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The phylogenetic diversity and structure of the seasonally dry forests in the Neotropics

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Abstract

Aim: Exceptions to the quasi-ubiquitous latitudinal diversity gradient (LDG) have been poorly studied. A reverse LDG, when species richness (SR) increases away from the Equator, has been suggested for several taxa and entire biomes. The Neotropical seasonally dry tropical forests (SDTF) are a well-known example of a reverse LDG that could be caused by the climatic stability of Pleistocene Refugia and dispersion from distinct source areas. Here, we test these predictions under a spatial and phylogenetic framework.

Location: Neotropics.

Taxon: Woody plants.

Methods: We used a recent species-level seed plant phylogeny and the DRYFLOR dataset to evaluate the geographic patterns of phylogenetic diversity (PD) and structure of woody plant assemblages associated with the Neotropical SDTFs. We conducted spatial regressions to test the effect of climatic instability since the Last Glacial Maximum (LGM) on assemblages' residual PD (controlling for SR) and null model analysis to evaluate their phylogenetic structure using the Net Relatedness Index.

Results: Phylogenetic diversity of the Neotropical SDTFs increased away from the Equator, likely driven by SR. This pattern was not related to climatic instability since the LGM. Phylogenetic structure of SDTF assemblages showed considerable spatial patterning, with significant phylogenetic clustering in the Mesoamerica and Caatinga regions.

Main conclusion: The reverse latitudinal SR gradient of the Neotropical SDTF assemblages is mirrored by their PD. Phylogenetic history seems to have influenced such patterns differently across the Neotropics with no relationship to climatic stability since the LGM, where particular SDTF nuclei previously suggested as Pleistocene refugia served as cradles and source areas for the current diversity pattern of the biome.

KEYWORDS

latitudinal diversity gradient, Palaeoclimate, phylogenetic diversity, phylogenetic structure, Pleistocene refugia, Seasonally Dry Tropical Forests

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1 | INTRODUCTION

Several hypotheses have been proposed to account for the dominant latitudinal diversity gradient (LDG) of increasing species richness (SR) from the poles to the Equator, including ecological/contemporary (e.g. habitat heterogeneity, productivity) and evolutionary/historical (e.g. diversification, climatic stability) explanations (Fine, 2015). Conversely, little attention has been paid to the description and explanation of reverse LDG, when SR increases away from the Equator (Morales-Castilla & García-Valdés, 2014), which includes several taxa across continents (Kindlmann et al., 2007; Morales-Castilla & García-Valdés, 2014) and even whole biomes (Banda et al., 2016). The Neotropical seasonally dry forests (SDTF) are a well-known example of reverse LDG (Gentry, 1995) where the SR of various clades such as woody plants (Banda et al., 2016), freshwater arthropods (Morinière et al., 2016) and birds (Prieto-Torres et al., 2019) increases away from the equator.

The SDTF has an extensive and discontinuous geographical distribution across Latin America and the Caribbean, reaching up to ~30° in latitude on either side of the equator (Pennington et al., 2006). It is distributed across heterogeneous topographic, climatic and edaphic conditions (Banda et al., 2016; Portillo-Quintero & Sánchez-Azofeifa, 2010). The main environmental characteristics in the distributional range of this biome are mean annual precipitations up to 700–1,800 mm, and drought periods from 3 up to 6 months (Gentry, 1995; Murphy & Lugo, 1986). The dominant life form are deciduous and semi-deciduous trees (i.e. that lose between 50% and 100% of their foliage annually during the dry season) that form extensive forests in which different landscape units intermingle, e.g. coastal dunes, mangroves, gallery forests, pastures and cultivated areas (Sánchez-Azofeifa et al., 2013). Patches of SDTF, known as nuclei, are bounded historically by other natural vegetation types (now including their anthropogenic transformations), which contributes significantly to the beta diversity of SDTF at continental, regional and local scales and its elevated number of endemisms of different taxa (Ceballos, 1995; Pennington et al., 2000, 2006, 2009; Prieto-Torres et al., 2019).

Quaternary climatic shifts have been hypothesized as main determinants of current diversity gradients in several taxa (Haffer, 1969; Svenning et al., 2015). More specifically, the Pleistocene refugia hypothesis suggests that climatically stable areas during the late Quaternary would have allowed several lineages to establish and diversify (Svenning et al., 2015), resulting in higher SR in these areas compared to climatically instable areas (Klopfer, 1959). A particular version of this hypothesis to explain the current diversity gradient of SDTF in South America is the Pleistocene Arc Hypothesis (PAH; Prado, 2000; Prado & Gibbs, 1993), which posits that the present-day fragmentary distribution of SDTF are remnants of a once continuous biome that reached its maximum extension during the Last Glacial Maximum (LGM), from north-eastern Brazil to northern Argentina and Paraguay and from the eastern Andes in Bolivia spreading into the Amazonia and the Caribbean coast (cf. Pennington et al., 2000, 2009; Prado & Gibbs, 1993). According to the PAH, some of the extant remnants of SDTF, namely, the Brazilian Caatinga, Misiones and the Andean Piedmont nuclei (Prado, 2000; Prado & Gibbs, 1993), could be considered as refugia as they were uninterruptedly covered by SDTF despite the Pleistocene climatic fluctuations. However, the relevance of this nuclei as actual climatic refugia for SDTF since the LGM has not been explicitly evaluated.

