Why and how so many Species coexist in Tropical Moist Forests

by

Jason VLEMINCKX*

*Laboratory of Plant Ecology and biogeochemistry, Université libre de Bruxelles, av. F.D. Roosevelt, 1050 Brussels (Belgium)

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Summary

Tropical rainforests host an incomparable biodiversity, vastly surpassing that of temperate regions. The relative stability of warm and humid climatic conditions over geological time has been a major factor in fostering such richness while limiting extinctions, and in promoting the diversification of highly specialized ecological niches. But locally, how can we explain the maintenance of so many taxa living side by side, i.e. the alpha-diversity? While environmental heterogeneity relatively well explains patterns of diversity at local and regional scales, the mechanisms that allow for the coexistence of hundreds of species at fine spatial scale, within a seemingly homogeneous habitat, remain largely debated. However, a growing body of research suggests that negative density-dependent mechanisms, mediated by microhabitat partitioning and natural enemies (herbivores, parasites, pathogens), play a crucial role in maintaining plant species coexistence, which in turn supports the coexistence of organisms that depend on primary producers. This article explores the key factors underlying the origin and maintenance of tropical moist forest biodiversity, integrating well-established hypotheses with recent scientific advances.

Pourquoi et comment autant d’espèces coexistent en forêt tropicale humide ?

Mots-clés : coexistence des espèces, forêts tropicales humides, gradient latitudinal de diversité, limitation de similarité, niche écologique.

Résumé

Les forêts tropicales humides abritent une richesse en espèces par unité de surface incomparable, dépassant largement celle des zones tempérées. La relative stabilité des conditions climatiques chaudes et humides au cours des temps géologiques a été un facteur majeur permettant cette richesse, en ayant favorisé une diversification de niches écologiques hautement spécialisées. Bien que l'hétérogénéité environnementale explique relativement bien les patrons de diversité à des échelles locales et régionales, les mécanismes permettant la coexistence de centaines d'espèces à une fine échelle spatiale, au sein d'un habitat relativement homogène, restent largement débattus. Cependant, un nombre croissant de travaux publiés suggère que des processus de densité-dépendance négative, induits par la spécialisation de niche et les ennemis naturels des plantes (herbivores, parasites, pathogènes), jouent un rôle crucial dans le maintien de la coexistence des espèces végétales, ce qui, à son tour, favorise la coexistence et la diversité des organismes dépendant des producteurs primaires. Cet article explore les facteurs clés expliquant l'origine et le maintien de la biodiversité des forêts tropicales humides, en intégrant des hypothèses bien établies et des avancées scientifiques récentes.

Introduction

During the early 19th century, the German naturalist Alexander von Humboldt (1769-1859) was among the first to document an increase in species richness from the poles to the equator. This pattern, commonly known today as the Latitudinal Gradient of Diversity (Wallace, 1878; Willig *et al*. 2003), reaches its zenith in tropical moist forests (TMF). Despite covering only approximately 8% of the Earth's terrestrial surface—around 15 million square kilometres—these forests are estimated to harbour much more than 50% of the planet's terrestrial biodiversity (Wilson, 1988; Gibson *et al*. 2011; Barlow *et al.* 2018). TMFs are unparalleled in their species richness, with some areas supporting up to 400 tree species per hectare (Gentry, 1988). Understanding the factors explaining the origin and maintenance of such extraordinary biodiversity has long been a major concern in ecology and evolutionary biology. This question already "haunted" Charles Darwin, while his contemporary Alfred Wallace early suspected that the accumulation of warm and stable conditions through long periods of time was part of the explanation (Wallace 1878, Stebbins 1976). He was not far from the most presently accepted theories on the topic (Pianka, 1966; Fine, 2015; Schemske & Mittelbach 2017). In parallel, the rise of modern ecological science, particularly through the development of the ecological niche concept, has significantly advanced our understanding of the mechanisms that enable species coexistence. The niche of a species, in its most commonly used definition, refers to the abiotic and biotic factors that allow the species to survive, grow and reproduce (Hutchinson, 1957). Species have had more time to become habitat and trophic specialists (Fine 2015) in the tropics than in higher latitudes (Wright et al. 2006, Gillman et al. 2010), and may also have diversified relatively faster among animals and fungi than among trees as the latter have longer generation times (Holmes et al. 2025).

