



Revealing the influence of climatic variables on the distribution of legume dispersal traits in the Chaco

Giovani Carlos Andrella^{1, 3*} , Evaldo Benedito de Souza²  and Ângela Lúcia Bagnatori Sartori^{1, 3} 

Received: May 17, 2023

Accepted: September 25, 2023

ABSTRACT

Climate influences species distribution and selects different morphological traits. The Chaco biome has climatic gradients, leading us to question morphological trait distribution. Using Fabaceae as a study model, we aimed to understand how the dispersal traits of this family, such as fruit types, dispersal syndromes and dispersal units, are distributed along the climatic gradients in the Chaco. We performed a spatial analysis in order to generate spatial predictors and thus identify on which spatial scales climate and soil variables are relevant to the distribution of the traits. Also, we used Threshold indicator rate analysis to identify the variation of the traits along the gradients. Temperature seasonality, precipitation seasonality, and annual mean precipitation are significant predictors of the distribution of the analyzed traits. Anemochory and barochory show the occurrence of reductions in intermediate gradient values for temperature seasonality. Regarding precipitation seasonality, craspedium showed greater reductions. At intermediate values of the rainfall gradient, we observed an increase in the occurrence of drupes and follicles. Craspedium increases in drier regions. Understanding the dispersion patterns of Fabaceae, a group of significant ecological and ethnological relevance in the Chaco, should contribute to the consolidation of conservation plans in different dry forest areas in South America.

Keywords: Chaco, Dispersal syndromes, Dry forests, Fabaceae, Spatial analysis

Introduction

Environmental predictors such as climate and soil properties are some of the modulators of species distribution and richness around the globe on different spatial scales (Dell *et al.* 2011; Jara-Guerrero *et al.* 2011; Moles *et al.* 2014; Payne *et al.* 2018; Baptista *et al.* 2020; Assunção *et al.* 2022).

Scales can substantially affect the observed patterns and therefore need to be considered as part of observational ecological studies (Wiens 1989). For instance, at the individual level, temperature can result in changes in metabolic activity rates, and at the population level, it influences distributional patterns and species abundance (Dell *et al.* 2011; Payne *et al.* 2018). Precipitation is crucial in establishing plant

¹ Laboratório de Sistemática Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul – UFMS, Cidade Universitária s/n. 79070-900 Campo Grande - MS, Brazil.

² Laboratório de Ecologia Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul - UFMS. Cidade Universitária s/n. 79070-900 Campo Grande - MS, Brazil.

³ Programa de Pós-graduação em Biologia Vegetal, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande - MS, Brazil.

* Corresponding author: giovani.andrella@gmail.com



species, influencing vegetation composition and ecological interactions such as seed dispersal (Jara-Guerrero *et al.* 2011; Moles *et al.* 2014). Specifically, in dry forests, there is a lack of knowledge on how environmental characteristics and specific functional traits enable the survival of plant species in dry environments with marked seasonality (Pinho *et al.* 2019).

Tropical seasonally dry forests (SDTF) are regions with low rainfall, strong seasonality, and generally fertile soils (Murphy & Lugo 1986). In this context, the Chaco stands out as the largest continuous dry forest biome in South America, with a high richness of plant species, especially legumes, and is among the most threatened vegetation formations in the world due to deforestation (Hansen *et al.* 2013; Fehlenberg *et al.* 2017). For the Chaco are estimated that 20% of the natural vegetation has already been deforested, and the rest is fragmented (de la Sancha *et al.* 2021). Studies that focus on understanding patterns of diversity and morphological traits are of urgency in these environments due to the high anthropic pressure ranging from fragmentation and local extinctions to climate changes at the global level. Such studies would provide knowledge about the biome, permitting us to understand the diversity and ecological relationships of the organisms living in it.

The Chaco is characterized as a climatically heterogeneous biome (Prado 1993; Pennington *et al.* 2000). First, because of the presence of a rainfall gradient from east to west, historically, the biome has been divided into two sectors, with the wet sector, further east (over 1,200 mm.yr⁻¹), covering portions of Argentina, Brazil, and Paraguay and the dry sector, further west (500 to 700 mm. yr⁻¹) closer to the Andes, covering territories of Argentina, Paraguay, and Bolivia (Ramella & Spichiger 1989; Adamoli *et al.* 1990; Prado 1993). Second, due to the differences in temperature along the biome, with higher values in the north and lower values in the south (Hueck 1972). Another critical factor in the Chaco is the climatic seasonality, which significantly alters the landscape throughout the year, with very different rainfall and temperature values in different seasons and with other effects on biodiversity such as richness and distribution of species (Prado 1993; Chesson 2000; Pennington *et al.* 2000; Tonkin *et al.* 2017).

The variation of plant dispersal traits concerning environmental characteristics (*e.g.*, rainfall gradients) helps to understand distributional patterns, evolutionary and occupation processes (Alberto *et al.* 2013). Furthermore, seed dispersal is a critical factor for establishing plant species in a biome and for the spatial structuring of plant communities (Cousens *et al.* 2008; Jara-Guerrero *et al.* 2015). In this sense, considering the spatial configuration of communities using spatial variables in addition to climate ones, is crucial to understanding how the communities found in the Chaco are occupied and formed. In this context, Fabaceae represents an exciting model for the study of the biological relationships of its representatives with different climatic determinants. The family, of ancient origin, is widely

distributed in the Old and New World (Bouchenak-Khelladi *et al.* 2010) and has a wide morphological diversity (*e.g.*, fruit types). Fabaceae is represented by 361 species in the Chaco, mainly trees and shrubs (Noguchi *et al.* 2009; Sartori *et al.* 2018; Morales *et al.* 2019; Baptista *et al.* 2020).

Studies of extensive areas such as biomes have detected changes in morphological traits along climatic gradients (Cornwell & Ackerly 2009; Schellenberger Costa *et al.* 2017; Dong *et al.* 2020). For example, places with higher values of annual rainfall tend to have a greater diversity of plant species with a predominance of trees and zoochoric dispersion, while drier areas have less diversity and contain species with functional traits linked to water economy and dispersion by abiotic factors (Tabarelli *et al.* 2003; Esquivel-Muelbert *et al.* 2017; Leigh Jr *et al.* 2004). The same happens with temperature gradients, which interfere with ecological functions such as fruit maturation and the presence of dispersers (Jara-Guerrero *et al.* 2011). Environmental gradients in the Chaco show significantly different values at their extremes. This variation leads us to question the distribution of morphological traits with ecological roles along these gradients, as reported for other biomes. In general, climate filters species according to their functional characteristics, and considering the impacts that environmental gradients have on species diversity, we expect that there will be changes in species predominance and functional traits linked to dispersal at different locations along the gradients. Furthermore, studies that aim to understand the relationship between seasonality gradients and dispersal traits of plants are scarce and are very important for the understanding of the dynamics of distribution, dispersion, and occupation of areas by plant species.

Thus, finding patterns of variation of plant morphological traits according to environmental characteristics (*e.g.*, seasonality gradients) can help us understand the evolutionary processes and selection of these traits (Alberto *et al.* 2013). Therefore, the objective of our study was to understand (i) which environmental variables shape the different morphological traits of tree and shrub legumes and (ii) how the traits are distributed along gradients in the Chaco. Due to the different climatic gradients traditionally recognized in the Chaco and an exacerbated seasonality, as hypotheses, we postulate that (i) average annual precipitation and variables linked to seasonality have a more significant impact on the distribution of traits and (ii) traits linked to zoochoric dispersion are concentrated in more wet places of the Chaco, and dry fruits and dispersal by abiotic factors in drier places.

Materials and methods

Study area

The Chaco ecoregion covers approximately 1,080,000 km² (Olson *et al.* 2001) and is considered to be South America's largest continuous dry forest formation (Prado & Gibbs



1993; Pennington *et al.* 2000). Chaquen soils were derived from massive aeolian and river sediment accumulations during the Quaternary period (Pennington *et al.* 2000; Prado 1993). No rocks are found in Chaquen soils (except near mountain ranges), which are compacted and difficult to drain. Luvisols are the most common soil type, although cambisols and arenosols can also be found (Pennington *et al.* 2000; May *et al.* 2008). The climate is marked by strong seasonality and is classified as warm, humid, and temperate in the east (Humid Chaco) and semiarid in the west (Dry Chaco) (Lewis 1991; Pennington *et al.* 2000). The annual average temperature varies from 18° C in the south to 26° C in the north, with absolute maximum values reaching 48° C during the summer (Lewis *et al.* 1994). The area experiences severe winters and frosts can occur several times yearly (Prado 1993).