Beyond climatic dynamics at certain time periods, current diversity gradients are the result of evolutionary and biogeographic processes along the history of clades (Fine, 2015). For the SDTF, its long evolutionary history dating back to the Miocene (Becerra, 2005; Burnham & Carranco, 2004) has provided sufficient time for lineages to accumulate and/or diversify within this biome (Pennington et al., 2009). For instance, at the northern extent of its distribution, mountain uprising between the Oligocene and Miocene Epochs (30–20 Ma) provided the climatic conditions for the SDTF to establish, accumulate and diversify along the western coast of Mexico (western Mexico hypothesis; WMH, Becerra, 2005). Similar processes have been suggested for SDTF nuclei in South America, such as the Caatinga region in north-eastern Brazil that together with Mexico represent the largest, oldest and most species-rich SDTF nuclei (Banda et al., 2016). From these nuclei, the SDTF could have expanded towards other nuclei (Becerra, 2005; Cortes et al., 2015) because of climatic dynamics affecting evolutionary and biogeographic processes in the same way as proposed in the PAH but at deeper time scales (Fordham et al., 2019). Climatically stable regions are usually associated with low extinction rates where old lineages are likely to persist (refugia), hence, also referred as reservoirs or 'museums' of diversity (Stebbins, 1974). Besides, refugia can also act as 'cradles' for diversity by fostering speciation in some linages as novel biotic and abiotic opportunities appear over time (Haffer, 1969; Stebbins, 1974; Stewart et al., 2010). Therefore, contrasting the potential effect of climatic dynamics since the Pleistocene and evolutionary processes at deeper time scales can shed light on the long-debated causes of the observed diversity patterns of the SDTF.

Assessing the legacy of long-term climatic shifts and evolutionary processes on current biodiversity patterns requires including temporal information on climatic conditions (i.e. palaeoclimate) and phylogenetic relationships among clades (Svenning et al., 2015). Indeed, this integrative palaeoclimatic and phylogenetic approach has been used to evaluate the effect of Quaternary climatic dynamics on several aspects of biodiversity patterns (Fordham et al., 2018) as well as inferring their evolutionary drivers (Tucker et al., 2017). For instance, considering the residual phylogenetic diversity (rPD) of assemblages can inform about the relative importance of speciation, extinction and dispersal processes on SR gradients (Davies & Buckley, 2012; Fritz & Rahbek, 2012). Similarly, assemblage phylogenetic structure can further inform about ecological (e.g. niche divergence and environmental filters) and evolutionary (phylogenetic niche conservatism, diversification) processes behind species assembly and the resulting richness gradients (Cavender-Bares et al., 2009; Webb et al., 2002). Regarding the SDTF, the use of phylogenetic information has revealed at least three general patterns (Pennington et al., 2009): (a) strong phylogenetic niche conservatism of species confined to the SDTF, (b) SDTF nuclei are usually composed by relatively old monophyletic clades and (c) phylogenetic clustering within individual SDTF nuclei. Despite the relevance of such phylogenetic patterns to infer the origin and distribution of the SDTF, these patterns have not been evaluated along their complete distribution across the Americas nor explicitly combined with information on climatic dynamics required to properly evaluate prominent hypotheses about its origin and structure.

Here, we combined geographic, phylogenetic and climatic (past and present) information of SDTF assemblages to test the predictions of the PAH and WMH about the current distribution and diversity pattern of the SDTF across the Neotropics. We focused on woody plants associated with the SDTF to: (a) describe the latitudinal pattern of phylogenetic diversity (PD), (b) evaluate the relationship between climatic stability (i.e. difference between past and present climate) and rPD, and (c) investigate the phylogenetic structure of SDTF assemblages. First, following the reverse LDG presented by the SDTF (Banda et al., 2016; Gentry, 1995; Prieto-Torres et al., 2019), we expected (a) to find an increase of PD away from the Equator. Then, according to the PAH, and implicitly for the WMH, we expected (b) to find a negative relationship between climatic instability and rPD where nuclei with lower instability, thus, climatically stable (e.g. proposed refugia [PAH] and source areas [WMH]) will have higher rPD indicating an accumulation of evolutionary distinct lineages (Fritz & Rahbek, 2012; Massante et al., 2019), whereas nuclei with higher instability will have lower rPD implying the presence of relatively recently derived lineages or the extensive in situ speciation of geographically confined clades (Kissling et al., 2012). Furthermore, SDTF nuclei suggested as refugia could have served, firstly, as museums favouring the presence of old lineages but also as cradles for some lineages that later expanded their distribution to other nuclei. Accordingly, we expected c) the overall phylogenetic structure of SDTF assemblages within proposed refugia and source nuclei to be clustered at continental scales (Qian et al., 2014; Webb, 2000) but random at regional scales (Mesoamerica–northern South America and South America) owing to dispersal limitations across nuclei (Pennington et al., 2009), supporting the in situ diversification and later migration from the proposed refugia into other SDTF nuclei.