Understanding the mechanisms of species diversification and coexistence is essential for the conservation of these forests. Tropical rainforests are not merely reservoirs of biodiversity; they are vital to the health of our planet. These forests play a critical role in carbon sequestration, helping to mitigate climate change by storing about 55% of the world's forest carbon (Lewis *et al*. 2009). Additionally, they regulate the global climate, influence hydrological cycles, and provide essential ecosystem services such as water purification and soil stabilization, while representing an invaluable reservoir of genetic resources (Myers *et al.* 2000, Laurance & Peres 2006). Here I aim to provide a concise review of the factors explaining the origin ("why"?) of TMF diversity at large spatial and temporal scales, as well as the ecological mechanisms ("how"?) maintaining species coexistence at a local scale in these ecosystems.

Why so many species in tropical moist forests?

The factors explaining the remarkable species richness of TMF have prompted numerous hypotheses, linked to climate stability, biogeography and evolutionary speed. The following sections explore some of the most prominent theories.

The Climate Stability Hypothesis

One of the oldest and most widely accepted explanations for tropical biodiversity is the Climate Stability Hypothesis (Rohde, 1992; Willig et al., 2003; Pianka, 1966; Fine *et al*., 2015). This hypothesis suggests that the warm, humid, and relatively stable climatic conditions in tropical regions have persisted over geological time scales, providing a consistent environment that has been less affected by historical climatic fluctuations. During ice ages, extensive TMF refuges may have remained intact in several parts of the tropics, although this refugia hypothesis remains the subject of much debate (Rocha & Kaefer, 2019). The relatively low amplitude of inter-annual climatic disruptions in the tropics, coupled with minimal seasonal temperature fluctuations, high humidity levels, and lower extinction rates, has facilitated continuous speciation and the maintenance of high species diversity over long periods (Jansson & Davies, 2008).

The Time-Integrated Area Hypothesis

The Time-Integrated Area Hypothesis partly builds on the idea of climatic stability by incorporating the role of geographic area and evolutionary time (Fine & Ree 2006, Jetz and Fine 2012, Fine 2015). Tropical regions cover the surface of the globe located between latitudes 23°27' north and south, and comprise about 35% of the Earth's land surface, with vast land masses presenting a diversity of habitats that have been relatively climatically stable over evolutionary time scales compared to temperate regions (Mittelbach *et al*. 2007; Rohde, 1992; Willig *et al*. 2003). Habitat specialization and founder events over long evolutionary time have been a significant driver of the high levels of biodiversity observed in TMF (Wiens & Donoghue, 2004, Baraloto *et al*. 2021). The large land area of the tropics combined with long-term climate stability has not only facilitated speciation but also allowed for the persistence of diverse lineages over millions of years, including the preservation of highly ancestral lineages, making these ecosystems both a biodiversity cradle and a "museum" of ancient taxa (Wiens & Donoghue, 2004; Rull, 2008; Crisp & Cook, 2012), including the most ancestral angiosperm family Amborellaceae, endemic of New Caledonia.

The Productivity and Evolutionary Speed Hypotheses

The Productivity Hypothesis suggests that high rainfall amounts and high solar radiation in the tropics support intense and continuous plant growth, or primary production (Huston, 1994; Brown, 2014). High primary productivity provides a substantial energy base that can sustain large populations and a wide variety of species, each occupying a unique ecological niche (Fine, 2015). The Evolutionary Speed Hypothesis emphasizes that this continuous input of energy has led species to evolve at a rapid pace, allowing them to develop highly specialized niches (Huston 1994).