Uneven rainfall in the Chaco forms a decreasing east-to-west gradient, with values closer to 400 mm/year near the Andes but reaching 1500 mm/year in southeastern Paraguay. The dry sector of the Chaco corresponds to areas with rainfall averages of up to 700 mm/year (Adamoli *et al.* 1990; Prado 1993; Pennington *et al.* 2000) and includes large sections of Paraguay and parts of Argentina and Bolivia. The wet sector, which receives more than 1200 mm/year of rainfall, includes Argentina and the western border of Brazil. According to previous studies, except that by Andrella and Sartori (2021), the recognition of two sectors, dry and wet, does not consider irregular a rainfall between 700 and 1200 mm/year. The delimitation of the Chaco adopted in this study is based on Olson *et al.* (2001).

Data collection and morphological traits

We assembled a list of Fabaceae species by means of physical visits to herbaria such as PY and FCQ from Paraguay, ACOR and BAB from Argentina, LPB from Bolivia, and CGMS from Brazil. Next, the occurrence of Fabaceae species in the Chaco was obtained from the Global Biodiversity Information Facility (GBIF) website. Only records identified at the species or intraspecific level were considered. We removed duplicate occurrences, coordinates without decimal digits, and those georeferenced at sea, in capitals, in research institutions, and in the centroids of countries, provinces, and states. The data were then selected using QGIS 2.18 software, and collections within the Chaco ecoregion's limits were considered. Nineteen bioclimatic variables were obtained from the WorldClim database (<https://www.worldclim.org/>). In addition to climate variables, we also included clay content obtained from the Soilgrids database (<https://soilgrids.org/>), with a resolution of 250 m (Poggio *et al.* 2021, Table S1). To avoid saturation of the models, we performed Pearson correlation analyses between the environmental variables and selected the following variables: mean annual temperature, mean annual precipitation, seasonality of precipitation, and seasonality of temperature, all with < 68% autocorrelation.

Growth forms (trees and shrubs) were determined according to information provided by the collector and, in the absence of such information, were verified in the specialized literature or by consulting the exsiccates of online herbaria. Only trees and shrubs were considered. The species were identified based on the taxonomic literature, consultation with standard material, and comparisons with specimens from online herbaria (NY, MO, P) and were identified by specialists. Botanical names were checked and updated using online herbaria and the latest specialized literature. The fruits and the dispersion unit types were analyzed directly from the exsiccates and, when necessary, complemented with information available in the literature. The classification of fruits was based on Harris and Harris (1994). The criteria for the characterization of the fruits were: the aspects of their thick and/or swollen tissues, the occurrence of dehiscence (or not), the presence of dry tissue, the presence of wings, and the presence of spongy tissue. Based on their morphological characteristics, the species were classified as zoochoric, anemochoric, autochoric, barochoric, or hydrochoric, according to Van der Pijl (1982). We also considered the dispersion factor between biotic for zoochoric syndrome and abiotic for the others (Table 1).

Table 1. Traits evaluated in the legumes of the Chaco.

Growth form	Traits			
	Fruit type	Dispersal unit	Dispersal factor	Dispersal syndromes
Tree	Craspedium	Fruit	Biotic	Anemochory
Shrub	Cryptosamara	Seed	Abiotic	Barochory
	Legume <i>stricto sensu</i>			Zoochory
	Fleshy legume			Autochory
	Samara			Hydrochory
	Folicle			
	Drupe			

Data Analysis

A grid with hexagonal cells (11 × 11 km) was constructed to delimit the sampling units using the QGIS software (version 2.18.14). With this grid, 342 sample units were generated. To prevent the frequency of a given characteristic from being inflated due to the repetition of species in the sampling units, we excluded repeated species in each sampling unit. To verify the existence of spatial autocorrelation, we used the Mantel correlogram (Legendre & Legendre 2012; Fig. S1). For this, data on species traits were standardized (using the Hellinger method) and detrended (residues of the linear relationship between variables and geographic coordinates) (Legendre & Legendre 2012; Borcard *et al.* 2018). Spatial structuring was analyzed using a distance-based eigenvector matrix (dbMEMs) and the dbmem function of the adespatial package (Dray *et al.* 2012). We constructed the matrix of



dbMEMs by using the geographical coordinates matrix. The function *dbmem* generated 84 spatial variables. Each dbMEM represents a class of spatial structures based on geographic distances between samples, from least extensive to most extensive (in our case, from dbMEM 84 to dbMEM 1, respectively). This dbMEM analysis produced spatial models combining all spatial variables selected directly from the set of 84 dbMEMs with a positive spatial correlation.

We used canonical ordering (RDA) to relate plant characteristics with dbMEMs. The significant axes of the RDA were used as the response variable to the environmental variables. We applied model selection with the *forward.sel* function. After the selection five of the spatial variables (dbMEMs 9, 12, 16, 24, 75) were found to be significant. Next, to see how much of the variation in the data is explained by the dbMEMs, we ran a second RDA using only the five dbMEMs that were significant. To verify if the variation in the spatial structure of the data is related to the environmental variables, we tested the first axis of the second RDA as a response variable against the environmental variables. For this, we use a generalized linear model (GLM). To select the best set of environmental variables, we apply model selection using the *forward.sel* function. Furthermore, to verify whether the spatial structure responds differently at different scales, we separated the five significant dbMEMs into broad (dbMEM 9 and 12), medium (16 and 24), and fine (dbMEM 75) scales and analyzed them separately, following the steps described above (Legendre & Legendre 2012; Borcard *et al.* 2018). Here, we use the definition of broad and fine scales described by Wiens (1989) and Legendre and Legendre (2012).

To detect changes in plant characteristics across environmental gradients that were significant in the previous analysis, we used a Threshold Indicator Taxa Analysis (TITAN). This analysis is based on the principles of Indicator Species Analysis (IndVal) which aims to identify points of change in the abundance of taxa in a continuous gradient. TITAN provides a more sensitive and accurate alternative to existing methods for assessing community boundaries. For this, the analysis uses bootstrap resampling to estimate the uncertainty associated with the sample and thus select the taxa (in our case, plant traits) that most contribute to patterns of change along environmental gradients. This process sets attributes with 95% purity and reliability. These two criteria (purity and reliability) are essential to show which plant characteristics are primarily responsible for changes along environmental gradients (Baker & King 2010). Purity is the proportion of the changepoint response directions (positive or negative) between bootstrap replications that agree with the observed response. Reliability is estimated by the ratio of bootstrap changepoints whose IndVal scores consistently result in p-values below one or more user-determined probability levels (e.g., $P < 0.05$) (Baker & King 2010). The analysis also selects those indicator traits that, despite having <

95% purity and reliability, contribute substantially to the pattern of changes in environmental gradients. For this analysis, we used the *titan* function from the “TITAN2” package in an R environment (Baker *et al.* 2020).

Results

Morphological traits of the legumes

A total of 290 taxa of legumes (trees and shrubs) in the Chaco were evaluated (Table S2). Seven types of fruits were recorded, with legumes *sensu stricto* (86 species), fleshy legumes (83), craspedium (50), and samara (49) standing out (Fig. 1A). Throughout the Chaco, we found that abiotic dispersal occurred among 221 species and biotic dispersal among 69 species (Fig. 1B), with a predominance of autochory (148 species), followed by zoochory (69 species) (Fig. 1C). Abiotic dispersal was observed in 68 genera, such as *Mimosa* (50 species) and *Bauhinia* (20 species) with craspedium and legumes *sensu stricto*, respectively. Fruits related to biotic dispersal were found in 14 genera, with emphasis on *Neltuma* (27 species) and *Inga* (10 species), both of which produce fleshy legumes. *Senna* with high richness (29 species). Concerning the dispersion unit, there was a predominance of dispersion via seed (158 species) followed by dispersion via fruit (132 species). contributed with fruits dispersed by different agents. Trees were more numerous (156 species) than shrubs (134 species).

