INVESTIGATING THE SCALE-DEPENDENT RELATIONSHIPS OF PLANT-FRUGIVORE BIODIVERSITY USING BIG DATA IN A BIODIVERSITY HOTSPOT

By

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ABSTRACT

Plants are vital to all life on Earth, and many are experiencing extinction risk and other threats, which makes it important to understand plant diversity. Investigating the biodiversity patterns of interacting species can help us gain knowledge of the underlying processes of biodiversity patterns. Quantifying spatial patterns of biodiversity plays a critical role in determining conservation priorities and ecosystem function and clarifying the underlying processes of community assembly, species-area relationships, and environmental filtering. There is a lack of knowledge about how taxonomic diversity and functional diversity covary across spatial grains, and between interacting species like fruiting plants and frugivorous birds and mammals. This work investigates spatial grain-dependent relationships of taxonomic diversity and functional diversity in the Tropical Andes forests at various spatial grains. The results provide evidence that relationships for both fruiting plant-frugivore taxonomic and functional diversity were the strongest at the coarsest spatial grain (100 km), the fruiting plant-frugivore taxonomic diversity relationship was stronger than the functional diversity relationship across all spatial grains, and the scaling relationship for fruiting plant-frugivore taxonomic diversity was stronger than fruiting plant-frugivore functional diversity. These findings support the expectation that the relationship between plant-frugivore taxonomic diversity and plant-frugivore functional diversity are scale-dependent and differ from each other. Future work should further assess these relationships by incorporating different traits, frugivore diet portion, , generalist vs. specialist plant-frugivore interactions, intraspecific trait variation, and environmental drivers including spatiotemporal changes in land use, land cover, and climate.

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INTRODUCTION

Plants comprise much of the world's biodiversity and are essential to most life on earth. Plants make up the largest amount of global biomass at 15% or 450 Gt C (Bar-On *et al.*, 2018). They provide vital ecosystem services and are the foundation of all terrestrial ecosystems. Many plant species are facing extinction with estimates of species loss ranging from 40% to 64% (Brummitt *et al.*, 2015; Nic Lughadha *et al.*, 2020; IUCN, 2022; Brown *et al.*, 2023), and even greater for undescribed species at 3 in 4 (Brown *et al.*, 2023). However, there is less focus and funding for plant conservation, as many conservation initiatives are biased toward animals (Clark & May, 2002; Sitas *et al.*, 2009; Martín-López *et al.*, 2011; Balding & Williams, 2016). In the European Union, for example, animal species received three times more funding than plants between 1992 and 2020 (Adamo *et al.*, 2022). In the United States, plants make up 56% of the federal endangered and threatened species list (U.S. Fish & Wildlife Service, 2024); yet in 2020, they totaled approximately 2.04% of federal endangered species expenditures (U.S. Fish & Wildlife Service, 2020). This could be due to "plant awareness disparity", also referred to as "plant blindness", which is the human tendency to ignore or not notice plants leading to a devaluing of plants' importance (Wandersee & Schussler, 1999; Balding & Williams, 2016; Parsley, 2020). These biases contribute to the outstanding gaps in our understanding of plant biodiversity. For example, only 17% (64,240) of the 350,000 known species of vascular plants have been included on the International Union for Conservation of Nature Red List of Threatened Species (IUCN, 2022) - considered the most comprehensive and authoritative source on global extinction risk for species or the 'gold standard' for species conservation status (Rodrigues *et al.*, 2006; Betts et al., 2020; Cazalis, 2022). Even the plant-focused Botanica Gardens Conservation International ThreatSearch database only has conservation assessments for 180,000 taxa (BGCI, 2024). One study found that for endemic flora by country, 58% (127,

643) have no conservation assessment (Gallagher *et al.*, 2023). Around 2,000 plant species are described by science each year (Cheek *et al.*, 2020), and some estimate there are still an estimated 100,000 species yet to be discovered (Corlett, 2020). The Convention on Biological Diversity's Global Strategy for Plant Conservation set targets for 2011-2020 under several objectives: (1) plant diversity is well understood, documented, and recognized; (2) plant diversity is urgently and effectively conserved; (3) plant diversity is used in a sustainable and equitable manner; (4) education and awareness about plant diversity, its role in sustainable livelihoods and importance to all life on earth is promoted (CBD, 2011). It is now 2024 and while progress has been made on these targets, there is still work to be done to conserve plant biodiversity (Sharrock, 2020; Antonelli *et al.*, 2023a,b). With so many plants facing extinction risk and experiencing threats from habitat loss and transformation, climate change, deforestation, agricultural expansion, human infrastructure development, pollution, and invasive species, there is an urgent need to understand, support, and mitigate the loss of plant diversity (Feeley & Silman, 2010; Corlett, 2016; Harrison, 2020; Nic Lughadha *et al.*, 2020).

Macroecology and biogeography can be used to understand and explain patterns of biodiversity. The species-area relationship (SAR) describes how the number of species increases as the area sampled increases (Rosenzweig, 1995). Larger areas generally support more species because they encompass a greater variety of habitats and resources. They also have lower extinction rates because they can support larger populations, are less susceptible to stochastic events, and have a higher probability of receiving colonists from surrounding regions (Arrhenius, 1921; Rosenzweig, 1995). Larger populations enhance genetic diversity and reduce the risk of inbreeding and genetic drift, and they are more likely to benefit from the rescue effect or when immigration from nearby populations can prevent local extinctions (Arrhenius, 1921;

Rosenzweig, 1995). Habitat heterogeneity or the variation in habitat structure contributes to species diversity; diverse habitats within a region support higher biodiversity (Stein *et al.*, 2014). Larger areas tend to include more diverse habitats and microhabitats, which can support a wider range of species with different ecological requirements (Whittaker *et al.*, 2001). Larger areas are also more likely to contain more ecotones (transition zones between different habitats), which are often rich in species due to the overlap of species from adjacent habitats (Lemessa *et al.*, 2023). Environmental gradients, such as variations in temperature, precipitation, elevation, altitude, moisture, and soil nutrients also impact biodiversity. The geographic range limits of species can be defined by environmental gradients. Species distributions change as conditions move from optimal to suboptimal for different species along an environmental gradient, creating zones of higher and lower species richness through niche specialization (Carboni *et al.*, 2016). The species composition of communities can change rapidly along environmental gradients through species turnover as different species communities are found at different points along the gradient (Gaston, 2000; Chen *et al.*, 2016). Environmental gradients often correspond to changes in habitat types (e.g., from forest to grassland to desert), each supporting distinct assemblages of species (Keddy, 1992). Species may evolve physiological adaptations to survive specific conditions along an environmental gradient and exhibit behavioral adaptations to exploit different parts of an environmental gradient (Wong & Candolin, 2015; Riesch *et al.*, 2018). Environmental gradients can shape the complexity and dynamics of food webs or trophic interactions (Dézerald *et al.*, 2013; Kortsch *et al.*, 2019; Mestre *et al.*, 2022). Along environmental gradients, the intensity of biotic interactions such as competition and facilitation can vary, as environmental conditions influence the presence and strength of mutualistic relationships, thereby affecting the distribution and diversity of species dependent on these interactions (Eloranta *et al.*, 2022; O'Brien *et al.*, 2022; Ohlmann *et al.*, 2023). By leveraging the insights from macroecology and biogeography, we can better comprehend the processes and spatial distributions that shape biodiversity.

Quantifying spatial patterns of biodiversity is important for determining conservation priorities and clarifying the underlying processes of community assembly, species-area relationships, environmental filtering, and ecosystem function. There are multiple dimensions of diversity including taxonomic, phylogenetic, functional, genetic, and ecosystem (this thesis focuses on taxonomic and functional diversity). The most commonly used dimension is taxonomic diversity, often measured as species richness, or the number of species in a given area. Taxonomic diversity provides insights into species composition, offering a clearer understanding of the variety of species present in an ecosystem which is crucial for assessing how ecosystems function and their resilience and stability. Quantifying patterns of biodiversity using only taxonomic diversity, as has been focused on in the past, ignores crucial aspects of diversity and the context of a species' ecosystem; therefore, additional dimensions of diversity should be considered (Brum *et al.*, 2017; Eduardo, 2016; Girardello *et al.*, 2019; Zhang *et al.*, 2023). Functional diversity is a measure of the variation of traits between organisms and takes into account the roles species play in their environment. Quantifying functional diversity can provide valuable insights into how ecosystems function by revealing how different species contribute to ecological processes (Tilman, 2001). Different dimensions of biodiversity can respond differently to climate change (Edie *et al.*, 2018); focusing only on species richness as a measure of taxonomic diversity may under or over-estimate the responses of species diversity to climate change (Strecker *et al.*, 2011; Buckley & Kingsolver, 2012). Functional diversity of traits could better represent responses to global changes including climate change because these changes restrict the traits that will be present in an area (Wellstein *et al.*, 2011; Verheijen *et al.*, 2013; Estrada *et al.*, 2015). Quantifying biodiversity through taxonomic and functional diversity provides critical insights into the richness and roles of species within ecosystems. However, to fully understand how these patterns manifest and vary, it is crucial to consider the scale at which they are observed, as the patterns of biodiversity can shift significantly across different spatial and temporal scales.

Patterns of biodiversity also vary by spatial scale. Scale consists of two components: grain and extent. This thesis will focus on grain. Different spatial grains can reveal different biodiversity patterns: fine grains may capture detailed local variations and microhabitat differences, while coarse grains can highlight broader, landscape-level patterns and regional trends (Wu & Li, 2006). The species-area relationship (SAR) is also influenced by spatial grain in that fine grains might underestimate species richness due to limited sampling area, while coarse grains integrate over larger areas and can capture more species, potentially revealing a more complete picture of biodiversity (Arrhenius, 1921). Spatial grain affects the perceived habitat heterogeneity, with finer grains detecting small-scale features and variations crucial for understanding species' habitat preferences and distributions, while coarser grains capture broader patterns of habitat diversity and environmental gradients (Turner, 1989; Hui *et al.*, 2006). The landscape context, including the matrix and connectivity between habitats, varies with spatial grain, with fine grains capturing edge effects and local fragmentation, while coarse grains provide insights into landscape connectivity and the impact of surrounding land uses (Hui *et al.*, 2006; Fu *et al.*, 2011; Newman *et al.*, 2019).

Ecological processes operate at various scales, with local interactions like competition and predation occurring at fine grains, while broader processes such as climate gradients, dispersal, and landscape connectivity influence patterns at coarser grains (Wiens, 1989). Many ecological theories and models, such as metapopulation dynamics, island biogeography, and species distribution models, are scale-dependent (Ricklefs, 1987). Spatial grain is vital for conservation planning and management, as fine grains are essential for identifying critical habitats, microrefugia, and local biodiversity hotspots for targeted actions, while coarse grains aid in landscape-level planning, understanding regional biodiversity patterns, and prioritizing large-scale conservation areas (Wu *et al.*, 2000; Van Eetvelde & Aagaard Christensen, 2023). Understanding how patterns observed at one spatial grain scale up or down to other grains is crucial for ecological generalization and modeling, as patterns identified at fine grains may not hold at coarser grains and vice versa, with scaling relationships aiding in the prediction of biodiversity patterns across different spatial extents (Wiens, 1989). Ultimately, understanding how spatial grain affects biodiversity patterns is crucial for accurately assessing ecological dynamics and making informed conservation decisions, as it ensures that both fine-scale details and broad-scale trends are effectively captured and considered. This spatial perspective is equally important when examining specific ecological interactions, such as plant-frugivore relationships, where both the scale of observation and habitat context can significantly influence these mutualistic connections.

Plant-frugivore relationships are fundamental ecological interactions in many ecosystems, with many of these relationships being mutualistic. In these interactions, frugivores benefit from the nutritional value of fruit, while plants gain from seed dispersal, which is crucial for plant reproduction and biodiversity maintenance (Howe & Smallwood, 1982). This mutualism influences plant distribution, diversity, and the overall structure and functioning of ecological communities (Bascompte & Jordano, 2007). Frugivores contribute to seed dispersal in two main ways: through ingestion and excretion (endozoochory) or by carrying seeds externally (epizoochory) (Howe & Smallwood, 1982). Effective seed dispersal enhances plant genetic diversity and supports the colonization of new habitats (Schupp & Fuentes, 1995). Plants have evolved various fruit traits—such as color, size, and nutrient content—to attract specific frugivores, who select fruits based on these traits (Wheelwright & Orians, 1982). Plant-frugivore interactions create complex ecological networks that impact community structure and ecosystem functioning (Bascompte & Jordano, 2007). However, the effectiveness of frugivores as seed dispersers can vary across spatial and temporal scales, influenced by factors like habitat type, seasonal fruit availability, and frugivore behavior (Schupp *et al.*, 2010; Beckman & Sullivan, 2023). Frugivores play a critical role in forest regeneration, particularly in tropical ecosystems, by dispersing seeds away from parent plants, thus reducing competition and predation (Beckman & Rogers, 2013; Zwolak & Sih, 2020). Despite their importance, more research is needed on how climate change impacts fruiting phenology, frugivore behavior, and seed dispersal timing is crucial, as climate shifts can disrupt these interactions and affect plant reproduction and biodiversity (Mokany *et al.*, 2014; Geissler *et al.*, 2023). Research into the functional traits of both plants and frugivores can provide valuable insights into their contributions to seed dispersal and ecosystem functioning. Understanding plant-frugivore relationships is crucial for grasping how ecosystems function and maintain biodiversity. In particular, these interactions play a vital role in the diverse and complex ecosystems of the Tropical Andes, where unique plant-frugivore dynamics contribute to the region's rich biodiversity and ecological processes.

The Tropical Andes is the most species-rich terrestrial biodiversity hotspot in the world, located on the western side of South America in Venezuela, Colombia, Ecuador, Peru, and Bolivia between latitudes 11°N and 27°S and characterized by the Andes Mountains, which are the longest continental mountain range in the world. This region is renowned for its exceptional ecological richness, marked by dramatic elevational gradients that range from lowland rainforests to high-altitude páramos that create a diverse array of microhabitats, from cloud forests to grasslands, and contribute to varying climatic conditions, including extreme temperature fluctuations and diverse precipitation patterns (CEPF, 2015; Comer *et al.*, 2022). The Andes Mountains function as both ecological corridors and barriers, facilitating species migration and promoting speciation through isolation, which supports a high level of endemism (Pérez-Escobar *et al.*, 2022). Additionally, the mountainous terrain significantly influences local and regional climate patterns, with orographic lift generating crucial rainfall that sustains lush ecosystems (Bruijnzeel *et al.*, 2010). The Tropical Andes also serve as a vital source of freshwater, with glaciers, snowfields, and high-altitude wetlands acting as important water reservoirs that feed major rivers and agricultural areas downstream (CEPF, 2015; Comer *et al.*, 2022).

