nor 2) those elevations where the hump would be expected (ca. 1500 m) were sampled. Therefore, a hump-shaped pattern could likewise fit the observed data would we have continuous sample coverage all along the altitudinal gradient, as it has been already shown (Nogués-Bravo et al. 2008). A hump-shaped pattern would be very illustrative of how TMFs in the slopes of the Andes host more diversity at the regional scale than the nearby lowland Amazon forests (Gentry 1992, McFadden et al. 2019).

4.2 |Functional diversity

Our results indicate a monotonic decrease in functional diversity (i.e., functional strategies) along altitude across all the transects consistent for different Hill numbers (Figure 4 b). Functional traits offer clues concerning how plants cope with their surrounding abiotic and biotic environment. Therefore, upslope changes in temperature, water availability, atmospheric pressure, radiation or wind will influence key physiological or phenological processes such as photosynthesis, water and nutrient uptake AND growth that will be reflected on plant functional traits. In this sense, changes along altitude in TMFs have been widely documented for most informative functional traits, e.g., leaf size (Velázquez-Rosas et al. 2002, Schneider et al. 2003, Moser et al. 2007), wood density (Chave et al. 2006, Swenson and Enquist 2007) or growth forms (Vázquez and Givnish 1998). Comparatively, less studies have explored how functional diversity varies along altitudinal gradients (Thakur and Chawla 2019). Theory posits that along a gradient of environmental stress, the array of viable traits will be reduced as consequence of environmental filtering (Weiher and Keddy 1995, Cornwell and Ackerly 2009). In the case of altitude, the increasingly harsher and more restrictive conditions as we move upslope (Stevens 1992) will result in selective survival of only those taxa with the adequate traits whereas the rest with maladapted traits will be culled, either directly (i.e., certain traits will not make survival possible under certain conditions) or indirectly (i.e., some traits will not be sufficient to guarantee for survival under the competition of better adapted species exhibiting more adequate traits). Therefore, a loss in functional diversity (i.e., functional clustering sensu Weiher and Keddy [1995]) is expected to occur along altitudinal gradients as only species sharing key traits will be selected to survive (Graham et al. 2009, Machac et al. 2011). Although fewer than for taxonomic diversity, various studies have reported an altitudinal decrease in functional diversity for plants (Duivenvoorden and Cuello 2012, de Bello et al. 2013, Gazol et al. 2017, Schellenberger Costa et al. 2017, Thakur and Chawla 2019) and other organisms (Dehling et al. 2014, Bässler et al. 2016) and such evidences have been used to support the role of deterministic mechanisms, such as environmental filtering, in structuring plant communities (Swenson et al. 2012, Mori et al. 2013). In any case, it is worth remarking that two studies (Kluge and Kessler 2011, Zhang et al. 2014) encountered a hump-shaped pattern in functional diversity with a peak at mid altitudes (*ca*. 1300 m). In both cases, the authors concluded that environmental conditions were more stressful at lower and upper altitudes (lower precipitation in the former and lower temperatures in the later) in comparison to the mildest heat and moist conditions at middle ones (since precipitation peaks at middle elevation in many tropical mountains [Rahbek 1995, Boyle 1996]) that would be responsible of the peak in functional diversity. In this regard, same as for taxonomic diversity, would the cited studies reporting overall altitudinal decreases in functional diversity considered larger, ample enough altitudinal gradients could a hump shaped pattern be encountered. The same applies to our gradients: none of them reach altitudes below 800 m were environmental stress could impose severe functional restrictions potentially causing a decrease in functional diversity.

For functional diversity, the altitudinal decrease also occurs systematically for different Hill numbers. However, it is much less pronounced when functional entities are weighted by their abundance or their dominance (q=1 or q=2, respectively). An explanation might be that rare species are responsible of expanding the community functional hyperspace by exhibiting the more extreme functional traits values. When the environmental conditions set the limits for the occurrence of life, species exhibiting the most adequate traits will thrive while the rest fail (Bazzaz 1991, Keddy 1992), although few species displaying suboptimal, marginal values of those traits may still be able to survive. However, the fitness and performance of the formers will be likely hampered, thus explaining their lower abundance in comparison to species exhibiting the functionally most common, successful strategies (Cornwell and Ackerly 2010). Indeed, in hyper-diverse ecosystems such as tropical forests or coral reefs, most of the species have been demonstrated to account for similar, relatively limited functionality (functional redundancy) whereas the most distinct traits (functional rarity), responsible of a huge fraction of functional diversity, are mainly exhibited by rare species (Mouillot et al. 2013, 2014). A gross exploration of our results shows that dominant functional entities (q=2) encompass twofold less diversity than when entities are weighted by their abundance (q=1) and fourfold less than when all entities are considered as equally abundant (q=0), thus meaning that the less common functional strategies are those that account for broader functional hyperspace (Figure 4 b). These results, well in agreement with other studies, imply that the conservation of rare taxa goes far beyond their taxonomic uniqueness or aesthetic or cultural arguments because functional rarity – predominantly supported by them– and not functional redundancy is responsible of key ecosystem processes and a true and invaluable buffer against the contingencies arising from climate change or human perturbations (Walker et al. 1999, Cadotte et al. 2011, Violle et al. 2017).

4.3 | Phylogenetic diversity

Our results indicate that phylogenetic diversity (i.e., clades richness) decreases along altitude (Figure 4). This decrease is significant for q=0 and q=1, but not for q=2 (Table 2). These findings are well in agreement with the predictions of TNC hypothesis. According to TNC, only few closely related lineages would have historically acquired the suite of adaptations necessary to cope with the altitudinal increasingly colder temperatures (Latham and Ricklefs 1993) and hence the taxa at higher altitudes will be an impoverished, phylogenetically clustered subset of those from lower altitudes and thus their low phylogenetic diversity (Donoghue 2008). Although such a pattern has been already observed for other groups in Andean TMFs (e.g., hummingbirds [Graham et al. 2009, Dehling et al. 2014] or moths [Brehm et al. 2005]), studies conducted for trees in the same region suggest an opposite pattern. Both González-Caro et al. (2014) and Ramírez et al. (2019) revealed a tendency for an increase in woody plant phylogenetic alpha diversity and overdispersion towards Andean TMFs highlands. By also considering beta diversity, they demonstrated that there is a phylogenetic turnover along altitude. With those results, they concluded that the existence of temperate extratropical lineages in higher altitudes is responsible of the increase in phylogenetic alpha diversity and turnover and therefore they advocate for OTL hypothesis. In addition, by studying the mean clade age, Qian (2014) found that mean clade age tends to decrease along an altitudinal gradient in Andean TMFs, another prediction of the OTL model. Therefore, our results are contrary to evidences found by other authors and suggest instead the validity of the TNC hypothesis (although we did not account for beta phylogenetic diversity, considering our decrease in alpha diversity, we could not expect phylogenetic turnover but nestedness [sensu Baselga [2010]).

What could explain the opposing patterns between studies? Firstly, it is important to consider that González-Caro et al. (2014) and Ramírez et al. (2019) used phylogenetic metrics derived from a phylogeny resolved at species level (concretely net relatedness index –NRI– and nearest taxon index –NTI–; see Webb et al. [2008]), conversely to our metrics that derive from a megaphylogeny (Jin and Qian 2019). However, our metrics are tightly related (r=0,96 with NRI and r=0,91 with NTI, see Qian and Jin [2016]) and thus the comparison between studies is possible. In relation to Ramírez et al. (2019), which conclusions are based on results obtained from the study of a single transect, we believe that our experimental design is more robust since it considers four altitudinal transects spanning over a broad latitudinal extent and our conclusions more revealing since all transects show similar patterns. In relation to González-Caro et al. (2014) is important to consider that their altitudinal gradient is located along a vast extension that also encompasses stark edaphic and precipitation gradients. Such a fact makes difficult to untangle results concerning solely changes in phylogenetic diversity along altitude from the simultaneous influence of those potentially confounding factors on biogeographic and historical processes. In consequence, more studies about phylogenetic altitudinal patterns in Andean TMFs investigating alpha and beta and clade age are required to clarify whether TNC or OTL predictions better fit with observed woody plants trends along their slopes. In this regard, important implications should be considered depending on which hypothesis is valid. In the case that OTL was confirmed, caution should be taken when accepting phylogenetic proximity among species in TMFs as a surrogate for niche overlap or phylogenetic diversity as a surrogate for functional one –and vice-versa–, as functional traits would not be necessarily conserved but acquired (Webb et al. 2002, Losos 2008, Cavender-Bares et al. 2009)

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APPENDIX

TABLE S1. Pearson's correlations values between the facets of diversity for different Hill numbers. *: significative correlation ($p<0.05$); **: significative correlation ($p<0.01$); ***: significative correlation ($p<0.001$); light grey cells: correlations were not conducted since functional data were not available for Madidi and Pilón Lajas sites.

		Taxonomic vs functional	**Taxonomic vs phylogenetic**	**Functional vs phylogenetic**
Podocarpus	$q = 0$	0,93 (***)	0,93 (***)	0,85 (***)
	$q = 1$	0,94 (***)	0,34	0,35
	$q = 2$	0,93 (***)	-0,27	-0,15
Río Abiseo	$q = 0$	0,97 (***)	0,98 (***)	0,97 (***)
	$q = 1$	0,99 (***)	0,65 (***)	0,60 (***)
	$q = 2$	0,98 (***)	0,03	-0,01
Madidi	$q = 0$		0,95 (***)	
	$q = 1$		0,81 (***)	
	$q = 2$		0,55 (**)	
Pilón Lajas	$q = 0$		0,96 (***)	
	$q = 1$		0,48 (*)	
	$q = 2$		-0,11	
All sites	$q = 0$	0,80 (***)	0,93 (***)	0,80 (***)
	$q = 1$	0,83 (***)	0,58 (***)	0,47 (***)
	$q = 2$	0,83 (***)	0,03	-0,04

TABLE S2. Results from post-hoc tests to evaluate significative differences in diversity decrease among sites for different Hill numbers. -: no significative variation (p>0.05); *: significative variation (p<0.05); **: significative variation (p<0.01); ***: significative variation (p<0.001); light grey cells: no test conducted as interaction was not among the best models.

Taxonomic diversity	***q* = 0**	***q* = 1**	***q* = 2**
Podocarpus – Río Abiseo	-	*	*
Podocarpus – Madidi	-	***	***
Podocarpus – Pilón Lajas	-	**	**
Río Abiseo – Madidi	-	***	**
Río Abiseo – Pilón Lajas	-	-	-
Madidi – Pilón Lajas	-	***	*
Functional diversity	***q* = 0**	***q* = 1**	***q* = 2**
Podocarpus – Río Abiseo	*		
Phylogenetic diversity	***q* = 0**	***q* = 1**	***q* = 2**
Podocarpus – Río Abiseo	-	-	*
Podocarpus – Madidi	-	***	*
Podocarpus – Pilón Lajas	-	-	-
Río Abiseo – Madidi	-	*	-
Río Abiseo – Pilón Lajas	-	-	-
Madidi – Pilón Lajas	-	***	***

Text S1. Phylogenetic tree in Newick format based on Zanne et al. (2014).

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CHAPTER II

Linking patterns and processes of tree community assembly across spatial scales in tropical montane forests

Manuscript in press in Ecology

Abstract

Many studies have tried to assess the role of both deterministic and stochastic processes in community assembly, yet a lack of consensus exists on which processes are more prevalent and at which spatial scales they operate. To shed light on this issue, we tested two non-mutually exclusive, scale-dependent hypotheses: 1) that competitive exclusion dominates at small spatial scales; and 2) environmental filtering does so at larger ones. To accomplish this, we studied the functional patterns of tropical montane forest communities along two elevational gradients, in Ecuador and Peru, using floristic and functional data from 60 plots of 0.1 ha. We found no evidence of either functional overdispersion or clustering at small spatial scales, but we did find functional clustering at larger ones. The observed pattern of clustering, consistent with an environmental filtering process, was more evident when maximizing the environmental differences among any pair of plots. To strengthen the link between the observed community functional pattern and the underlying process of environmental filtering, we explored differences in the climatic preferences of the most abundant species found at lower and higher elevations and examined whether their abundances shifted along the elevation gradient. We found: 1) that greater community functional differences (observed between lower and upper tropical montane forest assemblies) were mostly the result of strong climatic preferences, maintained across the Neotropics; and 2) that the abundances of such species shifted along the elevational gradient. Our findings support the conclusion that at large spatial scales environmental filtering is the overriding mechanism for community assembly, since the pattern of functional clustering was linked to species` similarities in their climatic preferences, which ultimately resulted in shifts in species abundances along the gradient. However, there was no evidence of competitive exclusion at more homogeneous, smaller spatial scales, where plant species effectively compete for resources.

Keywords: community assembly, competitive exclusion, elevational gradients, environmental filtering, functional traits, spatial scale, tropical montane forest.

1 | INTRODUCTION

Which processes determine the structure and composition of communities? This question has generated a long discussion among naturalists for decades (Clements 1916, Gause 1934, MacArthur and Levins 1967, Wright 2002), becoming almost an obsession for ecologists and the core of community assembly research (Sutherland et al. 2013). In the quest for answers, scholars have proposed different explanations for the mechanisms shaping the structure and distribution of natural communities, with environmental filtering and competitive exclusion being among the most broadly embraced (Belyea and Lancaster 1999, Götzenberger et al. 2012, Kraft and Ackerly 2014). According to environmental filtering, the abiotic milieu acts as a sieve, allowing only species with certain traits or phenotypes to successfully establish and survive, whereas the rest fail (Bazzaz 1991, Weiher and Keddy 1995a, Diaz et al. 1998). However, competitive exclusion posits that coexisting species compete for the resources until one excludes the others. Thus, the least two species compete the more likely they are to co-occur (Diamond 1975, Abrams 1996, Dayan and Simberloff 2005). As an alternative to these niche-based explanations, the neutral assembly theory considers that all species are ecologically equivalent, and therefore communities would be the result of only dispersal limitation events and stochastic demographic processes (Hubbell 2001).

To address the community assembly issue, functional ecology has emerged as a more powerful and suitable tool than classical taxonomic approaches based on Linnaean binomials, since indices of species composition and abundances provide little information about the ecological strategies of those species (Fukami et al. 2005, Swenson 2012). Instead, the functional approach relies on species functional traits – easily measurable morphological or physiological characters of individuals relevant to growth, survival or reproduction (Westoby and Wright 2006, Funk et al. 2017)– as proxies of ecological performance and, consequently, capable of explaining how species interact with their abiotic and biotic environment (Keddy 1992, McGill et al. 2006, Violle et al. 2007). By using the functional ecology framework, environmental filtering has been identified as a major force shaping communities across a number of biomes, including drylands (Le Bagousse-Pinguet et al. 2017), alpine (de Bello et al. 2013a, López-Angulo et al. 2018), temperate (Cornwell and Ackerly 2009) and tropical forests (Kraft et al. 2008, Swenson and Enquist 2009, Lebrija-Trejos et al. 2010, Baraloto et al. 2012). Nevertheless, the overwhelming importance of environmental filtering on community assembly has lately been questioned based on a disregard towards spatial scale consideration (Chase 2014) and on the uncertainty regarding whether functional patterns can reliably indicate mechanisms (Mayfield and Levine 2010).

To account for spatial scale is of utmost importance ecology (Wiens 1989, Levin 1992, McGill 2010) and its implications on community assembly are undeniable (Whittaker et al. 2001, Kneitel and Chase 2004, Snyder and Chesson 2004, Münkemüller et al. 2013). For instance, at a broad spatial scale, environmental filtering seems to be prevail over other processes (e.g., neither cacti thrive in artic regions nor polar bears in the rainforest) while competitive exclusion has virtually no effect on individuals that are many kilometers apart, although it may have an effect at a smaller spatial scale, on individuals in close proximity. Nonetheless, ignoring spatial scale-related implications has often led to discrepancies about which processes dominate community assembly (discussed by Chase 2014, Chalmandrier et al. 2017). To incorporate the scale issue a hierarchical model has been proposed, according to which assembly mechanisms operate sequentially at different spatial scales (Weiher and Keddy 1995b, Götzenberger et al. 2012, HilleRisLambers et al. 2012). This model encompasses from evolutionary and biogeographic processes such as historical patterns of speciation, extinction or migration at large/regional scales to abiotic and biotic processes like environmental filtering or competitive exclusion at smaller/local scales. The former processes define a regional pool of potential colonizer species over which the latter operate at finer scales, yielding the final assembly of local communities. Under this paradigm, shifting the scope of the studied community and the species pool will allow to clarify whether distinct assembly processes are restricted to operate at certain spatial scales (Colwell and Winkler 1984, Weiher and Keddy 1995b, Swenson et al. 2007). For instance, environmental filtering may be more prevalent when the species pool is defined from a broad area encompassing strong abiotic heterogeneity –e.g., steep environmental or habitat gradients– while the studied community, established at a relatively narrower spatial scale, is constrained to an environmentally homogeneous area (de Bello et al. 2013b; Garzon-Lopez et al. 2014; reviewed in Kraft et al. 2015).

Community patterns based on co- occurring species composition and abundance combined with functional diversity have been broadly trusted to reflect different community assembly processes. However, interpreting them as unequivocal signals of actual assembly processes is arguable. Traditionally and according to the community assembly mechanisms above, two mutually- excluding scenarios for species co-occurrence have been proposed: i) species could diverge in their ecological strategies to achieve co-occurrence by avoiding competitive exclusion, thus functional overdispersion should be observed within the community (Watkins and Wilson 2003, Silvertown 2004, Stubbs and Wilson 2004, Cavender-Bares et al. 2009); or ii) species could converge in their ecological strategies as to enable them to thrive in the same abiotic environment, resulting instead in functional clustering (Keddy 1992, Cornwell et al. 2006, Ackerly and Cornwell 2007). Besides, if the traits are phylogenetically conserved, a phylogenetic overdispersion or clustering pattern should also be observed within the community, respectively (Webb et al. 2002). This dichotomy, nevertheless, is an oversimplification, because both theory (Chesson 2000; Grime 2006; Mayfield & Levine 2010) and practice (Burns and Strauss 2011, Narwani et al. 2013, Godoy et al. 2014) have proven it to be unwarranted, since clustering can also result from competitive exclusion as well as from other biotic processes. For example, the existence of selective herbivores (Uriarte 2000), pathogens (Parker et al. 2015) or pollinators (Sargent and Ackerly 2008) can specifically harm or favor groups of species exhibiting certain traits, thus affecting the whole community structure. Therefore, inferring unequivocally that environmental filtering drives community assembly just on the basis that a clustered functional pattern has been observed could be deluding (Götzenberger et al. 2016, Cadotte and Tucker 2017).

Our study aims to move forward the understanding of community assembly accounting for spatial scale implications and avoiding an over-reliance on community patterns. To achieve this, we studied functional diversity of woody plant communities along two elevational gradients in Andean tropical montane forests, one of the most complex and diverse ecosystems worldwide. We consider that at a given spatial scale only one single mechanism will have a heavier influence on community assembly. Under this premise we assume that, whereas competitive exclusion would mainly operate at small spatial scales at which the environment is relatively homogeneous, environmental filtering would chiefly emerge as a significant force shaping community assembly at larger scales at which there is enough environmental heterogeneity to trigger a functional community response. Therefore, we hypothesized that 1) if competitive exclusion drives the community assembly at small spatial scales (e.g., across neighbouring individuals within a plot), functional patterns would be over-dispersed in comparison to a null expectation; and 2) if environmental filtering rule at larger scales (e.g., across plots spaced hundreds of meters or at different elevations), functional patterns would be clustered. Furthermore, following the guidelines from Kraft et al. (2015) to clearly state the importance of the processes in the assembly of the community, we sought evidences that link the observed community patterns with the underlying assembly processes (e.g., correlations between thermal gradient and community functional patterns or species abundances, respectively). By doing so, this study will further contribute to unmask the spatial scales at which different assembly processes predominate.

2 | MATERIALS AND METHODS

2.1 | Study regions and field sampling

The study was conducted along two elevational gradients of tropical montane Andean forests: one in Podocarpus National Park (Ecuador) and the other in Rio Abiseo National Park (Peru) (Fig 1). These sites were chosen because both extend along wide elevational ranges (ca. 2000 m), over a continuous forest cover, each within a single river basin: the Bombuscaro River in Ecuador and the Montecristo-Abiseo River in Peru. Three elevational belts were defined at each site (lower, 800-1100 m.a.s.l.; intermediate, 1900-2100 m.a.s.l.; upper, 2700-2900 m.a.s.l.). At each belt, 10 plots of 0.1 ha (50 × 20 m) were established between 2015 and 2017 following Arellano et al. (2016) (Appendix S1: Table S1). Each plot was subdivided in 10 subplots of 0.01 ha (10 × 10 m). Plots were placed at least 300 m apart, avoiding areas visibly affected by natural disturbances (e.g., gaps caused by fallen trees or landslides). In each plot, all woody individuals ≥ 2.5 cm of diameter at breast height (DBH) rooted within the plot limit were inventoried and their height estimated, although for this study solely trees, treelets, shrubs and lianas were taken into an account. At least one voucher from every taxon was collected for identification. Overall, 18,272 individuals were inventoried in 60 plots: 9,366 in Ecuador and 8,905 in Peru (Appendix S1: Table S1).