Spatial analysis and relationships with environmental variables

The full RDA, with all dbMEMs (ie, including all scales), showed a relationship with plant characteristics (RDA: $R^2 = 0.28$; $\text{adj}R^2 = 0.05$; $F = 1.2$; $p = 0.027$). All five selected spatial variables (dbMEMs 9, 12, 16, 24, 75) were significant in the second RDA ($R^2 = 0.057$; $\text{adj}R^2 = 0.043$) (Fig. S2). Only the first axis of the RDA with this reduced model was significant (RDA anova table: $F = 16.5$; $p = 0.001$). The first significant canonical axis is a combination of dbMEM variables ranging from broad scale (dbMEM9) to fine scale (dbMEM75). The RDA with the five dbMEM explained 4.32% of the variance. In the relationship between all 5 selected dbMEMs (i.g. broad, medium and fine scales) and the environmental variables, temperature seasonality, average annual precipitation and precipitation seasonality were significant (Table S3)

Considering the scales separately, only the broad scale (dbMEMs 9 and 12) showed a significant relationship with the following environmental variables: Clay, temperature seasonality, mean annual precipitation and precipitation seasonality (Table S4). Autochory, dispersion via seed or fruit, legume and fleshy legume were the characteristics that most contributed to the general variation of the data (Fig. 2). On both the medium and fine scales, the



Revealing the influence of climatic variables on the distribution of legume dispersal traits in the Chaco

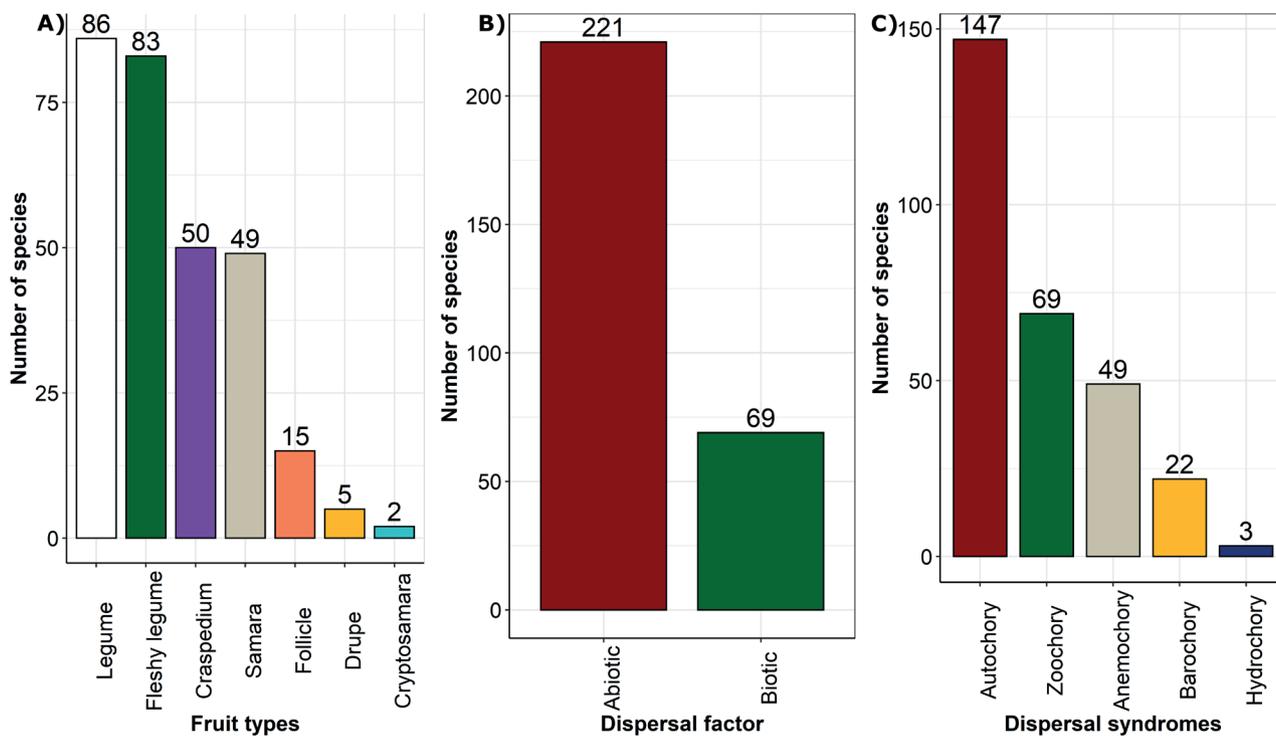


Figure 1. Morphological traits of legumes in the Chaco. **A)** Fruit types. **B)** Dispersal factors. **C)** Dispersal syndromes recorded in the Chaco.

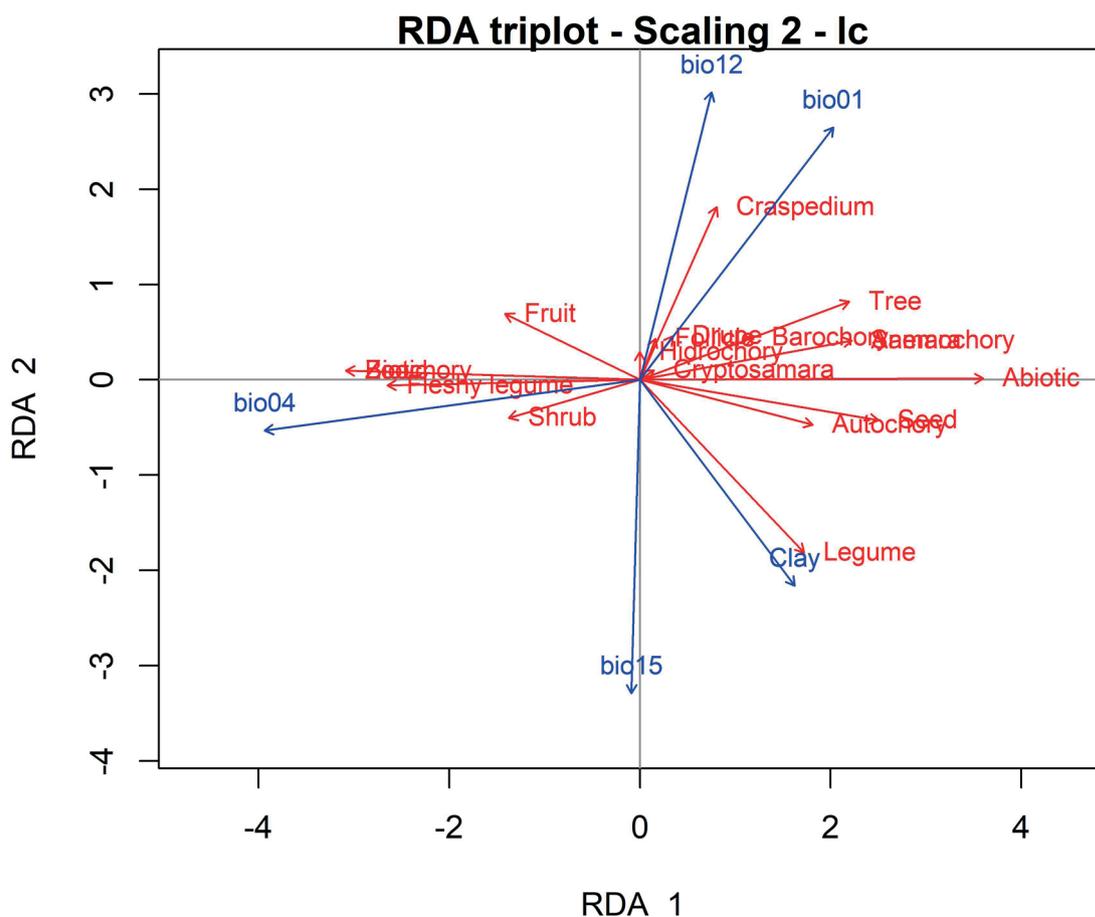


Figure 2. RDA plot showing the relationship between environmental variables and dispersal traits of legumes in the Chaco.