The consistently warm temperatures increase metabolic rates, especially among ectothermic organisms (such as insects and reptiles), leading to faster growth and shorter generation times (Wright *et al*. 2006). Accelerated life cycles provide more opportunities for mutations and natural selection to act, thereby enhancing speciation (i.e., the generation of new species) rates (Allen *et al*. 2007). Additionally, the stability of tropical climates over geological timescales, with relatively fewer disruptions from ice ages compared to temperate regions, has allowed species to accumulate and diversify without frequent extinction events (Jansson & Davies, 2008). While direct evidence linking warm temperatures to increased mutation rates is less established, the higher metabolic rates associated with tropical climates can lead to faster molecular evolution, as observed in some plant lineages (Gillman *et al*. 2010). Furthermore, the increasing variety of specialised niches has magnified the diversity of biotic interactions of all sorts, including predation, symbiosis, cooperation (e.g. animal-mediated pollination and seed dispersal), fostering species diversification even more (Wiens & Donoghue, 2004). Thus, overall, the combination of rapid evolutionary processes, stable environmental conditions, and the high complexity of ecological interactions have contributed to the extraordinary levels of biodiversity found in tropical forests.

The “Out of the tropics” Hypothesis

The Out-of-the-Tropics Hypothesis builds on explanations that integrate the previously discussed hypotheses, in particular the time-integrated area hypothesis (Fine 2015). It posits that the higher biodiversity observed in tropical regions compared to temperate and polar zones is primarily due to the tropics functioning as a "cradle" of diversity. In this view, the tropics have higher rates of speciation due to their relatively stable, warm humid climates, diverse habitats, and fewer large-scale environmental disturbances (Jablonski *et al*. 2006). Stability reduces extinction rates and allows species to accumulate over long periods. Many species that originate in the tropics eventually expand their ranges into temperate regions, but fewer species have time to evolve in temperate zones and then migrate into the tropics, leading to an asymmetrical flow of species from tropical to non-tropical regions (Jansson *et al*. 2013). The hypothesis is supported by fossil records, phylogenetic studies, and present-day biodiversity patterns, which demonstrate that a large proportion of global biodiversity has tropical origins (Mittelbach *et al*. 2007). The Out-of-the-Tropics Hypothesis thus provides a compelling explanation for the global latitudinal gradient in biodiversity, emphasizing the tropics as a crucial engine of species generation and global biodiversity.

How can so many species coexist?

Tropical Moist Forests are renowned for their exceptionally high levels of α-diversity, where a vast number of species coexist within a relatively small area. In some areas of Ecuador for instance, we can sometimes encounter more than 400 tree species per hectare (Valencia et al. 2004). Such levels of diversity often implies that the majority of species are locally rare, raising questions about the mechanisms that maintain this rarity. The concept of the ecological niche, as formulated by Hutchinson (1957), has provided a successful general framework to understand these patterns, suggesting that species with overlapping ecological niches are unlikely to coexist due to intense competition for similar resources. This idea builds on the principle of limiting similarity, which posits that species with very similar traits related to resource use cannot stably coexist (Gause, 1934; MacArthur & Levins, 1967). Biodiversity is then maintained through niche differentiation mechanisms, where species are adapted to exploit different resources. For instance, tree species vary in their light requirements. Fast-growing pioneer tree species are highly competitive in well-lit forest openings but could not survive under forest canopy, whereas at the opposite, shade-bearer species thrive in the understory vegetation layers (Swaine 1988 & Whitmore). However, limiting similarity may also refer to a wide variety of antagonistic biotic interactions, including enemy-mediated negative density dependence, where specific natural enemies prevent local species dominance and allow rare species to persist (Janzen, 1970; Connell, 1971). Together, these processes help maintain the extraordinary species richness observed in TMF, promoting both the coexistence of diverse species and the evolutionary processes that generate such diversity (Fine *et al*. 2004).