2 | MATERIALS AND METHODS

2.1 | Woody plant species and occurrence data

We obtained geographical and compositional data for SDTF floristic inventories (hereafter assemblages) across the Neotropics from the Latin American and Caribbean Seasonally Dry Tropical Forest Floristic Network (DRYFLOR; Banda et al., 2016). DRYFLOR is the most comprehensive database available for plant species associated with the SDTF, composed by 1,652 assemblages across the Neotropics. We downloaded data for all these assemblages from the DRYLOR website (www.dryflor.info/data). We limited our analysis to woody plants as they are the most recognizable physiognomy of the SDTFs and to those sites that fit the definition of SDTF provided by Pennington et al. (2009) and Banda et al. (2016). Thus, we excluded the Chaco woodland of central-South America characterized by frequent winter frosts (Pennington et al., 2000) and the semi-deciduous forests in Brazil bordering the Amazonian and the Atlantic rain forests where a considerable mixture of species from dry forests and wet forests are observed (Silva de Miranda et al., 2018). Nonetheless, consistent with other regional studies of the SDTF we included the semi-deciduous forests from the Misiones region (Pennington et al., 2000; Prado & Gibbs, 1993). We also removed several assemblages that only had one species matching with our phylogenetic hypothesis (see below). Accordingly, we only kept 805 of the 1,652 assemblages registered in DRYFLOR with a total of 4,443 species (Figure 1a). All woody plant species in the dataset were standardized to APG IV taxonomy using the *Taxonstand* (Cayuela et al., 2012) package for R 3.6.0 (R Core Team, 2018) for a better match with the phylogenetic data. Every SDTF assemblage was assigned to one floristic group following Banda et al. (2016): Mesoamerica, North-South America, the Antilles, the South American Pacific, the Andean piedmont, Misiones, central Brazil and Caatinga.

2.2 | Phylogenetic hypothesis and diversity metrics

To calculate phylogenetic metrics, we obtained a phylogenetic hypothesis for our pool of species based on a time-calibrated species-level plant mega-phylogeny from Smith and Brown (2018). This megaphylogeny was built by combining genetic data from GenBank (release 218.0), a synthetic phylogeny from the Open Tree of Life (release 9.1) and the time-calibrated backbone hypothesis for 758 Spermatophyta taxa by Magallón et al. (2015) (ALLMB tree). This phylogenetic hypothesis comprised ~90% of our total pool of species, with ~45% of these species containing genetic data and the remaining species begin included according to their taxonomic arrangement (Smith & Brown, 2018). Such synthetic phylogenies have been recently shown to perform equally well as fully genetic phylogenies, particularly for community phylogenetic analyses as the one performed here (Li et al., 2019).

For each SDTF assemblage, we estimated the number of species (SR), the PD, the rPD and the net relatedness index (NRI). We used the *picante* R-package (Kembel et al., 2010) to estimate PD and NRI. For PD, we followed Faith (1992); thus, PD equals the total branch length, excluding the root, of the phylogeny that connects all species within a particular assemblage. Because there is a strong correlation between SR and PD, we fitted a locally estimated scatterplot smoothing (LOESS) regression where PD is explained by SR and the resulting residuals were used to estimate rPD (Fritz & Rahbek, 2012). Positive rPD values indicate assemblages with higher PD than expected by their SR, suggesting the co-occurrence of early diverged and/or distantly related lineages within the assemblage, whereas negative rPD values indicate assemblages with lower PD than expected by their SR, implying the co-occurrence of recently derived and/or closely related lineages (Davies & Buckley, 2012; Fritz & Rahbek, 2012).