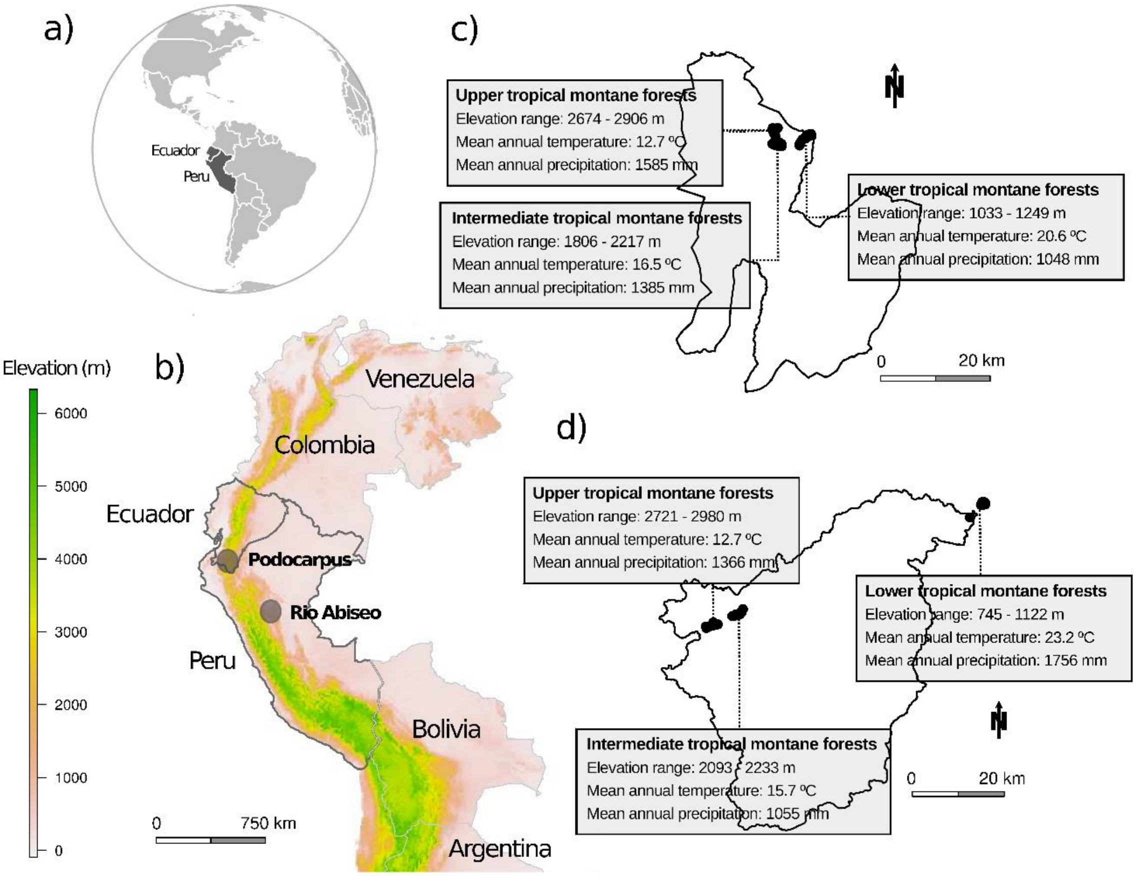

FIGURE 1. Location of the study sites. The two tropical montane Andean forests elevational gradients in Ecuador and Peru (a, b). Outlined areas represent Podocarpus National Park (c) and Rio Abiseo National Park (d), respectively. Ten plots of 0.1 ha were established at each of three elevational belts (lower, intermediate and upper) for each site, resulting in a total of 60 plots.

2.2 | Floristic data and functional characterization

Voucher specimens were identified at different herbaria from Ecuador (HUTPL, LOJA, QCA) and Peru (HAO, HUT, MOL, USM). After thorough taxonomic effort, 424 individuals from Ecuador (4.5 %) and 733 from Peru (8.23 %) could not be reliably assigned to a morphospecies level and were therefore excluded from the analysis (Appendix S1: Table S2). For Ecuador, the 8,942 identifiable individuals were assigned to 734 taxa, comprising 471 species and 263 morphospecies. For Peru, the 8,172 identifiable individuals were assigned to 526 taxa, including 189 species and 337 morphospecies. Standardization of taxonomic species names was conducted using the R package 'Taxonstand' (Cayuela et al. 2012, 2017).

For each taxon, the following functional traits were measured: specific leaf area (SLA), leaf thickness (LT), and wood density (WD). These traits address key woody plant functional strategy axes on which assembly mechanisms operate (Wright et al. 2004, Kraft et al. 2008, Baraloto et al. 2010). SLA was calculated from five leaves as the ratio of leaf surface area (measured with a portable laser leaf area meter CI- 202, CID Bio-Science, WA, USA) to leaf dry mass (after drying at 80 °C for 48 h). LT was measured with a digital calliper. Branch wood density was used as a proxy for WD, since both are strongly and positively correlated (Swenson and Enquist 2008). Sections of branches ca. 10 cm in length, as cylindrical as possible, were stripped of bark and their diameter and length measured in the field with a calliper to determine their fresh volume. Density of the branch section was calculated dividing its fresh volume by its dry mass (after drying at 80 °C for 48-72 h). Mean trait values were calculated for every taxon. All these protocols were based on Cornelissen et al. (2003) with just one exception: for SLA and LT leaves in full sun, at the upper canopy, were avoided in order to make these traits comparable between canopy and understory species. Functional data were collected for 723 taxa in Ecuador (98.5 % of the total identified), that include 8903 individuals (95 % of the total inventoried) and for 504 taxa in Peru (95.8 % of the total identified), that include 8016 individuals (90.01 % of the total inventoried). For a summary of community functional characterization, see Appendix S1: Table S3.

2.3 | Community assembly functional patterns

To elucidate how the consideration of different spatial scales may influence the relative effect of distinct deterministic mechanisms, the observed and the null functional trait distribution patterns were calculated for two spatial scale-related hypotheses (Fig 2): 1) trait distribution within a subplot compared with trait distribution among non- adjacent subplots from the same plot (small spatial scales); and 2) trait distribution within a plot compared with trait distribution among plots located along the elevational gradient (large spatial scales). Deviations in the observed functional distribution pattern from the null expectation would suggest the existence of different deterministic community assembly processes, such as environmental filtering or competitive exclusion, whereas a close match between distributions could be interpreted as evidence of stochastic community assembly (Connor and Simberloff 1979, Gotelli and Graves 1996).

For both cases, the observed community trait distribution was calculated as $U_{ST\text{-}obs} = 1-\sum Dw/\sum Da$, where Dw and Da are the trait Euclidean distances between pairs of co-occurring individuals (for all the individuals within each site) from distinct taxa randomly paired from within a subplot (Dw) and among subplots (Da) for hypothesis 1) and from within a plot (Dw) and among plots (Da) for hypothesis 2) (Hardy and Senterre 2007, Baraloto et al. 2012). Since the value of $U_{ST\text{-}obs}$ is dependent on the particular selection of a random subset of pairs of individuals, we iterated this procedure 1000 times and generated a distribution of $U_{ST\text{-}obs}$. By definition, U_{ST} can take both positive and negative values, where $U_{ST}>0$ indicates trait clustering and $U_{ST}<0$ trait overdispersion. To assess the significance of $U_{ST\text{-}obs}$, a null community trait distribution ($U_{ST\text{-}null}$) to have random assembly as null expectation was calculated using the same procedure for each of the hypotheses, but breaking down the observed community structure by random shuffling taxonomic identities among individuals (T1 randomization *sensu* Götzenberger et al. 2016). As a result, the original community structure remains unaltered because taxa richness and frequency are fixed, but trait values are independently reshuffled across taxa for each trait, thus not preserving the correlation structure across traits. We selected this randomization procedure over others because of its versatility: while it is particularly suitable for detecting competitive exclusion (via limiting similarity), it also performs well in detecting environmental filtering (Götzenberger et al. 2016). For each of the 1000 $U_{\text{ST-obs}}$ and $U_{\text{ST-null}}$ distributions we extracted the mean value as a summary statistic. Then, the distributions of the means of both the observed and null U_{ST} were compared using a one-tailed t-test, with a critical significance level of $\alpha=0.05$, since tests for the null hypothesis were unidirectional (Götzenberger et al. 2016). The whole analytic procedure was conducted independently for each site and replicated for two cohorts of co-occurring individuals: saplings (DBH<10 cm) and adults (DBH≥ 10 cm).

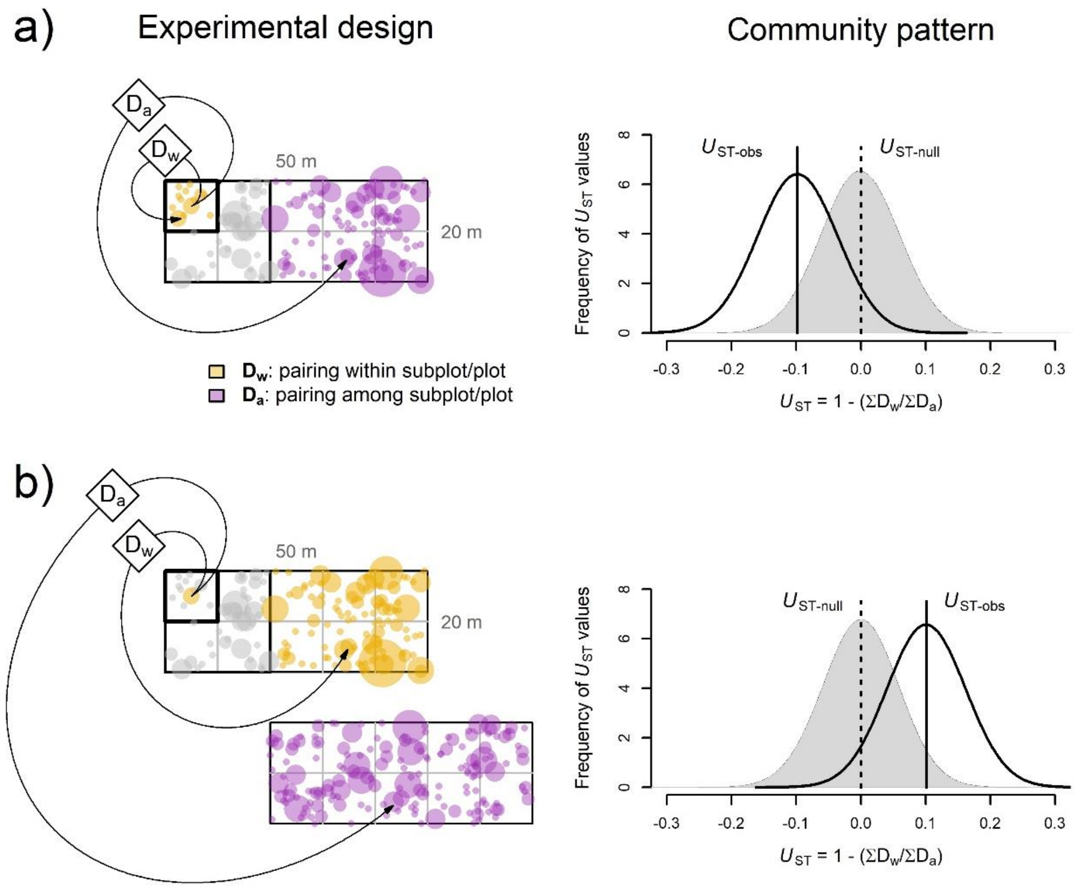

FIGURE 2. Sampling design and the respective community functional pattern for testing the existence of different community assembly processes at different spatial scales and the expected community functional patterns. According to hypothesis 1 (a), at small spatial scale –within plot–, an over-dispersed functional pattern occurs, which would be consistent with competitive exclusion. Conversely, in accordance to hypothesis 2 (b), at larger spatial scale –among plots–, a clustered functional pattern arises, which would suggest the existence of environmental filtering. UST is the mean functional trait Euclidean distance between pairs of co-occurring individuals from distinct taxa randomly paired within subplots (Dw) and among subplots (Da) for hypothesis 1 and within plot (Dw) and among plots (Da) for hypothesis 2.

2.4 | Assembly processes underlying community functional patterns

For environmental characterization of each plot we used the bioclimatic variables from CHELSA (Karger et al. 2017). Mean annual temperature (hereinafter MAT) was selected as small changes in this variable along our altitudinal gradients (spanning thermal ranges between 9 and 12 ºC in Ecuador and Peru, respectively; see Appendix S1: Table S1) are expected to have a strong effect on species distribution, since in the tropics species have evolved to have narrow thermal tolerances (Janzen 1967). In addition, MAT was highly correlated ($r>0.86$) with most bioclimatic variables, both in Ecuador and Peru. We used Mantel tests to statistically analyze the correlation between the observed community trait pattern for any pair of plots ($U_{\text{ST-obs}}$, *sensu* hypothesis 2) and the plots' environmental distance, calculated as the pairwise difference in MAT. To estimate the statistical significance of the correlation between MAT and $U_{\text{ST-obs}}$ we used a Monte Carlo test, permuting 200 times the elements of one of the distance matrices while holding the other constant.

The climatic preferences of the most abundant taxa in the lower and upper elevational belts (i.e., at both extremes of the elevational gradient) were computed for each one of the two study sites. To achieve so, we defined the most abundant species as those with 10 or more individuals within a single elevational belt (morphospecies excluded). In total we recognized 65 of such species for the lower tropical montane forest belt (henceforth, LTMF species) and 66 for the upper belt (UTMF species) for Ecuador, whereas there were 26 and 27 respectively for Peru (Appendix S1: Table S4). We then we retrieved occurrence data across the Neotropics for each of those species from the Global Biodiversity Information Facility (GBIF) and extracted the bioclimatic information from CHELSA for the locations where species were reported. The climatic preference of LTMF and UTMF species was defined as the mean ± 1.96 standard deviation of the MAT from those species' locations. Finally, the significance of the differences in climatic preferences between sets of LTMF and UTMF species was estimated comparing the mean MAT value for each set of species' locations with a one-tailed t-test, using a significance level of $\alpha=0.05$. All analyses were conducted using the 'vegan' R package (Oksanen et al. 2006).

As consequence of environmental filtering the species adapted to certain climatic preferences would be filtered out along the elevational gradient as climatic conditions change. To explore this, we quantified the number of individuals of LTMF and UTMF species at each of the three elevational belts (lower, intermediate and upper) and then analyzed how they changed with elevation in each of the two study sites using generalized linear mixed models (GLMMs) with a negative binomial error distribution (to account for statistical overdispersion; not to be confounded with functional overdispersion). Mean elevation at each belt, climatic preference (LTMF or UTMF) and their interaction were used as fixed terms, whereas species identity was used as a random factor. A random slope structure was used for mean elevation, indicating that the slope of the relationship between abundance and elevation may change randomly among species. We built all possible combinations of fixed and random factors. Overall, we fitted 15 models, including null models for both fixed and random effects (Appendix S1: Table S5), using the R packages 'glmmADMB' (Skaug et al. 2013) and 'MASS' (Venables and Ripley 2002). All models were compared using the Akaike Information Criterion corrected for small sample sizes (AICc) with the R package 'MuMIn' (Barton 2018). Models with a difference in AICc > 2 indicate that the worse model had virtually no support and could be omitted.

3 | RESULTS

3.1 | Community assembly functional patterns

No statistically significant evidence ($U_{ST\text{-}obs} \approx U_{ST\text{-}null}$) of functional overdispersion was found at small spatial scales for any of the three traits in either site (Fig 3). Thus, individuals within a subplot were not functionally more different from the rest of individuals of the same plot than expected by chance ($U_{ST\text{-}obs}$; Dw ≈ Da). The same overall results were obtained when the analyses were conducted independently for saplings and adults (Appendix S1: Fig S1).

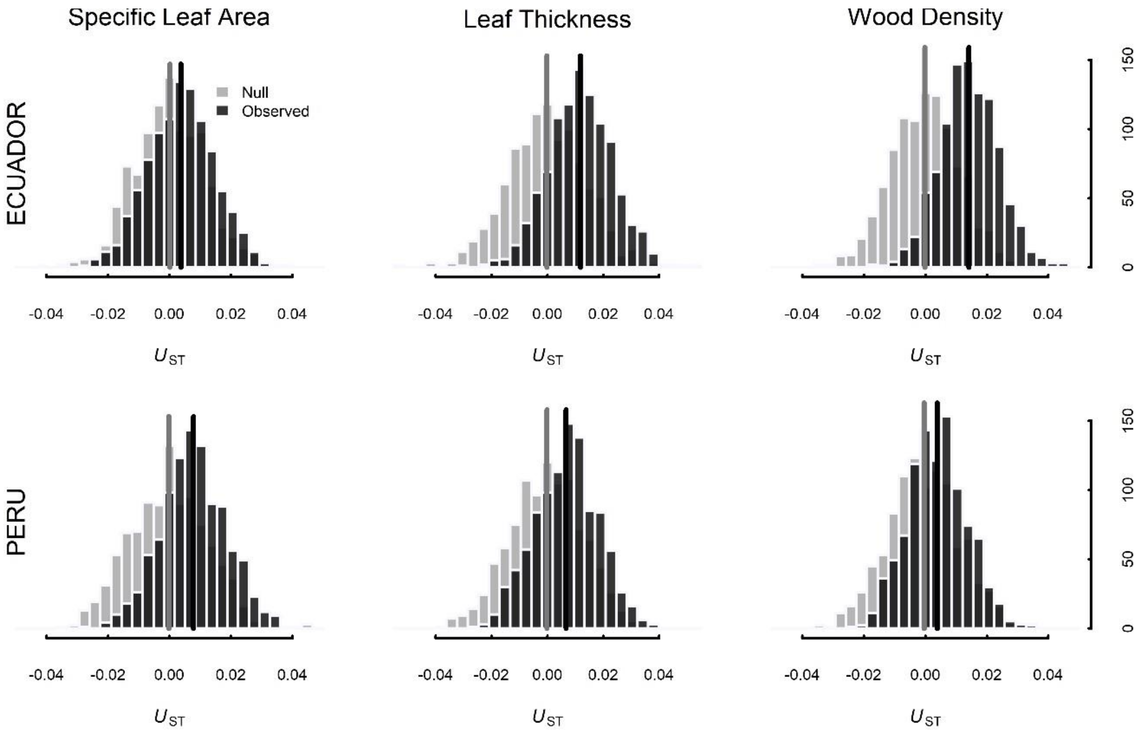

FIGURE 3. Hypothesis 1: community functional distances distribution patterns at small spatial scale (within plot). Frequency of distribution of $U_{ST\text{-}obs}$ (black) and $U_{ST\text{-}null}$ (grey) values at two geographical sites (Ecuador, upper charts; Peru, lower charts) as measured based on three functional traits (SLA, left; LT, center; WD, right) after 1000 randomizations, in all six cases. There were no significant differences (α=0.05) between $U_{ST\text{-}obs}$ and $U_{ST\text{-}null}$ for any of the traits at any of the sites.

Instead, when larger spatial scales were considered, there was statistically significant evidence ($U_{ST\text{-}obs} > U_{ST\text{-}null}$, $p \leq 0.01$) of functional clustering for all traits at both sites (Fig

4). Thus, the individuals within a plot were functionally more similar from the individuals of different plots than expected by chance ($U_{ST\text{-}obs}$; Dw < Da). The same overall results were obtained when the analyses were independently conducted for saplings and adults (Appendix S1: Fig S2).

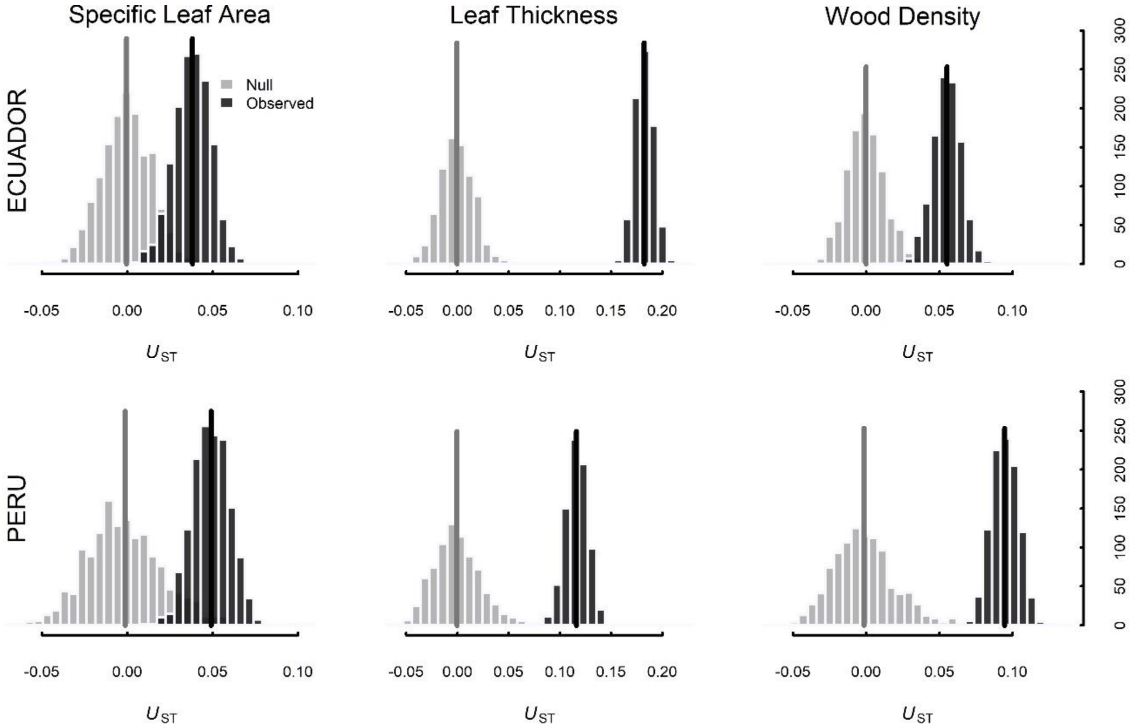

FIGURE 4. Hypothesis 2: community functional distances distribution patterns at large spatial scale (among plots). Frequency of distribution of $U_{ST\text{-}obs}$ (black) and $U_{ST\text{-}null}$ (grey) values at two geographical sites (Ecuador, upper charts; Peru, lower charts) as measured based on three functional traits (SLA, left; LT, center; WD, right) after 1000 randomizations, in all six cases. Differences between $U_{ST\text{-}obs}$ and $U_{ST\text{-}null}$ were significant ($p \leq 0.01$) for all traits at both sites.