Differentiation of highly specialized resource use niches

The principle of niche differentiation refers to how species use abiotic and biotic resources differently (in time or space), allowing them to occupy the same area without outcompeting each other (Chesson, 2000; Wright, 2002). Advancements in the field of functional ecology during the past two decades have provided much support for the role of resource use partitioning in explaining local species assembly (Sedio *et al*. 2012; Bergmann *et al*. 2020; Vleminckx *et al*. 2021). The variability in soil types, topography, and microclimates creates a mosaic of habitats that support species adapted to different specific abiotic conditions (John *et al*. 2007; Schemske *et al*. 2009; Vleminckx *et al*. 2018), thereby increasing overall diversity.

Enemy-mediated negative-density dependence

More than half a century ago, two American ecologists, Daniel H. Janzen (1970) and Joseph H. Connell (1971), independently formulated a hypothesis, presently known as the Janzen-Connell hypothesis, relating plant species coexistence with their natural enemies, in the specific context of TMF. The hypothesis posits that a seedling has more chance to survive if establishing far from its parent tree and surrounded by heterospecific and functional different individuals that are less likely to attract specific enemies (herbivores, pathogens, parasites) of the given seedling, thereby reducing the likelihood of a single species dominating an area. This mechanism is somewhat analogous to a dilution effect in disease ecology, where increased biodiversity dilutes pathogen transmission and thereby its potential to expand, often leading to lower disease prevalence in the host species (Keesing & Ostfeld 2021).

The Janzen-Connell effect has been well-established as a facilitator of plant species coexistence, contributing to the high levels of α-diversity observed in TMF (Wright, 2002; Comita *et al*. 2014; Levi *et al.* 2019). Works on the genera *Piper* (Piperaceae, Salazar *et al.* 2016), *Inga* (Fabaceae; Forrister et al. 2019), *Protium* (Burseraceae; Fine *et al.* 2004, 2006, 2013; Vleminckx *et al*. 2018), or even at community-level (Wang *et al*. 2023) provide further examples of how specific enemies may promote species coexistence among closely related species. Their work demonstrated that neighbouring plants tend to share more dissimilar leaf chemical defences than expected by chance, suggesting an enemy-mediated dilution effect. In the Amazon, Fine *et al*. (2006, 2013) showed that different herbivore communities and the selection of different growth-defence trade-offs on nutrient-depleted sandy soils and more fertile clayey soils may have amplified differential selection of chemical defences among ecotypes (habitat specialists) of the species *Protium subserratum* occurring on each edaphic habitat. These results imply that specific enemies can greatly enhance niche differentiation and accelerate both speciation and the evolution of plant defences along environmental gradients. Thus, herbivores may play a significant role in the origin of plant diversity in TMF, although further studies on additional plant genera are necessary to fully understand these dynamics. Furthermore, studies also revealed that plant species' sensitivity to a Janzen-Connell effect is highly correlated with their local abundance (Comita *et al*. 2010), thereby providing a key explanation on why some species dominate while others are rare. Additionally, natural enemies can limit the long-term dominance of highly specialized ecotypes that are highly competitive for particular habitats, which may help maintain local diversity (Gilbert, 2002).

Summary of key hypotheses explaining the origin and maintenance of tropical forest biodiversity

Table 1 summarizes the key hypotheses discussed above to explain the origin and maintenance of TMF biodiversity. Figure 1 shows how the latitudinal gradient of diversity can be obtained by modelling the factors explaining the origin of the high levels of biodiversity in tropical rainforests compared to higher latitudes. The R code used to reproduce these simulations is available in Appendix S1.

Table 1. Key hypotheses explaining the origin of tropical moist forest diversity (lines 1-5) and the mechanisms maintaining species coexistence in these ecosystems (two last lines).