RDA between dbMEMs (16, 24, and 75) and the response variables was significant (only the variation on axis 1), but no environmental variable explained this variation. That is, on fine and medium scales, separately, the spatial structuring of plant traits is not explained by any of the environmental variables.

Changes in plant traits along environmental gradients

For the detection of changes in traits along the gradients, we selected only the results involving all scales in the analysis of dbMEMs, i.e., temperature seasonality, mean annual precipitation and precipitation seasonality (Fig. 3). TITAN analysis (Table S5) of temperature seasonality revealed that the types of syndromes and types of fruit showed a marked reduction around the 375SD value (Fig. 4A, B), indicating that these traits reduce their frequencies starting from these values. In the precipitation gradient, in turn, fruit types showed an increase in frequency between 750 and 820 mm (Fig. 4C). For the seasonality of precipitation, fruit types showed a reduction of about 60CV (Fig. 4D) and the dispersion unit increased by about 30 CV (Fig. 4E).

Regarding temperature seasonality, the syndromes that showed a reduction along the gradient were hydrochoria at 350, anemochoria and, more pronouncedly, barochoria, both at 450 (Fig. 5A). Regarding fruit type, we detected a reduction of most types between 350 and 450, and a reduction of 550 for legumes (Fig. 5B). Along the precipitation gradient, fruit types showed increases mainly for drupe and follicle at 993 and 914 mm, respectively, and for craspedium at 450 (Fig. 5C). For precipitation seasonality, the drupe, follicle and craspedium fruits were reduced by 55, 60 and 83, respectively (Fig. 5D), and dispersion by the fruit showed an increase between 29 and 30 (Fig. 5E).

Only five traits showed Purity and Reliability above 95%, namely: the anemochoric and barochoric dispersion syndromes and the type of samara fruit in the seasonality and temperature gradients; drupe fruit in precipitation gradients and precipitation seasonality; and fruit as a dispersing unit also in the gradient of seasonality of precipitation (Fig. 5; Table S5). The other traits: hydrochoric dispersion and fruit types cryptosamara, drupe, follicle, craspedium and legume *s.s* for temperature seasonality; follicle, cryptosamara and craspedium fruit types for precipitation and precipitation seasonality, also shown in Fig. 5, reached < 95% purity and reliability, but contributed substantially to the overall changes shown in Fig 4.

Discussion

Dispersal traits of the legumes

In general, the diversity of Fabaceae fruits in the Chaco is mainly due to legumes *sensu stricto* (29.5%), fleshy legumes (28.8%), and craspedium (17%), which together account

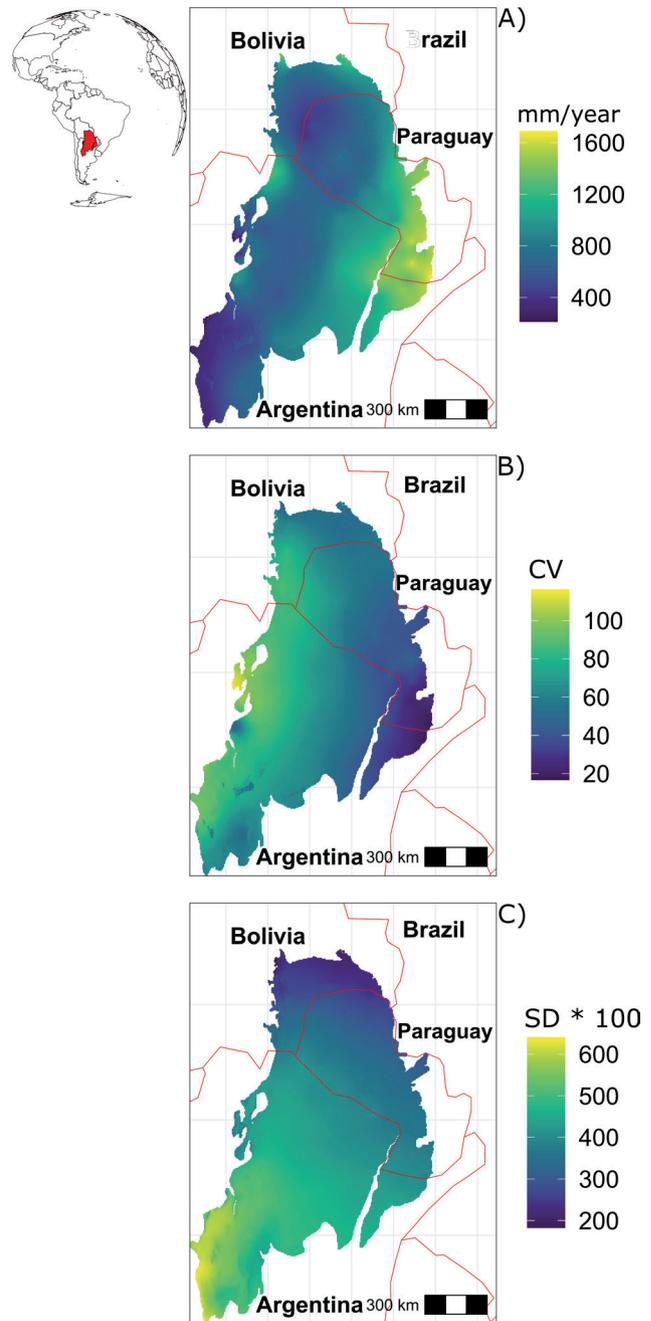


Figure 3. Maps of the climatic variables. Annual Precipitation (A). Precipitation Seasonality (B). Temperature Seasonality (C). Red lines represent country boundaries.

for 75% of all carpological types. Legume pods are most common among species in Caatinga areas (Griz & Machado 2001), chamber fruits and legume pods are the most representative in the Carrasco vegetation (De Vasconcelos *et al.* 2010) and legumes *sensu stricto* and fleshy fruits have similar proportions in the Cerrado (Jardim & Batalha 2009). Although legumes *sensu stricto* are recognized as the most frequent fruit types in the family (Lewis *et al.* 2005; Polhill 1994), fleshy legumes are abundant in the Chaco. Abiotic dispersal is prevalent (76.2%) among Chaco tree and shrub legumes. Abiotic dispersal in the Chaco mainly occurs by



Revealing the influence of climatic variables on the distribution of legume dispersal traits in the Chaco

autochory (legumes *sensu stricto* and craspedium) and anemochory (samara). Fruits included in this dispersal mode are characteristic of genera that show considerable richness (*Bauhinia* and *Mimosa*) and are responsible for 31% of all abiotic dispersal.

Autochory and legume fruit are directly related traits and, consequently, they represent the seed dispersal unit (Van der Pijl 1982). In the Chaco, Fabaceae species tend to include legume fruits with autochoric dispersion (see Fig. 1), possibly related to the evolutionary history of