These unique environmental features of the Tropical Andes create a complex and dynamic environment that supports an exceptional diversity of flora and fauna, contributing to the region's remarkable biodiversity and complex interactions among species. The area encompasses 1% of the terrestrial area of the planet, yet is home to 45,000 or 12% of the known species of vascular plants, and 20,000 of those plant species are endemic (Myers *et al.*, 2000; Mittermeier *et al*., 2011). The Tropical Andes includes 429 key biodiversity areas and only 25% of the primary vegetation remains intact (CEPF, 2015, 2021; Myers *et al.*, 2000). This region is also home to tremendous cultural diversity with an estimated 10 to 17 million Indigenous people of 40 ethnic groups, who steward more than 50% of the land in the hotspot (Cuvi, 2013; CEPF, 2015, 2021). The Andes Mountains hold cultural and economic significance for local communities, providing resources such as medicinal plants and materials for traditional practices (Cuvi, 2013). However, this biodiversity hotspot faces significant threats from deforestation, habitat fragmentation, and climate change, which jeopardize its ecological balance (Herzog *et al.*, 2011). The mountains in the region are sensitive indicators of climate change, with shifts in species distributions and glacier dynamics offering valuable insights into the effects of global warming on alpine and tropical ecosystems (Bruijnzeel *et al.*, 2010; Rabatel *et al.*, 2013; Christmann *et al.*, 2023). One study found that 80% of Andean tree species will reduce their habitat, while 10 percent will face extinction by 2050 (Garavito *et al.*, 2015). Another reported that many endemic species will become severely threatened due to reductions in their climatic niche (Ramirez-Villegas et al., 2014). More research is needed to understand how patterns of biodiversity will be impacted by these changes as the Tropical Andes is especially vulnerable to climate change (Herzog *et al.*, 2011; Tovar *et al.*, 2013, 2022; Fadrique *et al.*, 2018; Li *et al.*, 2018; Fuentes-Castillo *et al.*, 2020; Noh *et al.*, 2020; Manes & Vale, 2022). The Tropical Andes play a crucial role in regional and global ecological processes, such as carbon sequestration and water regulation, and support intricate ecological interactions, including vital plant-frugivore relationships that influence ecosystem functioning (Herzog *et al.*, 2011; CEPF, 2021). Understanding how plant-frugivore interactions operate within the diverse and complex habitats of the Tropical Andes is essential for comprehending the broader patterns of biodiversity in this hotspot, as these relationships drive seed dispersal, plant distribution, and ecosystem dynamics across varying spatial and environmental scales.

This thesis aims to investigate the grain-dependent relationships between fruiting plant-frugivore taxonomic and functional diversity in a biodiversity hotspot, the Tropical Andes. The analysis in Chapter 1 leverages open data repositories of occurrence and trait data for fruiting plants and frugivores. By investigating these relationships, this thesis contributes to our understanding of how plant-frugivore interdependence impacts the relationship of their taxonomic and functional diversity in space to use this information to better inform conservation prioritization. Ultimately, this knowledge improves our ability to assess biodiversity and prioritize the conservation of its related ecosystem functions and services.

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CHAPTER 1: THE GRAIN-DEPENDENT RELATIONSHIPS OF FRUITING PLANTS AND FRUGIVORES IN TROPICAL ANDES FORESTS

The following co-authors contributed to this chapter: Beth Gerstner, Pat Bills, and Phoebe Zarnetske

1.1 Abstract

Quantifying spatial patterns of biodiversity plays a critical role in determining conservation priorities and ecosystem function and clarifying the underlying processes of community assembly, species-area relationships, and environmental filtering. There is a growing body of literature that recognizes the need to move past solely focusing on taxonomic diversity (TD) to quantity biodiversity and has emphasized the advantages of using traits to determine functional diversity (FD), which reflects the roles species play in their communities and ecosystems. Yet there is a lack of knowledge about how taxonomic and functional diversity covary across spatial grains, and between taxonomic groups that depend on each other. Fruiting plant-frugivore communities are an ideal focal group for filling these gaps due to their consumptive and seed dispersal interactions. Here we focus on the Tropical Andes, a biodiversity hotspot, and quantify scale-dependent relationships of TD and FD for fruiting plants and frugivores using occurrence and trait data from big, open databases. The results indicate that relationships for both fruiting plant-frugivore taxonomic and functional diversity were the strongest at the coarsest spatial grain (100 km), the fruiting plant-frugivore taxonomic diversity relationship was stronger than the functional diversity relationship across all spatial grains, and the scaling relationship for fruiting plant-frugivore taxonomic diversity was stronger than fruiting plant-frugivore functional diversity. These findings provide evidence that the relationships between plant-frugivore taxonomic diversity and plant-frugivore functional diversity are scale-dependent and differ from each other.

1.2 Introduction

Understanding biodiversity patterns is crucial for conserving ecosystems and their functions, particularly in plant-frugivore interactions which play a key role in seed dispersal and plant community dynamics. However, while much research has been conducted on the taxonomic and functional diversity of plant and frugivore communities separately, the scale-dependency of their relationships with one another remains underexplored. Specifically, it is unknown how the interactions between plant-frugivore taxonomic diversity and functional diversity vary across different spatial grains. As spatial scaling relationships can affect macroecological conclusions and alter conservation and management decisions, uncovering any scale dependency is essential for robust biodiversity assessments. To fill this gap, we investigate the scale-dependent nature of these relationships, providing insights that can inform biodiversity conservation priorities and ecosystem management strategies.

Patterns of biodiversity reflect underlying processes of community assembly, species-area relationships, environmental filtering, and ecosystem functions (Gaston, 2000; Swenson, 2011; Díaz & Malhi, 2022). With many threats to biodiversity, such as land degradation, climate change, pollution, and invasive species, it is becoming even more crucial that we understand these patterns and processes to inform our conservation actions (Sala *et al.*, 2000; Hooper *et al.*, 2012). Biodiversity is a multidimensional measure of the variability of life, encompassing dimensions such as taxonomic and functional diversity (Naeem *et al.*, 2016; Díaz & Malhi, 2022). While taxonomic diversity measures the number and abundance of species, it does not consider the roles or functions that these species play within an ecosystem. In contrast, functional diversity explicitly accounts for the diversity of traits and the roles species perform in an ecosystem. This means that an ecosystem with high functional diversity has a variety of species performing different ecological roles, which can be crucial for maintaining ecosystem functions. Consequently, the loss of species with unique functional traits can significantly disrupt ecosystem processes, highlighting the importance of preserving both taxonomic and functional diversity.

Since taxonomic diversity and functional diversity measure different aspects of biodiversity, they are not always aligned. For example, a study investigating the relationship of species richness with three different functional diversity metrics for vegetation across a successional gradient of Atlantic Forest, southern Brazil found that all dimensions of functional diversity increased with species richness but differed by how much depending on the functional diversity metric used (Warring *et al*., 2016). Similarly, another meta-analysis found that while there was a positive correlation between species richness (taxonomic diversity) and functional diversity, the strength of this relationship varied depending on the specific functional traits present and the environmental conditions of the community (Flynn *et al.*, 2009). Incorporating both taxonomic and functional diversity into biodiversity assessments provides a more holistic understanding of ecosystem complexity and resilience, highlighting the necessity of preserving not just the number of species, but also the variety of ecological roles they perform to maintain healthy and functioning ecosystems.

Patterns of taxonomic and functional diversity vary across different spatial scales (Wiens, 1989; Levin, 1992). Studying biodiversity patterns across multiple spatial scales provides insights into various dimensions of diversity and helps elucidate the underlying processes that shape these patterns, such as landscape structure and ecological interactions. This approach enhances our understanding of biodiversity by offering a more comprehensive and nuanced representation of its distribution and dynamics. Scale-dependent patterns also help elucidate how species exploit different ecological niches (Levin, 1992). One component of scale is spatial grain, which is the resolution or size of the spatial units used. The relationship between taxonomic diversity and spatial grain generally follows the species-area relationship: as grain coarsens, more species are observed up to a point (Arrhenius, 1921; Preston, 1960, 1962; Macarthur & Wilson, 1967). For example, in a study of global vascular plant species richness at various spatial grains, there was a positive relationship between log grain size and log richness with some regional variation in relationship strength (Puglielli & Pärtel, 2023). Functional diversity also can vary by spatial grain. It is generally expected that finer spatial grains will exhibit higher functional diversity because they can capture detailed microhabitat variations and localized species interactions, which contribute to a richer array of functional traits. In contrast, coarser spatial grains tend to show lower functional diversity, as they integrate broader landscape-level processes and species turnover, potentially smoothing out finer-scale variations and interactions (Zambrano *et al.*, 2019).

Understanding scale-dependent patterns in taxonomic and functional diversity can contribute to the developing and refining ecological theories, such as species-area relationships and community assembly rules. Yet, our understanding of how taxonomic and functional measures of biodiversity covary across different spatial scales is still limited (Flynn *et al.*, 2011; Gonzalez *et al.*, 2020). One study of ants and spiders at various spatial scales of an individual tree, stand, site, and ecoregion found stronger scaling patterns of taxonomic diversity than functional diversity from local to regional scales (Mahon *et al.*, 2023). Other work with birds in the United States reported similar scaling patterns of taxonomic and functional diversity change at finer (50 km) and more intermediate (100 - 1600 km) scales with taxonomic diversity change exceeding functional diversity change at the coarser continental scale (Jarzyna & Jetz, 2018).

Quantifying the spatial relationships among these multiple dimensions can help refine and interpret the geographic distribution of any given species and trait syndrome, thus providing important advances in fundamental biogeography, modeling species distributions, and informing conservation (Dubuis *et al.*, 2013; Violle *et al.*, 2014; Abelleira Martínez *et al.*, 2016).

Recognizing the spatial relationships between taxonomic and functional diversity provides a valuable framework for exploring biodiversity interactions within ecosystems, such as the relationship between fruiting plants and frugivores. This ecological interaction highlights how both plant and animal diversity, along with their functional traits, influence ecosystem dynamics. Fruiting plants and frugivores—such as fruit-eating birds and mammals—engage in mutualistic consumptive and seed dispersal interactions. Fruiting plants provide essential food for frugivores; in turn, frugivores help maintain plant species diversity through seed dispersal and scarification, impacting species' geographic distributions, patterns of diversity, and ecosystem functions (Fleming & Estrada, 1993). Studies indicate that approximately 90% of plant species are involved in such plant-frugivore networks in tropical ecosystems globally (Jordano, 2000). Examining these interactions through the lens of taxonomic and functional diversity not only enhances our understanding of how species contribute to ecosystem processes but also informs effective conservation strategies. By integrating the study of plant-frugivore networks across different spatial scales, we can better appreciate how these interactions shape biodiversity patterns and maintain ecosystem resilience, guiding targeted conservation efforts that preserve both species diversity and ecosystem functions.

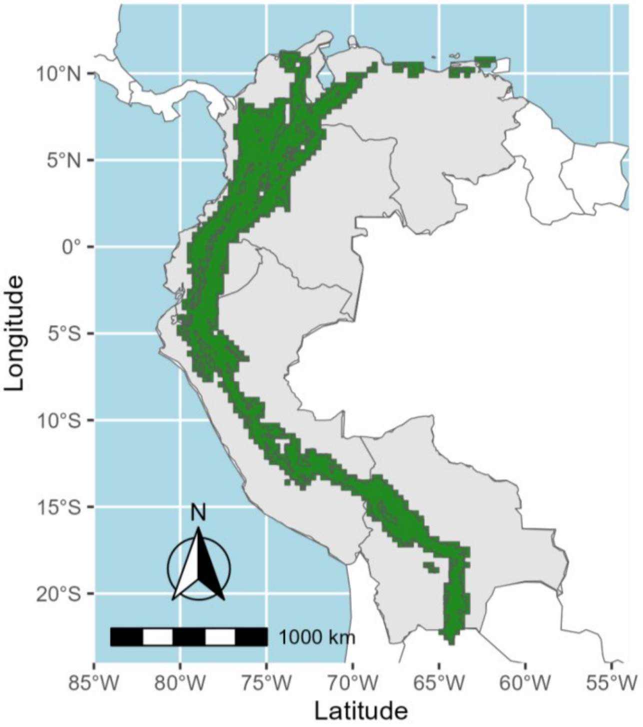
In this study, we aim to assess patterns of TD and FD of fruiting plants and frugivores in the forested areas of the Tropical Andes across various spatial scales. Specifically, we asked: (1) What spatial grains are fruiting plant-frugivore taxonomic diversity and fruiting plant-frugivore functional diversity most aligned/highly correlated? (2) What is the difference between the strength of the fruiting plant-frugivore taxonomic diversity relationship and the fruiting plant-frugivore functional diversity relationship? (3) What is the difference between the spatial scaling relationship of fruiting plant-frugivore taxonomic diversity and fruiting plant-frugivore functional diversity? We hypothesized that the greatest alignment between fruiting plant-frugivore taxonomic and functional diversity would be found at coarser grains, as more spatial heterogeneity is captured at finer scales and homogenized as grain coarsens; environmental or habitat heterogeneity and low rates of species turnover are more likely at coarser grains. We also expect that the alignment between fruiting plant-frugivore functional diversity will be stronger than the fruiting plant-frugivore taxonomic diversity relationship, as mutualistic interactions and trait matching are better captured through functional diversity instead of simply species co-occurrence. Finally, we expect that the fruiting plant-frugivore functional diversity scaling relationship will be weaker than the taxonomic diversity scaling relationship, as taxonomic diversity is expected to increase as scale broadens (species-area relationship) whereas functional diversity is expected to experience trait clustering and functional redundancy as scale broadens.

1.3 Methods

1.3.1 Study Region

The Tropical Andes region is in South America and consists of the countries of Colombia, Venezuela, Ecuador, Peru, and Bolivia. This region is a biodiversity hotspot: home to 10% of all known species across all taxa, over 30,000 vascular plant species, and the greatest number of endemic plants and vertebrate species in the world (Myers *et al*., 2000). Specifically, this study focuses on areas with the IUCN habitat designation ‘Forest-Subtropical/Tropical Moist Montane’ and ‘Forest-Subtropical/Tropical Moist Lowland’ (Keith *et al*., 2020) (Figure 1).

Figure 1: Map of the study region showing the Tropical Andes Forested area (in green) consisting of IUCN habitats Forest-Subtropical/Tropical Moist Montane and Forest-Subtropical/Tropical Moist Lowland within the Tropical Andes hotspot (precisely delineated using a shapefile obtained from the Critical Ecosystem Partnership Fund). Tropical Andes countries (gray outline).



1.3.2 Study Taxa

Plants and frugivores have many important ecological relationships through biotic interactions such as seed dispersal and consumption (Fleming & Estrada, 1993), and frugivory is essential to maintaining forest structure (Albert *et al.*, 2021). For this study, plant species potentially involved in frugivorous relationships included all fruiting flowering plant species with available data in the study region. In the study region, there are estimated to be 70,376 species, 4,381 genera, and 273 families of angiosperms which was determined using the checklist function of the GIFT R package (Denelle & Weigelt, 2023) on 2024-06-11. Frugivorous bird and mammal species were determined using Frugivoria (Gerstner *et al.*, 2023a, 2023b), which includes bird and mammal species with frugivorous diets above 10% diet composition.

1.3.3 Workflow

To adhere to Open Science principles, this study follows the Environmental Data Initiative's Thematic Standardization (Environmental Data Initiative, 2023) which streamlines data management and standardized protocols. As illustrated in the supplemental workflow diagram (Figure A1), the level 0 (L0) code retrieves the raw data, the level 1 (L1) code modifies and cleans the data, and the level 2 (L2) code runs analyses with the data. This study also implements FAIR (Findable, Accessible, Interoperable, and Reusable) data principles (Wilkinson *et al.*, 2016) to follow best practices of management, sharing, and use of research data.