Question	**Hypothesis**	**Explanation**	**Key studies**
Origin of diversity?	*Climate Stability*	Stable, warm, and humid conditions in tropical regions have persisted over long periods, allowing continuous speciation and high species diversity with minimal disruptions.	Rohde, 1992; Willig et al., 2003; Pianka, 1966; Fine et al., 2015; Jansson & Davies, 2008
	Time-Integrated Area	The large, stable land area of the tropics over evolutionary time provides diverse habitats that support species specialization, founder events, and preservation of ancient lineages.	Fine & Ree 2006, Jetz & Fine 2012, Fine 2015
	Productivity	High primary productivity due to consistent rainfall and sunlight supports diverse populations, facilitates niche differentiation, and reduces direct competition.	Huston, 1994; Brown, 2014; Fine et al., 2015
	Evolutionary Speed	Warm temperatures accelerate metabolic rates and life cycles, enhancing speciation rates. Stable tropical climate reduces extinction rates, allowing species accumulation.	Wright et al., 2006; Allen et al., 2007; Jansson & Davies, 2008; Gillman et al., 2010
	Out of the Tropics	The tropics act as a cradle of biodiversity, with high speciation rates and low extinction rates, allowing species to migrate outwards to temperate regions, creating a gradient of diversity.	Jablonski et al., 2006; Jansson et al., 2013; Mittelbach et al., 2007; Wiens & Donoghue, 2004
Maintenance of species coexistence?	*Niche Differentiation*	Species coexist by using different resources or habitats, minimizing competition. Variability in environmental conditions supports diverse adaptations and resource partitioning.	Hutchinson, 1957; Gause, 1934; MacArthur & Levins, 1967; Chesson, 2000; Wright, 2002; Bergmann et al., 2020; Vleminckx et al., 2021
	Enemy-Mediated Negative Density Dependence	Specific natural enemies prevent single species dominance and allow rarer species to persist.	Janzen, 1970; Connell, 1971; Comita et al., 2014; Levi et al., 2019; Salazar et al., 2016; Vleminckx et al., 2018; Fine et al., 2006, 2013