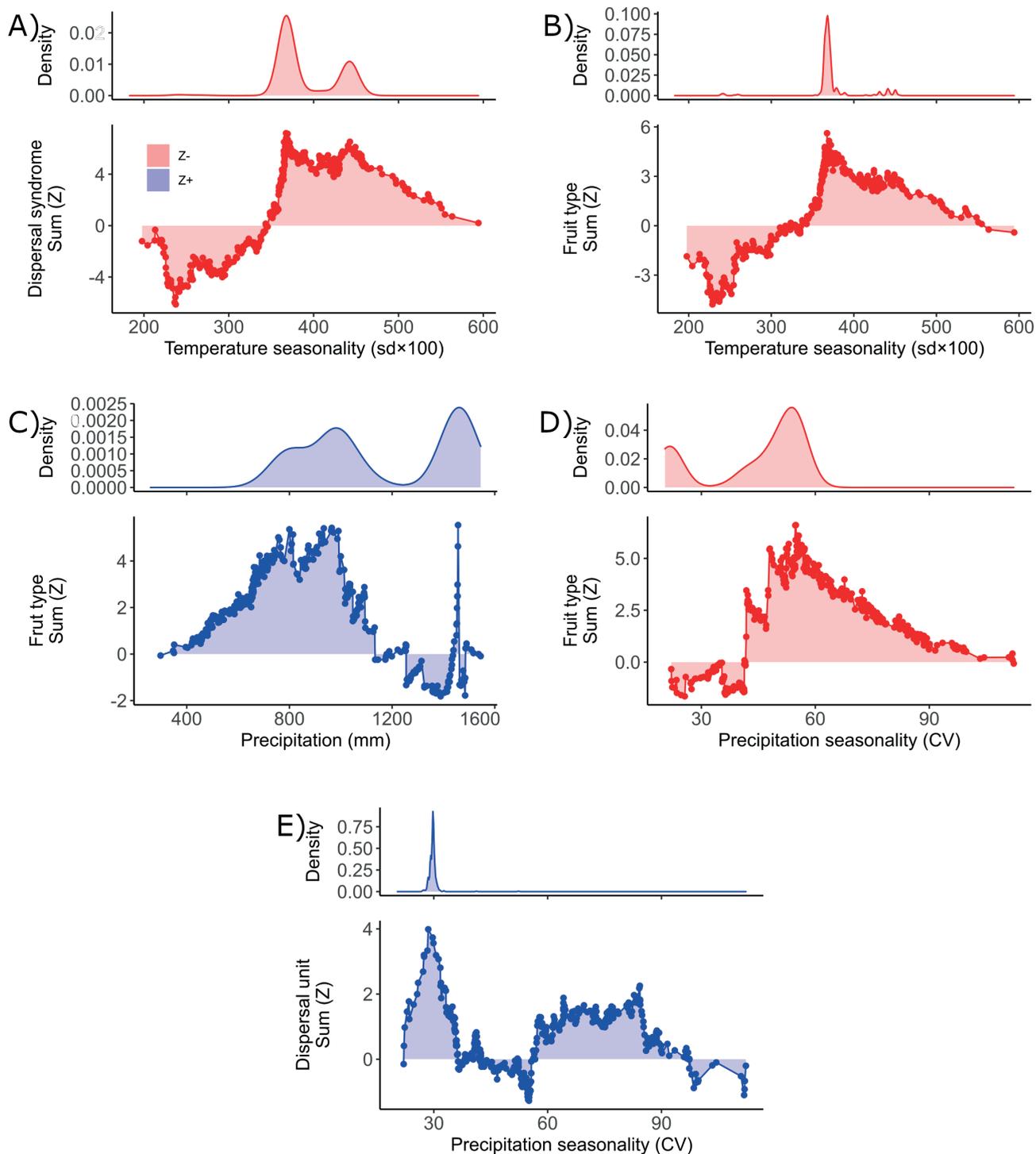


Figure 4. Change in plant attributes along the gradient of temperature seasonality, precipitation and precipitation seasonality. The bottom chart shows the magnitude of change of the attributes declining along the gradient (Z- = red colours) and of those increasing along the gradient (Z+ = blue colours). Peaks indicate points that produce larger amounts of change. Plateaus represent regions of constant change. The upper chart shows the estimated probability density of the sum Z.



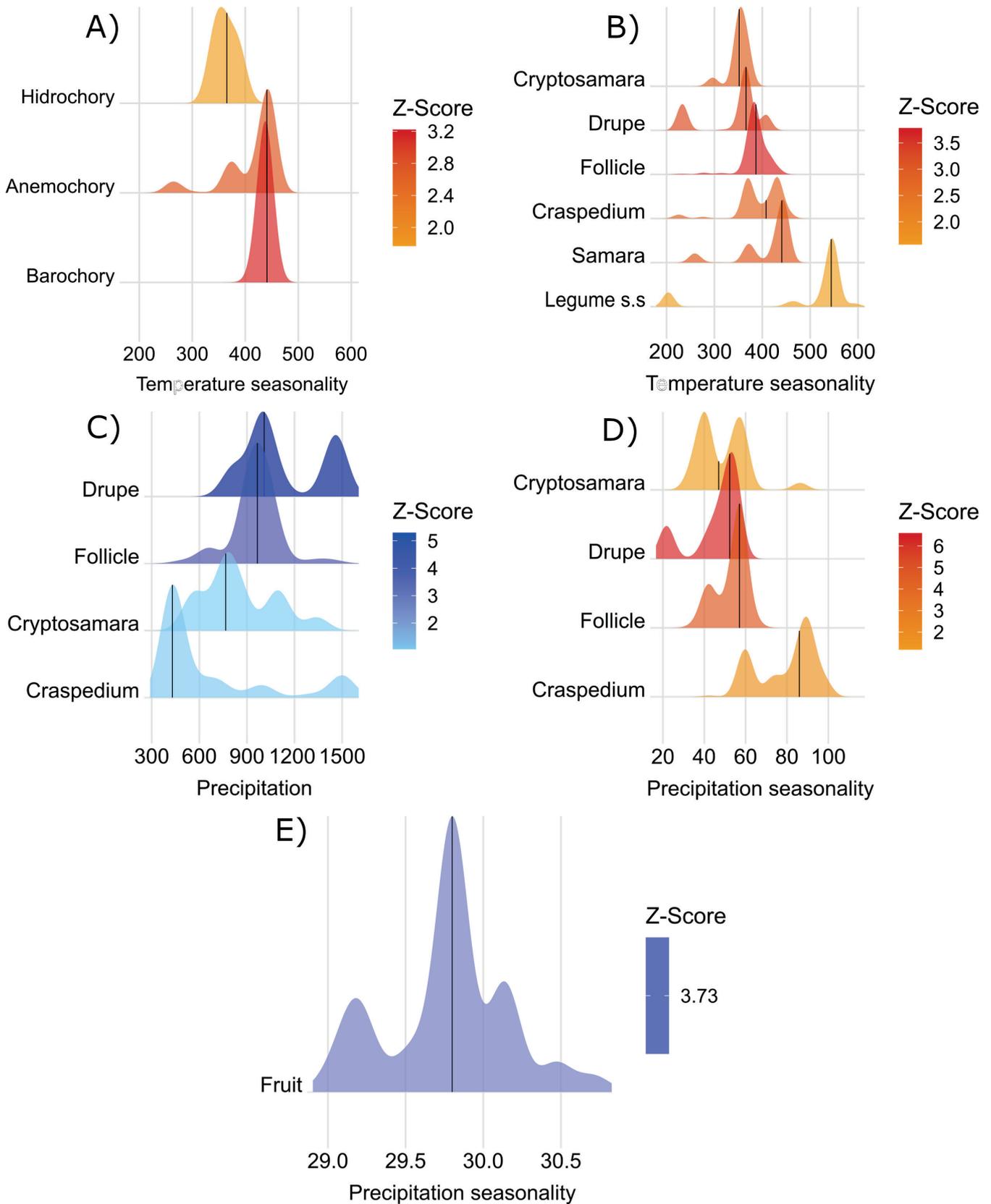


Figure 5. Change in the frequency of plant traits along the gradients. For temperature seasonality, dispersal syndrome (A) and fruit types (B). For mean annual precipitation and fruit types (C). For rainfall seasonality, fruit types (D) and dispersal unit (E). Higher Z score values indicate the attributes that best represent the Z+ (increase in frequency) and Z- (reduction in frequency) groups. Vertical black lines represent the environmental change point for each taxon based on the IndVal maximum.



Fabaceae and its distribution and occupation of areas, especially in dry biomes (Centeno-González *et al.* 2021; Koenen *et al.* 2021). In addition, fleshy legumes and zoochory are also well represented. It is worth remembering that fleshy fruits are important to the mastofauna of the Chaco and are produced by representatives of the genera *Neltuma*, *Strombocarpa*, *Libidibia* and *Vachellia*. These genera show seasonal alternations of fruiting. *Neltuma* and *Strombocarpa* species tend to fructify in the dry season, and species of *Vachellia* and *Libidibia* fructify in the rainy season – thus providing food for the local fauna throughout the year (Campos & Ojeda 1997; Cuéllar 2000). Animal species such as *Mazama gouazoubira* (Red deer), *Pecari tajacu* (Caititu), *Tayassu pecari* (Queixada) (Cuéllar 2000), *Lagostomus maximus*, and *Dolichotis patagonum* (Mara) (Bonino *et al.* 1997; Chillo *et al.* 2010; Kufner & Monge 1998) occur in the Chaco and feed on these legumes.