3.2 | Assembly processes underlying community functional patterns

Trait clustering pattern ($U_{ST\text{-}obs} > 0$) among pairs of plots increased when increasing differences in MAT (Fig 5). Those differences, as expected, were greater when comparing plots from lower and upper elevational belts (i.e., greater MAT differences) than when comparing among plots within the same elevational belt (i.e., smaller or no MAT differences). The correlation between MAT differences and trait clustering was positive and statistically significant ($p \leq 0.01$) for all three functional traits at both sites. The only exception was SLA in Peru, for which no significant variations in community trait pattern appeared in relation to differences in MAT.

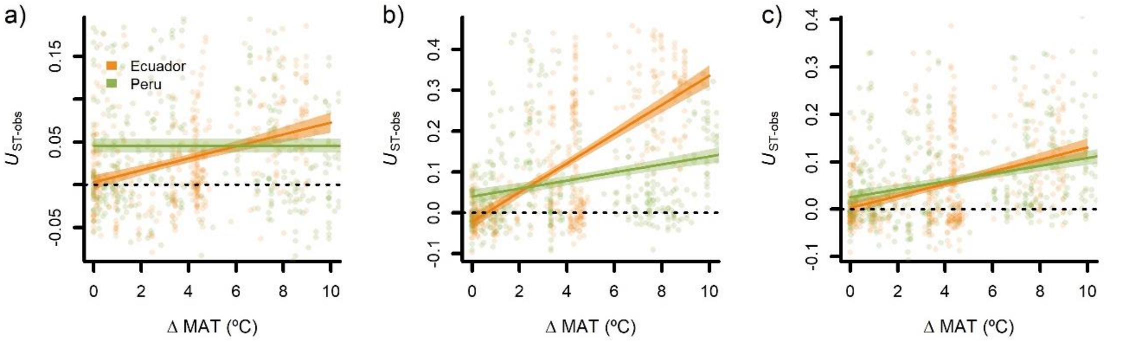

FIGURE 5. Plots pairwise functional and environmental comparison. X- axis represented environmental differences (in terms of Mean annual temperature; MAT) between pairs of plots. Y- axis represented differences in observed functional traits patterns ($U_{\text{ST-obs}}$) among plots for SLA, LT and WD. Trait clustering pattern ($U_{\text{ST-obs}} > 0$) increased positively as MAT differences increased. This correlation was significant ($p \leq 0.01$) for all traits at both sites, excepting for SLA in Peru.

The climatic preferences of the LTMF and UTMF species, defined using their MAT values across their entire Neotropical distribution ranges, were clearly segregated both in Ecuador and Peru (Figs 6 a-b). LTMF species showed a mean temperature optimum of 22.8 °C in Ecuador and 24 °C in Peru, whereas these optima were 15.5 °C and 18.2 °C, respectively, for UTMF species. There were statistically significant ($p \leq 0.01$) differences in MAT for LTMF and UTMF species, both in Ecuador and Peru.

The abundances of LTMF and UTMF species shifted across the different elevational belts (Figs 6 c-d). Best fit models for both sites included the most complex structure for both fixed effects and the simplest for random effects (Appendix S1: Table S5). Model predictions indicated that LTMF species were significantly more abundant at lower elevations than at the intermediate or, especially, higher elevations, from which some species were absent. Conversely, UTMF species were significantly more abundant at higher elevations than at the intermediate or, especially, lower ones, where some were missing.

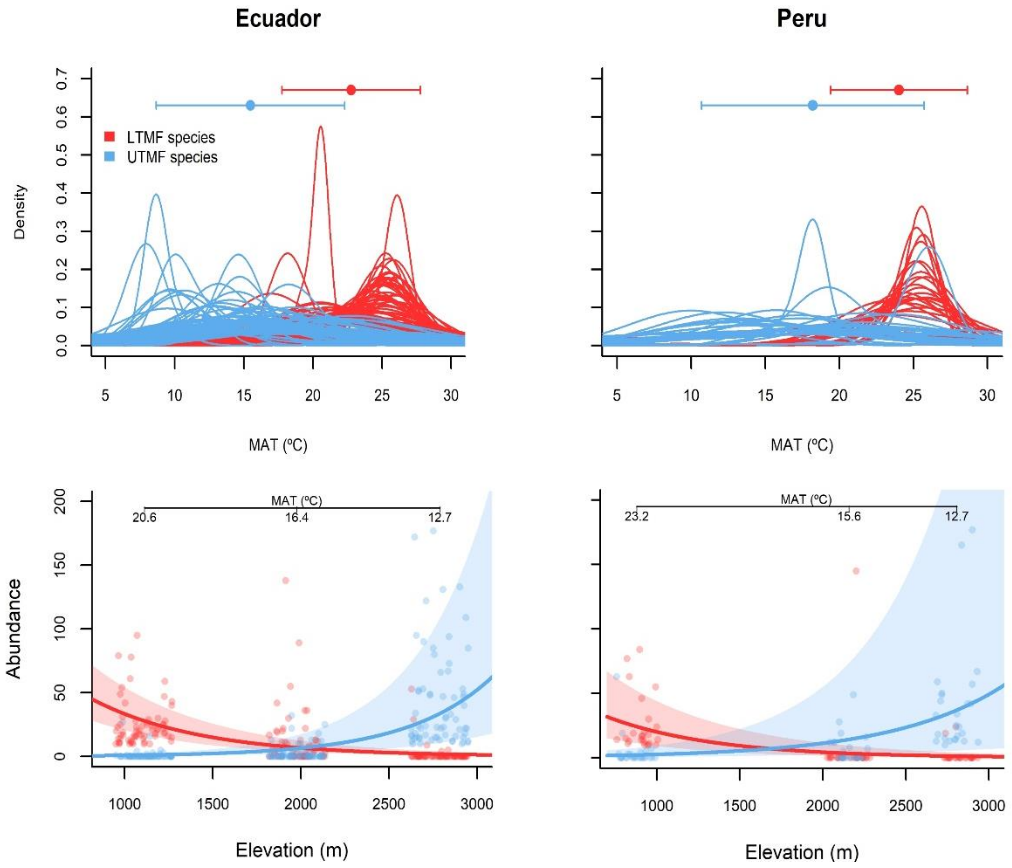

FIGURE 6. Climatic preferences for the upper and lower tropical montane forest most abundant (N≥10) species (UTMF and LTMF species, respectively) and their abundances along the elevational gradients. Climatic preferences in terms of MAT preferences of the UTMF and LTMF sets of species were segregated at the edges of the thermal gradient when the MAT values for those species' occurrences across their entire distribution range in the Neotropics were considered, both in Ecuador (a) and Peru (b). Dots represent the mean MAT and horizontal lines the 95 % confidence interval of the MAT for each set of species' climatic preferences. Difference in the means of MAT for LTMF and UTMF species´ climatic preferences was statistically significant ($p \leq 0.01$) in both sites. Shifts in UTMF and LTMF species' abundances along the elevation gradients in Ecuador (c) and Peru (d). Lines represent best fit model predictions with a 95 % confidence interval. Best fit models for both sites included altitude, climatic preference and its interaction as fixed terms, and species as a random factor.

4 | DISCUSSION

Our study approaches a fundamental question in ecology: identifying the ecological mechanisms shaping community assembly. Overall, we found that taking in account spatial scale is key for detecting the functional fingerprint of the underlying mechanisms driving community assembly. While we found no evidence of competitive exclusion at the smallest spatial scale, we detected strong evidence of environmental filtering at larger scales. In addition, further analyses conducted to link the community observed functional pattern with its underlying assembly process allows us to endorse the role of environmental filtering for community assembly.

4.1 | No evidence of competitive exclusion at small spatial scales

In this study we detected no evidence of competitive exclusion at small spatial scale. Competitive exclusion has been hypothesized to occur at small spatial scales, where individuals from different species effectively compete for local resources (Weiher and Keddy 1995b, Stoll and Weiner 2000), thus a pattern of trait divergence is expected as a consequence of limiting similarity (Watkins and Wilson 2003, Stubbs and Wilson 2004). Nevertheless, as obvious as may seem, scale dependence has sometimes been ignored. For instance, Baraloto et al. (2012) rejected the importance of competitive exclusion as an assembly process by comparing functional distances of species within 1 ha plots (Dw) and among plots separated by tens of kilometers (Da). In our opinion, their results ought to be interpreted with caution for two reasons. First, it makes little sense to test for competitive exclusion between plant individuals that are much spatially distant (e.g., up to 140 m apart from each other), then hardly competing for the same resources (e.g., light, soil nutrients). In relation to this, the scale at which competition between species operates is certainly organism-dependent, thus whereas sessile organisms like plants mostly compete for key resources at small spatial scales (up to few tens of meters), motile organisms such as birds or mammals can compete at much larger scales (up to few tens of kilometers). Consequently, studies need to consider the spatial scales at which community assembly processes are most likely to operate in relation to the group of organisms under study–e.g., if plants, a checkerboard pattern noticed at large spatial scales (Diamond 1975, 1982) could be misinterpreted as the effect of competitive exclusion–. Second, even if competitive exclusion existed between individuals within such a large plot, its trait overdispersion signal would be masked by the effect of among plots environmental differences on functional distance.

To avoid spatial scale biases, we searched for evidence of competitive exclusion at small spatial scale (i.e., within 10 x 10 m subplots). At this scale, co-occurring individuals can be assumed to directly compete for the same resources, while the effect of environmental filtering on functional distance can be ruled out because environmental conditions within a subplot are essentially the same (de Bello et al. 2013b). However, conversely to our expectation, we detected no evidence of a functional overdispersion pattern resulting from competitive exclusion for the traits we measured (Fig 3). Instead, our results suggest a random community assembly at this small scale, although there could be cryptic non-random dispersion with respect to traits that we did not measure (Gallien 2017). In addition, since most of the assembly processes operate more strongly at early stages of plant life cycles (Green et al. 2014), a functional pattern suggesting competitive exclusion may only become revealed when only considering saplings in the community, as they are most sensitive to competition (Falster and Westoby 2003, Wagg et al. 2017). To test this hypothesis, we checked whether functional overdispersion emerged for saplings but disappeared for adults. Again, no evidence of functional overdispersion was found for neither saplings nor adults (Appendix S1: Fig S1).

Whereas some studies have also found no evidence of functional overdispersion between co-occurring species at small spatial scale (Schamp et al. 2008, Thompson et al. 2010), others have. However, those studies that did find functional overdispersion, typically did not find it for all the analysed traits, and it was sometimes the case that functional overdispersion and clustering were both simultaneously reported within the same study system (Cavender-Bares et al. 2004, Mason et al. 2007, Kraft et al. 2008, Cornwell and Ackerly 2009, Swenson and Enquist 2009, Kraft and Ackerly 2010, de Bello et al. 2013b). The few studies that systematically reported the existence of limiting similarity (see Wilson 2007) were based on evidence found in relatively low diversity communities –e.g. sand dunes (Stubbs and Wilson 2004), lawns (Mason and Wilson 2006) or saltmarshes (Wilson and Stubbs 2012)–. Our results, in agreement with the lack of consensus found in earlier studies, suggest that in hyper-diverse plant communities, limiting similarity may not be a paramount force driving community assembly (Grime 2006) since in hyper-diverse systems, the functional hyperspace would be limited to be parsed out into many discrete and differentiated functional niches, each for one of the co-occurring species.

4.2 | Evidence of environmental filtering clearly linked to environmental heterogeneity at large spatial scale

In this study, we did find strong evidence of environmental filtering at large spatial scale. Given the more abiotically homogeneous and restrictive environment existing at small spatial scales, the potentially successful functional strategies that allow the survival of community members are narrowed, thus decreasing the role of environmental filtering for community assembly. But at large spatial scales that encompass different habitat conditions –such as topography or edaphic variables–, or that expand environmental gradients, there is consensus on the importance of environmental filtering. Under this scenario, the selection of just the suitable set of traits that allows species to thrive under certain environmental conditions would result in a functional clustering pattern (Fig 4). Nevertheless, the reliability of clustering patterns –in themselves widely accepted as indicators of environmental filtering– has been questioned lately because some biotic processes can also render clustering patterns (Sargent and Ackerly 2008). We agree with Kraft et al. (2015) on their assertion that experimental manipulations aimed to assess species failure to establish and persist in the absence of biotic interactions are the most robust proof of environmental filtering *sensu stricto*. We argue, however, that this is not only impractical in field studies, especially at logistically challenging tropical montane forests, but neither it is necessarily so meaningful from an ecological perspective. Instead, we trust that, according to Cadotte & Tucker (2017), as long as we can correlate changes in community functional clustering patterns, species abundances or population growth with the underlying shifts in environmental conditions, we can infer and advocate for the existence of a *sensu lato* environmental filtering process ongoing, regardless of simultaneously occurring biotic phenomena.

Our results show that only when large spatial scales that truly encompass environmental differences are considered (e.g., among pairs of plots from different elevational belts and, thus, affected by notable MAT differences), environmental filtering is revealed as an overriding influence for community assembly. Thus, the evidence of environmental filtering does not merely lay on the traditionally admitted clustering pattern itself, but on the fact that the pattern just arises when underlying environmental heterogeneity exists (Fig 5). In addition, our study reveals how such environmental differences cause changes in community features other than the clustering pattern. For instance, for the most abundant species in the lower and upper tropical montane forest –LTMF and UTMF species, respectively–, 1) their abundances dramatically shift between elevations (Figs 6 c-d) and 2) their climatic preferences are segregated at the edges of the thermal gradient (Figs 6 a-b). Those facts suggest that species distribution is mainly a consequence of species abiotic preferences –resulting from environmental filtering– and unlikely of other factors such as dispersal limitation –which is expected to play a negligible role in the continuous, non-fragmented forests within single river basins, as is the case in both our sites (Young 1990, Pennington et al. 2010)–. Besides, the fact that the climatic preferences of the LTMF and UTMF species are maintained across their entire distribution range in the Neotropics (Figs 6 a-b), reinforces the role of environmental filtering as a broadly prevalent mechanism for community assembly.

Thus far, indications of an environmental filtering fingerprint on tropical community assembly across different habitats have been reported mainly by considering habitat differences as a surrogate for environmental differences (e.g., topography in the Yasuní megaplot, Ecuador, by Kraft et al. 2008, or forest age and geological formation in Barro Colorado Island, Panama, by Garzon-Lopez et al. 2014). Besides, identifying the effect of environmental filtering has remained particularly challenging in species-rich forests, where, as a result of stochastic dilution, the signal of deterministic assembly processes may not be detectable, even if those processes are operating (Wang et al. 2016). However, our study provides a robust, scale and environmentally-based evidence supporting the importance of environmental filtering for community assembly.

5 | SUMMARY AND FURTHER PROSPECTS

The effect of environmental filtering in community assembly has been traditionally inferred from trait clustering patterns, as found by several studies targeted at various systems and taxonomic groups (e.g., trees in tropical forests (Baraloto et al. 2012), rockfishes in the ocean (Ingram and Shurin 2009), bees in mountains (Pellissier et al. 2013)). However, in order to be properly addressed, pertinent spatial scale related implications need to be taken into account (e.g., de Bello et al. 2009, Swenson and Enquist 2009, Münkemüller et al. 2013, Garzon-Lopez et al. 2014, Mori et al. 2015). Our results allow to clearly link the pattern with the mechanism by showing that the pattern is only revealed when environmental differences exist, and by demonstrating how those differences correlate with species` climatic preferences –maintained across their entire distribution range in the Neotropics– and abundances –along elevation–. This study, thus, contributes to emphasizing the importance of considering the implications of spatial scale to detect the extent at which assembly mechanisms act. Besides, it highlights the undeniably role of environmental filtering in community assembly and the usefulness of such concept, demonstrating that neither excluding biotic potentially confounding processes nor identifying abiotic tolerance ranges are strictly necessary for validating its effect. Future studies have the challenge of moving forward the discussion and shed light on the remaining details, such as whether the effect of environmental filtering equally influences low and highly diverse communities.

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Data Availability

The floristic data used in this manuscript are available upon request through ForestPlots (https://www.forestplots.net/en)

APPENDIX

TABLE S1. Elevational gradients and plots information.

Country	Belt	Elevation (masl)	MAT mean (°C)	MAT min (°C)	MAT max (°C)	*N*_ind. (Total)	*N*_ind. (DBH<10cm)	*N*_ind. (DBH≥10cm)
Ecuador	Lower	1114	20.6	19.9	21.1	2939	2247	692
	Interm.	1978	16.4	16.3	16.5	2623	1904	719
	Upper	2788	12.7	12.2	14.1	3380	2879	501
Elevation gradient: 1873 m			Temperature gradient: 8.9 °C			8942	7030	1912
Peru	Lower	881	23.2	22.1	23.9	2260	1695	565
	Interm.	2158	15.6	14.7	16.6	3069	2389	680
	Upper	2807	12.7	11.6	13.5	2843	2176	667
Elevation gradient: 2235 m			Temperature gradient: 12.3 °C			8172	6260	1912

Plot	Belt	Elevation (masl)	Longitude (°)	Latitude (°)	*N*_ind. (Total)	*N*_ind. (DBH<10cm)	*N*_ind. (DBH≥10cm)
Bombuscaro.A1	Lower	1084	-78.970967	-4.119717	276	75	201
Bombuscaro.A2	Lower	1053	-78.964472	-4.11275	231	47	184
Bombuscaro.A3	Lower	1057	-78.968575	-4.117603	367	80	287
Bombuscaro.A4	Lower	1104	-78.964869	-4.115967	375	90	285
Bombuscaro.A5	Lower	1033	-78.961969	-4.112369	411	86	325
Bombuscaro.A6	Lower	1084	-78.975627	-4.121194	210	41	169
Bombuscaro.A7	Lower	1129	-78.978097	-4.124908	197	50	147
Bombuscaro.A8	Lower	1216	-78.980158	-4.127579	225	70	155
Bombuscaro.A9	Lower	1249	-78.980554	-4.131513	254	65	189
Bombuscaro.A10	Lower	1130	-78.969242	-4.114559	393	88	305
Bombuscaro.B1	Interm.	1806	-79.009822	-4.132517	379	85	294
Bombuscaro.B2	Interm.	1837	-79.012364	-4.131953	240	53	187
Bombuscaro.B3	Interm.	1952	-79.0106	-4.128777	334	79	255
Bombuscaro.B4	Interm.	1851	-79.01511	-4.132622	274	79	195
Bombuscaro.B5	Interm.	1860	-79.016925	-4.130683	281	91	190
Bombuscaro.B6	Interm.	1901	-79.019635	-4.130672	334	83	251
Bombuscaro.B7	Interm.	2217	-79.013811	-4.126534	153	59	94
Bombuscaro.B8	Interm.	2060	-79.014515	-4.129384	250	80	170
Bombuscaro.B9	Interm.	2102	-79.022806	-4.130336	144	63	81
Bombuscaro.B10	Interm.	2190	-79.025295	-4.128751	234	47	187
Bombuscaro.C1	Upper	2817	-79.024139	-4.108305	379	33	346
Bombuscaro.C2	Upper	2796	-79.021398	-4.106056	230	65	165
Bombuscaro.C3	Upper	2851	-79.021215	-4.103533	549	51	498
Bombuscaro.C4	Upper	2906	-79.024935	-4.103009	287	48	239
Bombuscaro.C5	Upper	2900	-79.025027	-4.106183	307	46	261
Bombuscaro.C6	Upper	2729	-79.022835	-4.111277	248	39	209
Bombuscaro.C7	Upper	2703	-79.02112	-4.113053	531	64	467
Bombuscaro.C8	Upper	2738	-79.016544	-4.102644	202	50	152
Bombuscaro.C9	Upper	2765	-79.018394	-4.104557	262	30	232
Bombuscaro.C10	Upper	2674	-79.020317	-4.117274	385	75	310
Abiseo.A1	Lower	898	-76.90064876	-7.425792679	217	54	263
Abiseo.A2	Lower	819	-76.89783946	-7.425443058	131	37	94
Abiseo.A3	Lower	941	-76.89557457	-7.42320153	274	59	215
Abiseo.A4	Lower	963	-76.8981523	-7.422358751	221	59	162
Abiseo.A5	Lower	1122	-76.9011234	-7.422427413	280	70	210
Abiseo.A6	Lower	780	-76.89932701	-7.428049534	283	67	216
Abiseo.A7	Lower	912	-76.90167538	-7.426520599	218	48	170
Abiseo.A8	Lower	793	-76.90369262	-7.428030831	220	61	159
Abiseo.A9	Lower	745	-76.89503025	-7.42722709	188	48	140
Abiseo.A10	Lower	841	-76.92546548	-7.452708757	228	62	166
Abiseo.B1	Interm.	2117	-77.37919905	-7.638242162	188	70	118
Abiseo.B2	Interm.	2188	-77.37945734	-7.640717188	417	112	305
Abiseo.B3	Interm.	2152	-77.37676819	-7.637695184	365	86	279
Abiseo.B4	Interm.	2093	-77.37535081	-7.633662924	302	80	222
Abiseo.B5	Interm.	2144	-77.37375087	-7.631014495	188	44	144
Abiseo.B6	Interm.	2143	-77.38467284	-7.641890475	198	72	126
Abiseo.B7	Interm.	2189	-77.38777696	-7.64132199	272	63	209

Abiseo.B8	Interm.	2233	-77.38985881	-7.642639064	312	42	270
Abiseo.B9	Interm.	2222	-77.39154476	-7.644437335	470	58	412
Abiseo.B10	Interm.	2101	-77.39467987	-7.644555517	357	53	304
Abiseo.C1	Upper	2721	-77.4343626	-7.662887997	203	51	152
Abiseo.C2	Upper	2767	-77.43325685	-7.659604498	221	50	171
Abiseo.C3	Upper	2791	-77.42355934	-7.660472591	381	88	293
Abiseo.C4	Upper	2759	-77.43799153	-7.663807385	228	40	188
Abiseo.C5	Upper	2778	-77.44189073	-7.664463109	215	29	186
Abiseo.C6	Upper	2866	-77.44718356	-7.664857815	369	86	283
Abiseo.C7	Upper	2980	-77.44599411	-7.667557811	334	102	232
Abiseo.C8	Upper	2775	-77.43226167	-7.656645726	219	70	149
Abiseo.C9	Upper	2821	-77.42753392	-7.660043499	427	93	334
Abiseo.C10	Upper	2810	-77.43010882	-7.662008254	246	58	188

TABLE S2. Population taxonomic information for studied tropical montane forest communities in Ecuador and Peru.