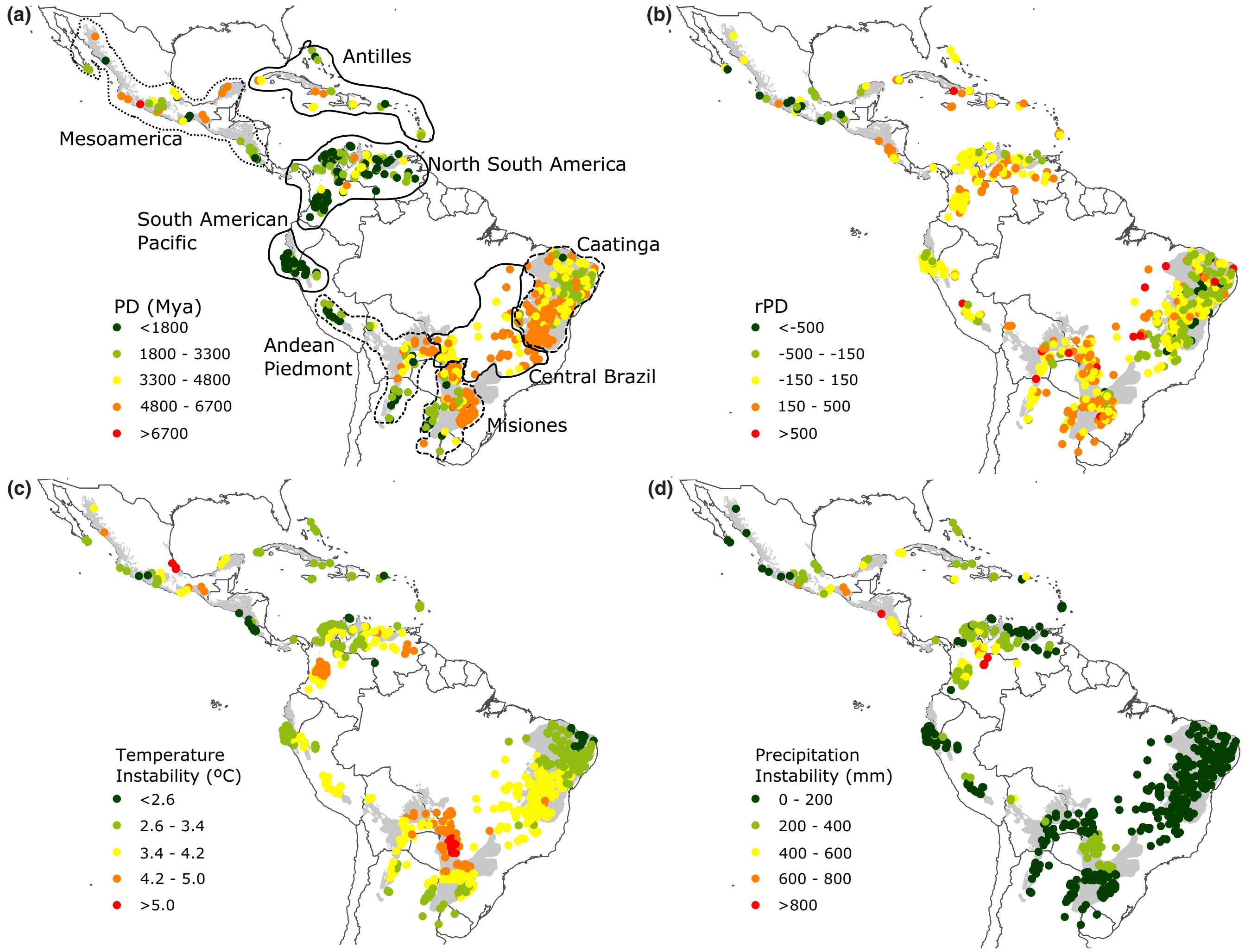

FIGURE 1 Geographic patterns of phylogenetic diversity and climatic instability since the LGM of SDTF assemblages across the Neotropics. Grey areas represent the current distribution of the SDTF biome. (a) phylogenetic diversity (PD) and floristic groups following Banda et al. (2016), where the dotted line represents the predicted source nucleus for the WMH and the dashed line represents the proposed refugia nuclei by the PAH as source areas; (b) residual PD (rPD) pattern, where green colours represent a high negative rPD (less PD than predicted by SR), whereas red colours represent a high positive rPD (more PD than predicted by SR); (c) temperature instability since the LGM and (d) precipitation instability since the LGM

2.3 | Climatic variables and instability

To test the effects of climatic stability during the late Quaternary on current diversity patterns of SDTF woody species, we used a time window of ~22,000 years between the LGM and the present. We used the LGM given that the Pleistocene Refugia hypothesis is suggested to have its most significant effects during that time (Prado & Gibbs, 1993; Svenning et al., 2015). The contemporary climate was characterized by Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP), which were obtained from Worldclim 1.4 at 2.5′ resolution (Hijmans et al., 2005). Mean temperature and precipitation during the LGM were extracted from the Community Climate System Model (CCSM) version 4 (Collins et al., 2006) and MIROC-ESM (Watanabe et al., 2011) at the same resolution as the contemporary climate. LGM temperature and precipitation were then summarized as the mean of the two models (Feng et al., 2017; Kissling et al., 2012). Then, we calculated climatic anomalies as the difference between the contemporary climate and LGM climate and defined climatic instability as the absolute values of these anomalies (McDonald-Spicer et al., 2019). All the climatic variables were extracted for each of the SDTF assemblages by their geographic coordinates and processed using the computational environment R 3.6.0 (R Core Team, 2018) and the *raster* package (Hijmans et al., 2011).

2.4 | Statistical analyses

To describe the latitudinal gradient in PD of SDTF, we fitted a general additive model (GAM) where the absolute latitude predicts the PD. Then, to assess the effects of climatic instability and test the existence of proposed refugia/source areas as expected by the PAH and

WMH, we applied Simultaneous Autoregressive models (SARs). SARs are linear regression models that incorporate the spatial autocorrelation structure of a given data set by including a spatial weights matrix defined by the distance among assemblages (i.e. closer assemblages receive higher weights). As such, SARs account for patterns in the response variable not predicted by explanatory variables but related to the assemblages' locations and, thus, avoid biased statistical inferences (e.g. Type I errors; Kissling & Carl, 2008). We calculated SAR error models where the climatic variables (contemporary, past and instability) for MAT and MAP predicted rPD. We used the *mgcv* (Hastie, 2017) and the *spedp* (Bivand & Piras, 2015) R packages to perform the GAM and SAR analyses, respectively, employing R 3.6.0.

2.5 | Phylogenetic structure

To further evaluate the existence of the proposed refugia nuclei and source areas, we also quantified the phylogenetic structure among species within SDTF assemblages using the Net Relatedness Index (NRI). We expected that those proposed areas would show considerable phylogenetic clustering. NRI measures the standardized effect size of the observed mean pairwise distance of all species within an assemblage (MPD_o) relative to that of random assemblages (MPD_r) from a species pool (Webb, 2000). NRI is defined as follows:

$$\mathrm{NRI} = -1\,\frac{MPD_o - MPD_r}{S_{MPDr}}$$

where $S_{MPDr} MPD_o$ is the standard deviation of the null model. Significantly positive NRI values (>1.96) indicate phylogenetic clustering of species (i.e. on average, species are more closely related than expected by chance), whereas significantly negative NRI values (<−1.96) indicate phylogenetic overdispersion of species (i.e. on average, species are more distantly related than expected by chance) (Webb, 2000). We used a null model that randomizes taxon labels on the phylogeny for the species included in the sampling pool but maintaining the SR (Kissling et al., 2012). To consider the effects of spatial scale on the processes shaping the phylogenetic structure of assemblages (Cavender-Bares et al., 2009; Kissling et al., 2012), we tested the deviation of NRI from the null expectations based on species pools at two spatial scales: (a) at the continental scale across the Neotropics, included all the 805 sites in our dataset and (b) at the regional scale, considering separate regions: the Mesoamerica–northern South America pool and the South America pool. These species pools were defined using the floristic groups proposed by Banda et al. (2016), where the northern South American species were very closely related those in Mesoamerican.