Spatial Analysis and Relationships with environmental variables

Temperature seasonality (bio04), mean precipitation (bio12), precipitation seasonality (bio15), and clay content were significant regarding legume traits when considering all scales and the broad scale separately. It is known that the effect of climatic variables on the distribution pattern of plant species and their characteristics occurs on large scales (tens or hundreds of kilometers). While on fine scales (a few kilometers or meters), what determines variations are biotic relationships, population dynamics, and local abiotic factors such as microrelief, microclimate, and edaphic characteristics (Woodward & Williams 1987; Levin 1992; Legendre & Legendre 2012; Dubuis *et al.* 2013).

In general, temperature and precipitation are essential predictors of plant traits globally (Moles *et al.* 2014). For the Chaco, however, our analyses showed that the seasonality of both climatic variables shapes the distribution of morphological traits of Fabaceae and, considering that the family is highly representative in terms of richness and abundance in the biome (Lima *et al.* 2015; Morales *et al.* 2019), we expect a similar pattern to be found for the vegetation in general. It is worth mentioning that the Chaco is formed by a mosaic of dry vegetation, with the presence of forested, savannah, and monodominance regions of species (*e.g.*, *Schinopsis balansae*) (Prado 1993) and, in the case of more extensive geographic scales, all vegetation structure in the biome is correlated to abiotic factors such as climate (Assunção *et al.* 2022).

Although the clay variable was significant when considering only large scale separately, it is a fact that soil data are essential variables to consider when dealing with the spatiality and distribution of plants (Velazco *et al.* 2017). In the case of clay content, it is known that the proportion of clay shapes the distribution of vegetation since it is linked to water retention in the soil (Larcher 1995). For the

Chaco, this must be a vital characteristic for plants since it is an arid environment with a heterogeneous and highly seasonal climate (Prado 1993). The dbMEM approach allows producing a set of uncorrelated spatial predictors that can be integrated into explanatory models to show the effect of a spatial phenomenon on different scales (*e.g.*, dispersion) (Peres-Neto & Legendre 2010).

Changes in plant traits along environmental gradients

Regions with intermediate values in the temperature seasonality gradient (~375 SD x 100) show a reduction of morphological traits, that is, the predominance of few traits. These locations correspond to those with the highest richness of legumes in the Chaco (Andrella & Sartori 2021) and tend to show less variation among syndromes and fruits. On the other hand, areas with higher temperature seasonality tend to have a low richness of species in the Chaco but show diverse dispersal strategies. In Fabaceae, it is common to observe different dispersion strategies for the same type of fruit. Follicles, for example, may show autochory dispersion when the seeds lack arils or sarcotesta or zoochory when these tissues are present (Van der Pijl 1982).

Hydrochoric, anemochoric, and barochoric species are more vulnerable to yearly temperature changes and are less represented in places with more significant seasonal temperature variations in the Chaco. Many species with a barochoric syndrome, among those studied here, have fruits with fleshy tissues (*Chloroleucon* and *Hymenaea*) and possibly have dispersion by secondary agents after the fall of the mother plant (Macedo & Prance 1978). Studies indicate that, in dry forests, the prevalence of fleshy fruits (*e.g.*, fleshy legumes and drupes) during the rainy season is linked to the seasonality of temperature, which directly influences the development and maturation of fruits (Jara-Guerrero *et al.* 2011; Herrera & Pellmyr 2009). Thus, places with very strict temperature seasonality should have less representation of fleshy fruit species, which are more sensitive to this variable.

Anemochory reduction also occurs in locations in the southern Chaco region, where there is wide temperature variation throughout the year and low average annual precipitation (see Fig. 3A, C). We believe that the reductions in anemochory and barochory also occur due to the decrease in richness of legume species in the regions south of the Chaco (Morales *et al.* 2019) regarding more humid environments, as is the case for the Paraguayan and Brazilian Chaco (Carvalho & Sartori 2015; Sartori *et al.* 2018; Morales *et al.* 2019; Andrella & Sartori 2021). On the other hand, drier places with more rigorous climates, such as the dry and sierra Chaco (Chaco sub-regions, Olson *et al.* 2001; Morales *et al.* 2019), tend to have plant species with xerophytic characteristics and with zoochoric dispersion, as is the case for *Neltuma* and *Strombocarpa*, which have fleshy fruits, and the Chaco Seco as a center of diversity (Catalano *et al.* 2008; Hughes *et al.* 2022). Thus, abiotic syndromes may be reduced due to the replacement of dispersal strategies



in these places by syndromes with biotic characteristics, even if at smaller proportions. Hydrochory is a syndrome restricted to places where rivers are abundant, as in the humid Chaco (e.g., Paraguay and Brazil; Olson *et al.* 2001).

Places with more significant precipitation seasonality are also the drier ones in the Chaco, close to the Andes, where we observe the presence of species related to arid regions (e.g., *Neltuma* and *Mimosa*). However, in general, these species are less abundant, as also observed in other studies (Morales *et al.* 2019; Andrella & Sartori 2021). Thus, when we consider the seasonality of precipitation, we find that the representativeness of specific genera with drupe-type fruit (*Andira*) and follicles (*Erythrina* and *Copaifera*) tends to be reduced in the middle of the gradient (54 and 57CV). Such genera are well represented in humid places, where precipitation seasonality tends to be lower than in dryer Chaco regions close to the Andes (see Fig. 3). Fruits such as craspedium, common in *Mimosa* species, decrease in places with high seasonal precipitation in the Chaco. The preference for species with dry fruits such as craspedium in these locations can be seen as a response to hydrological issues due to the lower requirement of water availability for fruiting, as already pointed out in several other studies of dry forests (Howe & Smallwood 1982; Tabarelli *et al.* 2003; Correa *et al.* 2015). Our results showed an increase in the occurrence of fruit as a dispersal unit at the beginning of the precipitation seasonality gradient (~30CV). Thus, considering that these locations are also of high humidity, the presence of species with baroque dispersion such as *Andira* and *Hymenaea* (Andrella & Sartori 2021), which disperse seeds via fruit, may have contributed to the increase in this trait in such locations.

The precipitation gradient in the Chaco is of considerable amplitude, from ~200 mm to the west and ~1500 mm to the east (Bucher 1982; Prado 1993; Rossi 2010). When considering the types of legume fruits, there was an increase in their variation between 750 and 820 mm/year (see Fig. 4C), which indicates an intermediate value between the extremes of the gradient. Regions with these precipitation values in the Chaco are in contact with other biomes such as the Cerrado, Bosques Chiquitano, and Pantanal (Prado *et al.* 1992), suggesting that the high diversity of fruits at these gradient values are influenced by the coexistence of species with different dispersal strategies such as zoochory (*Neltuma*), autochory (*Bauhinia*), anemochory (*Lonchocarpus*) and barochory (*Hymenaea*), which also have different fruit types, growth habits, and dispersal units. This increase in fruit variation at intermediate values is represented by drupe and follicle (see Fig. 5C), which may have fleshy tissues and arylate seeds, allowing zoochoric dispersal. *Craspedium* shows a significant increase at the beginning of the gradient, also indicating the occurrence of marked autochory in regions with drier climates in the Chaco, as confirmed by studies of plant communities where dispersion by abiotic factors tends to occur in drier places (Tannus *et al.* 2006).

Conclusion

Annual precipitation, temperature seasonality, and precipitation seasonality affect the distribution of morphological traits of tree and shrub leguminous species in the Chaco. Furthermore, there is an accumulation of different characteristics, such as dispersion syndromes and types of fruit, in specific places along the gradients, such as the Dry and Humid Chaco. Analyzing dispersal patterns based on the types of fruits of particular plant families can contribute to understanding the occupation dynamics of different biomes. In this study, we show for the first time the influence of seasonality on characteristics linked to plant dispersal throughout the Chaco. However, further studies concerning macroecology related to biotic factors, such as the distribution of dispersers and pollinators and ecological interactions between the members of the plant community, among others, may bring more meaningful answers about how the plant community disperses in the Chaco as a whole. Understanding the patterns of diversity and dispersion of Fabaceae, a group of significant ecological, evolutionary, and ethnological relevance in the Chaco, should contribute to consolidating conservation plans in different forest areas in South America.