		Ecuador			Peru		
Total number of individuals	*N*_ind	9366	species	morphospecies	8905	species	morphospecies
Community composition (taxonomically characterized)	*N*_ind	8942 (95,5 % identifiable)	7427 (83 %)	1515 (17 %)	8172 (91,7 % identifiable)	3775 (46,2%)	4397 (53,8 %)
	*N*_taxa	734	471 (64,2 %)	263 (35,8 %)	526	189 (35,9 %)	337 (64,1 %)
Community composition (taxonomic & functionally characterized)	*N*_ind	8903 (95%)	7395(83,1%)	1508 (16,9 %)	8016 (90 %)	3771 (47 %)	4245 (53 %)
	*N*_taxa	723 (98,5%)	466 (64,4 %)	257 (35,6 %)	504 (95,8 %)	186 (36,9 %)	318 (63,1 %)

TABLE S3. Functional information for studied tropical montane forest communities in Ecuador and Peru.

			Ecuador		Peru	
Functional trait	Units	Belt	*N* ind	Mean	*N* ind	Mean
Specific Leaf Area (SLA)	mm^2 mg^{-1}	Lower	971	16.2	922	16.6
		Intermediate	504	16.1	582	13.5
		Upper	295	15.1	289	14.3
			range: 2.95 – 57.95		range: 2.69 – 66	
Leaf thickness	mm	Lower	1028	0.19	927	0.18
		Intermediate	511	0.22	584	0.20
		Upper	273	0.35	301	0.32
			range: 0.05 – 0.95		range: 0.05 – 0.94	
Wood density	g cm^{-3}	Lower	973	0.42	899	0.42
		Intermediate	480	0.41	587	0.37
		Upper	193	0.46	299	0.35
			range: 0.06 – 1.30		range: 0.06 – 1.26	

TABLE S4. Lower and upper tropical montane forest (LTMF and UTMF) most abundant (N≥10) species in Ecuador and Peru.

Ecuador			
LTMF species (*N*=66)		**UTMF species (*N*=67)**	
Specie	**Family**	**Specie**	**Family**
Xylopia cuspidata Diels	Annonaceae	*Ilex andicola* Loes.	Aquifoliaceae
Cordia nodosa Lam.	Boraginaceae	*Ilex rupicola* Kunth	Aquifoliaceae
Dacryodes peruviana (Loes.) H.J.Lam	Burseraceae	*Schefflera dielsii* Harms	Araliaceae
Protium ecuadorense Benoist	Burseraceae	*Schefflera ferruginea* (Willd. ex Schult.) Harms	Araliaceae
Trattinnickia lawrancei Standl.	Burseraceae	*Brunellia inermis* Ruiz & Pav.	Brunelliaceae
Celtis schippii Standl.	Cannabaceae	*Hedyosmum purpurascens* Todzia	Chloranthaceae
Hedyosmum sprucei Solms	Chloranthaceae	*Hedyosmum translucidum* Cuatrec.	Chloranthaceae
Tovomitopsis membranacea (Planch. & Triana) D'Arcy	Clusiaceae	*Clethra ovalifolia* Turcz.	Clethraceae
Garcinia madruno (Kunth) Hammel	Clusiaceae	*Clethra pedicellaris* Turcz.	Clethraceae
Asplundia aulacostigma Harling	Cyclanthaceae	*Clusia alata* Planch. & Triana	Clusiaceae
Asplundia schizotepala Harling	Cyclanthaceae	*Clusia ducu* Benth.	Clusiaceae
Sloanea eichleri K.Schum.	Elaeocarpaceae	*Clusia elliptica* Kunth	Clusiaceae
Aparisthmium cordatum (A.Juss.) Baill.	Euphorbiaceae	*Clusia latipes* Planch. & Triana	Clusiaceae
Nealchornea yapurensis Huber	Euphorbiaceae	*Baccharis oblongifolia* (Ruiz & Pav.) Pers.	Compositae
Aniba muca (Ruiz & Pav.) Mez	Lauraceae	*Piptocoma discolor* (Kunth) Pruski	Compositae
Aniba panurensis (Meisn.) Mez	Lauraceae	*Weinmannia balbisiana* Kunth	Cunoniaceae
Cinnamomum triplinerve (Ruiz & Pav.) Kosterm.	Lauraceae	*Weinmannia cochensis* Hieron.	Cunoniaceae
Endlicheria formosa A.C.Sm.	Lauraceae	*Weinmannia fagaroides* Kunth	Cunoniaceae
Endlicheria griseosericea Chanderb.	Lauraceae	*Weinmannia lentiscifolia* C.Presl	Cunoniaceae
Endlicheria lorastemon Chanderb.	Lauraceae	*Weinmannia pinnata* L.	Cunoniaceae
Licaria cannella (Kostermans ex Rodrigues) Kurz	Lauraceae	*Weinmannia pubescens* Kunth	Cunoniaceae
Nectandra membranacea (Sw.) Griseb.	Lauraceae	*Weinmannia reticulata* Ruiz & Pav.	Cunoniaceae
Ocotea cernua (Nees) Mez	Lauraceae	*Weinmannia rollottii* Killip	Cunoniaceae
Ocotea insularis (Meisn.) Mez	Lauraceae	*Gaultheria reticulata* Kunth	Ericaceae
Grias peruviana Miers	Lecythidaceae	*Macrocarpaea sodiroana* Gilg	Gentianaceae
Inga thibaudiana DC.	Leguminosae	*Ocotea benthamiana* Mez	Lauraceae
Centronia laurifolia D. Don	Melastomataceae	*Ocotea infrafoveolata* van der Werff	Lauraceae
Clidemia sessiliflora (Naudin) Cogn.	Melastomataceae	*Ocotea sericea* Kunth	Lauraceae
Graffenrieda cucullata (Triana) L.O. Williams	Melastomataceae	*Persea hexanthera* L.E. Kopp	Lauraceae
Miconia decurrens Cogn.	Melastomataceae	*Persea weberbaueri* Mez	Lauraceae
Miconia punctata (Desr.) D. Don ex DC.	Melastomataceae	*Axinaea scutigera* Triana	Melastomataceae

Miconia theaezans Cogn.	Melastomataceae	*Graffenrieda emarginata* (Ruiz & Pav.) Triana	Melastomataceae
Guarea macrophylla Vahl	Meliaceae	*Graffenrieda harlingii* Wurdack	Melastomataceae
Guarea subandina W.Palacios	Meliaceae	*Meriania furvanthera* Wurdack	Melastomataceae
Batocarpus orinocensis H.Karst.	Moraceae	*Meriania maguirei* Wurdack	Melastomataceae
Clarisia racemosa Ruiz & Pav.	Moraceae	*Meriania tomentosa* (Cogn.) Wurdack	Melastomataceae
Helicostylis tomentosa (Poepp. & Endl.) J.F.Macbr.	Moraceae	*Miconia bolivarensis* Wurdack	Melastomataceae
Pseudolmedia laevigata Trécul	Moraceae	*Miconia caelata* (Bonpl.) DC.	Melastomataceae
Pseudolmedia macrophylla Trécul	Moraceae	*Miconia cajanumana* Wurdack	Melastomataceae
Sorocea trophoides W.C.Burger	Moraceae	*Miconia cladonia* Gleason	Melastomataceae
Trophis mexicana (Liebm.) Bureau	Moraceae	*Miconia loxensis* (Bonpl.) DC.	Melastomataceae
Otoba parvifolia (Markgr.) A.H.Gentry	Myristicaceae	*Miconia media* (D. Don) Naudin	Melastomataceae
Virola calophylla (Spruce) Warb.	Myristicaceae	*Miconia theaezans* Cogn.	Melastomataceae
Otoba glycycarpa (Ducke) W.A.Rodrigues & T.S.Jaram.	Myristicaceae	*Ruagea hirsuta* (C. DC.) Harms	Meliaceae
Eugenia oerstediana O.Berg	Myrtaceae	*Myrcianthes rhopaloides* (Kunth) McVaugh	Myrtaceae
Neea divaricata Poepp. & Endl.	Nyctaginaceae	*Ternstroemia cleistogama* Kobuski	Pentaphylacaceae
Hieronyma duquei Cuatrec.	Phyllanthaceae	*Ternstroemia lehmannii* (Hieron.) Urb.	Pentaphylacaceae
Piper papillicaule Trel. & Yunck.	Piperaceae	*Hieronyma macrocarpa* Müll.Arg.	Phyllanthaceae
Piper peltatum L.	Piperaceae	*Podocarpus oleifolius* D.Don	Podocarpaceae
Geissanthus ecuadorensis Mez	Primulaceae	*Cybianthus cuatrecasasii* Pipoly	Primulaceae
Condaminea corymbosa (Ruiz & Pav.) DC.	Rubiaceae	*Geissanthus ecuadorensis* Mez	Primulaceae
Faramea jasminoides (Kunth) DC.	Rubiaceae	*Myrsine andina* (Mez) Pipoly	Primulaceae
Faramea quinqueflora Poepp.	Rubiaceae	*Myrsine sodiroana* (Mez) Pipoly	Primulaceae
Faramea torquata Müll.Arg.	Rubiaceae	*Prunus guanaiensis* Rusby	Rosaceae
Hippotis brevipes Spruce ex K.Schum.	Rubiaceae	*Prunus opaca* Walp.	Rosaceae
Joosia aequatoria Steyerm.	Rubiaceae	*Cinchona mutisii* Lamb.	Rubiaceae
Ladenbergia heterophylla (Wedd.) Standl.	Rubiaceae	*Cinchona pubescens* Vahl	Rubiaceae
Palicourea cutucuana C.M.Taylor	Rubiaceae	*Palicourea andaluciana* Standl.	Rubiaceae
Remijia chelomaphylla G.A.Sullivan	Rubiaceae	*Palicourea hospitalis* Standl.	Rubiaceae
Ciliosemina pedunculata (H.Karst.) Antonelli	Rubiaceae	*Palicourea loxensis* C.M.Taylor	Rubiaceae
Meliosma herbertii Rolfe	Sabiaceae	*Solanum anceps* Ruiz & Pav.	Solanaceae
Casearia sylvestris Sw.	Salicaceae	*Styrax foveolaria* Perkins	Styracaceae
Pouteria torta (Mart.) Radlk.	Sapotaceae	*Symplocos bogotensis* Brand	Symplocaceae
Pourouma cecropiifolia Mart.	Urticaceae	*Symplocos fuscata* B. Ståhl	Symplocaceae

Leonia glycycarpa Ruiz & Pav.	Violaceae	*Symplocos nuda* Bonpl.	Symplocaceae
		Drimys granadensis L.f.	Winteraceae

Peru			
LTMF species (*N*=26)		**UTMF species (*N*=27)**	
Specie	**Family**	**Specie**	**Family**
Spondias testudinis J.D. Mitch. & D.C. Daly	Anacardiaceae	*Aphelandra acanthifolia* Hook.	Acanthaceae
Tapirira guianensis Aubl.	Anacardiaceae	*Oreopanax oroyanus* Harms	Araliaceae
Styloceras laurifolium (Willd.) Kunth	Buxaceae	*Lozanella enantiophylla* (Donn.Sm.) Killip & C.V.Morton	Cannabaceae
Clusia hammeliana Pipoly	Clusiaceae	*Hedyosmum racemosum* (Ruiz & Pav.) G.Don	Chloranthaceae
Buchenavia pulcherrima Exell & Stace	Combretaceae	*Weinmannia auriculata* D.Don	Cunoniaceae
Hevea guianensis Aubl.	Euphorbiaceae	*Vallea stipularis* L.f.	Elaeocarpaceae
Eschweilera coriacea (DC.) S.A.Mori	Lecythidaceae	*Hydrangea peruviana* Moric. ex Ser.	Hydrangeaceae
Grias peruviana Miers	Lecythidaceae	*Nectandra acuminata* (Nees & C. Mart.) J.F. Macbr.	Lauraceae
Mimosa guilandinae (DC.) Barneby	Leguminosae	*Nectandra olida* Rohwer	Lauraceae
Apeiba membranacea Spruce ex Benth.	Malvaceae	*Nectandra utilis* Rohwer	Lauraceae
Matisia bicolor Ducke	Malvaceae	*Axinaea tomentosa* Cogn.	Melastomataceae
Matisia bracteolosa Ducke	Malvaceae	*Guarea kunthiana* A.Juss.	Meliaceae
Matisia grandifolia Little	Malvaceae	*Morus insignis* Bureau	Moraceae
Sterculia frondosa Rich.	Malvaceae	*Piper augustum* Rudge	Piperaceae
Guarea kunthiana A.Juss.	Meliaceae	*Piper crassinervium* Kunth	Piperaceae
Otoba parvifolia (Markgr.) A.H.Gentry	Myristicaceae	*Piper dasyoura* (Miq.) C. DC.	Piperaceae
Duroia hirsuta (Poepp.) K.Schum.	Rubiaceae	*Piper areolatum* (Miq.) C. DC.	Piperaceae
Randia armata (Sw.) DC.	Rubiaceae	*Myrsine coriacea* (Sw.) R.Br. ex Roem. & Schult.	Primulaceae
Simira rubescens (Benth.) Bremek. ex Steyerm.	Rubiaceae	*Prunus huantensis* Pilg.	Rosaceae
Casearia arborea (Rich.) Urb.	Salicaceae	*Cinchona pubescens* Vahl	Rubiaceae

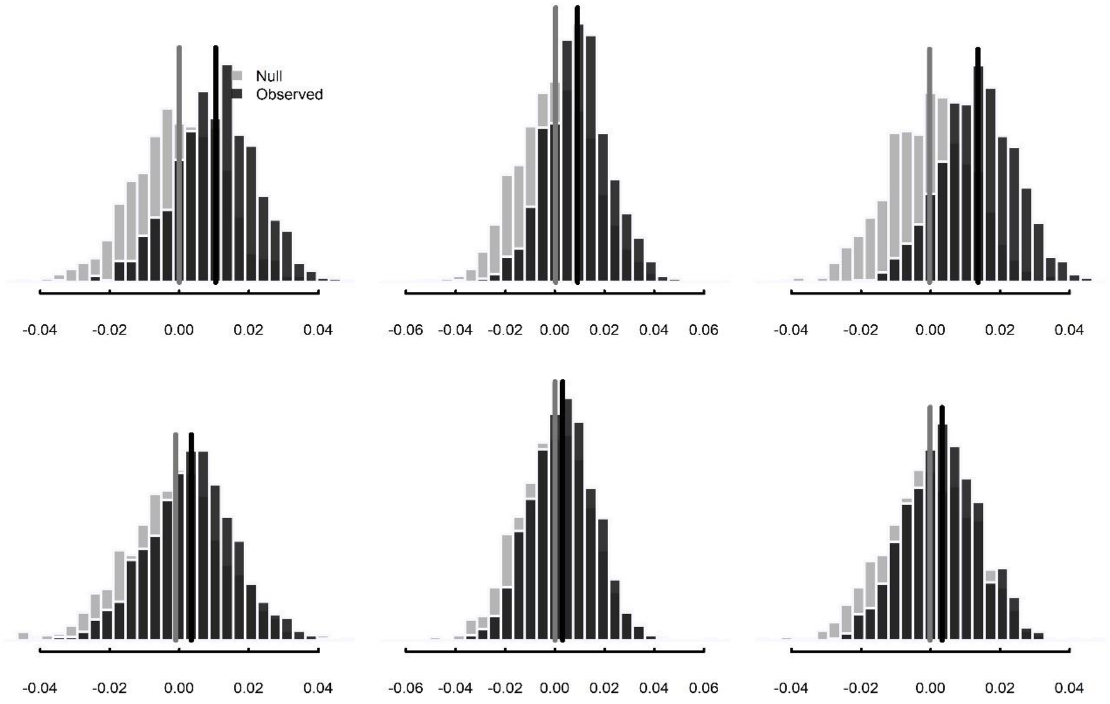
Allophylus myrianthus Radlk.	Sapindaceae	*Palicourea perquadrangularis* Wernham	Rubiaceae
Talisia cerasina Radlk.	Sapindaceae	*Psychotria carthagenensis* Jacq.	Rubiaceae
Pourouma cecropiifolia Mart.	Urticaceae	*Meliosma frondosa* Cuatrec. & Idrobo	Sabiaceae
Leonia glycycarpa Ruiz & Pav.	Violaceae	*Allophylus myrianthus* Radlk.	Sapindaceae
Rinorea guianensis Aubl.	Violaceae	*Solanum barbulatum* Zahlbr.	Solanaceae
Rinorea viridifolia Rusby	Violaceae	*Turpinia occidentalis* (Sw.) G.Don	Staphyleaceae
		Styrax pavonii A.DC.	Styracaceae

TABLE S5. Proposed generalized mixed linear models (GLMMs) to explain abundance shifts and their respective AICc values at both sites. Best fit model is represented in bolt.

Model structure	AICc	
	Ecuador	Peru
Abundance ~ 1	2834,632	1158,561
Abundance ~ elevation	2834,444	1151,118
Abundance ~ preference	2825,886	1154,315
Abundance ~ elevation + preference	2825,380	1153,066
Abundance ~ elevation * preference	2544,534	1081,682
Abundance ~ 1 + (1|specie)	2836,662	1153,082
Abundance ~ elevation + (1|specie)	2836,483	1149,725
Abundance ~ preference + (1|specie)	2827,923	1153,125
Abundance ~ elevation + preference + (1|specie)	2827,435	1151,844
Abundance ~ elevation * preference + (1|specie)	**2486,098**	**1041,300**
Abundance ~ 1 + (elevation|specie)	2835,763	1143,037
Abundance ~ elevation + (elevation|specie)	2837,715	1144,848
Abundance ~ preference + (elevation|specie)	2831,975	1145,142
Abundance ~ elevation + preference + (elevation|specie)	2830,758	1146,812
Abundance ~ elevation * preference + (elevation|specie)	2489,611	1044,551

FIGURE S1. Hypothesis 1: community functional distances distribution patterns at small spatial scale (within plot) for saplings (DBH<10 cm) and adults (DBH≥10 cm). Frequency of distribution of UST-obs (black) and UST-null (grey) values at two geographical sites (Ecuador, upper charts; Peru, lower charts) as measured based on three functional traits (SLA, left; LT, center; WD, right) after 1000 randomizations, in all six cases. There were no significant differences (α=0.05) between UST-obs and UST-null for any of the traits at any of the sites.