3 | RESULTS

The average PD across SDTF assemblages was 3,594.2 Myr (*SD* = 2,259.28, median = 3,293.80, range 91.50–1,396.20). The Brazilian Caatinga, Central Brazil and Misiones floristic groups had the higher average PD (4,776.96; 4,590.5 and 4,540.1 Myr, respectively), whereas the South American Pacific and northern South America also had the lower average PD (1,414.05 and 2,278.48 Myr, respectively) and the Antilles, the Andean piedmont and Mesoamerica had intermediate PD values (3,252.86; 3,771.17 and 3,868.64 Myr, respectively) (Figure 1a).

When PD was controlled by SR to obtain the relative PD, rPD values ranged from −2,469.45 to 1,606.92, with a mean of −2.1 (*SD* = 292.69). The lowest average of rPD was observed in Mesoamerica (−455.37) followed by the Brazilian Caatinga (−131.02), whereas the highest average was found in the Antilles (188.19). The South American Pacific, northern South America, Misiones, the Andean piedmont and Central Brazil showed low rPD values to those expected by SR (0.03, 45.8, 56.33, 79.53 and 83.26 respectively) (Figure 1b).

Regarding the climatic stability across SDTF assemblages from the LGM to the present, the average temperature instability was 3.5°C with a minimum of 1.8°C and a maximum of 5.8°C (Figure 1c), whereas the average precipitation instability was 172.2 mm with a minimum of 0 mm and a maximum 1,037.5 mm with ~69% of SDTF assemblages having a precipitation instability lower than 200 mm annually (Figure 1d).

The GAM ($R^2 = 0.253$, $p < 0.01$) showed that PD increased away from the Equator and towards the Tropics of Cancer and Capricorn, following the reverse LDG previously documented for the SDTF (Figure 2). High PD assemblages were located in the Brazilian Caatinga, Misiones and Central Brazil floristic groups, contributing together with western Mexico and the Yucatan Peninsula to define the reverse latitudinal gradient in PD as the assemblages close to the Equator had the lowest PD. SAR models, although significant ($p < 0.01$), showed that climatic instability had little explanatory power for the observe rPD ($R^2_{\mathrm{Nagelkerke}} < 0.10$). SAR models for present and past precipitation (MAP) showed the highest explanatory power of rPD among the evaluated models ($R^2_{\mathrm{Nagelkerke}} = 0.168$ and 0.162 respectively, Table 1).

At the continental scale, the phylogenetic structure (NRI) of SDTF assemblages ranged from −4.42 to 18.26 (median = 1.33). The average across these assemblages was not significantly different from zero (1.57), indicating an overall random phylogenetic structure. Nonetheless, several SDTF assemblages across the Neotropics showed significant phylogenetic structure as exemplified by the mean NRI values across different floristic groups. For instance, Mesoamerica had the highest mean NRI (4.11) and the most clustered assemblage (18.26), followed by the Brazilian Caatinga (mean NRI = 3.06), whereas in other floristic groups the mean NRI did not differ significantly from zero (Figure 3a). At the regional scale, for the Mesoamerican–northern South American pool, NRI of assemblages ranged from −1.32 to 17.08, with an average of 0.99; showing an overall random phylogenetic structure. The two floristic groups of this regional pool, Mesoamerica and North-South America, showed a lower NRI value in comparison with their values under the continental pool (4.11 to 3.57 and 0.87 to 0.58