Supplementary material

The following online material is available for this article:
 Table S1 - Environmental variables used in spatial analysis.
 Table S2 - List of Chaco legume species.
 Table S3 - Relationship between RDA1 and environmental variables (with all dbmems; broad, medium and fine scales together).
 Table S4 - Relationship between RDA1 and environmental variables (broad scale only).
 Table S5 - Results of the TITAN analysis. *ienv.cp* - environmental change point for each taxon based on IndVal maximum (used if *imax* = TRUE). *zenv.cp* - environmental change point for each taxon based on z maximum (default, *imax* = FALSE). *freq* - number of non-zero abundance values per taxon. *IndVal* - Dufrene and Legendre 1997 IndVal statistic, scaled 0-100%. *obsiv.prob* - probability of an equal or larger IndVal from random permutation. This is an uncorrected value that doesn't account for the analysis of multiple taxa in the same data set nor repeated estimates of across n partitions of the predictor (x value). To reiterated, this is not a valid test of indicator "significance", nor have the authors ever advocated its use in this manner (see Baker and King 2010). It is used in the calculation of reliability, which assesses the effect of nBoot replicates on the *obsiv.prob*; reliability, when coupled with purity, is a defensible metric for identifying robust indicator taxa. *Zscore* - IndVal z score. *purity* - proportion of replicates matching observed maxgrp assignment. *reliability* - proportion of replicate *obsiv.prob*



values ≤ 0.05 . z.median- median score magnitude across all bootstrap replicates. filter- logical (if >0) indicating whether each taxa met purity and reliability criteria, value indicates maxgrp assignment.

Figure S1 - Mantel correlogram for traits of legume species in the chaco. Positive values indicate positive autocorrelation. Significant values are represented by dark squares.

Figure S2 - RDA plot showing the relationship between spatial variables (dbMEMs) and dispersal traits of legumes in the Chaco.

Acknowledgments

We thank Thomaz Sinani and Geraldo Alves Damasceno-Junior for valuable suggestions; We also thank UFMS (Universidade Federal de Mato Grosso do Sul) and the Programa de Pós-Graduação em Biologia Vegetal for partial support of the present study. This study was also financed in part by the CAPES (Coordination of Superior Level Staff Improvement) - Finance Code 001.

References

- Adamoli J, Sennhauser E, Acero JM, Rescia A. 1990. Stress and disturbance: Vegetation dynamics in the dry Chaco Region of Argentina. *Journal of Biogeography* 17: 491-500.
- Alberto FJ, Derory J, Boury C, Frigerio JM, Zimmermann NE, Kremer A. 2013. Imprints of natural selection along environmental gradients in phenology-related genes of *Quercus petraea*. *Genetics* 195: 495-512.
- Andrella GC, Sartori ALB. 2021. Riqueza, distribuição e distinção taxonômica de leguminosas arbóreas e arbustivas no Chaco. In: Sartori ALB, De Souza PR, Arruda RCO (eds.). *Chaco caracterização, riqueza, diversidade, recursos e interações*. Campo Grande, Editora Universidade Federal de Mato Grosso do Sul. p. 142-164.
- Assunção VA, Sartori ÂLB, Mansano VF. 2022. Floristic structuring of woody plants from the Chaco in light of abiotic factors. *Rodriguésia* 73: e00262019.
- Baker ME, King RS, Kahle D. 2020. An introduction to TITAN2. Version 2.4.900. <https://cran.r-project.org/web/packages/TITAN2/vignettes/titan2-intro.pdf>. 2 Sep. 2022.
- Baker ME, King RS. 2010. A new method for detecting and interpreting biodiversity and ecological community thresholds: Threshold Indicator Taxa Analysis (TITAN). *Methods in Ecology and Evolution* 1: 25-37.
- Baptista MSP, Assunção VA, Bueno ML, Casagrande JC, Sartori ÂLB. 2020. Species representativeness of Fabaceae in restrictive soils explains the difference in structure of two types of Chaco vegetation. *Acta Botanica Brasílica* 34: 559-569.
- Bonino N, Sbriller A, Manacorda MM, Larosa F. 1997. Food partitioning between the Mara (*Dolichotis patagonum*) and the introduced hare (*Lepus europaeus*) in the Monte desert, Argentina. *Studies on Neotropical Fauna and Environment* 32: 129-134.
- Borcard D, Gillet F, Legendre P. 2018. *Numerical ecology with R*. 2nd. ed. Springer, International Publishing.
- Bouchenak-Khelliadi Y, Maurin O, Hurter J, Van Der Bank M. 2010. The evolutionary history and biogeography of Mimosoideae (Leguminosae): An emphasis on African acacias. *Molecular Phylogenetics and Evolution* 57: 495-508.
- Bucher EH. 1982. Chaco and Caatinga - South American Arid Savannas, Woodlands and Thickets. In: Huntley BJ, Walker BH (eds.). *Ecology of Tropical Savannas*. Ecological Studies. Berlin, Heidelberg, Springer. vol. 42, p. 48-79.
- Campos CM, Ojeda RA. 1997. Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. *Journal of Arid Environments* 35: 707-714.
- Carvalho FS, Sartori ÂLB. 2015. Reproductive phenology and seed dispersal syndromes of woody species in the Brazilian Chaco. *Journal of Vegetation Science* 26: 302-311.
- Catalano AS, Vilardi JC, Tosto D, Saidman BO. 2008. Molecular phylogeny and diversification history of *Prosopis* (Fabaceae: Mimosoideae). *Biological Journal of the Linnean Society* 93: 621-640.
- Centeno-González NK, Martínez-Cabrera HI, Porras-Múzquiz H, Estrada-Ruiz E. 2021. Late Campanian fossil of a legume fruit supports Mexico as a center of Fabaceae radiation. *Communications Biology* 4: 41.
- Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.
- Chillo V, Rodríguez D, Ojeda RA. 2010. Niche partitioning and coexistence between two mammalian herbivores in the Dry Chaco of Argentina. *Acta Oecologica* 36: 611-616.
- Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109-126.
- Correa DE, Álvarez E, Stevenson PR. 2015. Plant dispersal systems in Neotropical forests: Availability of dispersal agents or availability of resources for constructing zoochorous fruits?: Dispersal systems in Neotropical forests. *Global Ecology and Biogeography* 24: 203-214.
- Cousens R, Dytham C, Law R. 2008. *Dispersal in plants: A population perspective*. Oxford, Oxford University Press.
- Cuellar SRL. 2000. Fenología de plantas frutales importantes em la dieta de vertebrados frugívoros en el Chaco Boliviano. In: Cabrera E, Mercolli C, Resquin R (eds.). *Manejo de fauna silvestre em Amazonia y Latinoamérica*. La Paz, Fundación Moises Bertoní. p. 47-56.
- de la Sancha NU, Boyle SA, McIntyre NE *et al.* 2021. The disappearing Dry Chaco, one of the last dry forest systems on earth. *Landscape Ecology* 36: 2997-3012.
- De Vasconcelos SE, De Araújo FS, Lopes AV. 2010. Phenology and dispersal modes of wood species in the Carrasco, a tropical deciduous shrubland in the Brazilian semiarid. *Biodiversity and Conservation* 19: 2263-2289.
- Dell AI, Pawar S, Savage VM. 2011. Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences* 108: 10591-10596.
- Dong N, Prentice IC, Wright IJ *et al.* 2020. Components of leaf-trait variation along environmental gradients. *New Phytologist* 228: 82-94.
- Dray S, Pellissier R, Coutron P *et al.* 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82: 257-275.
- Dubuis A, Giovanettina S, Pellissier L, Pottier J, Vittoz P, Guisan A. 2013. Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. *Journal of Vegetation Science* 24: 593-606.
- Esquivel-Muelbert A, Baker TR, Dexter KG *et al.* 2017. Seasonal drought limits tree species across the Neotropics. *Ecography* 40: 618-629.
- Fehlenberg V, Baumann M, Gasparri NI, Piquer-Rodríguez M, Gavier-Pizarro G, Kuemmerle T. 2017. The role of soybean production as an underlying driver of deforestation in the South American Chaco. *Global Environmental Change* 45: 24-34.
- Griz LMS, Machado ICS. 2001. Fruiting phenology and seed dispersal syndromes in caatinga, a tropical dry forest in the northeast of Brazil. *Journal of Tropical Ecology* 17: 303-321.
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A. 2013. High-resolution global maps of 21st-century forest cover change. *Science* 334: 850-854.
- Harris JG, Harris MW. 1994. *Plant identification terminology: An illustrated glossary*. Utah, Spring Lake Publishing.
- Herrera CM, Pellmyr O. 2009. *Plant animal interactions: An evolutionary approach*. John Wiley & Sons.
- Howe HF, Smallwood J. 1982. *Ecology of seed dispersal*. *Annual Review of Ecology and Systematics* 13: 201-228.
- Hueck K. 1972. *As florestas da América do Sul: Ecologia, composição e importância econômica*. São Paulo, Editora da Universidade de Brasília, Editora Polígono.