SAPLINGS



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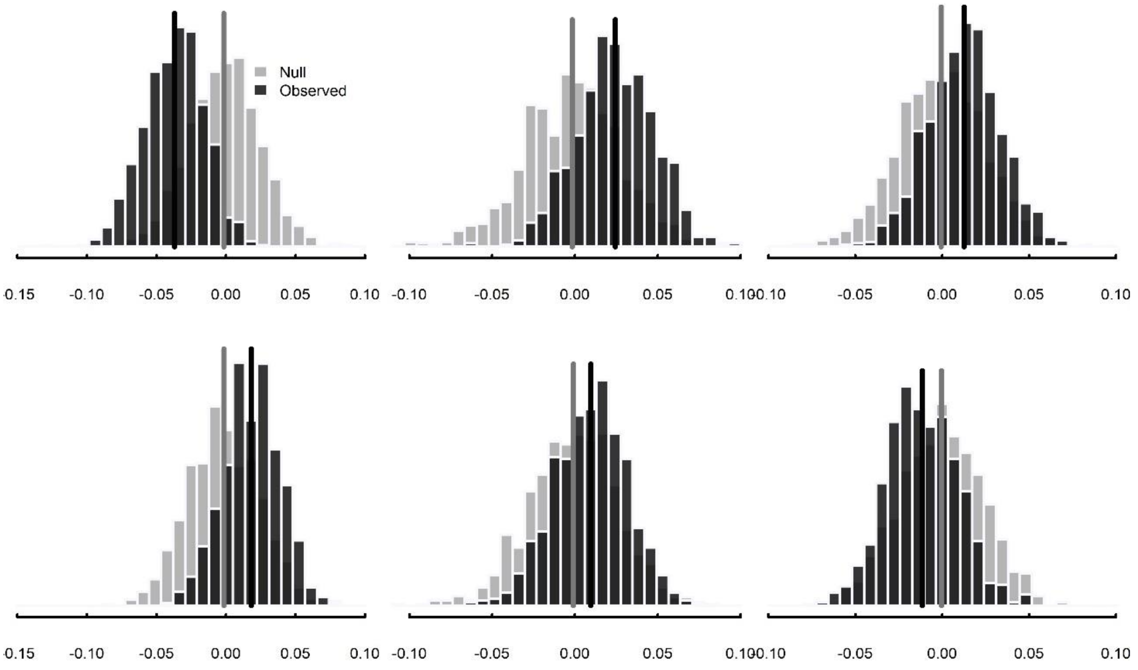
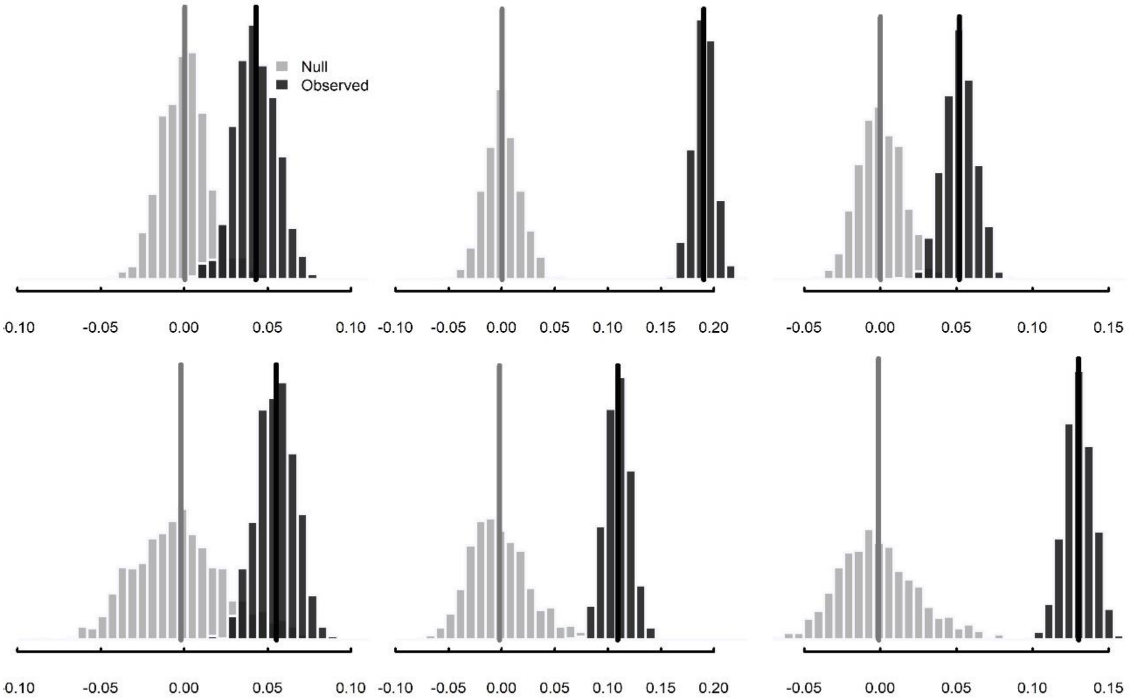


FIGURE S2. Hypothesis 2: community functional distances distribution patterns at large spatial scale (among plot) for saplings (DBH<10 cm) and adults (DBH≥10 cm). Frequency of distribution of $U_{\text{ST-}obs}$ (black) and $U_{\text{ST-}null}$ (grey) values at two geographical sites (Ecuador, upper charts; Peru, lower charts) as measured based on three functional traits (SLA, left; LT, center; WD, right) after 1000 randomizations, in all six cases. Differences between $U_{\text{ST-}obs}$ and $U_{\text{ST-}null}$ were significant ($p \leq 0.01$) for all traits at both sites with the exception of SLA for adults in Peru.

SAPLINGS



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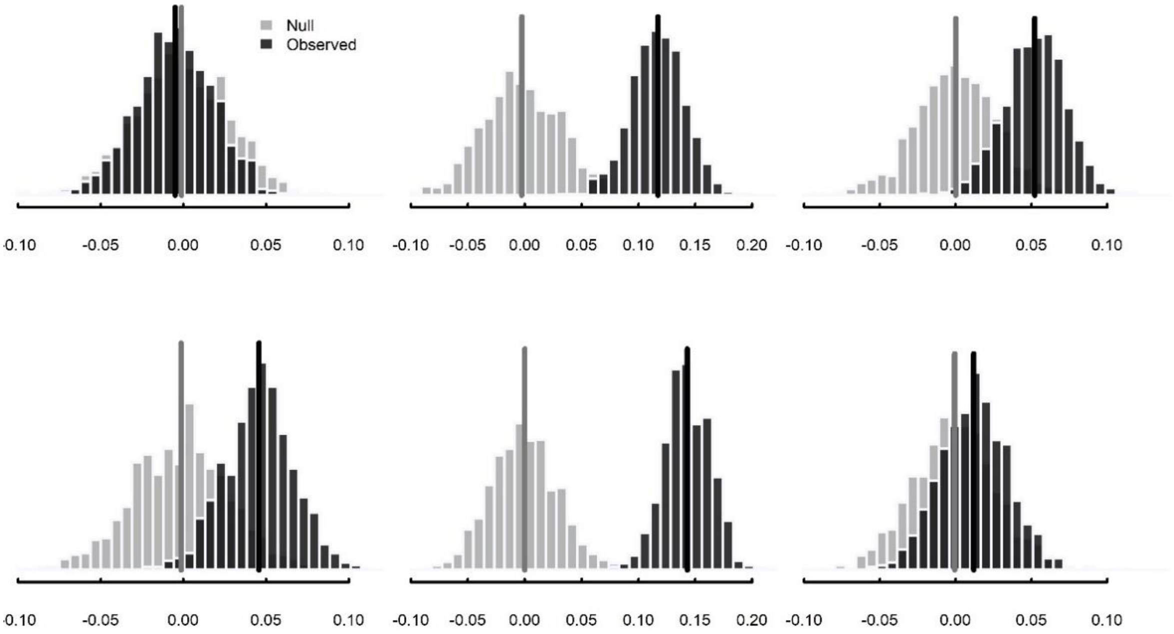

CHAPTER III

Altitudinal changes in compound leaf species in tropical Andean communities: Ecological advantages or evolutionary causes?

To be submitted to Global Ecology and Biogeography

Abstract

Aim To quantify changes in compound leaf (CL) patterns along altitudinal gradients and to explore, if any, the underlying CL ecological advantages (CL may favor drought tolerance, promote rapid growth or confer mechanical tolerance against wind) and evolutive causes (CL may be more common among the more recent lineages).

Location Andean tropical montane forests, South America.

Major taxa studied Woody plants.

Methods All species found in 390 plots from 11 altitudinal gradients of tropical montane forest were segregated as having simple or compound leaves. We used generalized linear mixed-effects models (GLMMs) to ascertain trends in the proportion of CL species richness and abundance with altitude, and to explore whether they were linked to different variables– drought, maximum height, wood density, leaf thickness or taxa age– to investigate possible underlying ecological or evolutionary drivers of such trends.

Results Abundance of CL taxa and, especially, richness decreased with altitude (from *ca*. 30 % CL species at 500 m elevation to 15 % at 3000 m), although this pattern was weaker when taxa in the Fabaceae were removed from the analyses. Overall, no support was found to the different ecological advantages or evolutionary causes hypothesized to explain those patterns.

Main conclusions This study clearly states that CL are more common at lower altitudes, becoming less common towards higher altitudes. However, there is no support for the hypotheses that those patterns are the result of the alleged ecological advantages of a CL –except for a rapid growth, for which partial support was found– or they are simply an evolutionary consequence given their historic origin.

Keywords compound leaves; drought tolerance; rapid growth; mechanical tolerance; tropical montane forest; altitudinal gradient; Andes

1 | INTRODUCTION

Despite all functioning as light-trapping surfaces, it is striking the enormous diversity of leaf types, sizes and forms: even though we solely focus on trees, they can range from as tiny as a few millimeters (*Polylepis microphyla*) to as big as several meters (*Raphia taedigera*) or from tough and thick (*Clussia spp.*) to soft and thin (*Hymenophyllum spp.*). This fact is particularly shocking because all the trade-offs ruling the vast plethora of leaf designs ultimately obey to a worldwide leaf economics spectrum (Wright et al., 2004). According to this, any leaf design is constrained within a single functional axis (Reich et al. 1998), spanning from those manufactured with low investment that are highly productive but short living to those costly to produce and low efficient but that in turn live longer. However, what underlies to the main aspect of foliar morphological classification remains unknown; *i.e.*, why are leaves either simple or compound?

In contrast to simple leaves (SL), which consist on a single surface, compound leaves (CL) are formed by a lamina dissected in multiple units or leaflets arranged along a fibrous axis termed rachis. In angiosperms, CL have independently evolved several times from SL (Cronquist 1988, Bharathan and Sinha 2001) and can be seen as an extreme case of lobulation. The molecular pathways regulating leaf dissection –and ultimately leading to leaf compoundness– appear to be modulated by environmental inputs (reviewed in Chitwood & Sinha 2016). In particular, same as environmental variables like temperature, rainfall or soil nutrients are related with certain functional traits (Castro-Díez et al. 1997, Niinemets 2001, Wright et al. 2001, 2017, Royer et al. 2008, Ordoñez et al. 2009, Goldsmith et al. 2017), climate could also explain the adaptative value of a leaf being simple or compound. Nonetheless, the subsequent ecological advantages and functional significance of CL are still under debate (Aarssen 2012, Milla 2012).

Most of the studies on the ecological significance of CL revolve around Givnish`s (1978, 1984) seminal idea, who surmised that CL act as cheap disposable non woody "twig" (*i.e.*, a CL is homologous to a small branch with several leaves, but cheaper to generate). This would confer ecological advantages to CL bearers under two scenarios. 1) In arid areas or during drought episodes or dry seasons, as CL reduce water loss in comparison to SL both by better convectively cooling down and/or by ultimately being disposed if necessary –henceforth "drought tolerance hypothesis"–. This idea makes sense because a non-disposable woody-barked twig fostering SL evapotranspirates more than an equivalent CL (Gates, 1980). 2) Under scenarios where rapid vertical growth is paramount, displaying leaflets in fibrous, non-woody, ephemeral twigs, which are only required for a short period of time, would allow to allocate the saved resources to rapid vertical growth –hereinafter "rapid growth hypothesis"–. In fact, CL species growth rates seem to be faster than SL ones (Malhado et al. 2010, Yang et al. 2019), being thus possible that CL confer an advantage to pioneer or early successional, gap-dependent species. 3) Alternatively, few studies (Vogel 1989, Niklas 1999) have shown that the architecture of CL reduces drag under strong winds compared to its SL counterparts: the leaflets fold into a cylinder-like aerodynamic structure instead as behaving as a "flag" (as SL do) and hence transmit little wind strength to branches and stems. Something similar would happen if CL are cheaper (sensu Givnish) and CL species drop their leaves when facing strong winds to reduce drag and survive (Zimmerman et al. 1994, Duryea and Kampf 2007). Any of these mechanisms would help CL trees to resist winds – hereinafter “mechanical tolerance hypothesis”–. However, all these CL alleged ecological advantages have received limited empirical support (see Stowe & Brown [1981] and Malhado et al. [2010] for drought tolerance or Vogel (1989) for mechanical tolerance) or were not confirmed (see Popma et al. [1992] and Niinemets [1998] for pioneer and gap-dependant species) with the exception of rapid growth (Malhado et al. 2010, Yang et al. 2019).

But what if CL evolved instead as a trade-off of in favour of something else than direct ecological advantages? A novel idea (Aarssen 2012) speculates that, at least in angiosperms, transition from an ancestral, large SL to a smaller CL is just a way to deploy a given leaf mass across an increased leaf number, as producing more leaves implies generating a larger “bud bank” (leafing intensity premium hypothesis *sensu* Kleiman & Aarssen, 2007). The latter would be advantageous since a larger reservoir of buds or a greater fecundity potential would increase survival chances after a disturbance. In addition, the more axillary meristems the more candidates to experience DNA replication errors, eventually increasing the likelihood for novel adaptative mutations that would be transmitted through the germ line. Hence, if CL merely represent an evolutive trade-off to reduce leaves` size while increasing their number, regardless of any ecological advantage involved at the individual level, CL would be more common among phylogenetically younger taxa just because it is a derived character –hereinafter “evolutionary hypothesis”–. This possibility remains untested to our knowledge (Milla 2012).

This study aims to cast light on CL ecological advantages and functional significance by investigating changes on leaf compoundness along altitude in 11 Andean tropical montane forests (TMFs). TMFs extent along altitudinal gradients, which offers a powerful tool to address the influence of environmental changes on functional traits and ecological communities (Colwell et al. 2008, Malhi et al. 2010). Hence, our aims were i) to quantify changes in CL richness and abundance patterns along altitude; and ii) to explore, if any, the CL ecological drivers underlying such patterns on the basis of three hypotheses:

> (1) Drought tolerance: albeit TMFs are characterized by high rainfall, the warmer temperatures of lower altitudes could potentially lead to less water availability and higher hydric stress (Körner 2007), especially if precipitation seasonality exists. In this sense, if CL are better adapted to drought-prone conditions than SL, the former would be favoured at lower altitudes.
>
> (2) Rapid growth: in lower altitudes TMFs have several canopy layers, with light becoming increasingly limited closer to the ground (Bruijnzeel et al. 2011). Hence, rapid growth is crucial for saplings to escape darker understorey layers fast. Conversely, fog prevalence in upper altitude TMFs, together with the absence of several canopy layers would cause rapid growth to be less relevant as

we move upslope. Consequently, if CL are associated with rapid growth, they would have less presence at higher altitudes.

(3) Mechanical tolerance: at lower altitudes, the TMFs complex vertical structure with several canopy layers includes the existence of tall, emerging trees very exposed to strong winds. Contrarily, upper TMFs have a denser and more uniform, rather short structure and generally lack tall emerging trees (Richter 2008, Mulligan 2011). Hence, these emergent trees in lower TMFs would be subjected to a wind selective pressure that would favor the prevalence of CL.

If any ecological advantage could be attributed to CL, leaf architecture could be used as a very informative, easily determined qualitative functional trait that could help to explain the community structure of current forests (McGill et al. 2006) and make generalizations to predict their composition under global change scenarios (Gornish and Prather 2014, Kimball et al. 2016). In addition, iii) we also explored potential evolutionary causes for CL patterns, according to which CL may be more common among more recent angiosperms taxa (Aarssen 2012). If confirmed, beyond contributing to explain CL patterns, this approach could reveal interesting insights on the TMFs evolutionary history and biogeography.

2 | MATERIALS AND METHODS

2.1 | Study region and field sampling

The study was conducted in 11 altitudinal transects of Andean TMFs (henceforth “sites”) scattered along a latitudinal gradient, spanning across Colombia, Ecuador, Peru, Bolivia and Argentina (Figure 1). In all cases, plots were placed in areas of mature forest, avoiding those visibly affected by human or natural disturbances (e.g., gaps caused by fallen trees or landslides). Number of plots per site, plot size and minimum diameter at breast height (DBH) of stems varied among sites, ranging from 12 to 67 plots, from 0.04 to 1 ha, and from 2.5 to 10 cm, respectively (Table 1). Within each plot, all woody individuals with DBH equal or above the respective minimum DBH were censused. The full dataset comprised 390 plots and 95,191 stems belonging to 4489-4133 species (including morphospecies), 699-687 genera and 151-147 families (those ranges consider the existing taxonomic uncertainty, since vouchers from different datasets have not been crosschecked).

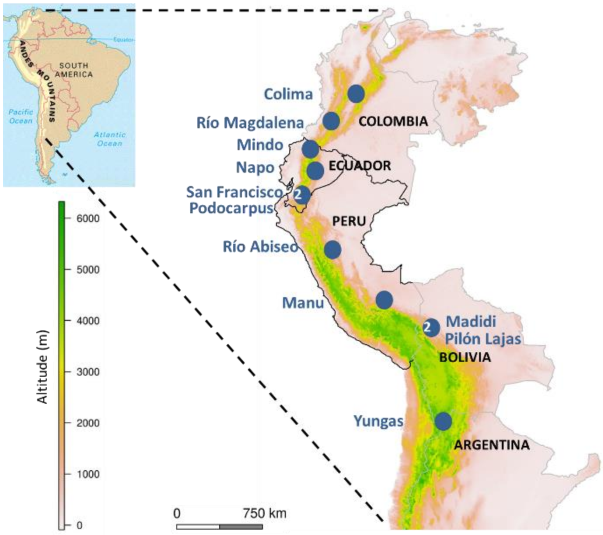

FIGURE 1. Map with the location of the 11 Andean tropical montane forest altitudinal gradients (blue dots), scattered along a latitudinal gradient, spanning from Colombia to the north of Argentina. The gradients comprised 390 plots.

TABLE 1. Geographical (country, coordinates, altitudinal range), plots (number, size, minimum DBH, number of trees) and taxonomic (number of taxa, genera and families) information for the altitudinal gradients explored in the study. Coordinates represent the centroid of plots for each site.

Site	**Country**	**Longitude**	**Latitude**	**Elevational range (m)**	***N* plots**	**Plot size (ha)**	**min DBH (cm)**	***N* families**	***N* genera**	***N* taxa**	**N *trees***	**N *trees (no Faba)***	**% *trees* Faba**
Colima	Colombia	-75,53	4,59	2208 - 3525	12	0.25	5	65	134	269	5207	5186	0,5
Río Magdalena	Colombia	-75,73	2,40	125 - 3600	33	1	10	93	372	1140	14373	13797	4,1
Mindo	Ecuador	-78,71	0,23	394-3128	15		10	58	133	200	1616	1575	2,6
Napo	Ecuador	-77,51	-1.04	400 - 3978	92	0.04	10	84	241	635	2885	2671	7,5
San Francisco	Ecuador	-79,07	-4,06	1020 - 2900	67	0.04	10	72	167	374	2267	2208	2,7
Podocarpus	Ecuador	-79,00	-4,12	1033 - 2906	30	0.1	2.5	86	276	748	9730	9451	2,9
Rio Abiseo	Peru	-77,06	-7,49	745 - 2980	30	0.1	2.5	99	282	550	9145	8873	3
Manu	Peru	-70.72	-12,86	200 - 3450	12	1	7.5	88	267	722	9472	9332	1,5
Madidi	Bolivia	-68,93	-14,75	1166 - 3061	27	0.1	2.5	87	231	459	8562	8515	0,6
Pilón Lajas	Bolivia	-68,37	-15,56	1224 - 3106	27	0.1	2.5	87	206	460	9933	9786	1,5
Yungas	Argentina	-64,52	-23,03	396 - 2304	45	1	10	54	117	148	22001	19266	12,5

2.2 | Leaf structure characterization

Information of SL or CL architecture was assigned to each taxa (i.e., each species or morphospecies) based on taxonomic expertise combining field and herbaria vouchers observation, digital data and image repositories and regional floras, especially Gentry (1996). We are aware that working at taxa resolution instead of at genus or family level may introduce a potential bias by overstating the influence of taxa exhibiting same leaf architecture simply by the fact that they share a recent common ancestor. To avoid this and untangle CL patterns from an underlying potential phylogenetic signal (Givnish 1978), we accounted for this issue in the statistical analyses (see Malhado et al., 2010; Stowe & Brown, 1981). To do so, the largest family of CL trees (Fabaceae) was excluded when the analyses were conducted at the plot level (see 2.3 and 2.4.1) and genera and family were included as random factors when were conducted at the taxa level (see 2.4.2 and 2.4.3). Taxonomic standardization of the species names was performed using 'Taxonstand' (Cayuela et al. 2012, 2017).

2.3 | Patterns of CL along altitude

Patterns of leaf compoundness were tested using two variables at the plot level: CL richness (the proportion of taxa exhibiting CL) and CL abundance (the proportion of individual stems bearing CL). Since the minimum DBH differed among sites (Table 1), we standardized analyses by considering only all taxa and individuals of DBH ≥ 10 cm. The dataset used to report CL patterns included 61,457 stems from 3600 taxa, that dropped respectively to 57,656 and 3343 when Fabaceae members were excluded.

2.4 | Hypothesis testing

2.4.1 The drought tolerance hypothesis

The adaptative value of CL to drought was assessed by exploring the relation between CL abundance and richness and a set of bioclimatic predictor variables representative for hydric availability. For each plot, information concerning the following variables was retrieved from CHELSA Climatology dataset (Karger et al. 2017) with a resolution of 30 arc seg: annual precipitation (mm), precipitation of the driest quarter (mm), precipitation of the driest month (mm), precipitation of the warmest month (mm), and precipitation seasonality (coefficient of variation of monthly mean precipitation). All the variables showed a high correlation between each other (Pearson`s $r>0.75$), except for precipitation seasonality (which showed a correlation of $r=-0.56$, $r=-0.72$, $r=-0.70$ and $r=-0.18$ with the four other variables, respectively). Albeit soil conditions or slope may substantially influence each site local water availability, the considered variables are expected to account for major differences existing along the altitudinal gradient. This analysis was conducted for the same subset of stems as in 2.3.1.

2.4.2 The rapid growth hypothesis

We tested whether values for two plant functional traits related to plant growth – namely wood density (WD) and leaf thickness (LT)– differed between CL and SL taxa. On one hand, WD is a fundamental trait of the wood economy spectrum (Chave et al. 2009) that captures a trade-off according to which species with lighter wood grow and die faster, while species with denser wood grow more slowly and live longer (Enquist et al., 1999; Swenson, 2012). On the other hand, LT is a proxy for the equivalent trade-off in the leaf economy spectrum (Poorter et al. 2009) –i.e., thinner leaves grow and die faster while thicker ones do the contrary–. Therefore, if CL favors rapid growth, the probability of displaying CL will be higher among taxa characterized both by lower WD and LT mean values. This hypothesis was addressed using only the subset of sites –San Francisco, Napo, Podocarpus and Río Abiseo– from where WD and LT were acquired. Functional traits were measured following standardized protocols (Cornelissen et al. 2003). In total 1337 taxa belonging to 362 genera and 113 families for WD and 1152 taxa from 342 genera and 109 families for LT were included in the analysis. For each taxa, trait values were calculated as the mean from an average of three individuals.

2.4.3 The mechanical tolerance hypothesis

To test this hypothesis, we sought a relationship between the probability of a taxon bearing CL and its height. Since tree height was neither consistently measured nor estimated across all sites, we used maximum DBH (DBHmax) as its proxy (Sumida et al. 2013). The largest height value for each taxa across the entire dataset was appointed as DBHmax. To avoid a potential bias caused by estimating a taxa DBHmax from just a few, non-very representative samples –e.g., undersampled or less abundant taxa, or those for which most of sampled individuals were still at young stages–, we conducted the analyses considering only taxa with abundance $N \geq 10$. In total 54547 trees belonging to 950 taxa, 319 genera and 99 families were included in the analysis.