1.3.4 Data

1.3.4.1 Tropical Andes Moist Montane and Lowland Forest Habitat Subset

A shapefile of the IUCN habitat designation of 'Forest-Subtropical/Tropical Moist Montane' and 'Forest-Subtropical/Tropical Moist Lowland' (Keith *et al.*, 2020) was generated by subsetting the global IUCN habitat classification (Jung *et al.*, 2020) to the Tropical Andes hotspot using the shapefile obtained from the Critical Ecosystem Partnership Fund and the above habitat designations. Rasters of Forest-Subtropical/Tropical Moist Montane and Forest-Subtropical/Tropical Moist Lowland were cropped using a shapefile of the Tropical Andes hotspot and combined into one raster, then converted to a shapefile to represent all forested areas of the Tropical Andes hotspot. This resulting shapefile "Tropical Andes Forest" defined the extent for all subsequent analyses.

1.3.4.2 Occurrence Data

All flowering plant species (angiosperms) with occurrence data in the Tropical Andes Forest were retrieved from GBIF on 2024-01-18 using the rgbif R package (Chamberlain *et al.*, 2023; GBIF.org, 2024), resulting in 4,519,792 point occurrence records of 40,288 species.

Bird and mammal occurrence data for the 1,733 species in Frugivoria (Gerstner et al., 2023a, 2023b) in the Tropical Andes Forest were retrieved from GBIF on 2023-08-02 using the rgbif R package (Chamberlain *et al.*, 2023; GBIF.org, 2023), resulting in 8,885,330 point occurrence records of 1,360 species.

1.3.4.3 Trait Data

Traits were selected for their ecological importance in interaction(s) between plants and frugivores. Trait values describe species-level measurements and therefore do not account for intraspecific variation. Plant traits included plant height (m), fruit mass (mg), dispersal syndrome, plant lifespan (years), fruit type, seed mass (mg), seed length (mm), seed width (mm), and growth form. Plant trait names are standardized conforming to the standards of the TOP Thesaurus of Plant Characteristics (Garnier *et al*., 2017; *ThesauForm*). Frugivore traits included body size (mm), body mass (g), diet category, and generation time (years). Trait values and categories are available in the Appendix (Table A2).

Plant trait data were retrieved from three databases: BIEN (Maitner *et al*., 2018), TRY (Kattge *et al*., 2020), and GIFT (Weigelt *et al*., 2020). Records available in the BIEN 4.2 dataset were retrieved through the BIEN R package (Maitner *et al.*, 2018) on 2023-10-25 for the following traits: "whole plant dispersal syndrome", "whole plant height", "maximum whole plant longevity", "maximum whole plant height", "minimum whole plant height", "longest whole plant longevity", "fruit type", "maximum fruit length", "minimum fruit length", "seed mass", "whole plant growth form", and "whole plant growth form diversity". This resulted in a total of 10,667,620 trait records for 87,300 species. Data available in the TRY database (Kattge *et al.*, 2020) was acquired on 2023-10-24 and pre-processed using the rtry R package (Lam *et al.*, 2023) for the following traits: “plant height vegetative”, “fruit dry mass”, “dispersal syndrome”, “plant lifespan (longevity)”, “fruit type”, “fruit texture inside”, “fruit surface type”, “dispersal unit type”, “fruit dehiscence type”, “fruit length”, “dispersal unit length”, “seed dry mass”, “seed length”, “seed width”, and “plant growth form”. This resulted in 32,118,997 trait records for 242,559 species. Data available in the GIFT 3.0 database (Weigelt *et al.*, 2020) was acquired using the GIFT R package (Denelle & Weigelt, 2023) on 2023-10-25 for the following traits: “plant_height_mean”, “plant_height_min”, “plant_height_max”, “dispersal syndrome”, “lifespan”, “fruit_type_1”,” fruit_dryness_1”, “fruit_length_min”, “fruit_length_max”, “fruit_length_mean”, “seed_mass_min”, “seed_mass_max”, “seed_mass_mean”, “seed_length_min”, “seed_length_max”, “seed_length_mean”, “seed_width_min”, “seed_width_max”, “seed_width_mean”, and “growth_form”. This resulted in 480,880 trait records for 225,033 species.

Bird and mammal trait data in the Moist and Montane Forest of the Tropical Andes were retrieved from the Frugivoria database (Gerstner *et al.*, 2023a, 2023b) on 2023-08-01. Frugivoria is a trait database of ecological, life-history, morphological, and geographic traits for mammals and birds exhibiting frugivory in contiguous moist montane forests and adjacent lowland forests of Central and South America (Gerstner *et al.*, 2023a, 2023b). This resulted in 40,074 trait records for 1,432 species for the following traits: “body size”, “body mass”, “diet category”, and “generation time”.

1.3.4.4 Cleaning Occurrence Data

Occurrence data for plants and frugivores were cleaned using the CoordinateCleaner R package (Zizka *et al.*, 2019) to remove duplicate records and problematic geographic coordinates (coordinates of biodiversity institutions, country capitals, country centroids, equal longitude and latitude, coordinates in the ocean, and plain zeros). Cleaning resulted in 1,886,120 plant occurrence records of 39,972 species and 1,721,825 frugivore occurrence records of 1,219 species; both from the timeframe of 1800 to 2023.

1.3.4.5 Plant Data Taxonomic Harmonization

The various databases have slightly different taxonomic backbones and recent taxonomic revisions are not always applied to previous records resulting in disparities in naming conventions between databases. A lookup table of original names and accepted names was created for plants with species scientific names from GBIF, BIEN, GIFT, and TRY to harmonize taxonomy between databases. A list of 487,201 unique, valid species names was compiled across the four data sources. For the first pass, the TNRS R package (Maitner *et al*., 2023) was used and matches were found for 472,680 species. The remaining 14,548 species names were classified as disparities (illegitimate, no opinion, invalid, or " "). Next, the bdc R package (Ribeiro *et al.*, 2022, 2023) using the Catalogue of Life database (Bánki *et al.*, 2023) was used to try to resolve the previous disparities and found matches for 5,177 species. Records were discarded if no acceptable names were found, which occurred for 9,371 species. This resulted in a lookup table for 476,010 species. After updating the data sources with the lookup table, the GBIF occurrence data contained 1,759,786 records of 38,676 species, the TRY trait data contained 3,760,571 records of 213,389 species, the BIEN trait data contained 10,381,323 records of 80,249 species, and GIFT trait data contained 479,530 records of 222,335 species.

1.3.4.6 Fruiting Plant Species Subset

A species list of fruiting plants was generated using species with trait information for traits related to fruits: "Fruit dehiscence type", "Fruit dry mass", "Fruit length", "Fruit surface type", "Fruit texture inside", "Fruit type", "fruit type", "fruit_dryness", "fruit_length_max", "fruit_length_mean", "fruit_length_min", "fruit_type", "maximum fruit length", and "minimum fruit length". Any plant species that had information for any of these traits was considered to be a fruiting plant. This resulted in 3,185 species, which were used to subset the plant occurrence and the rest of the plant trait data only to include fruiting species. Subsetting the plant occurrence and trait records by this species list resulted in the GBIF occurrence data containing 669,947 records of 3,185 species, the TRY trait data containing 674,028 records of 3,166 species, the BIEN trait data containing 456,110 records of 2905 species, and GIFT trait data containing 24,186 records of 3,161 species.

1.3.4.7 Plant Trait Standardization

Fruiting plant trait data was combined from the three sources and standardized for the following traits, selected based on their species coverage (traits with at least 100 species records in a single database): dispersal syndrome, fruit mass, fruit length, fruit type, growth form, plant height, plant lifespan, seed mass, seed length, and seed width. Numeric traits had non-numeric records filtered out and data was converted to ensure consistent units for each trait (if needed).. Non-numeric traits had numeric records removed. Categorical traits of dispersal syndrome, fruit type, and growth form had various possible values across the sources. Dispersal syndrome values were assigned to the following classifications: anemochorous, anthropochorous, autochorous, hypochlorous, myrmecochorous, zoochorous, and unspecialized. If trait values included words that matched the classification definition, it was assigned that classification; for example, a dispersal type of ‘bird’ would be assigned to zoochorous. Fruit type was harmonized into the following classifications: achene, aggregate berries, aggregate follicles, aggregate nutlets, berry, capsule, drupe, fleshy, follicle, legume, lomentum, nut, pod, pome, samara, schizocarp, siliqua, squash, syncarpous, unspecified, utricle. Most fruit type values already matched one of the classifications, but there were a handful of values that were different forms of the same classification (drupe and Drupaceous), as well as less specific fruit types that were grouped into other (apocarpous, pseudosyncarpous, vegetative, dry, fleshy). Growth form data was only used from the GIFT database to remove the need to reclassify trait values, which uses the following classifications: herb, shrub, tree, and other. The identify_outliers function from the rstatix R package (Kassambara, 2023) was used to investigate outliers for numeric traits. For each trait, one value was assigned per species using the geometric mean for numeric traits and mode for categorical traits. The resulting standardized trait data contained 16,776 records of 3,181 species.

1.3.4.8 Plant Trait Imputation

Plant species with no available information for a given trait, the case for 15,035 trait records, were assigned to the genus or family level where possible retrieved from BIEN (Maitner *et al.*, 2018) and GIFT (Weigelt *et al.*, 2020) with genus prioritized over family. This added 1,647 records of 6 traits at the genus level and 2,904 records of 6 traits at the family level. The remaining gaps of 10,489 trait records were filled through imputation using the mice R package (Buuren *et al.*, 2023), adding records for 10 traits of 3,166 species.

1.3.4.9 Frugivore Trait Subset

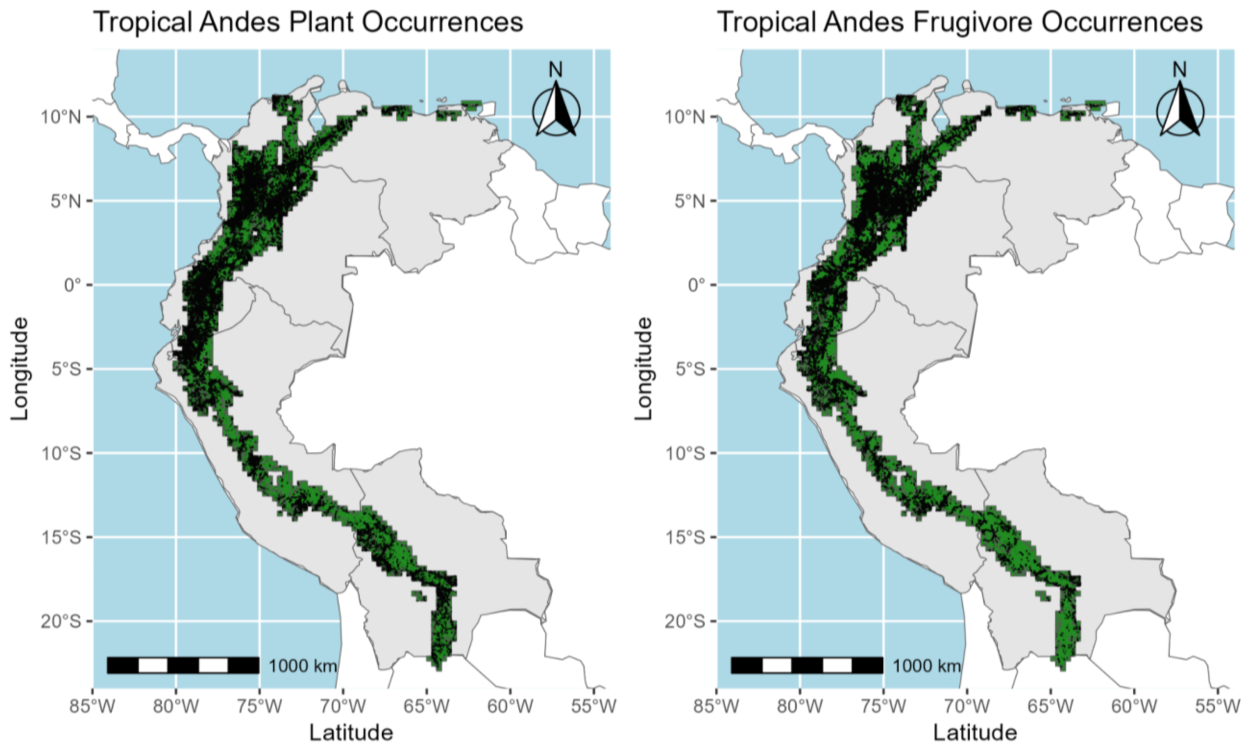
A species list was generated using the cleaned frugivore occurrence data, resulting in 1,143 species. The trait data from Frugivoria was subset by this species list, resulting in 4,514 records for 1,143 species.

1.3.4.10 Occurrence Data with Full Trait Coverage Subset

The frugivore trait subset was used to create a species list with complete trait records. The cleaned frugivore occurrence data was then filtered by the complete trait species list, resulting in 1,667,892 records for 1,074 species, 370 genera, and 64 families.

Similarly for plants, the imputed plant trait dataset was used to create a list of fruiting plant species with complete trait records. The subset fruiting plant occurrence data was then filtered by the complete trait species list, resulting in 658,609 records for 3,128 species, 1,359 genera, and 213 families.

Figure 2: Point occurrence plots showing the final occurrence datasets of fruiting plant species and frugivore (bird and mammal) species in the Tropical Andes Forest.



1.3.4.11 Creating Presence-Absence Matrices

The finalized plant and frugivore occurrence data was transformed to a projected CRS Peru96 / UTM zone 19S along with the Tropical Andes Forest and Tropical Andes countries from rnaturalearth (Massicotte *et al.*, 2023). The projected occurrence data was used to create presence-absence matrices at the various spatial grains described below using the letsR R package (Vilela & Villalobos, 2015; Villalobos, 2020).

1.3.5 Analyses

All analyses were conducted using R 4.4.0 (R Core Team, 2024) via RStudio 2024.04.2 (Posit team, 2024).

1.3.5.1 Spatial Grains

The grain size of the analyses was varied systematically to investigate plant-frugivore biodiversity scaling relationships from finer to coarser grains. Analyses were conducted at the following grains: 5 km, 10 km, 25 km, 50 km, 75 km, and 100 km. Using the sf R package (Pebesma *et al.*, 2024), grid cells of the desired size were intersected with the Tropical Andes Forest to generate a grid with only those cells overlapping with the forest habitat. A cell, in a spatial context, is a defined unit of space within a grid.

1.3.5.2 Taxonomic Diversity

Taxonomic diversity was quantified as species richness and calculated by summing the number of species present within each grid cell for a given grain using occurrence data for plants and frugivores. Specifically, the projected occurrence data was aggregated to the various grains of interest using the mean for the aggregate function of the raster R package (Hijmans *et al.*, 2023). Parallel processing was used for coarser grains to speed up the computations using the foreach (Daniel *et al.*, 2022a) and doParallel (Daniel *et al.*, 2022b) R packages.