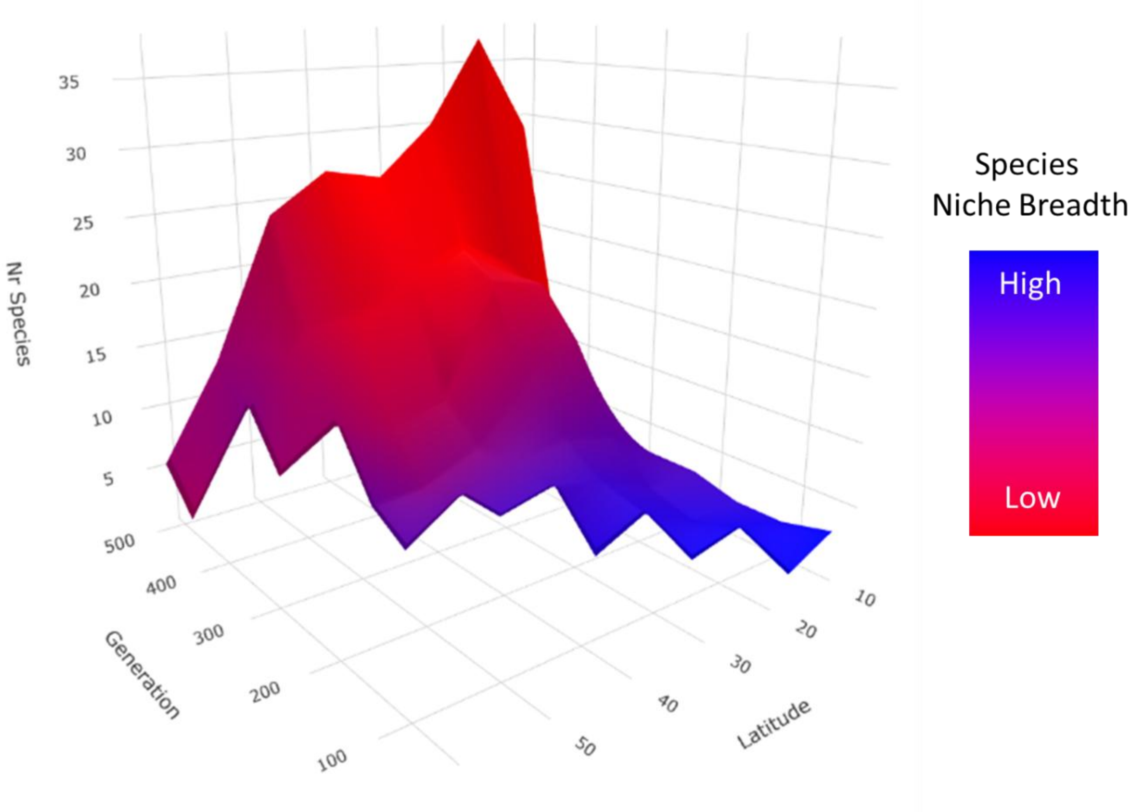

Figure 1. Visualisation of the Latitudinal Diversity Gradient, obtained by simulating the effects of tropical climate stability, higher tropical productivity, speciation and niche specialization over 500 generation times (see Appendix S1 for details). Here the simulation results in a peak of 37 species after 500 generation times (speciation rate exaggerated for the purpose of the analysis). Consistently with hypotheses presented in Table 1, species richness decreases with latitude and increases with generation times. Niche breadth (colour gradient) decreases with generation time due to niche specialization, a process occurring faster near the equator than at higher latitudes.

Conclusion and research perspectives

The extraordinary biodiversity of tropical rainforests can be attributed to a complex interplay of evolutionary and ecological factors. Stable climatic conditions, large geographic areas, high productivity, and rapid evolutionary processes all contribute to the richness of these ecosystems. Additionally, interactions among species, including competition, predation, and symbioses, play a crucial role in maintaining this diversity by driving niche differentiation and preventing competitive exclusion.

Despite major advances in understanding why tropical forests harbour so many species, several important questions remain unresolved, notably regarding the relative influence of abiotic versus biotic factors on local species coexistence at the community level, the extension and inter-connectivity among TMF refugia during glacial periods, and how long-term evolutionary processes integrate with local environmental contexts to shape the present-day biodiversity patterns. A key priority is to further develop approaches that link the long-term evolutionary history of species with the ecological processes shaping present-day communities. For example, combining studies of how lineages have spread and diversified over time with analyses of species' ecological traits could help clarify how ancient patterns of diversification continue to influence the remarkable diversity we see in tropical forests today.

Another promising direction is to uncover hidden aspects of niche differentiation, such as variation in chemical defences, soil microbial associations, and fine-scale habitat preferences, both aboveground (leaf and stem functions) and belowground (root systems) which may explain why so many species can coexist in seemingly similar environments. Emerging tools like metabolomics, environmental DNA sequencing, and field experiments offer exciting ways to detect these aspects.

Finally, understanding how genetic and phenotypic diversity within species contributes to coexistence and resilience to climatic changes is becoming increasingly important, as local adaptation may buffer communities against these changes. Also, predicting the future of tropical biodiversity will require models that integrate ecological interactions mediating species coexistence, such as negative density dependence effects, with information on how quickly species can evolve or shift their distribution ranges. This is particularly urgent given that climate changes, deforestation, and changes in disturbance regimes could potentially disrupt the balance between plants and their natural enemies, which may impact diversity. By combining long-term field data acquisition, experimental studies, and simulations, future research should lead to a more mechanistic and predictive understanding of the biodiversity organization and dynamics of TMF. These insights will be essential, not only for advancing ecological theories but also for designing effective conservation strategies in the world's most diverse ecosystems.

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