2.4.4 The evolutionary hypothesis

To asses this hypothesis we calculated the proportion of species with SL and CL only for all angiosperm genera across our dataset and sought a relationship between this proportion and the genera`s phylogenetic age. To estimate those ages we built a phylogenetic tree (Text S1) using the R package ‘V.PhyloMaker‘ (Jin and Qian 2019) on the implemented dated mega-tree ‘GBOTB.extended.tre‘ –which for seed plants was derived from Smith & Brown (2018) mega-tree–. We utilized the function ‘phylo.maker‘ with genera as terminals and got their dates of origin after their most recent common ancestors. For this analysis we worked with 614 genera (91,3 % of the 672 angiosperms` genera in our dataset).

2.5 | Statistical analyses

To assess how leaf compoundness patterns changed along the altitudinal gradient, we fitted generalized linear mixed-effects models (GLMMs) with a binomial error distribution to relate the proportion of CL richness and CL abundance per plot with altitude as a fixed term (Table S1). To investigate the drought tolerance hypothesis, we fitted GLMMs to relate the proportion of CL richness with five bioclimatic variables related to drought as fixed terms in separate models. In all these cases, site was used as a random factor (Table S2).

To test the rapid growth and the mechanical tolerance hypotheses, we also fitted GLMMs with a binomial error distribution to relate whether a given taxa was CL or not (a binary response variable) with WD or LT and DBHmax as fixed terms, respectively (Table S3). In all these cases, family and genera nested within family were used as random factors. Finally, to test the evolutionary hypothesis, we followed a similar approach by fitting generalized linear models (GLMs) to relate the proportion of CL taxa within a genus with the genus age (Table S4).

For each response variable, model selection was based on the comparison of alternative models using the corrected Akaike Information Criterion (AICc). Models with a difference in AICc > 2 suggest that the worse model had virtually no support and could be omitted. All statistical analyses were conducted with the R packages ‘glmmADMB‘ (Skaug et al. 2013), ‘MASS‘ (Venables and Ripley 2002) and ‘MuMIn’ (Barton 2018).

3 | RESULTS

3.1 | Patterns of CL along altitude

CL richness and CL abundance shifted along altitude (Figure 2a and 2b). Model predictions indicated that both CL richness and abundance were higher at lower altitudes, although the relationship of CL richness with altitude was stronger than that of CL abundance (e.g., from ca. 30 % CL species and 27 % CL individuals at 500 m to 15 % and 20 % at 3000 m, respectively). The same pattern was found when taxa belonging to Fabaceae were excluded from the analysis, although in this case the relationship with altitude was weaker. In both cases –with and without Fabaceae¬ and for both variables –richness and abundance– best fit models included the most complex structure for fixed and random effects (Table S1).

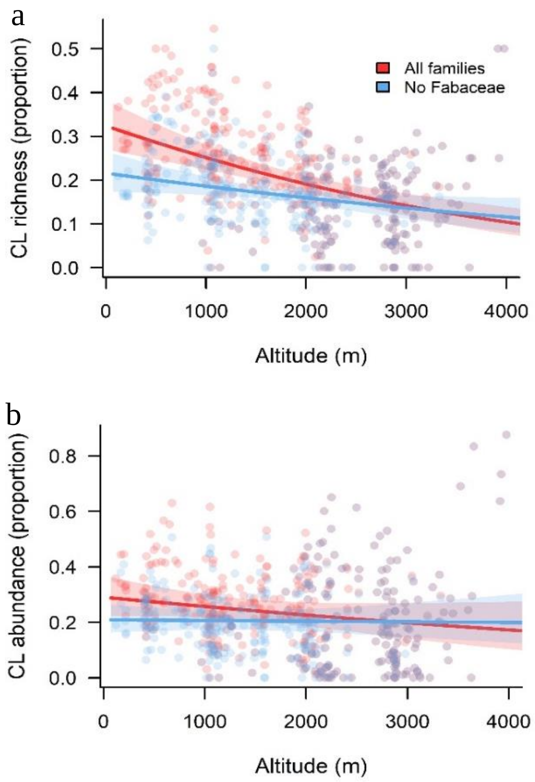

FIGURE 2. Compound leaves (CL) patterns along altitude. a) CL richness refers to the proportion of taxa having CL and b) CL abundance to the proportion of individual trees bearing CL. For standardization purposes, analyses were conducted considering only all taxa and individuals of DBH ≥ 10 cm. "All families"= all taxa included; "No Fabaceae"= taxa belonging to Fabaceae excluded.

3.2 | Hypothesis testing

3.2.1 The drought tolerance hypothesis

CL richness did not shift in response to drought (Table S2). Model predictions indicated that CL richness was independent from any of the drought related bioclimatic variables (Figure 3 for precipitation seasonality and Figure S2 for the remaining drought related predictors) since best fit models did not necessarily include the most complex structure for fixed effects (i.e., no effect of the climatic predictors). The same pattern was found when taxa belonging to Fabaceae where excluded from the analysis, although in this case the AICc values were smaller. Interestingly, alternative models (less parsimonious than the best) would suggest a lower proportion of CL species under drought related conditions, opposite to our expectation.

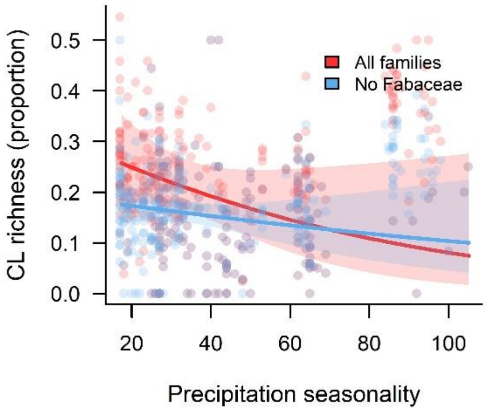

FIGURE 3. Compound leaves (CL) patterns respecting drought tolerance hypothesis. CL richness –- proportion of taxa having CL– in relation to precipitation seasonality. For standardization purposes, analyses were conducted analyses were conducted considering only all taxa and individuals of DBH ≥ 10 cm. "All families"= all taxa included; "No Fabaceae"= taxa belonging to Fabaceae excluded.

3.2.2 The rapid growth hypothesis

CL were not consistently more common among the fastest growing taxa. On the one side, when WD was considered, model predictions indicated that the probability of a taxon having CL was independent from its WD (Figure 4a, Table S3). On the other side, although for LT the models suggested that the probability of having CL was higher among taxa with lower LT values (Figure 4b, Table S3), this probability was only marginally higher.

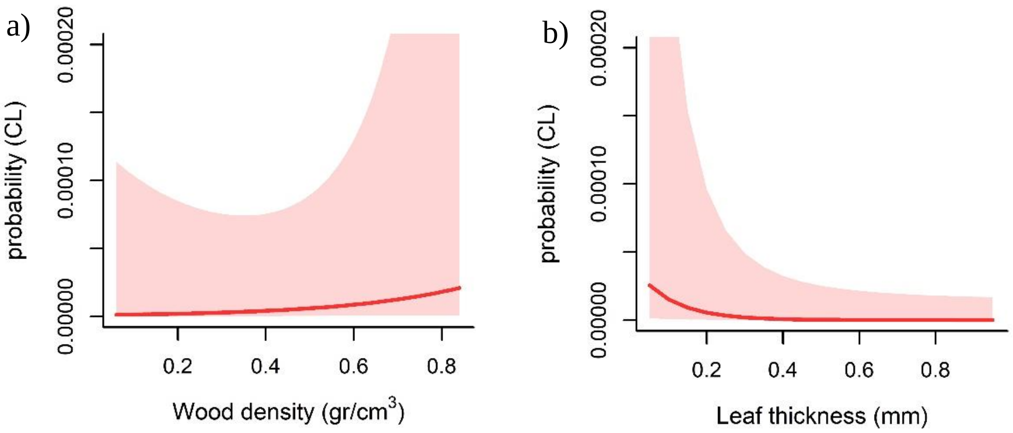

FIGURE 4. Probability of having compound leaves (CL) respecting rapid growth hypothesis. a) probability of a taxa bearing CL in relation to wood density and b) in relation to leaf thickness. This analysis was conducted considering only data for Napo, San Francisco, Podocarpus and Rio Abiseo gradients.

3.2.3 The mechanical tolerance hypothesis

CL were as frequent among the tallest trees as among shorter ones (Figure 5). Model predictions indicated that the probability of a taxon bearing CL was independent from its potential DBHmax (Table S3). The same results were found when the analyses were conducted for all individuals, not just the abundant taxa of N ≥ 10 (data not shown).

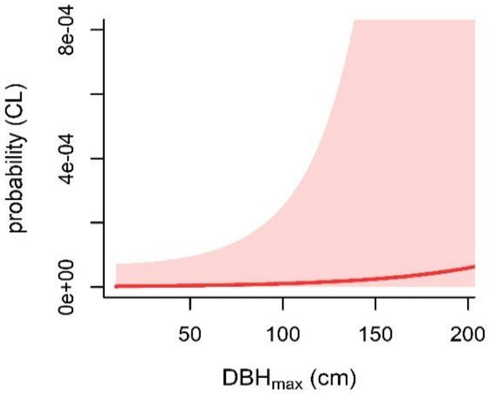

FIGURE 5. Probability of a having compound leaves (CL) respecting mechanical tolerance hypothesis. Probability of a taxa bearing CL in relation to its maximum diameter at breast height (DBH$_{max}$). This analysis was conducted considering only taxa of abundance *N* ≥ 10.

3.2.4 The evolutionary hypothesis

CL were not more common among the most recent genera (Figure 6). Model predictions revealed that the proportion of CL taxa within a genus was independent from the genus age (Table S4).

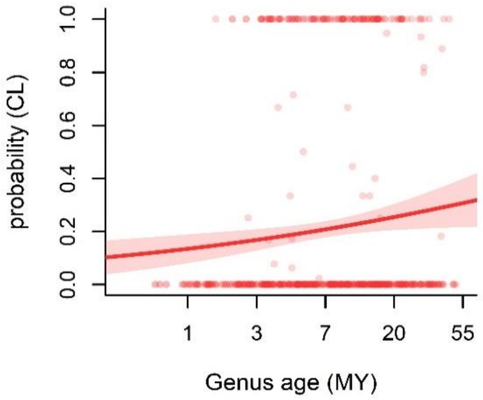

FIGURE 6. Probability of a having compound leaves (CL) respecting evolutive hypothesis. Probability of a genus taxa bearing CL in relation to its age ("MY"= Millions of years).

4 | DISCUSSION

By assembling what to our knowledge is the largest dataset to explore CL patterns along altitude, we found that the occurrence of CL species decreases with altitude, a pattern that is consistent across the tropical Andean range. Although this fact may be presumably due to certain (their causality yet to be determined) ecological advantages of CL species or to underlying evolutionary causes, our results do not support specific ecological drivers other than rapid growth, –and this one only in part–.

4.1 | Patterns of CL along altitude

Our study clearly shows that CL species richness decreased with increasing altitude, albeit this pattern was not as clear for CL abundance (Figure 2 and Table S1). This result was firstly reported by Beard (1944) based on his "impression" that along altitude in "montane formations the predominant leaf-type is reduced from compound to simple" in the Neotropics. Later, other studies quantitatively confirmed this pattern. For example, the proportion of CL species decreased from 36 % at 380 m to 9 % at 1710 m in Ecuador (Grubb et al., 1963), from 19 to 15 % below and above 365 m, respectively, in Puerto Rico (Little and Wadsworth 1964, Little et al. 1974) and from 30 % at 1220 m to ca. 10 % at 2010 m in Mexico (Velázquez-Rosas et al. 2002). With this study we went beyond local studies and found a pattern that can be generalized to the entire tropical Andes (Malhado et al. 20110 did something similar for the Amazon). The fact that the altitudinal pattern is still maintained –albeit weaker¬– when members of Fabaceae were removed from the analyses suggests that CL patterns might be not solely the product of biogeographical factors underlying the differential distribution of particular phylogenetic groups (Givnish, 1978). Rather, it indicates that CL may confer some ecological advantages that would explain those patterns.

4.2 | Hypothesis testing

4.2.1 The drought tolerance hypothesis

CL richness did not shift in relation with any of the drought related bioclimatic variables, neither with nor without Fabaceae members as part of CL species (Figures 2 and S2; Table S2). Hence, our findings suggest that CL confer no drought tolerance. This result can contribute to clarify the contradictory results from former works: although Malhado et al. (2010) found solely a "relatively weak" association between different metrics of water availability and CL trees in the Amazon, Stowe & Brown (1981) concluded that CL trees have a preference "for regions with high spring and summer temperatures and low moisture availability" in North America. However, concerning Stowe & Brown (1981) conclusions, two facts suggest that they must be taken with caution: i) statistically their results are flawed since they use a stepwise regression procedure to test the significance of 36 bioclimatic variables, with high collinearity among them, over a dataset of 37 geographic regions and, besides, ii) the maps used to determine those variables date from at least 50 years ago, so their locations climatic characterization lacks the current approaches resolution. Our results and all those facts lead us not to advocate for CL drought tolerance hypothesis.

But, what if a potential CL adaptative value under drought may just arise after a certain water scarcity threshold has been overcome? Considering that CL are very characteristic of warm, seasonally arid habitats as savannas, thorn forests and deserts (Givnish 1978) or that the % of CL species increases from evergreen forests in well-watered areas towards drought tree velds and scrubs in more arid ones in South Africa (Bews 1925) and from montane to lowland and semi deciduous rainforests in Venezuela (Rollet

1990), an alternative explanation emerges: the relatively limited drought in tropical rain forest systems may be not enough to trigger a plant community composition in which CL are clearly favored. In this sense, tropical systems would not be suitable to unveil the potential CL adaptative value against drought and further studies are required in other ecosystems where drought is harsher.

4.2.2 The rapid growth hypothesis

Our results are only partially consistent with CL favouring rapid growth (Figure 4) although hitherto, from all the alleged CL ecological advantages, this is the more evidence-based supported one from our results. The most recent study in this sense claimed that the higher hydraulic efficiency and photosynthetic rates for CL trees enable them to growth faster (Yang et al. 2019), although this conclusion was based upon the comparison of only four SL and four CL temperate forest species. Hence, the most robust evidence for this hypothesis still belongs to Malhado et al. (2010), who reported that the annual diameter growth rates of trees bearing CL across Amazonia were 30% greater than their SL counterparts. However, this pattern was mostly driven by Fabaceae members –e.g., when merely individuals from Fabaceae were considered as CL, the differences in growth rate between SL and CL increased 50 % whereas when Fabaceae were excluded from the CL group, it decreased to just 3 %–, leading them to only claim for “some” support for this hypothesis. Therefore, our results indicating that CL are only partially more common among the fastest growing taxa are not surprising (Figure 4 and Table S3), especially given the differences in the methodological approaches between both studies: while Malhado et al. (2010) directly measured growth rate we estimated it indirectly via wood density (WD) and leaf thickness (LT). Since these functional traits are just proxies for growth potential (Enquist et al. 1999, Köhler et al. 2000, Poorter et al. 2009, Edwards et al. 2014), we may have missed a great part of the statistical signal required to find differences between CL and SL species, if existing –we found that the probability of bearing CL was not higher among low WD taxa and only slightly higher among low LT ones–. In the case of WD, this fact coincides with Malhado et al. (2010), who found differences in growth rate between CL and SL but did not for WD. In addition, the fact that in our study we used twig WD as a proxy of stem WD –albeit tightly correlated, twig typically underestimates stem ca. 20 % (Swenson and Enquist 2008) – may likely diminish even more the power of using WD to explore this question. Hence, future studies revisiting the rapid growth hypothesis better rely on the usage of direct evidences rather than on indirect, functional traits-based ones.

Aside from those results, considering the trade-offs of WD related implications reveals a complex functional interplay according to which the different ecological advantages proposed for CL are likely mutually exclusive. For instance, WD could facilitate either rapid growth or drought tolerance/ mechanical tolerance, but hardly all simultaneously: if lighter WD facilitated CL species to grow faster, this would diminish their drought tolerance –as WD is positively related with xylem cavitation, light wooded species would be more prone to suffer a deathly xylem failure under low water availability environments (Hacke et al. 2001)– and their mechanical tolerance –as WD is positively related to mechanical strength, light wooded species would be less resistant to stem breakage (Putz et al. 1983, Zimmerman et al. 1994)–.

4.2.3 The mechanical resistance hypothesis

Our results do not endorse that CL confer mechanical tolerance to the tallest, canopy emergent trees (Figure 5 and Table S3). This would have contributed to explain higher proportion of CL at lower altitudes (see 3.1 and 4.1), since there TMFs are characterized by displaying a complex structure with canopy emergent trees while at upper altitudes TMFs tend to be arranged on a monolayer like structure without emergent trees (Koike et al. 1990, Withmore 1998) and thus with no need for CL to be favored. Besides, this would have matched with the drought tolerance hypothesis (see 4.2) in the sense that, as those trees in the upper strata are more prone to suffer evapotranspiration as consequence of direct sunlight than those in the understorey, the % of CL species would increase from the understorey to the canopy (see Cain, de Oliveira Castro, Pires, & da Silva, 1956).

However, the fact that we cannot advocate for the mechanical tolerance hypothesis to explain CL altitudinal patterns is not surprising at all, since our argumentation lays on a premise –CL suffer less wind drag than SL– very limited, as Vogel (1989) and (Niklas 1999) compared very few species (e.g., Vogel only considered five SL and three CL species and found relatively lower drag for just two out of the three CL ones). Thus, the alleged lower drag under strong winds experienced by CL should be thoroughly confirmed with studies embracing more species before accepting its generalisation. In the same sense Cain et al. (1956) observations, as already pointed out by Rollet (1990), can neither be generalized, since the CL understorey to canopy pattern was only found, and even with irregularities, in three out of five forests for CL richness and two out of four for CL abundance.

4.2.4 The evolutionary hypothesis

A recent, still untested idea speculates that CL may have aroused as a mere evolutive trade-off to increase leaf number, a fact that would confer several advantages to angiosperms (Aarssen 2012). Hence, a largest amount of more modern, CL taxa would be generated in the lowland Amazon forests and at lower TMFs elevations and would prevail there, thus explaining the reported CL altitudinal patterns. However, since according to our findings CL are not more common among the most modern taxa, the previously conjectured explanation cannot be supported. (Figure 6 and Table S4).

In any case, Aarssen (2012) idea envisions that, aside from CL, two alternative ways for an ancestral large SL to generate a larger number of smaller leaves exist: a) reducing SL dimensions or b) increasing SL lobing. Under this assumption, CL would be evolutionarily more modern than a large SL, but equivalent to a small or lobed SL. Therefore, the more pertinent way to test whether CL are more common among the more modern taxa would be by sorting species` leaves into those four categories (i.e., SL large, SL small, SL lobed or CL), as it would make possible to compare CL versus only the really ancestral SL taxa. Unfortunately, we do not have information about lobulation or average lamina size to conduct this type of analysis.

5 | CONCLUSIONS AND FUTURE PERSPECTIVES

This study supports the long-standing perception that in tropical forests CL are more common at lower altitudes. However, our findings do not support any CL ecological advantage favouring that pattern, with the only exception of a modest support for rapid growth. This is not surprising given that the evidence reported in former studies for such advantages is also weak, if any. Consequently, attempts to use CL as a functional trait to explain community composition seems a moot point to us. In this sense, the results of van der Sande et al. (2019) based on the use of CL as a conservative trait correlated negatively with precipitation and positively with erosion and fire related scenarios should be reconsidered, given that those relations rely on a single study –statistically flawed, conducted in temperate zones (Stowe and Brown 1981), which results were extrapolated to tropical areas– while ignore more recent and suitable evidences (Malhado et al. 2010).

Temperature is the bioclimatic variable most correlated with altitude and therefore it might be ultimately responsible of the CL patterns. To investigate this and other ideas, more exhaustive, mechanistic and physiologically based studies of CL (e.g., Yang et al. [2019]) rather than based on indirect-evidence to better assess the potential ecological advantages of CL. If any finally could be reliably assigned to CL, leaf type could be trusted as an easily-measurable functional trait that could provide insights about which species would be more successful under global change scenario.

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APPENDIX

TABLE S1. Results from generalized linear mixed-effects models (GLMMs) on the proportion of compound leaves (CL) richness and abundance in relation to altitude. For standardization purposes, analyses were conducted excluding all taxa and individuals of DBH ≥ 10 cm. “All families”= all taxa included; “No Fabaceae”= taxa belonging to Fabaceae excluded.

Fixed effect	Random effect	AIC	
		All families	No Fabaceae
CL Richness along altitude			
-	-	1954,57	1611,18
-	Site	1753,38	1545,21
-	Altitude |Site	1639,99	1520,40
Altitude	-	1731,29	1584,80
Altitude	Site	1641,45	1538,72
Altitude	Altitude |Site	**1628,30**	**1517,61**
CL Abundance along altitude			
-	-	9352,92	8638,89
-	Site	8185,58	7325,57
-	Altitude |Site	**7025,09**	**7001,30**
Altitude	-	8916,91	8626,04
Altitude	Site	7853,88	7326,82
Altitude	Altitude |Site	**7024,90**	**7003,28**

Figure S1. Compound leaves (CL) patterns in relation to different drought related bioclimatic variables. a) Annual precipitation, b) Precipitation of the driest month, c) Precipitation of the driest quarter, d) Precipitation of the warmest quarter. CL richness refers to the proportion of taxa exhibiting CL. For standardization purposes, analyses were conducted excluding all taxa and individuals of DBH < 10 cm. "All families"= all taxa included; "No Fabaceae"= taxa belonging to Fabaceae excluded.