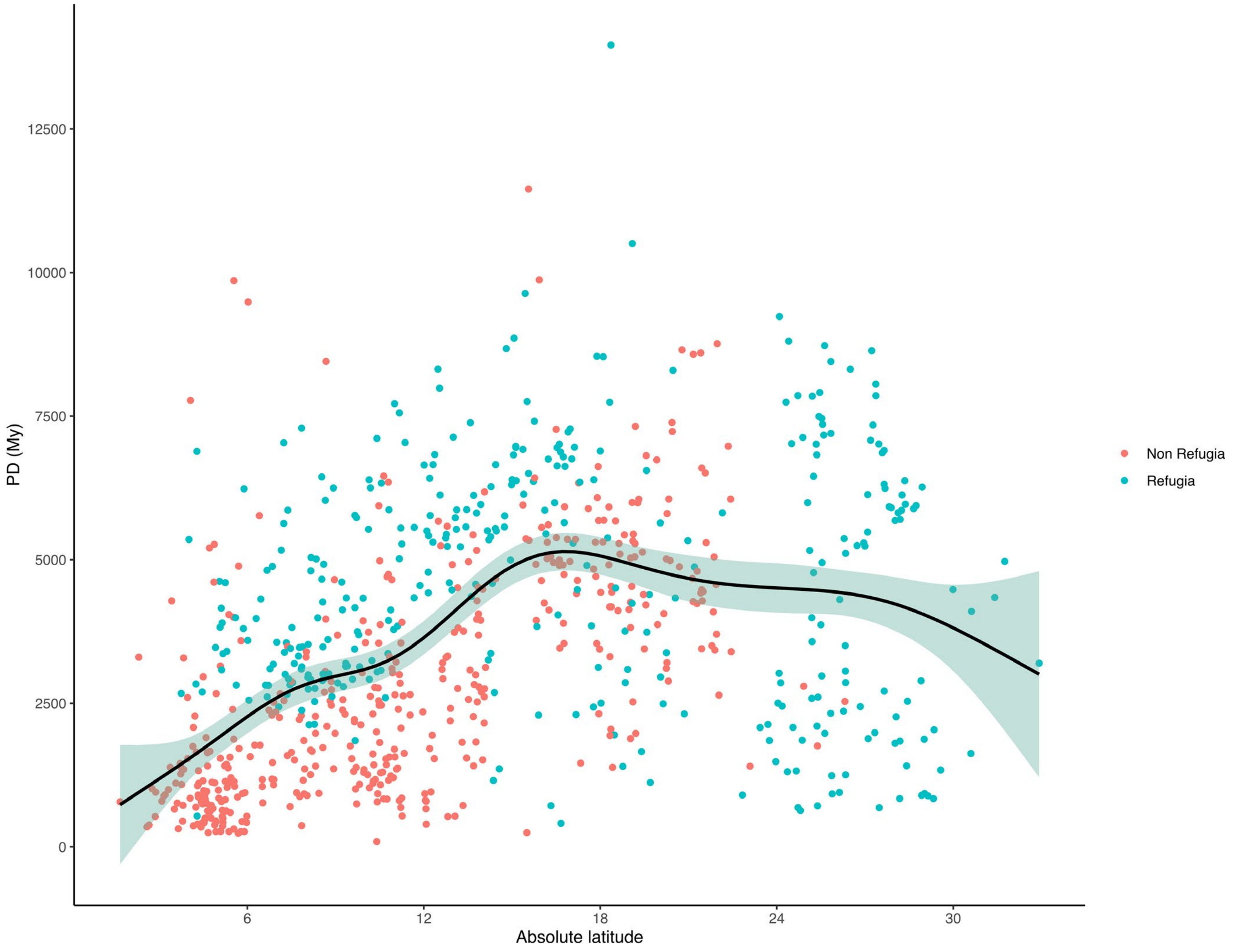

FIGURE 2 PD plotted against absolute latitude. The fitted GAM (black line), with absolute latitude predicting PD ($R^2 = 0.253$, $F = 28.73$, $p < 0.01$), shows a gradual increase in PD with latitude, reaching its peak around 17° of latitude. Blue dots represent assemblages located on the proposed refugia and source nuclei by the PAH and WMH (Refugia in the inset), whereas red dots are assemblages from other SDTF not considered as refugia (Non-refugia in the inset)

TABLE 1 SAR models results of the effects of climate and climatic instability on residual phylogenetic diversity (rPD) of Neotropical SDTF assemblages. MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation

Predictor	$R^2_{\text{Nagelkerke}}$	*p*-val	AIC	ESTIMATE	EST *p*-val
MAT	0.080972	<0.01	11,048	−0.83163	>0.05
MAP	0.16869	<0.01	10,969	0.204372	<0.01
MAT from the LGM	0.081336	<0.01	11,047	−0.82897	>0.05
MAP from the LGM	0.16202	<0.01	10,975	0.2348	<0.01
MAT Instability	0.077536	<0.01	1,1500	1.4722	>0.05
MAP Instability	0.089536	<0.01	11,040	0.23482	<0.01

respectively). For the South American pool, NRI values ranged from −3.27 to 7.42 with an average of 1.96, showing a marginal but significantly clustered phylogenetic structure. Still, there were three assemblages with overdispersed phylogenetic structure, two in central Brazil and one in the Andean Piedmont. Overall, all the floristic groups in the South American Pool increased their mean NRI (Figure 3b).

4 | DISCUSSION

We found evidence supporting the existence of a reverse latitudinal gradient in PD of the SDTF woody plants, following the same reverse LDG shown by plant (Banda et al., 2016; Linares-Palomino et al., 2011; Pennington et al., 2006, 2009) and bird SR (Prieto-Torres et al., 2019) across this biome. To the south and north of the Equator,

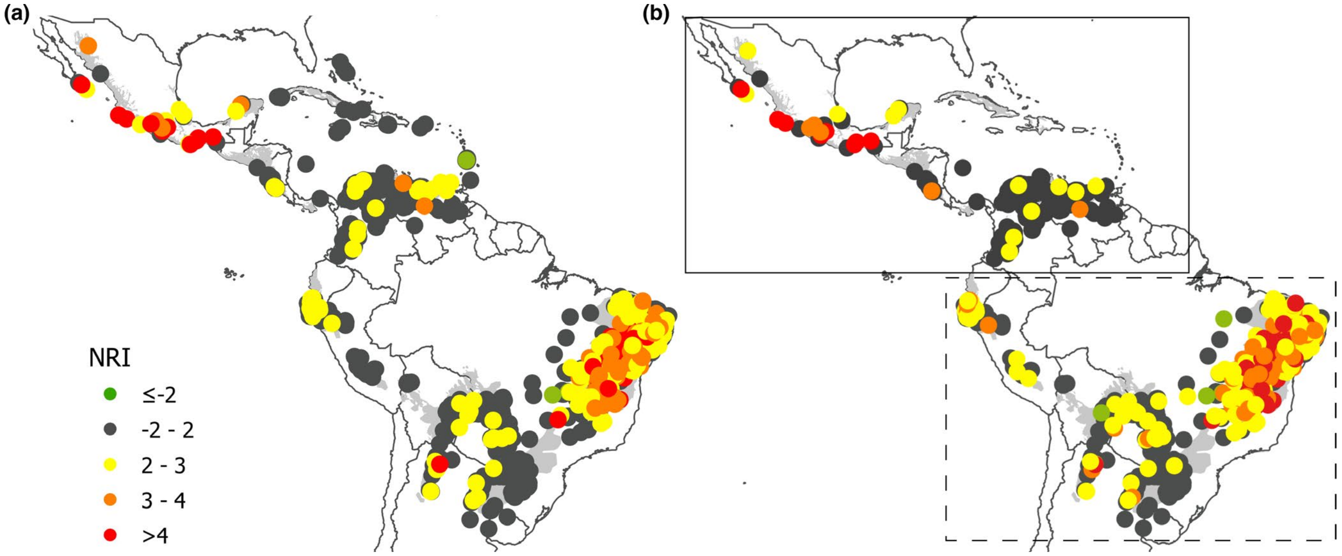

FIGURE 3 Geographic pattern of SDTF assemblages' phylogenetic structure relative to (a) the continental species pool and (b) the regional species pools, where the black square represents the Mesoamerican–northern South American region and the dotted line square represents the South American region. Green values indicate overdispersion, grey values indicate random structure, yellow values indicate low clustering, orange values indicate medium clustering and red values indicate high clustering