1.3.5.3 Functional Diversity

Functional diversity was calculated as functional dispersion. Functional dispersion was determined using the mFD R package (Magneville *et al.*, 2022, 2023) for plants and frugivores using species-trait matrices and species-assemblage matrices for plants and frugivores generated from occurrence and trait data. Functional dispersion is a multidimensional metric that captures species dispersion in a multidimensional trait space and is not influenced by species richness (Laliberté & Legendre, 2010). To compute the functional distance matrices for plants and frugivores, the Gower distance was used since both taxa had categorical and continuous traits. Gower distance handles categorical traits by converting them into binary values, where matching categories are scored as 0 and mismatched ones as 1, then normalizes the contribution of each categorical trait based on the number of possible categories (Gower, 1971; Legendre & Legendre, 2012). The overall Gower distance combines both categorical and continuous distances, usually by averaging or summing them (de Bello *et al.*, 2021). Parallel processing was used for all grains except for 100 km to speed up the computations using the foreach (Daniel *et al.*, 2022a) and doParallel (Daniel *et al.*, 2022b) R packages.

1.3.5.4 Diversity Relationships

For each spatial grain, regression plots were generated using cell values of plant taxonomic diversity vs. frugivore taxonomic diversity, and plant functional diversity vs. frugivore functional diversity. For each plot, two models were fit to the data to generate trendlines: linear and exponential for taxonomic diversity relationships and linear and quadratic for functional diversity relationships using the ggtrendline R package (Mei *et al.*, 2022). The R^2 (coefficient of determination) and slope coefficient of each trendline were calculated to determine the strength of the fit and the relationship between the variables.

1.4 Results

1.4.1 Taxonomic Diversity

The relationship between fruiting plant and frugivore taxonomic diversity was strongest at a spatial grain of 100 km. For all spatial grains, the taxonomic diversity of plants and frugivores showed variation across the study area (Figure 3). The relationship between plant and frugivore taxonomic diversity was positive with the strongest relationship at the coarsest spatial grain (100 km) for both linear and exponential trendlines with the smallest AIC, BIC, and RSS (Figure 4, Table 1).

Table 1: Model summaries for fruiting plant-frugivore taxonomic diversity relationships at each spatial grain. Model performance is evaluated by R^2, p value, N (sample size; the number of cells), AIC, BIC (Bayesian Information Criterion), and RSS (residual sum of squares).

Grain	Model	R^2	p value	N	AIC	BIC	RSS
5 km	Linear	0.113	<0.001	90599	913910	913938	127505943
	Exponential	0.147	<0.001	90599	910390	910428	122644414
10 km	Linear	0.208	<0.001	48306	503339	503365	94783352
	Exponential	0.247	<0.001	48306	500925	500960	90159377
25 km	Linear	0.394	<0.001	15357	166947	166970	47304809
	Exponential	0.442	<0.001	15357	165683	165714	43562570
50 km	Linear	0.549	<0.001	5352	59296	59315	20284665
	Exponential	0.61	<0.001	5352	58478	58504	17403506
75 km	Linear	0.632	<0.001	2858	31910	31928	11794585
	Exponential	0.703	<0.001	2858	31303	31327	9530748
100 km	Linear	0.699	<0.001	1841	20513	20530	7416476
	Exponential	0.77	<0.001	1841	20022	20044	5675002

Figure 3: Taxonomic diversity (species richness, S) for plants and frugivores across the Tropical Andes, at spatial grains of 5 km, 10 km, 25 km, 50 km, 75 km, and 100 km. Data was projected CRS Peru96 / UTM zone 19S; Lat/Long is shown for visualization purposes.

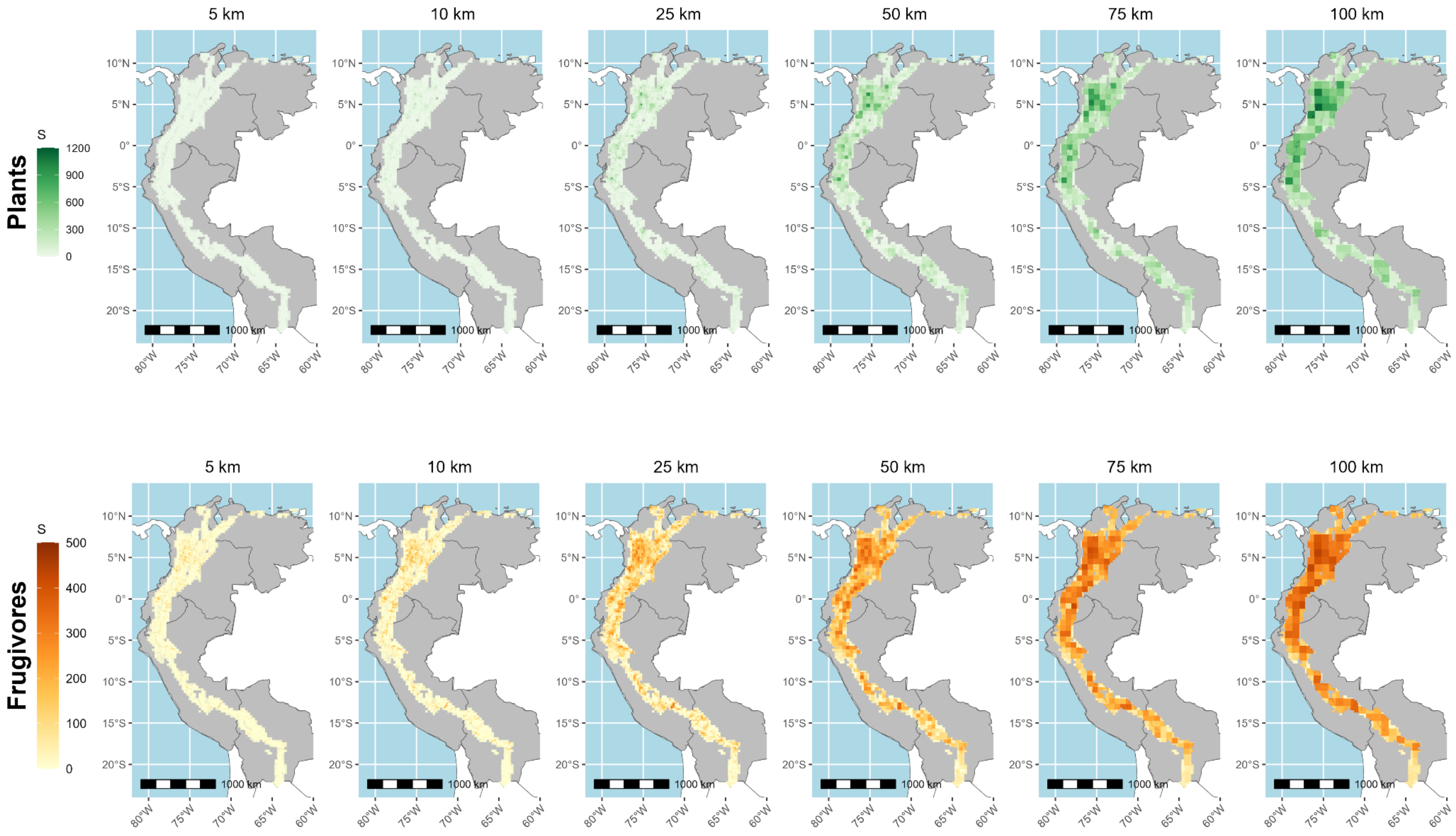
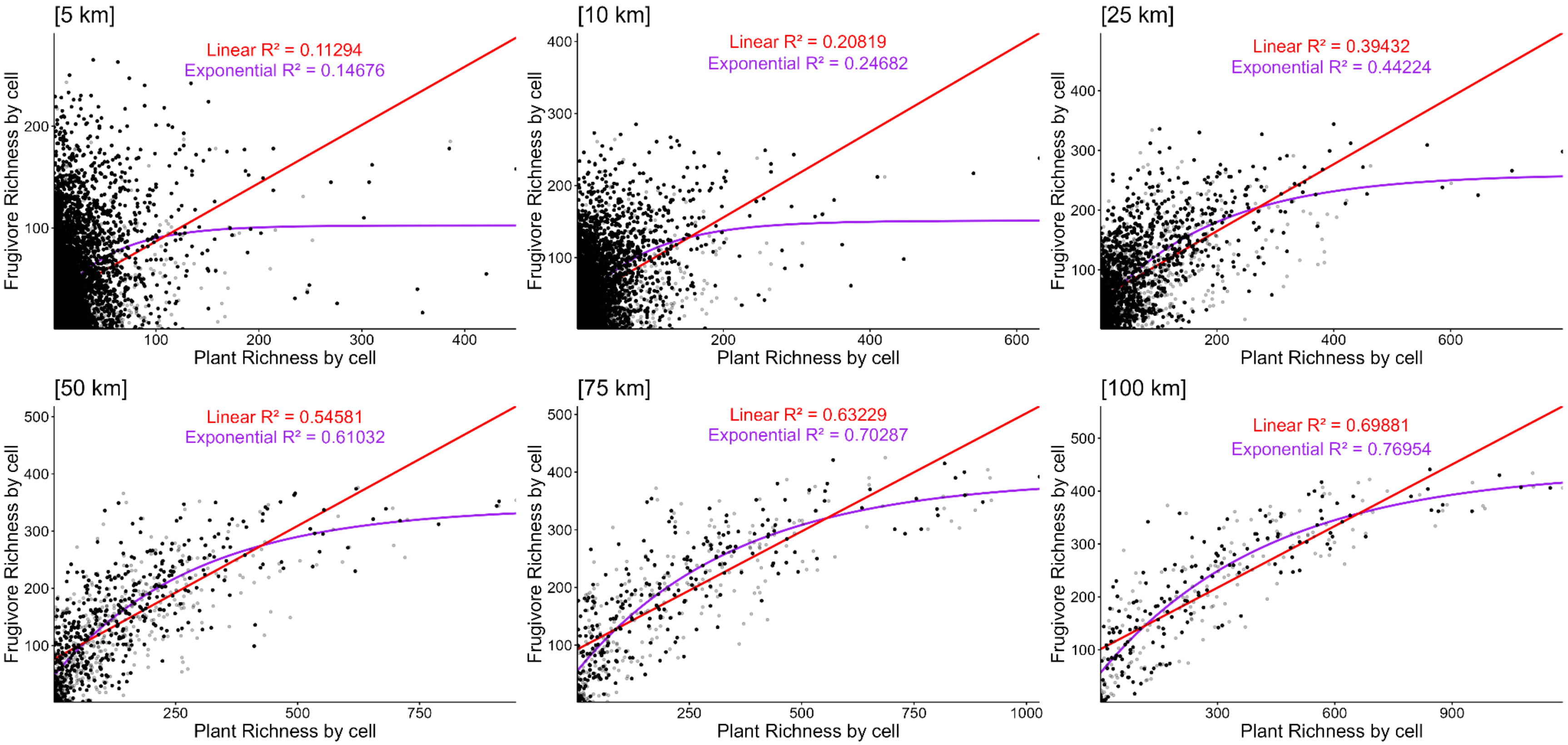


Figure 4: Correlations between fruiting plant and frugivore richness for spatial grains of 5 km, 10 km, 25 km, 50 km, 75 km, and 100 km. Each grain was fit with a linear and exponential trendline. Grey dots indicate fewer points and black dots indicate overlap of multiple points. Cells with 0 values were excluded.



1.4.2 Functional Diversity

The relationship between fruiting plant and frugivore functional diversity was strongest at a spatial grain of 100 km. For all spatial grains, the functional diversity of plants and frugivores measured as functional dispersion showed variation across the study area (Figure 5). The relationship between plant and frugivore functional diversity was positive at most spatial grains with the strongest at the coarsest spatial grain (100 km) for both linear and quadratic trendlines with the smallest AIC, BIC, and RSS (Figure 6, Table 2).

Table 2: Model summaries for fruiting plant-frugivore functional diversity relationships at each spatial grain. Model performance is evaluated by R^2, p value, N (sample size; the number of cells), AIC, BIC (Bayesian Information Criterion), and RSS (residual sum of squares).

Grain	Model	R^2	p value	N	AIC	BIC	RSS
5 km	Linear	0.002	0.16623	856	2649	2663.3	1098.9
	Quadratic	0.035	<0.001	856	2622.6	2641.6	1063
10 km	Linear	0.105	<0.001	34422	82444	82469	22103
	Quadratic	0.212	<0.001	34422	78043	78076	19449
25 km	Linear	0.092	<0.001	12624	28169	28191	6880
	Quadratic	0.159	<0.001	12624	27202	27231	6371.5
50 km	Linear	0.265	<0.001	4721	9455.1	9474.5	2045.5
	Quadratic	0.359	<0.001	4721	8805.5	8831.3	1781.8
75 km	Linear	0.283	<0.001	2492	5227.4	5244.9	1185.9
	Quadratic	0.349	<0.001	2492	4986.2	5009.5	1075.6
100 km	Linear	0.541	<0.001	1675	1795.1	1811.3	285.37
	Quadratic	0.776	<0.001	1675	595.73	617.43	139.29

Figure 5: Functional diversity measured as functional dispersion (FDis) for fruiting plants and frugivores across the Tropical Andes, at spatial grains of 5 km, 10 km, 25 km, 50 km, 75 km, and 100 km. Data was projected CRS Peru96 / UTM zone 19S; Lat/Long is shown for visualization purposes.