- Hughes CE, Ringelberg JJ, Lewis GP, Catalano SA. 2022. Disintegration of the genus *Prosopis* L. (Leguminosae, Caesalpinioideae, mimosoid clade). *PhytoKeys* 205: 147-189.
- Jara-Guerrero A, De la Cruz M, Espinosa CI, Méndez M, Escudero A. 2015. Does spatial heterogeneity blur the signature of dispersal syndromes on spatial patterns of woody species? A test in a tropical dry forest. *Oikos* 124: 1360-1366.
- Jara-Guerrero A, De la Cruz M, Méndez M. 2011. Seed dispersal spectrum of woody species in South Ecuadorian dry forests: Environmental correlates and the effect of considering species abundance. *Biotropica* 43: 722-730.
- Jardim AVF, Batalha MA. 2009. Dispersal syndromes related to edge distance in Cerrado sensu stricto fragments of central-western Brazil. *Brazilian Archives of Biology and Technology* 52: 1167-1177.
- Koenen EJM, Ojeda DI, Bakker FT *et al.* 2021. The origin of the legumes is a complex paleopolyploid phylogenomic tangle closely associated with the cretaceous–paleogene (K–Pg) mass extinction event. *Systematic Biology* 70: 508-526.
- Kufner MB, Monge S. 1998. Dieta De *Lagostomus maximus* (Rodentia, Chinchillidae) en áreas sometidas a intervención humana en el desierto del Monte, Argentina. *Iheringia, Série Zoologia* 184: 175-184.
- Larcher W. 1995. Physiological plant ecology: Ecophysiology and stress physiology of functional groups. New York, Springer.
- Legendre P, Legendre L. 2012. Numerical ecology. Elsevier.
- Leigh Jr EG, Davidar P, Dick CW, Terborgh J, Puyravaud JP, ter Steege H, Wright SJ. 2004. Why do some tropical forests have so many species of trees? *Biotropica* 36: 447-473.
- Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Lewis GP, Schrire B, Mackinder B, Lock M (eds.). 2005. Legumes of the world. London, United Kingdom, Royal Botanic Gardens, Kew.
- Lewis JP, Pire EE, Vesprini JL. 1994. The mixed dense forest of the Southern Chaco: Contribution to the study of flora and vegetation of the Chaco VIII. *Candollea* 49: 159-168.
- Lewis JP. 1991. Three levels of floristical variation in the forests of Chaco, Argentina. *Journal of Vegetation Science* 2: 125-130.
- Lima JR, Tozzi AMGA, Mansano VF. 2015. A checklist of woody Leguminosae in the South American corridor of dry vegetation. *Phytotaxa* 207: 38.
- Macedo M, Prance GT. 1978. Notes on the vegetation of Amazonia II. The dispersal of plants in Amazonian white sand campinas: The campinas as functional islands. *Brittonia* 30: 203-215.
- May JH, Zech R, Veit H. 2008. Late Quaternary paleosol–sediment-sequences and landscape evolution along the Andean piedmont, Bolivian Chaco. *Geomorphology* 98: 34-54.
- Moles AT, Perkins SE, Laffan SW *et al.* 2014. Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science* 25: 1167-1180.
- Morales M, Oakley L, Sartori ALB *et al.* 2019. Diversity and conservation of legumes in the Gran Chaco and biogeographical inferences. *PLoS One* 14: e0220151.
- Murphy PG, Lugo AE. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67-88.
- Noguchi DK, Nunes GP, Sartori ALB. 2009. Florística e síndromes de dispersão de espécies arbóreas em remanescentes de Chaco de Porto Murtinho, Mato Grosso do Sul, Brasil. *Rodriguésia* 60: 353-365.
- Olson DM, Dinerstein E, Wikramanayake ED *et al.* 2001. Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience* 51: 933-938.
- Payne NL, Meyer CG, Smith JA *et al.* 2018. Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator. *Global Change Biology* 24: 1884-1893.
- Pennington TR, Prado DE, Pendry CA. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27: 261-273.
- Peres-Neto PR, Legendre P. 2010. Estimating and controlling for spatial structure in the study of ecological communities: Spatial structure in ecological communities. *Global Ecology and Biogeography* 19: 174-184.
- Pinho BX, Tabarelli M, Engelbrecht BMJ, Sfair J, Melo FPL. 2019. Plant functional assembly is mediated by rainfall and soil conditions in a seasonally dry tropical forest. *Basic and Applied Ecology* 40: 1-11.
- Poggio L, De Sousa LM, Batjes NH *et al.* 2021. SoilGrids 2.0: Producing soil information for the globe with quantified spatial uncertainty. *SOIL* 7: 217-240.
- Polhill RM. 1994. Complete synopsis of legume genera. In: Bisby FA, Buckingham J, Harborne JB (eds.). *Phytochemical dictionary of the Leguminosae*. New York, Chapman and Hall. vol. 1, p. 49-54.
- Prado DE, Gibbs PE, Pott A, Pott VJ. 1992. The Chaco-Pantanal transition southern Mato Grosso, Brazil. In: Furley PA, Proctor J, Ratter JA (eds.). *Nature and dynamics of forest-savanna boundaries*. London, Chapman & Hall. p. 451-470.
- Prado DE, Gibbs PE. 1993. Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden* 80: 902.
- Prado DE. 1993. What is the Gran Chaco vegetation in South America? I: A review. Contribution to the study of flora and vegetation of the Chaco. *Candollea* 48: 145-172.
- Ramella L, Spichiger R. 1989. Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal: Contribución al estudio de la flora y de la vegetación del Chaco. I. *Candollea* 44: 639-680.
- Rossi CA. 2010. El Sistema Silvopastoril en la Región Chaqueña Árida y Semiárida Argentina. Buenos Aires, Inta.
- Sartori ALB, Pott VJ, Pott A, De Carvalho FS. 2018. Checklist of angiosperm from the Chaco of Mato Grosso do Sul. *Iheringia, Serie Botanica* 73: 22-33.
- Schellenberger Costa D, Gerschlaue F, Pabst H *et al.* 2017. Community-weighted means and functional dispersion of plant functional traits along environmental gradients on Mount Kilimanjaro. *Journal of Vegetation Science* 28: 684-695.
- Tabarelli M, Vicente A, Barbosa DCA. 2003. Variation of seed dispersal spectrum of woody plants across a rainfall gradient in north-eastern Brazil. *Journal of Arid Environments* 53: 197-210.
- Tannus JL, Assis MA, Morellato LPC. 2006. Fenologia reprodutiva em campo sujo e campo úmido numa área de cerrado no sudeste do Brasil, Itirapina-SP. *Biota Neotropica* 6: 27.
- Tonkin JD, Bogan MT, Bonada N, Rios-Touma B, Lytle DA. 2017. Seasonality and predictability shape temporal species diversity. *Ecology* 98: 1201-1216.
- Van der Pijl L. 1982. Principles of dispersal in higher plants. Berlin, Springer.
- Velazco SJE, Galvão F, Villalobos F, De Marco P. 2017. Using worldwide edaphic data to model plant species niches: An assessment at a continental extent. *PLoS One* 12: e0186025.
- Wiens JA. 1989. The ecology of bird communities. Vol I. Cambridge, Cambridge University Press.
- Woodward FI, Williams BG. 1987. Climate and plant distribution at global and local scales. Cambridge, Cambridge University Press.