assemblages with high PD coincide with the proposed refugia nuclei and source areas by the PAH (Prado & Gibbs, 1993) and the Western Mexico Hypothesis (WMH; Becerra, 2005) respectively. It seems that in the past these nuclei accumulated lineages over time from either local speciation and/or low extinction of early diverged lineages as shown by their clustered phylogenetic structure and negative rPD, with some derived lineages later expanding their distribution towards the equator (Becerra, 2005; Cortes et al., 2015) forming assemblages of low PD composed by both closely and distantly related species as evidenced by their random phylogenetic structure. However, the proposed climatic explanation (stability) for these phylogenetic patterns was not supported by our findings, as shown by the SAR models where climatic instability had little explanatory power on the observed rPD. This result undermines the role of climatic dynamics (at least since the LGM) and suggests the effect of evolutionary and biogeographic processes at deeper time scales in driving current diversity patterns of these forests. Indeed, SDTF presents significant geographic phylogenetic structure across the Neotropics beyond the 'phylogenetic integrity' (Pennington et al., 2009) exhibited by this biome when compared to Neotropical moist forests (Segovia et al., 2020).

Spatially, PD of SDTF assemblages showed a reverse latitudinal gradient congruent with that of SR, suggesting that phylogenetic history could either fully explain or not explain species richness at all (Fritz & Rahbek, 2012). Therefore, such reverse latitudinal pattern of PD is not particularly informative or surprising in this case. However, when considering the spatial pattern of rPD across SDTF assemblages, thus, controlling for SR, we found evidence of phylogenetic history influencing species richness differently across the Neotropics. Indeed, SDTF assemblages with negative and positive rPD indicate regions where diversification and dispersal have played a role in the formation of the observed species richness patterns. For instance, within the continent, Mesoamerica and Caatinga regions showed a concentration of assemblages with markedly negative rPD, whereas the other continental regions had positive but rather close to zero rPD. This pattern of negative rPD (low PD relative to SR) in these regions can be explained by the in situ radiation of geographically confined clades, such as the genus *Bursera* in Mexico (De-Nova et al., 2012; Sosa et al., 2018) and the genera *Coursetia* and *Luetzelburgia* in Caatinga (Queiroz et al., 2017). Conversely, SDTF assemblages in the Antilles, which are also far from the equator, showed positive rPD (high PD relative to SR). This insular pattern can be the result of strong environmental filtering brought about by hurricanes, drought and extreme edaphic conditions that may have favoured evolutionary distinct lineages with convergent attributes in this insular environment (Franklin et al., 2018; Murphy & Lugo, 1986) and perhaps accompanied by lower in situ diversification compared to Mesoamerica and Caatinga regions.

The PAH originally proposed that extant SDTF nuclei are remnants of a once continuous distribution of this biome across South America during the LGM (Prado, 2000; Prado & Gibbs, 1993). Accordingly, some of these nuclei remained covered by SDTF despite the climatic fluctuations of this time period and, thus, may have been climatically stable refugia providing enough time for lineages to accumulate and diversify (Haffer, 1969; Klopfer, 1959; Svenning et al., 2015). As such, these climatically stable nuclei would be expected to show positive rPD compared to instable regions. In direct contradiction to this, we found that many assemblages within the Caatinga region, one of the proposed refugia nuclei for SDTF (Prado & Gibbs, 1993), had negative values of rPD indicating that most of their species are closely related, perhaps reflecting local diversification. This finding is congruent with the outcomes of the SAR models where no effect of climatic stability was observed on rPD. This evidence adds to the questioning about the role of Late Quaternary climatic changes as determinants of current SDTF diversity patterns in particular (Mayle, 2004), and biodiversity patterns in general (Fordham et al., 2019). Furthermore, our observed PD and rPD patterns contradict the recent predictions of Costa et al. (2018) for the SDTF, mainly for the Caatinga. According to these authors, Caatinga should present low SR and PD, thus, rPD around zero, owing to its high instability since the LGM. Instead, we found that Caatinga has some of the highest SR and PD, as well as highest negative rPD assemblages, supporting the idea that climatic stability since the LGM could have exerted low impact on current diversity patterns, at least in South America (Fordham et al., 2019). Still, it is possible that climatic dynamics at deeper time periods than the LGM, such as those resulting from Milankovitch oscillations (10–100 thousand years cycles), could have influenced evolutionary processes responsible for current diversity patterns as has been suggested for the LDG (Fine, 2015; Jansson & Dynesius, 2002). However, directly evaluating such deep time climatic dynamics requires data that are not yet available.

Water availability is one of the defining attributes of the SDTF (Pennington et al., 2009). Accordingly, we found that mean annual precipitation in both the LGM and contemporary climate were the only variables with significant explanatory power of rPD across SDTF assemblages, suggesting that precipitation regimes could have been more critical for lineage establishment and diversification than climatic stability. Indeed, seasonal drought represents a strong environmental filter for SDTF species, directly affecting their distribution and assembly (Pinho et al., 2019). More generally, precipitation regimes have been recently shown to influence the PD of tropical tree assemblages with high PD at intermediate precipitation levels (Neves et al., 2020). In our case, the observed positive relationship between past and current precipitation with rPD agrees with these recent findings, as our SDTF assemblages showing high PD (and rPD) and high precipitation within this particular biome seem to match those assemblages with high PD and intermediate precipitation across lowland tropical South America. Still, the fact that many of our studied assemblages had similar amounts of precipitation in both time periods with only a few assemblages showing precipitation instabilities (>200 mm annually) may explain why climatic stability is not related to the current diversity pattern of the SDTF (Collevatti et al., 2013; Werneck et al., 2011).