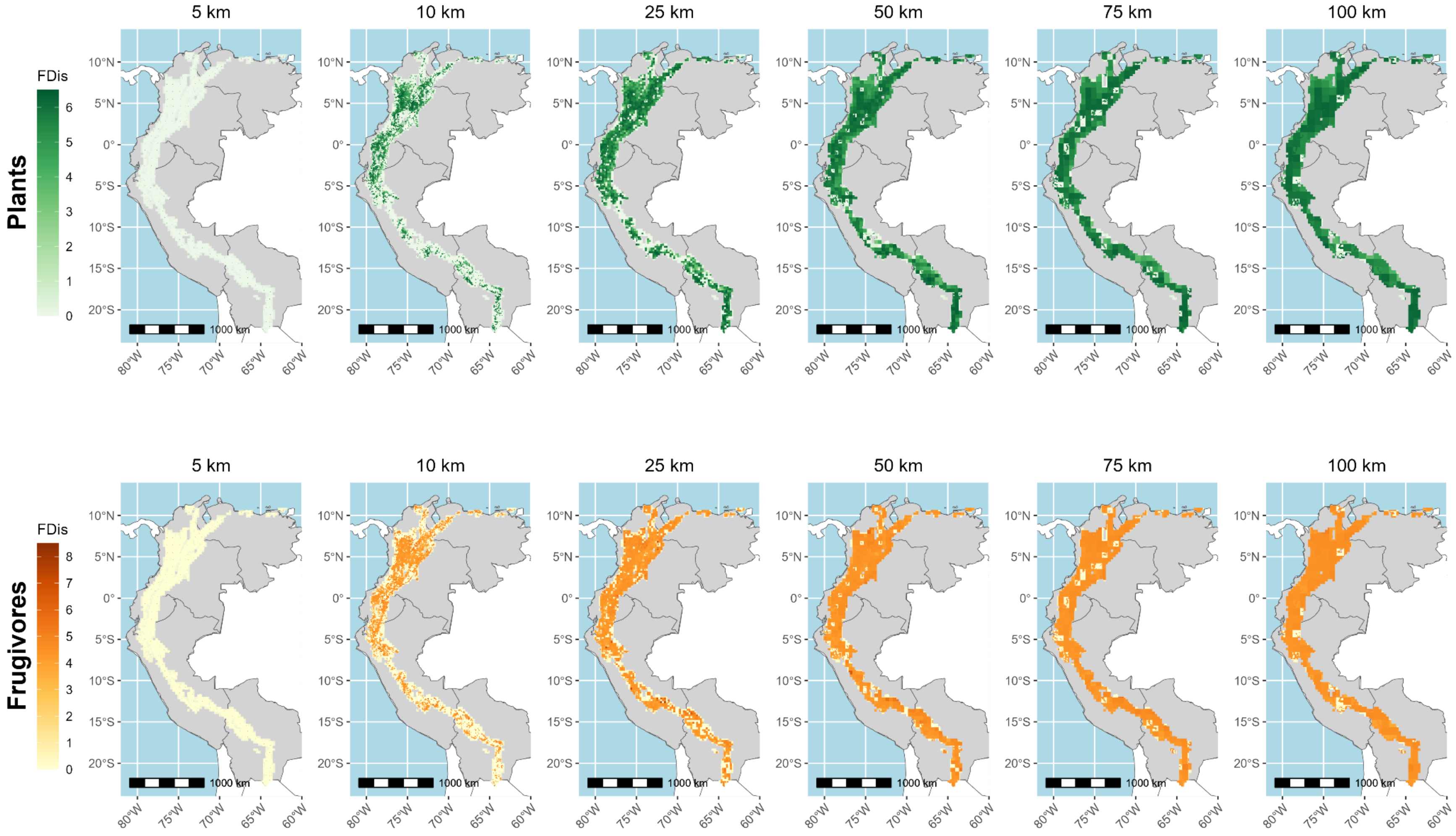
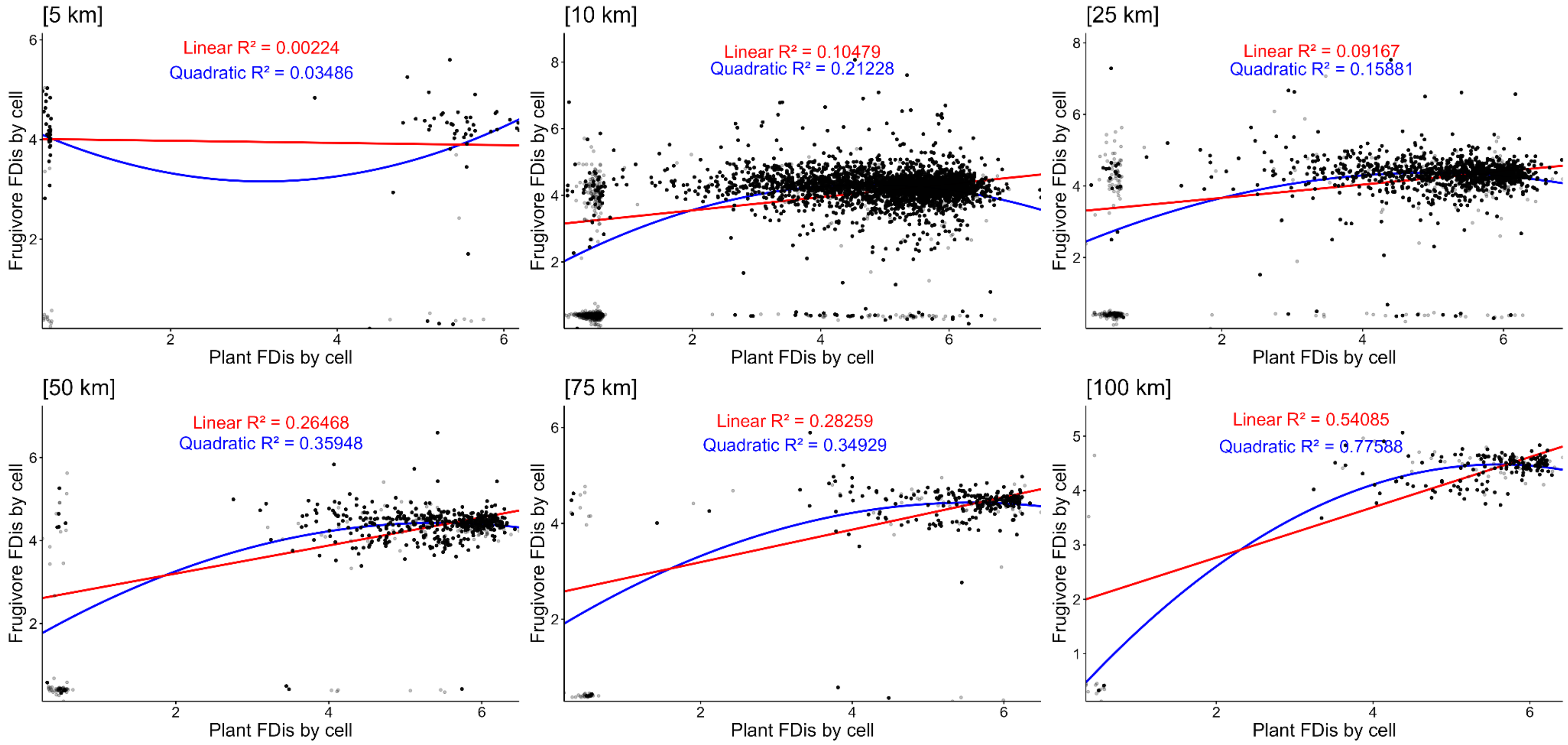


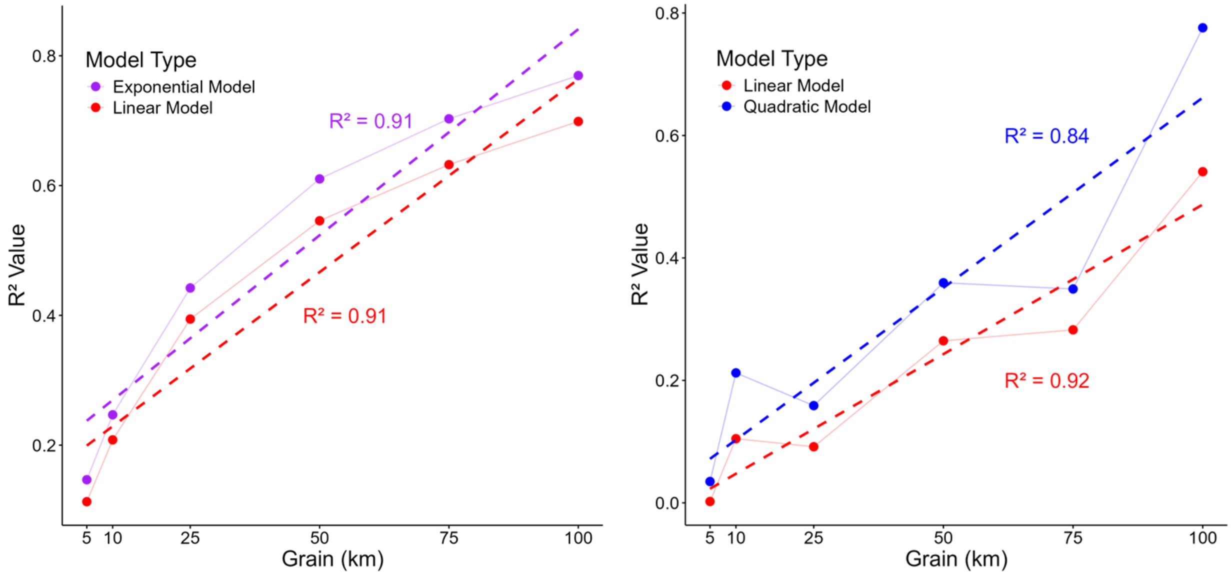
Figure 6: Correlations between plant and frugivore functional dispersion for spatial grains of 5 km, 10 km, 25 km, 50 km, 75 km, and 100 km. Each grain was fit with a linear and quadratic trendline. Grey dots indicate fewer points and black dots indicate overlap of multiple points. Cells with 0 values were excluded.



1.4.3 Diversity Relationships

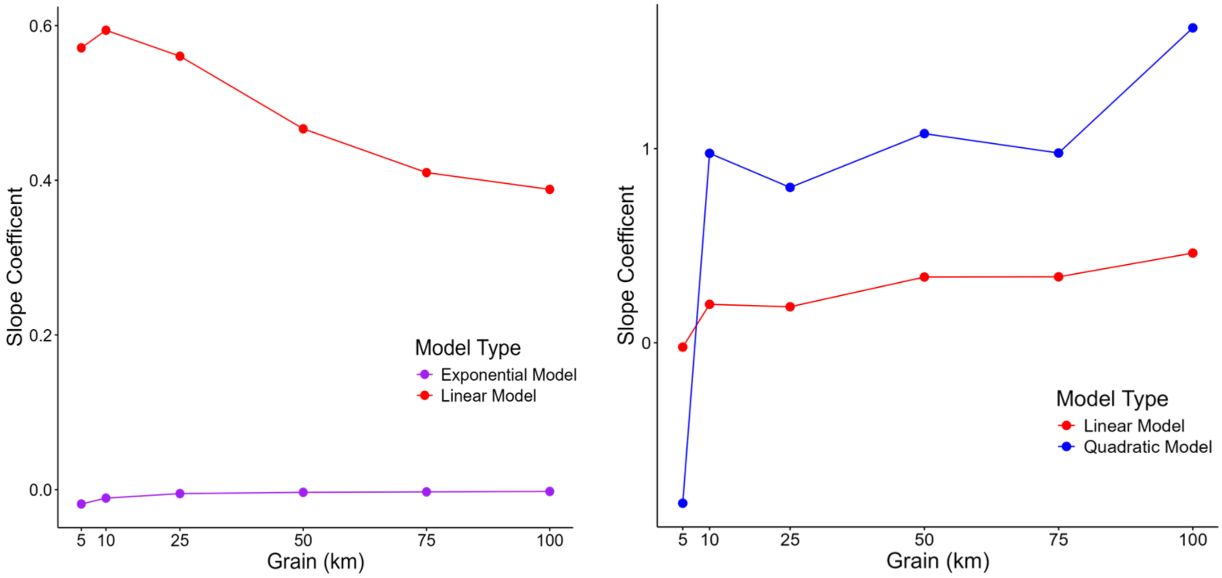
There was a significant relationship between grain and R^2 value for richness for both trendline types. The relationship was positive and linear for both the linear and exponential models with $R^2 = 0.91$. There was also a significant relationship between grain and R^2 value for FDis for both trendline types. For the linear model, there was a positive linear relationship with R = 0.92. For the quadratic model, there was a positive linear relationship with R = 0.84.

Figure 7: Comparing the relationship between R^2 values and grains for richness and FDis for both model types. Linear trendlines were fit to each relationship to show strength (dotted lines).



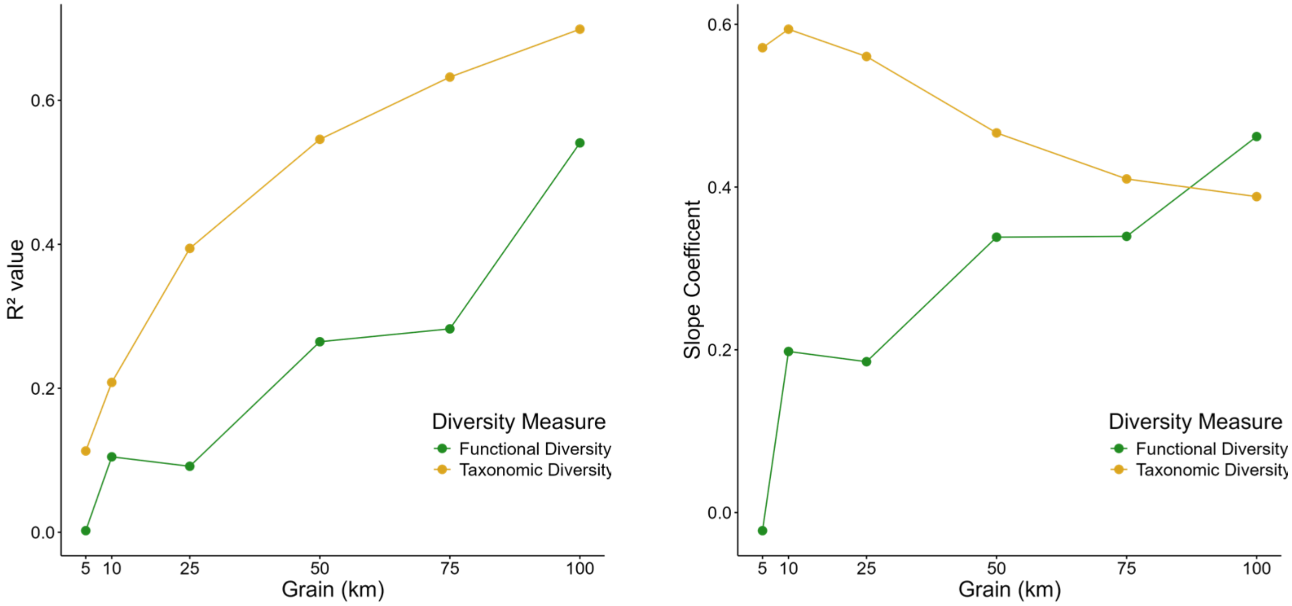
The relationship between grain and slope coefficient for richness varies by model type. The linear model starts with a high slope coefficient at 5 and 10 km but decreases steadily from 10 to 100 km. The exponential model has a constant slope coefficient with minimal change for all grains. For FDis, the relationship between grain and slope coefficient is more similar between the two model types. The linear model increases from 5 to 10 km, slightly declines from 10 to 25 km, increases from 25 to 50 km, slightly declines from 50 to 75 km, and increases from 75 to 100 km. The quadratic model rapidly increases from 5 to 10 km, then slightly decreases from 10 to 25 km, increases from 25 to 50 km, decreases from 50 to 75 km, and greatly increases from 75 to 100 km.

Figure 8: Comparing the slope coefficients for each grain for both Richness (left plot) and FDis (right plot).



When comparing the linear model results for the fruiting plant – frugivore taxonomic and functional diversity relationships, we can see that the R^2 value was higher for the taxonomic diversity relationship across all spatial grains and the slope coefficient was also higher for taxonomic diversity across most spatial grains compared to functional diversity. Overall, the taxonomic diversity had a stronger scaling relationship than functional diversity which does not match our expectations.

Figure 9: Comparing the R^2 (left plot) and slope coefficients (right plot) for each grain for the linear models of Richness and FDis.



1.5 Discussion

Understanding the spatial relationships and patterns of taxonomic and functional diversity of fruiting plants and frugivores in the forested areas of the Tropical Andes is essential because it informs conservation efforts, enhances our knowledge of biodiversity dynamics, and aids in predicting and mitigating the impacts of environmental changes on these critical mutualistic networks. We found the relationship between fruiting plant and frugivore taxonomic diversity was positive with the strongest at a spatial grain of 100 km; the same was true for functional diversity. The taxonomic relationship was stronger across all spatial grains than the functional diversity relationship. We also found evidence of scale dependence for both taxonomic and functional diversity.