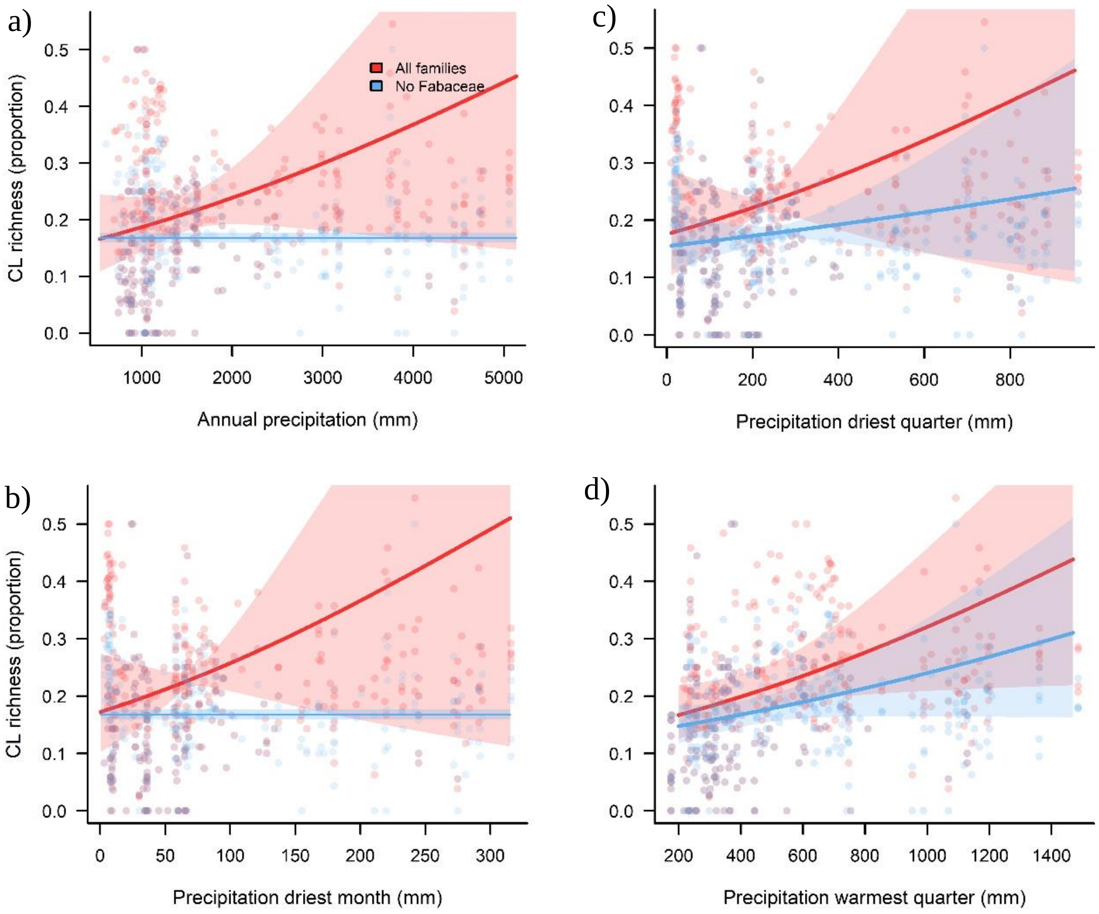

Table S2. Results from generalized linear mixed-effects models (GLMMs) on the proportion of compound leaves (CL) richness in relation to different drought related bioclimatic variables. For standardization purposes, analyses were conducted excluding all taxa and individuals of DBH ≥ 10 cm. “All families”= all taxa included; “No Fabaceae”= taxa belonging to Fabaceae excluded.

Fixed effect	Random effect	AIC	
		All families	No Fabaceae
CL Richness in relation to precipitation seasonality (Precip. seas.)			
-	-	1954,57	1611,18
-	Site	1753,38	1545,21
-	Precip. seas. |Site	**1703,09**	**1527,29**
Precip. seas.	-	1895,24	1581,52
Precip. seas.	Site	1742,08	1547,06
Precip. seas.	Precip. seas. |Site	**1702,95**	**1528,13**
CL Richness in relation to annual precipitation (Ann. precip.)			
-	-	1954,57	1611,18
-	Site	1753,38	1545,21
-	Ann. precip. |Site	**1710,95**	**1528,22**
Ann. precip.	-	1949,71	1612,74
Ann. precip.	Site	1733,43	1546,86
Ann. precip.	Ann. precip. |Site	**1711,18**	**1529,78**
CL Richness in relation to precipitation of the driest month (Prec. driest mon.)			
-	-	1954,57	1611,18
-	Site	1753,38	1545,21
-	Prec. driest mon. | Site	**1698,13**	**1514,86**
Prec. driest mon.	-	1956,41	1609,73
Prec. driest mon.	Site	1749,25	1547,03
Prec. driest mon.	Prec. driest mon. | Site	**1698,83**	1523,39
CL Richness in relation to precipitation of the driest quarter (Prec. driest quar.)			
-	-	1954,57	1611,18
-	Site	1753,38	1545,21
-	Prec. driest quar. | Site	**1694,40**	**1521,74**
Prec. driest quar.	-	1956,40	1609,39
Prec. driest quar.	Site	1747,80	1547,07
Prec. driest quar.	Prec. driest quar. | Site	**1695,48**	**1522,94**
CL Richness in relation to precipitation of the warmest quarter (Prec. warmest quar.)			
-	-	1954,57	1611,18
-	Site	1753,38	1545,21
-	Prec. warmest quar. | Site	**1717,30**	**1534,44**
Prec. warmest quar.	-	1897,59	1600,84
Prec. warmest quar.	Site	1729,76	1538,88
Prec. warmest quar.	Prec. warmest quar. | Site	**1716,06**	**1533,50**

Table S3. Results from generalized linear mixed-effects models (GLMMs) on the proportion of compound leaves (CL) richness in relation to rapid growth and mechanical tolerance hypotheses. For rapid growth, the taxa mean wood density and the leaf thickness were used as proxies. For mechanical resistance, the taxa maximum diameter at breast height (DBH_{max}) was used as a proxy. For standardization purposes, analyses were conducted excluding all taxa and individuals of DBH ≥ 10 cm.

Fixed effect	Random effect	AIC
CL proportion in relation to rapid growth (via wood density)		
-	Family/Genus	**242,85**
Wood density	-	**243,87**
Wood density	Family/Genus	1169,71
CL proportion in relation to rapid growth (via leaf thickness)		
-	Family/Genus	220,56
Leaf thickness	-	**217,58**
Leaf thickness	Family/Genus	967,28
CL proportion in relation to mechanical resistance		
-	Family/Genus	**506,84**
DBH_{max}	-	**506,72**
DBH_{max}	Family/Genus	3414,03

Table S4. Results from generalized linear models (GLMs) on the proportion of compound leaves (CL) richness within a genus in relation to in relation to the evolutive hypothesis. Genus age was used to estimate the evolutive time of each genus. Analysis was conducted only for taxa belonging to angiosperms.

CL proportion in relation to evolutive time	
-	**3869,83**
Genus age	**3869.27**

Text S1. Phylogenetic tree in Newick format used for the evolutionary hypothesis analyses based on Zanne et al. (2014).

((((((((((((((((((((((((((((((((Tachia_sp1:14.8236)Tachia:14.8236,(Macrocarpaea_sp1:14.8236)Macrocarpaea:14.8236,(Symbolanthus_sp1:14.8236)Symbolanthus:14.8236)Gentianaceae:22.381642,(((Mandevilla_sp1:18.8041)Mandevilla:18.8041,(Odontadenia_sp1:18.8041)Odontadenia:18.8041,(Orthosia_sp1:18.8041)Orthosia:18.8041,(Rauvolfia_sp1:18.8041)Rauvolfia:18.8041,(Tabernaemontana_sp1:18.8041)Tabernaemontana:18.8041,(Aspidosperma_sp1:18.8041)Aspidosperma:18.8041,(Couma_sp1:18.8041)Couma:18.8041,(Forsteronia_sp1:18.8041)Forsteronia:18.8041,(Geissospermum_sp1:18.8041)Geissospermum:18.8041,(Himatanthus_sp1:18.8041)Himatanthus:18.8041,(Lacmellea_sp1:18.8041)Lacmellea:18.8041,(Macoubea_sp1:18.8041)Macoubea:18.8041,(Malouetia_sp1:18.8041)Malouetia:18.8041)Apocynaceae:9.146931,(((Strychnos_sp1:17.2216)Strychnos:17.2216)Loganiaceae:11.895604):0.41634):5.27365):6.77608,((Ladenbergia_sp1:28.435)Ladenbergia:28.435,(Chomelia_sp1:28.435)Chomelia:28.435,(Macrocnemum_sp1:28.435)Macrocnemum:28.435,(Ciliosemina_sp1:28.435)Ciliosemina:28.435,(Malanea_sp1:28.435)Malanea:28.435,(Cinchona_sp1:28.435)Cinchona:28.435,(Margaritopsis_sp1:28.435)Margaritopsis:28.435,(Condaminea_sp1:28.435)Condaminea:28.435,(Notopleura_sp1:28.435)Notopleura:28.435,(Coussarea_sp1:28.435)Coussarea:28.435,(Tocoyena_sp1:28.435)Tocoyena:28.435,(Warszewiczia_sp1:28.435)Warszewiczia:28.435,(Wittmackanthus_sp1:28.435)Wittmackanthus:28.435,(Paederia_sp1:28.435)Paederia:28.435,(Coutarea_sp1:28.435)Coutarea:28.435,(Palicourea_sp1:28.435)Palicourea:28.435,(Dialypetalanthus_sp1:28.435)Dialypetalanthus:28.435,(Pentagonia_sp1:28.435)Pentagonia:28.435,(Dioicodendron_sp1:28.435)Dioicodendron:28.435,(Pogonopus_sp1:28.435)Pogonopus:28.435,(Duroia_sp1:28.435)Duroia:28.435,(Posoqueria_sp1:28.435)Posoqueria:28.435,(Elaeagia_sp1:28.435)Elaeagia:28.435,(Emmeorhiza_sp1:28.435)Emmeorhiza:28.435,(Agouticarpa_sp1:28.435)Agouticarpa:28.435,(Faramea_sp1:28.435)Faramea:28.435,(Alibertia_sp1:28.435)Alibertia:28.435,(Ferdinandusa_sp1:28.435)Ferdinandusa:28.435,(Alseis_sp1:28.435)Alseis:28.435,(Genipa_sp1:28.435)Genipa:28.435,(Amaioua_sp1:28.435)Amaioua:28.435,(Guettarda_sp1:28.435)Guettarda:28.435,(Arachnothryx_sp1:28.435)Arachnothryx:28.435,(Psychotria_sp1:28.435)Psychotria:28.435,(Randia_sp1:28.435)Randia:28.435,(Remijia_sp1:28.435)Remijia:28.435,(Rudgea_sp1:28.435)Rudgea:28.435,(Schizocalyx_sp1:28.435)Schizocalyx:28.435,(Hillia_sp1:28.435)Hillia:28.435,(Bathysa_sp1:28.435)Bathysa:28.435,(Hippotis_sp1:28.435)Hippotis:28.435,(Borojoa_sp1:28.435)Borojoa:28.435,(Isertia_sp1:28.435)Isertia:28.435,(Calycophyllum_sp1:28.435)Calycophyllum:28.435,(Joosia_sp1:28.435)Joosia:28.435,(Capirona_sp1:28.435)Capirona:28.435,(Kutchubaea_sp1:28.435)Kutchubaea:28.435,(Chimarrhis_sp1:28.435)Chimarrhis:28.435,(Schradera_sp1:28.435)Schradera:28.435,(Simira_sp1:28.435)Simira:28.435,(Sommera_sp1:28.435)Sommera:28.435,(Stenostomum_sp1:28.435)Stenostomum:28.435,(Stilpnophyllum_sp1:28.435)Stilpnophyllum:28.435)Rubiaceae:1.934967)Gentianales:14.564527,(((((((((((((((((Duranta_sp1:14.1955)Duranta:14.1955,(Lippia_sp1:14.1955)Lippia:14.1955,(Citharexylum_sp1:14.1955)Citharexylum:14.1955)Verbenaceae:0.812672,((Handroanthus_sp1:12.4138)Handroanthus:12.4138,(Jacaranda_sp1:12.4138)Jacaranda:12.4138,(Tabebuia_sp1:12.4138)Tabebuia:12.4138,(Tecoma_sp1:12.4138)Tecoma:12.4138,(Amphilophium_sp1:12.4138)Amphilophium:12.4138,(Anemopaegma_sp1:12.4138)Anemopaegma:12.4138,(Arrabidaea_sp1:12.4138)Arrabidaea:12.4138,(Delostoma_sp1:12.4138)Delostoma:12.4138,(Fridericia_sp1:12.4138)Fridericia:12.4138)Bignoniaceae:4.376157):5.841632,((Exarata_sp1:8.37278)Exarata:8.37278,(Schlegelia_sp1:8.37278)Schlegelia:8.37278)Schlegeliaceae:18.29978):0.402276):0.411261):2.273981):2.929385,(((((Besleria_sp1:18.6973)Besleria:18.6973,(Columnea_sp1:18.6973)Columnea:18.6973)Gesneriaceae:1.313555):0.828288):1.431136,((Buddleja_sp1:18.7289)Buddleja:18.7289)Scrophulariaceae:3.509661):0.094686):0.332342,((Hyp 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8 | GENERAL DISCUSSION

Naturalists initially devoted their time to describe the biodiversity that surrounded them. With the centuries, their eagerness to discover new forms of life spurred them to enrol into exploration voyages to remote lands where they become awed by the existence of an inordinate amount of animals and plants never seen before. In the particular case of the Tropics, their own texts show that naturalists were almost in shock. After that initial astonishment, when they analysed more into the detail the particularities of faunas and floras from different territories, they started to understand that some life forms, although very far from each other, share certain similarities and adaptations to the environments that surround them. Then, naturalists` research got more sophisticated and moved from simply describe biodiversity to understand its distribution and the underlying factors that determine this distribution. Probably, the most important cornerstone in this sense took place around two hundred years ago, when the prusian naturalist Alexander von Humboldt set sail on the most intellectually ambitious to date scientific journey to gather data aiming to elaborate an unified theory of the natural world (Rahbek et al. 2019b). Since then, two centuries of scientific research have dramatically improved our understanding of biodiversity. By studying and comparing biodiversity within and across biomes, now we understand many of the factors that determine its distribution. However, the discussion has become much more complex and still many questions remain unresolved.

During the last decades two facts have played a major role in advancing the understanding of community assembly mechanisms. One the one hand the consideration of biodiversity facets others than the taxonomic one has permitted to understand the ecological and evolutionary processes that have shaped the distribution of biodiversity (Swenson 2011, 2012). On the other hand, the incorporation of spatial scale related considerations (McGill 2010, Chase 2014) has allowed to determine the relative extent of those processes and to identify under which circumstances they exert their influence (Chalmandrier et al. 2013, Münkemüller et al. 2013, Garzon-Lopez et al. 2014). The latter lead to the development of a hierarchical community assembly model, according to which different community assembly mechanisms operate sequentially, at increasingly finer spatial scales, to yield the observed biodiversity distribution patterns (Weiher and Keddy 1995b, Götzenberger et al. 2012). This model comprises from evolutionary processes such as historical patterns of speciation, extinction or migration, that mostly act at large spatial scales, to abiotic and biotic processes, like environmental filtering or competitive exclusion, mainly performing at smaller scales. In this regard, the general aim of this thesis is to use the taxonomic, functional and phylogenetic diversity framework to shed light into the community assembly processes and mechanisms that determine the distribution of woody plants in Andean tropical montane forests (TMFs) along altitudinal gradients. To accomplish so, we firstly described patterns on the three facets of biodiversity along altitudinal gradients and then used a multi- spatial scale approach to validate some of the hierarchical model postulates and to clarify which assembly mechanisms drive species occurrence in biological communities.

The three facets of biodiversity –taxonomic, functional and phylogenetic– showed a monotonic decrease with altitude consistently across four altitudinal gradients of TMFs (Chapter I). A decrease in taxonomic diversity along altitude has been broadly reported worldwide in different montane systems and for different forms of life. But the generalization of the altitudinal decrease in taxonomic diversity was questioned by Rahbek (1995), who on a meta-study found that a hump-shaped pattern with a taxonomic richness peak at middle altitudes was equally or even more pervasive. In this sense, although our results report an altitudinal decrease in taxonomic diversity a hump shaped pattern could not be disregarded to be found if those altitudes around which the hump could be expected (*ca*. 1500 m) would have been sampled (Nogués-Bravo et al. 2008). In any case, the mere exploration of taxonomic patterns on themselves conveys very limited information about the ecological and evolutive mechanisms generating those patterns.

Functional diversity informs about how the ecological strategies that the organisms display to cope with their surrounding environment. We calculated functional diversity based only on three functional traits: leaf thickness, specific leaf area and wood density. Those traits represent two fundamental axis of functional variation: the leaf economy spectrum (Wright et al. 2004) and the wood economy spectrum (Chave et al. 2009). Nevertheless, other traits exist –such as root, chemical defences or seed-traits– that fall into alternative functional axes (Lavorel and Garnier 2002, Funk et al. 2017). However, we left out these traits given the complexity of acquiring them in the field. Furthermore, we dismissed retrieving their data from global functional trait databases (e.g., TRY [Kattge et al. 2011]), for two reasons. First, given the taxonomical uncertainty we, should have required to exclude all the taxa identified above species level, thus meaning 36 and 64 % of taxa from Ecuador and Peru, respectively. Second, besides the natural plasticity and intraspecific variation of functional traits, relying in the usage of traits values from other studies would imply incorporating an additional source of variation due to differences in measuring inherent to distinct teams handling styles, despite standardized protocols. Hence, we consider that our communities are more realistically characterized by using only functional data acquired by our own, single team. Although accounting also for other traits would have been very desirable, the usage of leaf and wood economy spectra more representative traits allows us to capture a huge proportion of functional strategies in plant communities. The altitudinal decrease in functional diversity (Chapter I) in the two altitudinal gradients functionally characterized suggest that, as we move upslope, there will exist less strategies that permit life, which makes sense given the increasingly harsher and more restrictive conditions (e.g., temperature). This decrease on functional diversity gives some clues about the existence of an overwhelming influence of environmental filtering mechanism structuring plant communities as we move uphill, but more evidences in this sense are required.

In the quest of environmental filtering evidences, one of the most broadly trusted probes of his influence on community assembly are trait dispersion patterns. The central idea of environmental filtering concept is that the organisms that manage to stablish and survive on certain abiotic conditions is because they are all enabled with and share functional traits that confer them the ability to tolerate those conditions (Bazzaz 1991, Weiher and Keddy 1995a). This logic leads to expect that the effect of environmental filters must result on a trait clustering/ convergence on key functional strategies among community members (Keddy 1992). Nevertheless, others assembly processes can also lead to trait clustering. For instance, biotic related factors such us the existence of selective herbivores (Uriarte 2000) or the absence of pollinators(Sargent and Ackerly 2008) can specifically favour groups of species exhibiting certain traits, thus resulting on a community functional clustering pattern too. This is particularly interesting because biotic processes such as competition have been traditionally seen as to provoke community trait overdispersion/ divergence by considering that co-existing species on a given site must diverge in their ecological strategies to avoid competitive exclusion (Watkins and Wilson 2003, Silvertown 2004). In addition to question the significance of opposing dispersion patterns in terms of community assembly mechanisms, it is also important to consider the spatial scale at which those mechanisms are expected to occur. In this regard, it would make little ecological sense to assess the effect of environmental filtering among communities located across an area environmentally homogeneous, as abiotic conditions would be essentially the same. Contrarily, environmental filtering should better be explored by comparing communities scattered across a broad area containing high abiotic heterogeneity, thus considering large spatial scales (*i.e.*, across environmental gradients). The same underlying logic applies for studying competitive exclusion: it makes little sense to investigate competition at large spatial scales at which species are so spaced that can hardly be competing for the same resources. Instead, investigations of competition should better be conducted at small spatial scales (*i.e.*, within environmentally homogeneous locations). Nonetheless, spatial scale related considerations have been sometimes blatantly ignored (Chase 2014).

In our study we took into consideration those ideas and investigated the existence of environmental filtering at large spatial scales –*i.e.*, among plots scattered along the altitudinal gradients, which account for variation on abiotic variables inherent with altitude (Körner 2007)–. Our results indicate a trait clustering pattern for our three traits studied –specific leaf area, leaf thickness and wood density– at both two studied sites in comparison to a null functional trait distribution (Chapter II). In addition, to unambiguously state the effect of environmental filtering, we conducted several complementary analyses (Chapter II). First, we determined whether changes in community functional structure were correlated with changes in community environmental conditions by comparing functional and environmental distances among plots. Our results determine that the trait clustering pattern just arises at large spatial scales embracing enough thermal differences (*i.e.*, when the compared plots belong to different altitudinal belts) while at smaller spatial scales accounting for much less thermal heterogeneity *(i.e.*, when comparing plots from the same altitudinal belt) a clustering pattern was not found. Then we investigated whether changes in environmental conditions could be related with other community features else than the clustering pattern. We selected the most abundant species in the lower and upper belts of TMFs and 1) demonstrated using GLMMs that their abundances dramatically shift along altitude –*i.e.*, the environmental thermal gradient– and that the 2) the climatic preferences –in terms of thermal niches– of those species are segregated at the opposing edges of a thermal gradient across their whole Neotropical distribution range (obtained from GBIF).