The phylogenetic structure of assemblages also reveals deep-time evolutionary and biogeographic processes (Kissling et al., 2012), which in our case suggests the existence of potential source areas for the SDTF regardless of their climatic dynamics since the LGM. The overall random phylogenetic structure of SDTF assemblages at the continental scale may suggest that these assemblages equally comprise both closely and distantly related lineages. However, some assemblages, especially in Mesoamerica and Caatinga, showed significant phylogenetic clustering at this scale, implying that these nuclei could have served as source areas for the SDTF given the presence of closely related lineages that diversified in situ. Indeed, Queiroz et al. (2017) suggested that the Caatinga plant diversity arose mostly from in situ diversification during the mid-Miocene to the Pliocene (~15–3 Myr) harbouring many unique and species-rich plant lineages, agreeing with our observed phylogenetic clustering and negative rPD of this nucleus. Moreover, this agrees with the high phylogenetic geographic structure in which all species in a given region are each other's closest relative, evidencing niche conservatism, as reported for some SDTF genera (*Coursetia*, *Poissonia* and *Ruprechtia*; Pennington et al., 2006). Similarly, SDTF assemblages of western Mesoamerica showed high phylogenetic clustering implying processes of in situ diversification and niche conservatism of lineages such as *Bursera* (Becerra, 2005). However, these assemblages, particularly those in western Mexico, have been proposed to have ~20–35 Myr (Becerra, 2005; Sosa et al., 2018) compared to the Caatinga assemblages with ~3–15 Myr (Queiroz et al., 2017). Such age differences across SDTF assemblages are the core of the WMH for the origin of this biome (Becerra, 2005). In fact, the old age and regional diversification within Mexico have resulted in patterns of neo- and paleo-endemism in the Mexican dry forests, suggesting that these areas would have served as both cradles and museums for the SDTF in the Neotropics (Sosa et al., 2018). Despite age differences between the Mesoamerica and Caatinga nuclei, their comparatively larger area and age compared to other SDTF nuclei could have equally allowed them to serve as source areas for this biome perhaps through a time-integrated area effect as recently proposed by Banda et al. (2016).

At the regional scale, phylogenetic structure of SDTF assemblages showed different patterns than at the continental scale but still support the existence of sources areas in both Mesoamerica and South America. For instance, in South America a considerable number of assemblages that were random under the continental pool increased their phylogenetic clustering under the South American pool, such as those within Central Brazil, the South American Pacific and the Andean piedmont nuclei. This phylogenetic structure at more regional scales could support the PAH idea of previously widespread clades that fragmented into isolated lineages that later diversified in situ, forming separate nuclei composed by closely related species (Linares-Palomino et al., 2011; Pennington et al., 2006, 2009). Still, such pattern does not seem to have been driven by climatic stability since the Pleistocene but by earlier events related to the diversification and dispersal of SDTF lineages throughout their evolutionary history (Pennington et al., 2009). Regarding Mesoamerican assemblages, some of these changed from highly clustered at the continental scale to random phylogenetic structure under the Mesoamerican–northern South American pool. This could be explained by their sharing of a high proportion of lineages within this regional pool but not so much between this and the South American pool (e.g. Zygophyllaceae), suggesting dispersal limitations across regions (Becerra, 2005; Pennington et al., 2009). Overall, the significant phylogenetic structure observed mainly in Mesoamerica and Caatinga together with the lack of a relationship between these patterns and climatic stability since the LGM highlight the role of evolutionary and biogeographic processes that occurred beyond this time period in driving current SDTF diversity patterns. Testing the effect of such processes requires spatially explicit estimates of speciation, extinction and dispersal rates as well as their temporal variation that are beyond the scope of this study but that can be assessed with recent methods (Villalobos et al., 2020).

5 | CONCLUSIONS

Our findings add to those studies failing to support the effect of climatically stable refugia proposed by the PAH on the current diversity patterns of SDTF (Becerra, 2005; Cortes et al., 2015; Mayle, 2004). Nonetheless, some predictions of the PAH were supported by our data: from the Caatinga nucleus, diversification in situ from which numerous migration events could have populated other areas of SDTF. However, these evolutionary and biogeographic events may have occurred long before the Pleistocene. This is the case under the WMH and supported by our findings, suggesting the existence of source areas for the current SDTF in western Mesoamerica as a result of such deep time events. As such, the proposed source areas for the seasonally dry forest in South America by the PAH and in Mesoamerica by the WMH remain valid and support the existence of unique floristic associations within each of these two regions, perhaps associated with different timing of radiation and adaptations of woody plants to seasonally dry environments along northern and southern regions (Banda et al., 2016; Becerra, 2005; Cortes et al., 2015).

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DATA AVAILABILITY STATEMENT

The data used in this study are freely available from the sources cited in the Materials and Methods section. All scripts to conduct the analyses are available at: https://github.com/fabro/NewWorld_SDTF

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BIOSKETCH

Axel Arango is currently a PhD student at Instituto de Ecología A.C. (INECOL) under the supervision of F.V. He is greatly interested in global biodiversity patterns and the mechanisms that drove them to their current state. This study resulted from his Master's thesis jointly supervised by R.G. and F.V.

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