Consistent with our expectations, relationships for both plant-frugivore taxonomic and functional diversity were the strongest at the coarsest spatial grain (100 km). This could be attributed to the sampling effect when more data is considered at larger grains. It also can be explained by the species-area relationship and species turnover - smaller areas tend to have higher rates of species turnover than larger areas (Vellend, 2001; Qian *et al.*, 2005). Habitat or environmental heterogeneity also could be influencing this pattern, as environmental variability increases as grain coarsens (Heidrich *et al.*, 2020).

The results indicate that the fruiting plant-frugivore taxonomic diversity relationship was stronger across all spatial grains, which contradicts our initial expectations. This may be due to high functional redundancy in the study area, where multiple species fulfill similar ecological roles (Eisenhauer *et al.*, 2023). Taxonomic diversity, or species richness, often reflects more immediate and observable changes in community composition compared to functional diversity (Cadotte *et al.*, 2011). If different frugivores are associated with a broad range of fruiting plants, the taxonomic diversity of both groups may exhibit a clearer, more direct correlation. This finding might also be explained by functional trait overlap; if frugivores or fruiting plants share similar traits or if functional traits are unevenly distributed among species, the functional diversity relationship could appear weaker (Flynn *et al.*, 2011). In contrast, taxonomic diversity measures the number of distinct species directly, which can reveal stronger patterns across spatial scales. Additionally, the grain and scope of data collection could influence the detection of functional diversity. If the dataset or sampling methods are more effective at capturing taxonomic diversity, this could result in a stronger observed relationship (Schleuter *et al*., 2010). Community assembly processes might also contribute to stronger taxonomic diversity relationships if fruiting plants and frugivores have co-evolved or exhibit strong ecological interactions that drive species diversity (Bannar-Martin *et al.*, 2018). Furthermore, functional traits may not always capture the full ecological complexity of interactions. Selected traits might not be specific enough to frugivory to fully account for the diversity of interactions between frugivores and fruiting plants, whereas taxonomic diversity provides a more direct measure of these interactions (Jordano, 2000). Finally, taxonomic diversity may better reflect the stability and resilience of ecological networks, as a variety of interacting species across different scales could lead to more consistent relationships in taxonomic terms (Duffy *et al.*, 2007).

Fruiting plant-frugivore taxonomic diversity had a stronger scaling relationship than fruiting plant-frugivore functional diversity, which was also contrary to our expectations. Some of the same reasons that explained the pattern of a stronger fruiting plant-frugivore taxonomic diversity relationship across all spatial grains can be used to explain this result. Factors such as functional redundancy and functional trait overlap can weaken the functional diversity relationship (Flynn et al., 2011). Environmental heterogeneity, increasing with spatial scale, can enhance taxonomic diversity by supporting different species in different environments (Stein *et al.*, 2014). Additionally, the ecological complexity of interactions might not be fully captured by functional traits, leading to a weaker functional diversity relationship (Lavorel & Garnier, 2002).

Some limitations of this study include trait selection, frugivore definition, and not considering generalists vs specialists. The traits selected for this study were limited by available data in large databases. Other fruiting plant-frugivore studies have used more frugivory-specific morphological traits such as gape size, bill width, bill length, and wing shape for frugivores; fruit length, fruit width, fruit color, fruit diameter, fruit shape, fruit color, pulp to seed ratio, seed number per fruit, forest strata, dehiscence, fruiting period length, and presence of fleshy tissue for plants (Blendinger *et al.*, 2016; Bender *et al.*, 2018; Zhang *et al.*, 2022). Plant trait data is also more limited in overall species coverage across databases compared to vertebrates (Feng *et al.*, 2022), due in part to the sheer number of plants compared to vertebrates. We also defined frugivores in this study to be birds and mammals with at least 10% of their diets being fruit, which could be too low to capture the specific ecological interactions between fruiting plants and frugivores. Other studies have used frugivorous diets above 50% (McFadden *et al.*, 2022). We also grouped birds and mammals as frugivores. Future studies may want to consider them separately as they have different feeding strategies and preferences, seed dispersal mechanisms, ecological roles, habitat preferences, mobility and range, body sizes, and physiological traits (Janson, 1983; Schupp *et al.*, 2010; Fleming & John Kress, 2011). Finally, considering the differences between generalists and specialists is also important, as generalists interact with a wide variety of species, while specialists have a narrower range of interactions. Generalists may provide stability to ecosystems by maintaining interactions even when specific species decline. Conversely, specialists might be more vulnerable to changes but are crucial for certain ecosystem functions (Solé & Montoya, 2001; Elmqvist *et al.*, 2003). Additionally, generalists often exhibit functional redundancy, where multiple species perform similar roles, thereby contributing to ecosystem stability. In contrast, specialists frequently have unique roles that cannot be easily replaced, making them critical for specific ecological processes (Devictor *et al.*, 2010). Furthermore, generalists may disperse seeds of many plant species over a wide area, whereas specialists tend to disperse seeds of fewer plant species but in a more targeted manner (Dehling *et al.*, 2021). Despite these limitations, the study provides valuable insights into the spatial scaling relationships between taxonomic and functional diversity in fruiting plant-frugivore interactions. Addressing these limitations will enhance our understanding of these relationships and improve the robustness of conclusions drawn from similar studies.

Future related studies should consider intraspecific trait variation, seasonality, temporal changes, and environmental drivers. Intraspecific trait variation affects functional roles within species and interactions with the environment, influencing competition, resource use efficiency, and ecosystem functioning (Bolnick *et al.*, 2011; Mitchell & Bakker, 2014; Chardon *et al.*, 2020; Zhou *et al.*, 2024). It indicates how populations might adapt to environmental changes, aiding predictions of responses to climate change and habitat degradation. For example, Martins et al. (2024) found that birds near their range limits feed more on fruits matching their beak size, illustrating trait variation's role under stress. Variation within species also contributes to functional redundancy (Rosenfeld, 2002). Seasonality and life cycles (e.g., flowering, fruiting, migration) are crucial for understanding species' roles and interactions (Cleland *et al.*, 2007; Forrest & Miller-Rushing, 2010). Climate change alters seasonal patterns, affecting species distributions and interactions. Monitoring temporal changes predicts ecosystem responses to future environmental changes. Environmental variables like temperature, precipitation, soil type, and light availability shape habitat suitability and species distributions, influencing biodiversity patterns (Tilman *et al.*, 2014). These considerations will enhance our understanding of biodiversity patterns.

This study provided evidence that the relationship between plant-frugivore taxonomic diversity and plant-frugivore functional diversity are scale-dependent and differ from each other. Future directions for this research not only could address the stated limitations, but also consider these relationships with environmental variables, varying the spatial or temporal extent, and including other dimensions of biodiversity. Such advancements will deepen our understanding of biodiversity patterns of interacting species and their underlying processes, ultimately contributing to more effective conservation strategies and ecosystem management.

1.6 Data Availability Statement

All the code used in this study for data processing, analysis, and visualizations, is publicly available on GitHub at https://github.com/bioXgeo/neotropical_plants/. The data used in this study will be available through the Environmental Data Initiative (EDI) upon publication of this manuscript.

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APPENDIX

Figure A1: Workflow diagram

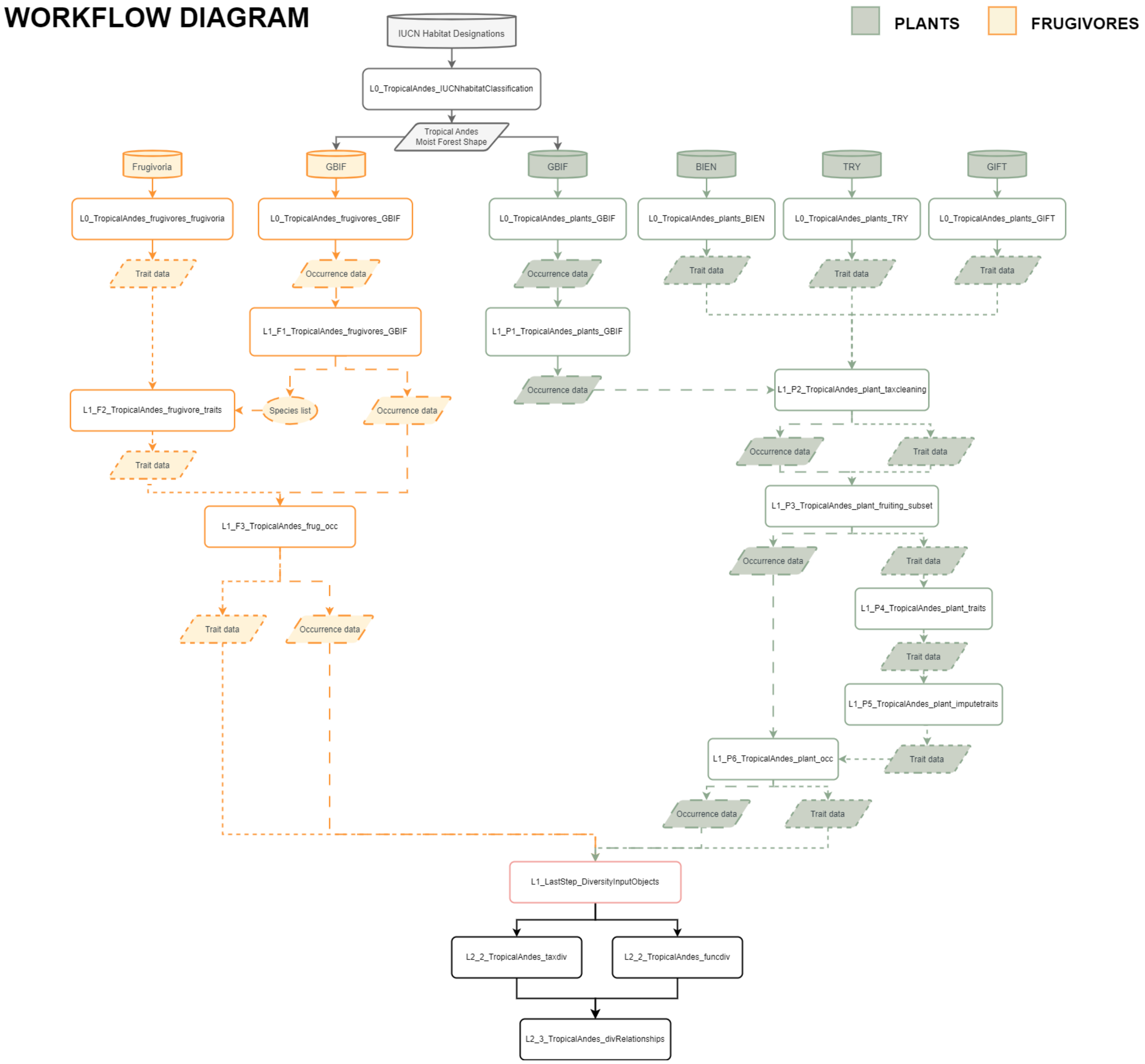

Table A1: Plant trait names and units across plant trait databases (BIEN (Maitner et al., 2018), TRY (Kattge *et al.*, 2020), and GIFT (Weigelt *et al.*, 2020)) as orginally sourced. See methods for trait selection process. Trait name IDs are shown in parentheses and originate from each database.

Trait	BIEN name	BIEN unit	GIFT name (ID)	GIFT unit	TRY name (TraitID)	TRY unit
Plant height	whole plant height, maximum whole plant height, minimum whole plant height	m	Plant_height_mean (1.6.3), Plant_height_min (1.6.1), Plant_height_max (1.6.2)	m	Plant height vegetative (3106, 3107)	m
Fruit mass					Fruit dry mass (919)	mg
Dispersal syndrome	whole plant dispersal syndrome	Categorical	Dispersal syndrome (3.3.1)	Categorical	Dispersal syndrome (28)	Categorical
Plant lifespan/ longevity	maximum whole plant longevity, longest whole plant longevity	years	Lifespan (2.2.1)	years	Plant lifespan (longevity) (59)	years
Fruit type	fruit type	Categorical	Fruit_type_1 (3.16.1)	Categorical	Fruit type (99)	Categorical
Fruit length	maximum fruit length, minimum fruit length	mm	Fruit_length_min (3.13.1), Fruit_length_max (3.13.2), Fruit_length_mean (3.13.3)	cm	Fruit length (918)	mm
Seed mass	seed mass	mg	Seed_mass_min (3.2.1), Seed_mass_max (3.2.2), Seed_mass_mean (3.2.3)	g	Seed dry mass (26)	mg
Seed length			Seed_length_min (3.10.1), Seed_length_max (3.10.2), Seed_length_mean (3.10.3)	mm	Seed length (27)	mm
Seed width			Seed_width_min (3.11.1), Seed_width_max (3.11.2), Seed_width_mean (3.11.3)	mm	Seed width (239)	mm
Growth form	whole plant growth form	Categorical	Growth_form (1.2.1)	Categorical	Plant growth form (42)	Categorical

Table A2: Trait types and expected values before trait harmonization.

Trait	Units	Type	Expected values
Plant height	m	Numerical	Values ranging from 0 to 1817
Fruit mass	mg	Numerical	Values ranging from 0 to 1500
Dispersal syndrome		Categorical	"zoochorous", "autochorous", "anemochorous", "anthropochorous", "myrmecochorous", "unspecialized", "hydrochorous"
Plant lifespan/longevity	years	Numerical	Values ranging from 0.75 to 1000
Fruit length	mm	Categorical	Values ranging from 0 to 2000
Seed mass	mg	Numerical	Values ranging from 0 to 1600000
Seed length	mm	Numerical	Values ranging from 0 to 2000
Seed width	mm	Numerical	Values ranging from 0 to
Growth form		Categorical	"Herb", "shrub", "tree", "other"
Body size	mm	Numerical	Values ranging from 18 to 2220
Body mass	g	Numerical	Values ranging from 4.85 to 140000.63
Diet category		Categorical	"PlantSeed", "FruiNect", "Omnivore", "Invertebrate", "VertFishScav"
Generation time	years	Numerical	Values ranging from 0.41 to 100.00

Table A3: Taxonomic backbone of the various trait and occurrence databases.

Database name	Taxonomic backbone	Source
BIEN	Taxonomic Name Resolution Service (Boyle et al., 2013) which consults World Flora Online (WFO, 2023) and World Checklist of Vascular Plants (Govaerts et al., 2021)	(Maitner et al., 2018)
TRY	World Flora Online (WFO, 2023), as well as the Leipzig Catalogue of Vascular Plants (LCVP) (Freiberg et al., 2020), and TROPICOS (Missouri Botanical Garden, 2023)	(Boenisch & Kattge, 2023)
GBIF	Catalogue of Life (Bánki et al., 2023) and is supplemented by other sources like the International Barcode of Life (The International Barcode of Life Consortium, 2023), World Checklist of Vascular Plants (Govaerts et al., 2021), the Leipzig Catalogue of Vascular Plants (LCVP) (Freiberg et al., 2020), and many more	(GBIF Secretariat, n.d.)
GIFT	World Checklist of Vascular Plants (Govaerts et al., 2021) and iPlant's Taxonomic Name Resolution Service (Boyle et al., 2013)	(Biodiversity, Macroecology & Biogeography group, 2023)
Frugivoria	IUCN Redlist (IUCN, 2022)	(Gerstner et al., 2023b)

Full citations available in Chapter 1 Reference list.