The decrease in functional diversity (Chapter I) and the emergence of a trait clustering pattern along altitude (Chapter II), together with changes in community characteristic others than the pattern itself –shifts in altitudinal distribution and segregated thermal preferences of the most abundant species (Chapter II)– permits us to advocate for an environmental filtering effect along altitudinal gradients in TMFs. Some authors suggest that claims for environmental filtering must adhere to a strict interpretation of this concept, which considers that is necessary to demonstrate that a given specie has the potential to arrive at a certain location and be able to stablish and survive in absence of other species (Kraft et al. 2015). This perspective, which needs of experimental manipulations to be validated, is intended to guarantee that the survival is only conditioned by the ability of a potential resident specie to surpass by itself the sieve imposed by the environmental conditions, without the presence of other surrounding species that can alter –diminish or enhance– its chances of survival. This nuance rests on the fact that a potential resident specie 1) although not having the most suitable traits may still survive to the environmental restrictions in absence of competitors (better adapted species which otherwise would ultimately displace it) or 2) even when lacking a necessary trait a facilitator (a specie that provides to another one shelter, nutrients or any other requirement that the last cannot obtain by itself) enables its survival. Hence, we agree with Kraft et al. (2015) on their assertion that experimental manipulations to assess species ability to establish and persist in the absence of other species would be the most robust proof of environmental filtering *sensu stricto*. We argue, however, that this is not only impractical in field studies, especially at logistically challenging TMFs, but also not necessarily meaningful in community ecology terms. In agreement with Cadotte and Tucker (2017) we believe that as far as we can correlate changes in community functional clustering patterns, species abundances, population growth or functional traits with the underlying shifts in environmental conditions, we can infer and advocate for the existence of a *sensu lato* environmental filtering process ongoing.

In TMFs several plant functional traits change with altitude from lowlands to highlands. The same occurs for others vegetation features: canopy height, presence of climbers, principal leaf size class, etc (Bruijnzeel et al. 2011). We considered one of those features –namely compound leaves– for seeking further evidences of environmental filtering. For many functional traits, distinct studies have reported changes along altitude and given solid ecological explanations for those changes based on changes on environmental conditions along the gradient (e.g., specific leaf area [Moser et al. 2007, Pescador et al. 2015] or wood density [Chave et al. 2006, Swenson et al. 2011]). However, although several studies at local level have indicated that compound leaves decrease along altitude, no explanation has been found for this fact. To shade light in the causes of this pattern, we investigated whether the environmental filters along altitude could explain the altitudinal decrease in compound leaves (Chapter III) under the light of the alleged ecological advantages that compound leaves have in comparison to simple leaves –e.g., higher drought tolerance (Givnish 1978, Stowe and Brown 1981), higher growth rate (Givnish 1978, 1984) or increased wind tolerance (Vogel 1989)–. By using GLMMs and collating the largest to our knowledge database of altitudinal gradients for this purpose, consisting on eleven TMFs transects, we clearly stated that the abundance and especially richness of compound leaved taxa decreased with altitude. However, we found no conclusive support to the fact that their altitudinal shifts could be explained by environmental constraints favoring compound leaves at lower altitudes. Our results are well in agreement with most modern investigations for compound leaves ecological advantages, which found limited to no support for any of the alleged compound leaves ecological advantages (Malhado et al. 2010, Yang et al. 2019). In this sense, the altitudinal trend must respond to reasons others than environmental filter selection against compound leaves. If any of the ecological advantages would have been demonstrated, we could not only explain the altitudinal pattern, but also advocate for the usage of leaf architecture –simple or compound– as an easily measurable informative, qualitative functional trait (van der Sande et al. 2019).

Phylogenetic diversity reveals how historical and evolutionary processes have shaped species distribution (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2009). Our results show a decrease in phylogenetic diversity as we move upslope (Chapter III) in the four altitudinal gradients studied. These results imply that the same theory originally proposed to explain the decreasing latitudinal trend in species diversity –termed Tropical Niche Conservatism or TNC [Latham and Ricklefs 1993]– can also explain the altitudinal patterns in tropical mountains too, supporting the idea that the altitudinal patterns mirror the latitudinal ones. According with the TNC, tropical species exhibit a heavy niche conservatism and therefore just a subset of phylogenetically related lowland lineages acquired the adaptations necessary to cope with the increasingly colder conditions as they expanded uplands during the Andean uplift. Hence, the highlands species assemblages would be mere phylogenetic impoverished and clustered subsets of their respective lowland floras which would have migrated across environmental filters, and those clades would have subsequently radiated (Donoghue 2008, Graham et al. 2009). This theory, which implies an environmental filtering effect along altitude, was not supported by few studies of altitudinal gradients in Andean TMFs (González-Caro et al. 2014, Qian 2014, Ramírez et al. 2019). In any case, the theory that those three investigations suggest –termed out of the tropical lowlands or OTL– does not deny an environmental filtering effect but considers that the clades that manage to thrive and survive highlands are not necessarily related, because the acquisition of traits was performed by several, not necessarily related lineages. This fact would have also allowed that tropical lowlands species managed to move in latitude towards the poles and ultimately migrate back to the tropical Andean highlands using the high altitude corridor that mountains offer (Qian and Ricklefs 2016).

In addition to study historical and evolutionary processes, the phylogenetic approach has also been used for addressing abiotic and biotic ecological assembly rules under the assumption that the more tightly related two taxa are the more ecological similarities they share in terms of functional traits and niche occupation (Webb 2000, Vamosi et al. 2009). This postulate implies that phylogenetic diversity can be used as a surrogate for niche overlap (Cavender-Bares et al. 2004, Pausas and Verdú 2010) and, therefore, environmental filtering or competitive exclusion are expected to cause on co-occurring species phylogenetic dispersion patterns –clustered or overdispersed, respectively– equivalent to the functional ones (Swenson 2013). However, this statement must be taken with caution, since the phylogenetic signal (Mouquet et al. 2012) of functional traits has proven not to be as common as originally assumed (Losos 2008, Cahill et al. 2008, Gerhold et al. 2015). But in Guyana tropical forests, Baraloto et al. (2012) found a significant albeit weak phylogenetic signal which suggests that phylogenetic diversity is a relatively good surrogate of functional diversity. A phylogenetic signal was also found to occur along a precipitation gradient in two tropical forests (Hardy et al. 2012). Therefore, in next studies it would be interesting to repeat the analysis from our Chapter I in which we investigated the functional dispersion pattern between plots scattered along the altitudinal gradient but using phylogenetic distances between individuals instead of functional ones and check whether we get the same results. If that was the case and the phylogenetic clustering pattern was also positively correlated with the shifts in environmental conditions (e.g., the altitudinal thermal gradient), we could not only advocate for the usage of phylogenetic diversity as a proxy of functional one in TMFs, but also consider the clustering as an extra evidence to support the validity of TNC predictions.

Lastly, another interesting finding of our study was the absence of support for competitive exclusion operating at small spatial scales (Chapter II). We explored this assembly mechanism within subplots because we were conscious that the spatial scale at which competition between plant organisms is more likely to act is at small spatial scales: within subplots, co-occurring species can be assumed to directly compete for the same, limited resources and according with limiting similarity principle, divergence on the functional strategies of the co-occurring species will maximize their chances of coexistence. However, we detected no evidence of a functional overdispersion pattern consistent with competitive exclusion for the traits we considered, although such a pattern cannot be disregarded if we had considered other traits on which species assemblages might have diverged (Gallien 2017, Li et al. 2018). Some authors unambiguously reported evidences of limiting similarity (Wilson 2007), but their claims rely on evidences found in relatively low diversity communities –e.g., lawns [Mason and Wilson 2006], sand dunes [Stubbs and Wilson 2004] or saltmarshes [Wilson and Stubbs 2012]–. Our results, in accordance with the lack of consensus found in other studies, suggest that limiting similarity might not be a paramount force driving community assembly (Grime 2006), at least In hyper- diverse systems as TMFs, where the functional hyperspace would be limited to be parsed out into as many discrete and differentiated functional niches as co-occurring species.

9 | CONCLUSIONS

The results obtained in this thesis can be boiled down into the following main conclusions:

1) Taxonomic, functional and phylogenetic diversity decrease along altitude in Andean tropical montane forests. The decrease in functional and phylogenetic facets of diversity gives some clues about the existence of different community assembly mechanisms which could not be revealed if only attending to the classical taxonomic scope.

2) The functional diversity decrease suggests that the upslope increasingly colder temperatures operate as an environmental filter that selects only for those species capable to adapt and survive while culls the rest.

3) The phylogenetic diversity decrease suggests that those species that historically migrated towards highlands and succeeded belong to few closely related clades originated in tropical warm lowlands, in agreement with the Tropical Niche Conservatism hypothesis.

4) The effect of environmental filtering was confirmed beyond a trait clustering pattern that just appeared at large spatial scales (between plots at different altitudinal belts) that embrace strong environmental differences. This was accomplished by demonstrating that along the altitudinal gradient plant species exhibit strong climatic preferences –maintained across their whole Neotropical distribution range– and their abundances dramatically shift.

5) Compound leaves species richness and abundance decrease along altitude. However, as no support was found for any of the compound leaves alleged ecological advantages, these altitudinal trends cannot be hypothesized to be triggered by environmental filters. Therefore, compound leaves do not seem to be suitable for being used as a qualitative, easily measurable informative functional trait.

6) At small spatial scales (within subplots), where individuals from different species do effectively compete for finite resources, no evidence of a functional overdispersion pattern suggesting a competitive exclusion process was found –at least for the traits we measured–. This result indicates that in hyper-diverse communities where the functional hyperspace would be limited to be parsed out into as many discrete and differentiated functional niches as co-occurring species, limiting similarity may not be a paramount force driving community assembly.

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11 | ACKNOWLEDGMENTS / AGRADECIMIENTOS

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… y lo que he encontrado durante el mismo

Este doctorado comenzó en septiembre de 2015, pero yo llevaba mucho tiempo imaginándolo… Por entonces yo había terminado un master en Suecia y podía empezar un doctorado allí, pero quería trabajar en ecología tropical (las razones requerirían un par de páginas) y buscaba doctorado en el tema. Estando en Madrid, mientras que terminé el máster y hasta que regresé a Suecia como técnico en la universidad, hablando con Nuria se me ocurrió que tal vez podría buscar algún grupo en España que investigase en ese ámbito (aunque aquí los recursos y los salarios del mundo académico son inferiores, si encontraba un proyecto que me gustase no tendría inconveniente en volver a casa). Así fue como buscando en el RJB de Madrid encontré que su director, Jesús Muñoz –a quien siempre estaré agradecido por lo que hizo–, había trabajado en áreas tropicales. Le escribí y me dijo que me pusiera en contacto *ipso facto* con Luis Cayuela porque estaba buscando alguien con mi perfil. Así hice. No puedo imaginar la cara de asombro cuando Luis recibió mi mensaje, puesto que ya tenía las entrevistas con candidatos para su proyecto cerradas y tenía que tomar una decisión en unos pocos días. Luis me dijo que fuera al día siguiente a la URJC a entrevistarme con él y con Manolo Macía. Una semana después me comunicaron que me querían a mí para solicitar una FPU al Ministerio en su proyecto. No me lo pensé dos veces. No quiero imaginarme como habrían sido las cosas si no me hubieran dado la oportunidad de ir a la entrevista o si hubiesen escogido a otro candidato.

El doctorado me ha llevado a Perú donde he vivido multitud de anécdotas. Vivir en ese país fue maravilloso y, como todo el mundo imagina, trabajar en las selvas montanas es una pasada. Pero es muy diferente entrar a la selva a trabajar que ir un par de días de turisteo: cuando entras a la selva lo haces por un mes en el que, con el paso de los días y el aislamiento –el contacto con el exterior se limita a llamadas esporádicas con un teléfono satelital– pierdes la noción del tiempo. En ese mes la carga de trabajo es brutal, pues la idea es entrar y terminar el trabajo en esa zona para no tener que volver, pues simplemente el entrar y salir hasta las zonas de trabajo requiere de hasta tres o cuatro días con los medios de transporte más variopintos –jeep, lancha, mula, pie– y de un séquito de ayudantes para introducir primero y sacar después todo el equipo y alimentos necesarios para que un grupo de 4- 7 personas vivan y trabajen. Todo eso implica una organización logística muy minuciosa y, además, una buena cantidad de dinero. Por eso la idea es hacer una única entrada y salida.

Las jornadas de trabajo (es decir, todos los días durante un mes salvo los que llueve tanto que trabajar se hace imposible) comienzan a las 7 cuando te levantas. A las 8.30 sales del campamento (un techo de plástico con unas tiendas de campaña) y caminas –o vadeas ríos, saltas árboles caídos o te arrastras bajo ellos, evitas desprendimientos…– incluso durante una hora hasta llegar a las parcelas de trabajo. Allí mides los árboles, tomas muestras, tomas fotos… y descansas un rato para comer. La selva alta de montaña no es como la selva baja… puede ser bastante fría y como llueva estás mojado todo el tiempo. Comer una comida que preparaste 4 o 5 horas antes y que está fría no invita precisamente a la sobremesa, si no a volver rápido al trabajo para entrar en calor. Continúas trabajando hasta las 5 o 5.30, hasta que calculas que el tiempo que queda hasta que caiga la noche es el suficiente para regresar al campamento sin que ésta te pille por el camino. Llegas y te das un baño, en un río en el mejor de los casos, o en algún hilillo de agua o pequeña charca cuando no hay otra cosa; el agua es fría y tampoco invita a la relajación. Entonces, cambias la ropa de trabajo por la ropa seca y relativamente limpia. Preparas la cena con gas o con una fogata, charlas un rato, bebes café y toca procesar las muestras recogidas en el día. Esto normalmente lleva un par de horas, pero en áreas de mucha biodiversidad la cantidad de muestras era tal que necesitábamos más de cuatro. Entonces, terminas y lo único que quieres es entrar en la tienda de campaña a dormir en un saco sobre un colchón hinchable que con las raíces y las piedras del suelo únicamente aguantó los primeros días y ahora está roto. Caes rendido. Lo cierto es que con el paso de los días se hace duro, sobre todo por el ritmo frenético de trabajo. Muchas veces la lluvia te impide trabajar durante un par de días, y cuando no llueve has de aprovechar al máximo antes de que vuelva a llover. Pero es absolutamente ma-ra-vi-llo-so. Todo el cansancio, todas las incomodidades, comer arroz con legumbres un día tras otro… todo merece la pena por un día que terminas la parcela un poco antes y volviendo tranquilamente al campamento te paras y te sientas un rato a contemplar la inmensidad de la selva que se extiende por las montañas más allá de donde alcanza la vista, por uno de los últimos días en el que te regalas un chapuzón en el río al sol del mediodía, por la sensación de saberte en un lugar remoto de naturaleza salvaje al que el turismo no llega, por el momento en el que te conjuras con tus compañeros para sacar adelante el trabajo cueste lo que cueste… Y la selva, la grandiosidad de la selva… Humboldt, Bates, Wallace… todos ellos han escrito al respecto… y otros muchos siguen haciéndolo… pero las sensaciones de estar ahí metido no se pueden describir. Los olores, los paisajes, las plantas, los sonidos… Cuando estás ahí dentro y a mitad de mes entra una persona del exterior y trae unos panes y una mermelada, sientes que eso es lo más delicioso que nadie pueda degustar en la faz de la Tierra. Cuando sales y llegas a la estación del guardaparques o a algún pueblo, dormir en un camastro y darte una ducha con agua tibia te parece un lujo. Y cuando llegas a una ciudad, entras en un mercado y ves las estanterías con tanta variedad de alimentos eres como un niño el día de Reyes –precisamente, la noche en la que escribo estas líneas–. Pero cuando llevas un par de semanas o un par de meses fuera de la selva, en la ciudad, todo eso se vuelve monótono, se torna superficial e incluso obsceno. Porque dentro de ti las ganas de volver a la selva comienzan de nuevo, cada vez con más fuerza, y no te las puedes quitar de encima.

… y a las personas que me han acompañado y lo han hecho inolvidable

En Madrid quiero agradecer a Luis Cayuela y a Manolo Macía. Ellos confiaron en mí y espero haber estado a la altura de sus expectativas. Trabajar con ellos ha sido una gozada: he aprendido muchísimo, nunca han sido unos jefes autoritarios –salvo para exigirme que haga oraciones más cortas y siempre han considerado mi opinión y me han ayudado en lo que he necesitado. Estoy convencido de que la ciencia sería todavía mejor si todos los jefes tuvieran su humanidad. También quiero agradecer a Íñigo Granzow, con quien siempre se aprende algo nuevo e interesante. A Gabriel Arellano, por sus valiosísimos comentarios y el consejo magistral de "empezar siempre por la parcela más lejana". A Victoria Cala, por su paciencia infinita con los suelos. Y a todo el mundo en la URJC. Biodiversos es un lugar con una densidad de calidad profesional y humana por m^2 que necesitaría tres departamentales para caber sin problemas: si necesitas algo muchas veces no hace falta ni pedirlo, pues si alguien se ha enterado ya estará tratando de ayudarte… y si tienes que pedirlo, todos harán lo posible por colaborar. Como anécdota, quiero recordar cuando tuve que vivir en Villalba las ocasiones en las que Luis Giménez y María Prieto me acercaron a Las Matas: no fueron muchas, pero me ahorrasteis un tiempo muy valioso. En otros lugares comer apiñados en una sala tan pequeña como la trófica seguramente generaría fricciones; aquí todo lo contrario. Y, por último, todos los compañeros y amigos del departamento, gracias por vuestros consejos, vuestros recordatorios, vuestras iniciativas y por contagiar optimismo por todo el Departamental… Esto va por todos: Jesús, Juanlu, Javi, Greta, Pilar, Juan, Óscar, Mario, Marina, Manu, Sandra Freire, Ana García, Ana Peralta, Sandra Rallo, Dani, Carlos, Laura, Clara, Sergio, Elena, Rocío, Joanna, Javi, Agus, Joaquín, Lara… y todas y cada una de las personas que no he citado y que generan un ambiente tan agradable sin el cual ir de Madrid a Móstoles sería infinitamente más pesado.

En Perú quiero agradecer a Norma y a Alex. Norma nos abrió las puertas de su laboratorio en la PUCP y nos acogió en el mismo… y nosotros, a cambio, se lo llenamos a rebosar durante meses con nuestros equipos y con un volumen de muestras que no hacía más que crecer y crecer cada vez que regresábamos del campo. Nunca podremos agradecer suficientemente su paciencia. Norma también nos prestó a los mejores estudiantes de su equipo de trabajo, los *patas* cusqueños… que resultaron ser las personas más comprometidas y profesionales que he conocido en este tiempo. Chicos extremadamente honestos, valientes, leales, inteligentes y honrados que se implican en la consecución de los objetivos como si ellos fueran los mismísimos investigadores principales del proyecto. Se trata de Alex, Carlos, José y Manuel, unos amigos y compañeros ante los que no puedo más que quitarme el sombrero. Alex fue el compañero con el que más tiempo he pasado en este proyecto. Lo conocí junto con Carlos en Trujillo, después de estar ellos esperando bajo la sombra de un enclenque árbol durante horas en el lugar acordado para encontrarnos, pues mi teléfono no me permitía contactarlos. Ahí empezaron dos semanas frenéticas de exploraciones a la parte baja y a la parte alta del Río Abiseo en busca de lugares con agua para acampar y trabajar y que fueron indescriptibles; un carrusel de experiencias, personas y aventuras. No cambio esos días por la fiesta más loca ni el viaje más glamuroso. Luego con Alex volví a ir a Juanjuí de exploración y trabajamos con los buenos de Grillo y Garrincha, comimos patacones y nos tocó empujar una lancha río arriba. Después, en Lima, pasamos muchas semanas como compañeros de laboratorio y con él y Mijail, Rudy y Héctor tenemos pendiente un Siete Sopas. En Perú también trabajé con Gabo y pasamos muy buenos ratos tanto en campo como haciendo los preparativos para entrar. Y tampoco puedo olvidarme de los guardaparques del Río Abiseo: Jhonny Ramos, Octavio Pecho, Tito Heras, Percy Franco, Guillermo Aguilar, Rafael Galán, Edelmer, Grover, Berardo... Sin su ayuda, conocimientos y apoyo logístico habría sido impensable llegar a los lugares donde llegamos. Lo mismo quiero agradecer al SERNANP (Servicio Nacional de Áreas Naturales Protegidas del Perú) y al Ministerio del Ambiente de Ecuador por facilitar los permisos para trabajar en sendos parques nacionales –Río Abiseo y Podocarpus, respectivamente– y por comprender la importancia que tiene la investigación para potenciar la conservación. Y también quiero recordar a la gente del sector Los Alisos en Pataz, Perú: gente aguerrida que nos ayudó a entrar en el Abiseo y sin los cuales todo el trabajo hubiera fracasado. Fueron muchos y no recuerdo los nombres de todos, pero especialmente quiero recordar a Percy Malqui (cuando nos trajo algo de fruta y galletas después de dos semanas dentro de la selva fue como un regalo caído del cielo), don Tolentino Cueva (se encargó de reunir gente, coordinar la logística e incluso adelantó dinero de su bolsillo, sin palabras), Anselmo (porque cuando dijo que se iba a ver a su caballo y que volvía en dos días todos aguantamos la respiración, pero cumplió su palabra y regresó, además de siempre trabajar de manera ejemplar) y Rosho (por su manera de trabajar eficiente, alegre, sin una mala cara o un mal gesto). Y también agradecer el trabajo de Reynerio y de sus hermanos. Y a gente como a Angel, Julia o Mara que trabajaron desinteresadamente como voluntarios.

12 |APPENDIX

During the development of the thesis Guillermo Bañares-de-Dios has also co-authored the following publication:

Lydia de la Cruz-Amo, **Guillermo Bañares-de-Dios**, Victoria Cala, Íñigo Granzow-de la Cerda, Carlos I. Espinosa, Alicia Ledo, Norma Salinas, Manuel J. Macía, Luis Cayuela, 2019. Trade-offs among aboveground, belowground and soil organic carbon stocks along altitudinal gradients in Andean tropical montane forests. Under revision in Frontiers in Plant Sciences.