Figure A2: A Sankey diagram visualizing the number of plant species through steps of the taxonomic harmonization process.

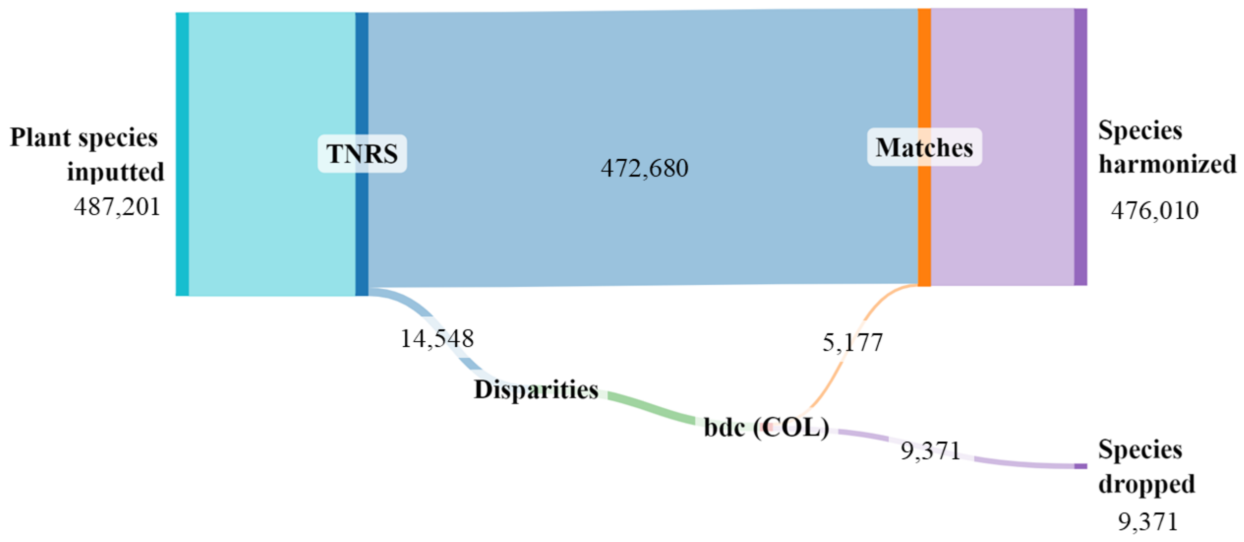

Table A4: Plant species harmonization species counts per step/package in harmonization process (Figure A2).

Package used (database)	Step	Number of species
	Plant species inputted	487,201
TNRS	Matches (accepted or synonyms)	472,680
TNRS	Disparities (Illegitimate, no opinion, invalid, or “ “)	14,548
	Plant species inputted	14,548
bdc (COL)	Matches (accepted or synonyms)	5,177
bdc (COL)	Disparities (Illegitimate, no opinion, invalid, or “ “)	9,371
	Species harmonized	476,010
	Species dropped	9,371

Table A6: Plant trait data species coverage across all trait databases during plant trait harmonization.

Trait Name	Number of species	Number of species with 1 record	Number of species with more than 3 records
Dispersal Syndrome	1932	402	942
Fruit Mass	337	120	195
Fruit Length	2035	435	461
Plant Height	2985	266	1845
Plant Lifespan	510	272	69
Seed Mass	2210	239	1823
Seed Length	1259	196	450
Seed Width	635	150	273
Growth Form	2862	2785	1
Fruit Type	2011	1307	26

Figure A3: Plant species coverage by trait after (a) trait standardization and (b) adding genus or family level traits. After imputation, all plant species coverage was at 100%.

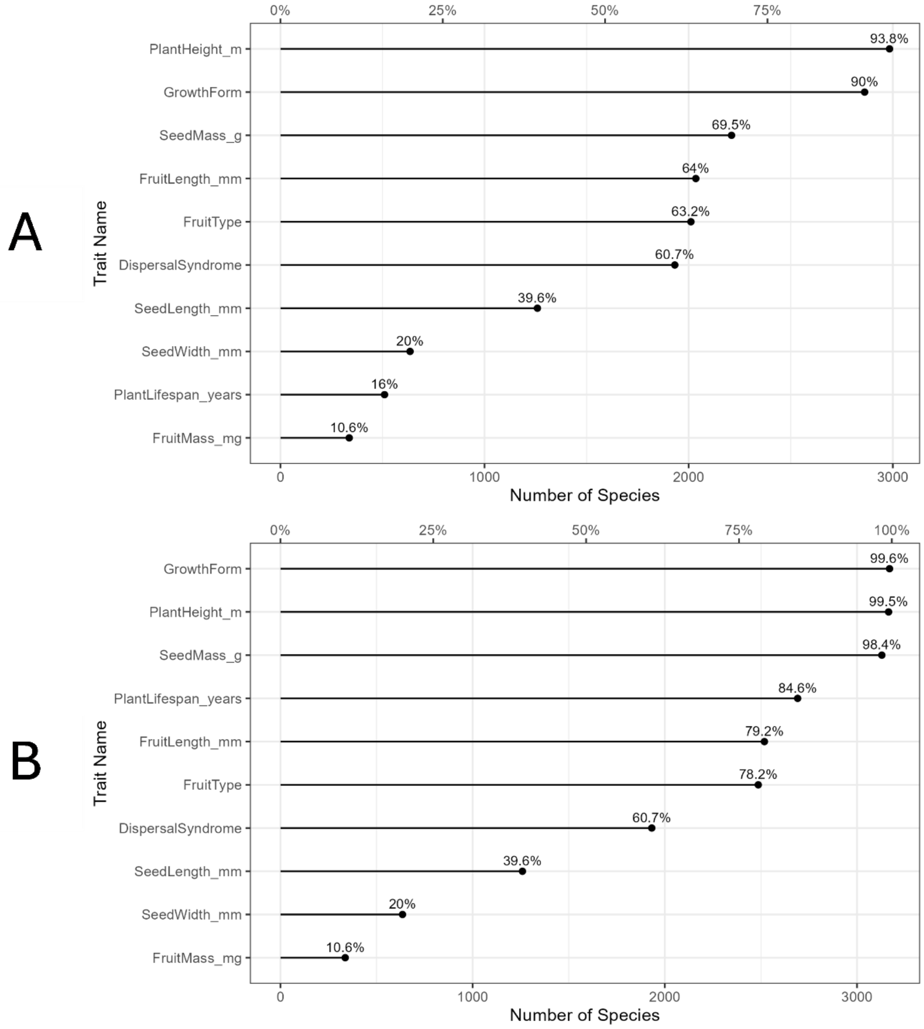

Figure A4: The comparison of the number of plant traits used per database source after trait cleaning but before getting one value per species.

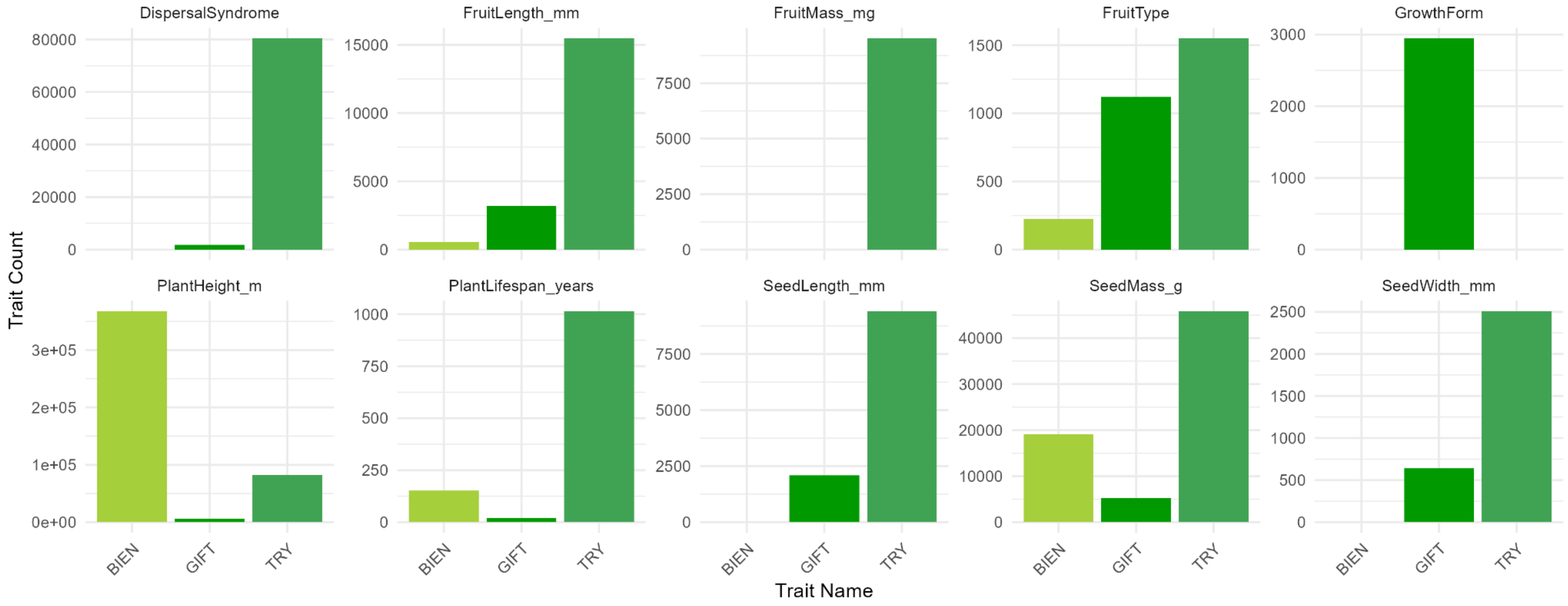

Figure A5: Counts of traits by the level of species, genus, family, or imputation for each trait type and overall. The final plant trait dataset consisted of 16,810 traits from the species level (52.78%), 1,647 traits from the genus level (5.17%), 2,904 traits from the family level (9.12%), and 10,489 traits were imputed (32.93%).

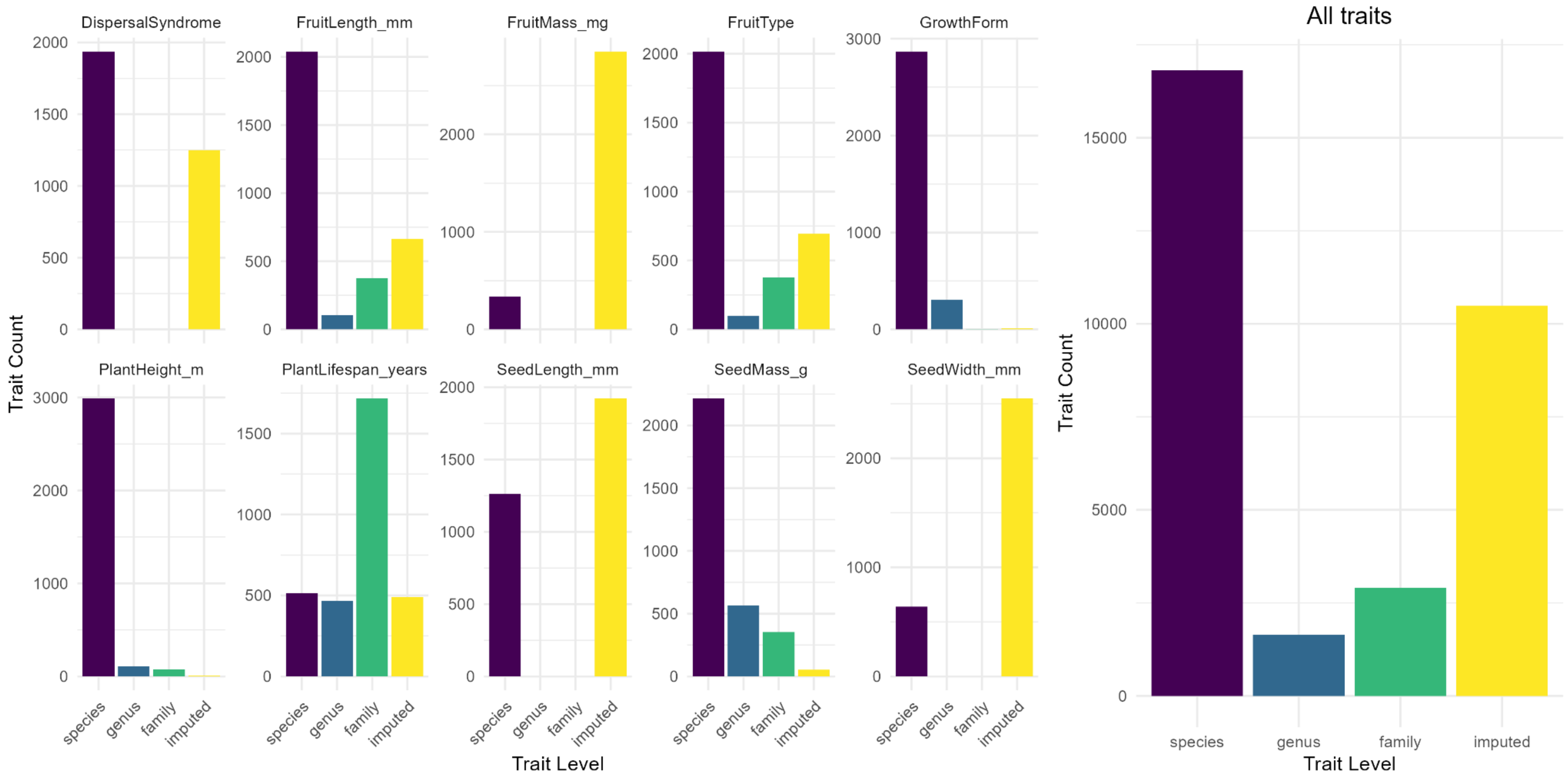

Figure A6: The taxonomic coverage of fruiting plants by family, genera, and species of the final dataset compared to the GIFT checklist data of all angiosperms in the Tropical Andes Forest generated using the GIFT R package (Denelle & Weigelt, 2023). The dataset contained 3,128 species, 1,359 genera, and 213 families in contrast to the GIFT checklist, which contained 70,376 species, 4,381 genera, and 273 families.

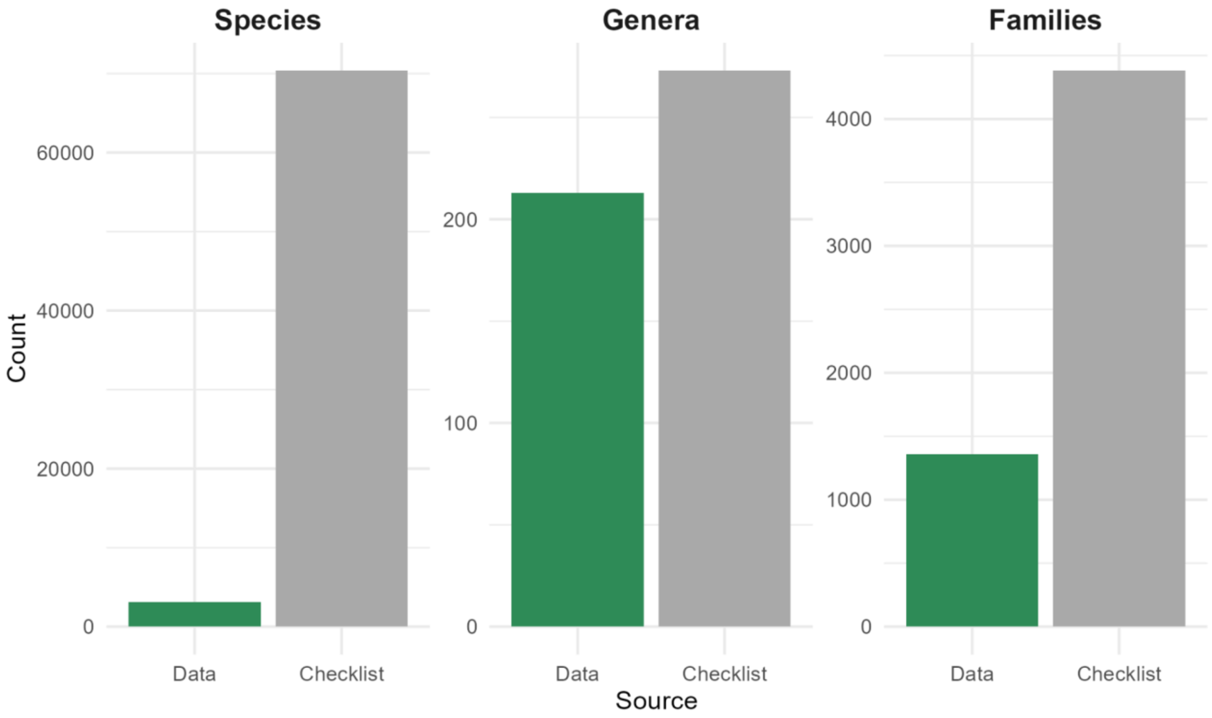

Figure A7: The number of plant and frugivore records, species, genera, and families represented in the data through various steps of processing the data. For plant data, the number of occurrence records for the raw data was 4,519,792, after cleaning 1,886,120, and with full trait coverage 658,609. The number of plant species for the raw data was 40,288, after cleaning 39,972, and with full trait coverage 3,128. The number of plant genera for the raw data was 4,083, after cleaning 3,793, and with full trait coverage 1,359. The number of plant families for the raw data was 307, after cleaning 293, and with full trait coverage 213. For frugivore data, the number of occurrence records for the raw data was 8,885,330, after cleaning 1,721,825, and with full trait coverage 1,667,892. The number of frugivore species for the raw data was 1,360, after cleaning 1,219, and with full trait coverage 1,074. The number of frugivore genera for the raw data was 400, after cleaning 398, and with full trait coverage 370. The number of frugivore families for the raw data was 66, after cleaning 66, and with full trait coverage 64.

Table A7: Extended R package citations and version numbers.

Package name	Version	Citation
bcd	1.15	Ribeiro B, Velazco S, Guidoni-Martins K, Tessarolo G, Jardim L (2024). bdc: Biodiversity Data Cleaning. R package version 1.1.5, https://brunobrr.github.io/bdc/ (website), https://github.com/brunobrr/bdc.
BIEN	1.24	Brian Maitner (2020). BIEN: Tools for Accessing the Botanical Information and Ecology Network Database. R package version 1.2.4. https://CRAN.R-project.org/package=BIEN
coordinateCleaner	3.0.1	Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, Svanteson S, Wengstrom N, Zizka V, Antonelli A (2019). "CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases." Methods in Ecology and Evolution, -7. doi:10.1111/2041-210X.13152, R package version 3.0.1, https://github.com/ropensci/CoordinateCleaner.
countrycode	1.6.0	Arel-Bundock V, Enevoldsen N, Yetman C (2018). "countrycode: An R package to convert country names and country codes." Journal of Open Source Software, 3(28), 848. https://doi.org/10.21105/joss.00848.
dplyr	1.1.4	Wickham H, François R, Henry L, Müller K, Vaughan D (2023). *dplyr: A Grammar of Data Manipulation*. R package version 1.1.4, https://github.com/tidyverse/dplyr, https://dplyr.tidyverse.org.
funbiogeo	0.0.0.9000	Casajus N & Grenié M (2024). funbiogeo: Functional Biogeography Analyses. R package version 0.0.0.9000, https://github.com/frbcesab/funbiogeo.
ggplot2	3.5.1	Wickham H (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.
ggpubr	0.6.0	Kassambara A (2023). ggpubr: 'ggplot2' Based Publication Ready Plots. R package version 0.6.0, https://rpkgs.datanovia.com/ggpubr/.
ggspatial	1.1.9	Dunnington D (2023). ggspatial: Spatial Data Framework for ggplot2. https://paleolimbot.github.io/ggspatial/, https://github.com/paleolimbot/ggspatial.

Table A7 (cont'd)

GIFT	1.3.2	Denelle P, Weigelt P (2024). GIFT: Access to the Global Inventory of Floras and Traits (GIFT). R package version 1.3.2, https://biogeomacro.github.io/GIFT/, https://github.com/BioGeoMacro/GIFT.
knitr	1.46	Xie Y (2024). knitr: A General-Purpose Package for Dynamic Report Generation in R. R package version 1.46, https://yihui.org/knitr/.
letsR	5.0	Bruno Vilela and Fabricio Villalobos (2015). letsR: a new R package for data handling and analysis in macroecology. Methods in Ecology and Evolution. DOI: 10.1111/2041-210X.12401
mFD	1.0.7	Magneville C, Loiseau N, Albouy C, Casajus N, Claverie T, Escalas A, Leprieur F, Maire E, Mouillot D, Villeger S (2022). mFD: mFD: an R package to compute and illustrate the multiple facets of functional diversity, volume 2022 number 1. https://onlinelibrary.wiley.com/doi/full/10.1111/ecog.05904.
mice	3.16.0	van Buuren S, Groothuis-Oudshoorn K (2011). "mice: Multivariate Imputation by Chained Equations in R." Journal of Statistical Software, 45(3), 1-67. doi:10.18637/jss.v045.i03.
purr	1.0.2	Wickham H, Henry L (2023). purrr: Functional Programming Tools. R package version 1.0.2, https://github.com/tidyverse/purrr, https://purrr.tidyverse.org/.
raster	3.4-5	Robert J. Hijmans (2020). raster: Geographic Data Analysis and Modeling. R package version 3.4-5. https://CRAN.R-project.org/package=raster
rgbif	3.79	Chamberlain S, Barve V, Mcglinn D, Oldoni D, Desmet P, Geffert L, Ram K (2024). rgbif: Interface to the Global Biodiversity Information Facility API. R package version 3.7.9, https://CRAN.R-project.org/package=rgbif Chamberlain S, Boettiger C (2017). "R Python, and Ruby clients for GBIF species occurrence data." PeerJ PrePrints. https://doi.org/10.7287/peerj.preprints.3304v1.

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rtry	1.0.0	Olee Hoi Ying Lam, Susanne Tautenhahn, Gabriel Walther, Gerhard Boenisch, Pramod Baddam and Jens Kattge (2022). rtry: Preprocessing Plant Trait Data. R package version 1.0.0. https://CRAN.R-project.org/package=rtry
sf	1.0-16	Pebesma, E., & Bivand, R. (2023). Spatial Data Science: With Applications in R. Chapman and Hall/CRC. https://doi.org/10.1201/9780429459016 Pebesma, E., 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10 (1), 439-446, https://doi.org/10.32614/RJ-2018-009
smoothr	1.0.1	Strimas-Mackey M (2023). smoothr: Smooth and Tidy Spatial Features. https://strimas.com/smoothr/, https://github.com/mstrimas/smoothr.
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taxize	0.9.100	Scott Chamberlain and Eduard Szocs (2013). taxize - taxonomic search and retrieval in R. F1000Research, 2:191. URL: https://f1000research.com/articles/2-191/v2 Scott Chamberlain, Eduard Szoecs, Zachary Foster, Zebulun Arendsee, Carl Boettiger, Karthik Ram, Ignasi Bartomeus, John Baumgartner, James O'Donnell, Jari Oksanen, Bastian Greshake Tzovaras, Philippe Marchand, Vinh Tran, Maëlle Salmon, Gaopeng Li, and Matthias Grenié. (2020) taxize: Taxonomic information from around the web. R package version 0.9.98. https://github.com/ropensci/taxize

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Terra	1.7-76	Hijmans R (2024). terra: Spatial Data Analysis. R package version 1.7-76, https://rspatial.github.io/terra/, https://rspatial.org/.
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CONCLUSION AND DISCUSSION

This research advances our understanding of the spatial grain-dependent relationships between fruiting plant-frugivore taxonomic and functional diversity in the Tropical Andes forests. The analysis in Chapter 1 leverages open data repositories of occurrence and trait data for fruiting plants and frugivores. By investigating these relationships, this research contributes to our understanding of how plant-frugivore interdependence impacts the relationship of their taxonomic and functional diversity in space to use this information to refine ecological theories and support conservation.

The analysis in Chapter 1 found that both plant-frugivore taxonomic and functional diversity relationships were the strongest at the coarsest spatial grain (100 km), the relationship of fruiting plant-frugivore taxonomic diversity was stronger than functional diversity across all spatial grains, and fruiting plant-frugivore taxonomic diversity had a stronger scaling relationship than fruiting plant-frugivore functional diversity. These findings reiterate the importance of using multiple dimensions of diversity and that biodiversity relationships are often grain-dependent, which helps provide a more nuanced understanding of ecological patterns and processes. It underscores the need to consider various spatial scales and dimensions of diversity in conservation planning and ecological research.

One of the limitations briefly touched upon in Chapter 1 is that the selection of traits was limited by available data in large databases, especially for plants. In addition to providing more funding and resources to fill in these gaps for both trait and occurrence data, other methods to increase data coverage may also be useful including digitizing specimens, community science, combining existing datasets, and remote sensing. Digitizing herbarium specimens has promise to contribute to knowledge of local diversity, as small herbaria contain unique records and have shown to be potential sources of plant trait measurements (Lavoie, 2013; Daru *et al.*, 2018;

Heberling *et al.*, 2019; Marsico *et al.*, 2020; Harris et al., 2021; Davis, 2022; Heberling, 2022; Hussein *et al.*, 2022). Citizen or community science is also gaining popularity as a way to contribute vital biodiversity data while also engaging people with nature (Amano *et al.*, 2016; Aristeidou *et al.*, 2021; Callaghan *et al.*, 2021, 2022). Harmonizing and combining small existing datasets may also provide key occurrence and trait data (Lenters *et al.*, 2021; Spear *et al.*, 2023). Remote sensing has also received notable attention as technologies advance and can measure certain traits over broad extents much quicker than in situ collection (Schneider *et al*., 2017; Rocchini *et al*., 2021; Angel & Shiklomanov, 2022). Using all the resources and methods available will enable a more complete picture of biodiversity and reduce the amount of bias and uncertainty in our ability to measure and conserve plant biodiversity.

Other considerations that future macroecological plant biodiversity studies should take into account include intraspecific trait variation, seasonality and changes over time, and environmental drivers of biodiversity. It is also important to consider intraspecific trait variation as it can influence the functional roles of individuals within a species and how individuals interact with their environment and contribute to ecosystem processes (Mitchell & Bakker, 2014; Chardon *et al.*, 2020; Zhou *et al.*, 2024). Different individuals within a species may exploit resources differently, impacting competition, resource use efficiency, and overall ecosystem functioning (Bolnick *et al.*, 2011). Intraspecific trait variation can indicate how populations might adapt to environmental changes or stressors, which helps predict responses to climate change, habitat degradation, or other disturbances (Chardon *et al*., 2020). For example, the study by Martins et al. (2024) illustrates how plant-frugivore relationships vary geographically, with birds at the edge of their range feeding more frequently on fruits that match their beak size, highlighting the influence of intraspecific trait variation under environmental stress. Variation within species contributes to functional redundancy, where multiple individuals or populations perform similar ecological roles (Rosenfeld, 2002). Seasonal and temporal variations are also important factors to consider. Taking into account species life cycles and phenological events (e.g., flowering, fruiting, migration) is crucial for accurately describing species' roles in ecosystems and their interactions with other species (Cleland *et al.*, 2007; Forrest & Miller-Rushing, 2010). The seasonal variation in the timing and intensity of species interactions, such as seed dispersal and pollination, helps explain how these interactions influence community composition and ecosystem processes (Elzinga *et al*., 2007; Memmott *et al.*, 2007). Seasonal patterns are being altered by climate change, affecting species distributions, migration patterns, and ecological interactions. Species may adapt to or shift in response to changing seasonal conditions. Monitoring changes over time helps predict how ecosystems will respond to future environmental changes and the impacts of climate change on biodiversity and ecosystem functioning. Finally, environmental variables could also be impacting patterns of biodiversity. Environmental variables such as temperature, precipitation, soil type, and light availability determine the suitability of habitats for different species. Understanding these factors helps explain current species distributions and predict potential range shifts. Changes in environmental conditions can alter the dynamics of species interactions and influence the availability of resources (Tilman *et al.*, 2014). All of these considerations will help us get closer to a more comprehensive understanding of patterns of biodiversity.

As we collectively work towards conserving biodiversity, we must keep in mind the irreplaceable role Indigenous people play. Indigenous people make up less than 5% of the global population, yet steward more than 25% of the earth and protect 80% of global biodiversity (Garnett *et al.*, 2018). Indigenous-managed lands often have higher levels of species richness than protected areas (Sze *et al.*, 2024). Cultural diversity often correlates with biological diversity, underlining the need to protect both (Levis *et al*., 2024). As many conservationists and conservation organizations promote the 30X30 initiative to protect 30% of the earth's land and seas by 2030 (Dinerstein *et al.*, 2019), supporting Indigenous land rights should be prioritized instead of reinforcing "fortress conservation", working towards decolonizing conservation policies (Domínguez & Luoma, 2020; Gewin, 2022). As incorporating Indigenous knowledge becomes more common in biodiversity research, Indigenous Data Sovereignty should be recognized by applying CARE: Collective benefit, Authority to control, Responsibility, and Ethics (Jennings *et al.*, 2023). Ultimately, acknowledging and respecting Indigenous stewardship and knowledge is not only a matter of justice but also a vital component of effective and sustainable conservation strategies. Without genuine collaboration and inclusion of Indigenous perspectives, efforts to understand and protect biodiversity may fall short of their full potential.

My intent for this thesis was to contribute to our understanding of the spatial patterns of fruiting plant-frugivore biodiversity in a biodiversity hotspot. I pursued these goals through a macroecology and biogeography lens with big data. By investigating these relationships, this work illuminates how interactions between fruiting plants and frugivorous birds and mammals affect the spatial patterns of their taxonomic and functional diversity, as well as the spatial scale dependence of those relationships. Any contribution I can make towards our understanding of biodiversity in this rapidly changing world is worth it as it brings us closer to better stewardship of global biodiversity.

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