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PERSPECTIVE

The two South American dry diagonals

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Abstract

South American drylands roughly form two diagonals both termed in the biogeographical literature as *the* "South American dry diagonal" (SADD). However, they correspond to two different geographical areas. One comprises the Caatinga, Cerrado and Chaco domains, thus encompassing the areas between northeastern Brazil and northwestern Argentina. The other stretches from Patagonia in southern Argentina to the Pacific deserts of northern Chile and Peru, thus also including the Monte, Prepuna and dry Puna domains. I termed them the eastern and western SADDs, respectively (i.e., eSADD and wSADD). In this mini review I attempt to summarize the major climatic features of the two South American dry diagonals, their possible origins, biogeographical patterns within and around them and to explore possible interconnections. The eSADD is generally more humid than the wSADD and has more pronounced rainfall seasonality, with precipitation concentrated in summer, while the wSADD tends to be less seasonal due to year-round aridity, with little precipitation largely occurring in winter. The origin of both diagonals appears to go back to the middle Miocene, associated with global cooling. Biogeographical studies show that these diagonals are important in structuring South American distribution patterns south of the Equator, both acting as barriers for humid-adapted lineages and corridors for arid-adapted taxa. Remarkably, the two diagonals appear to have few plant and animal taxa in common, which may explain why biogeographers speaking about one diagonal seem to ignore the existence of the other.

Highlights

- Two South American regions have been referred to as *the* South American dry diagonals.

- The first comprises the Caatinga, Cerrado and Chaco domains. The second encompasses Patagonia, Monte, Prepuna, dry Puna and Pacific Desert.

- These two diagonals are key in structuring South American distribution patterns, acting both as dispersal barriers and corridors.

- They appear to have little in common, both floristically and faunistically.

Keywords: Atacama, Caatinga, Cerrado, Chaco, Monte, Pacific Desert, Patagonia, Prepuna, Puna, SADD

Introduction

A rapid appraisal of the literature on South American biogeography reveals that when authors speak about *the* "South American dry diagonal" (SADD) they refer to two completely different things, resulting in two bodies of literature, which appear to largely ignore each other. The first notion of SADD refers to the concatenation of sub-humid, dry and semiarid domains stretching from northeastern Brazil into northwestern Argentina formed by the Caatinga, Cerrado and Chaco domains (Fig. 1A; Prado and

Gibbs 1993, Werneck et al. 2012, Santos-Silva et al. 2013, Fouquet et al. 2014, Azevedo et al. 2020a, Collevatti et al. 2020, Ledo et al. 2020, Neves et al. 2020, Rocha et al. 2020, Masa-Iranzo et al. 2021). The second refers to the arid and hyperarid domains distributed from southern Argentina into southwestern Ecuador formed by Patagonia, Monte, Prepuna, dry Puna and the Atacama and Peruvian deserts (Fig. 1B; Eriksen 1983, Houston and Hartley 2003, Bräuning 2009, Garreaud 2009, Moreira-Muñoz 2011, Marín et al. 2013, Aszalós et al. 2016). While
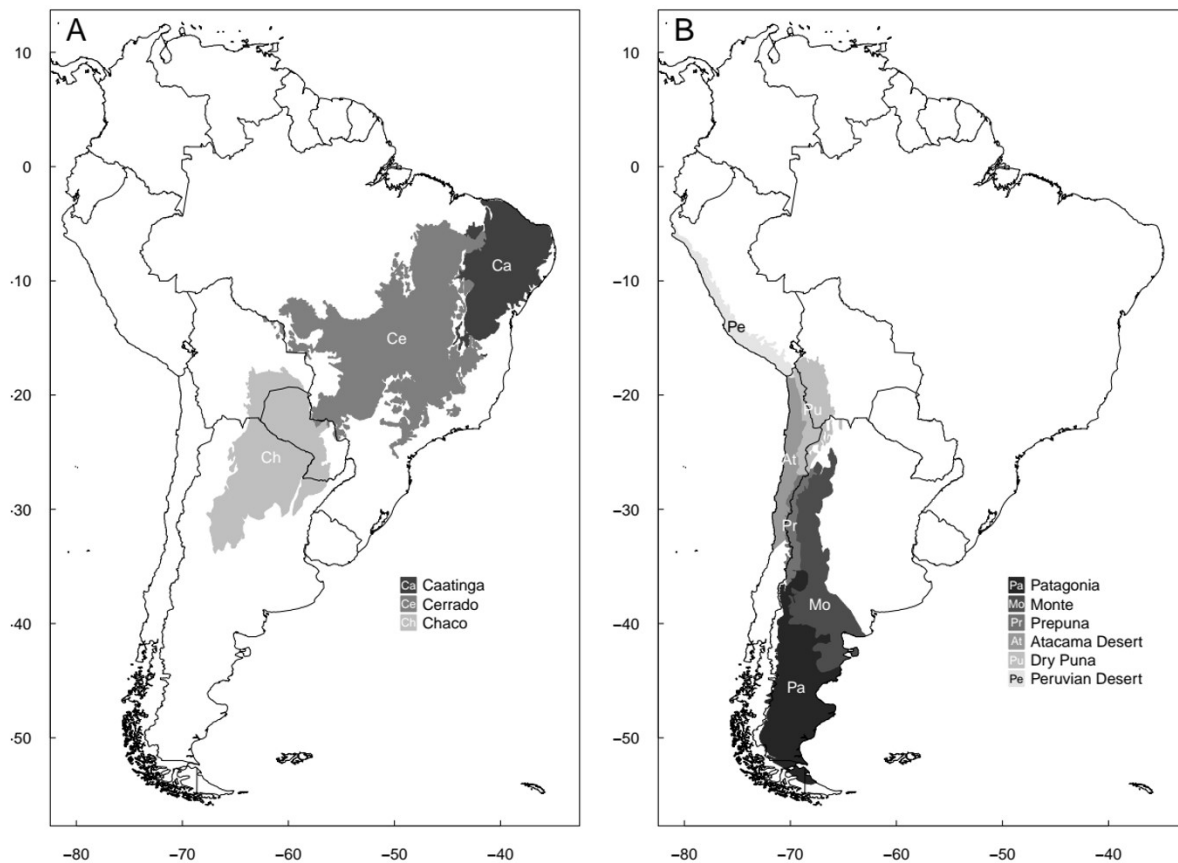
Figure 1. The two South American dry diagonals. A: Caatinga, Cerrado and Chaco (taken from Olson et al. 2001). B: Patagonia, Monte, Prepuna, dry Puna, Atacama and Peruvian deserts (taken from Romano 2017, based on Morrone 2015, except for the dry Puna, which was taken from Olson et al. 2001, because Morrone's definition of Puna includes humid regions)

the former is sometimes referred to as the "diagonal of open formations" (e.g., Vanzolini 1963, Ab'Sáber 1977, Werneck 2011, Zanella 2011, Fonseca et al. 2020), the latter is commonly referred to as the "South American arid diagonal" (SAAD; Martonne 1935, Ab'Sáber 1977, Bruniard 1982, Garleff and Schäbitz 1991, Messerli et al. 1997, Villagrán and Hinojosa 1997, Veit 1998, Ochsenius 1999, Abraham et al. 2000, 2009, 2020, Baranzelli et al. 2020, Salariato and Zuloaga 2020) or rarely as the "xeric diagonal" (Marín et al. 2013). To avoid confusion, I will henceforth refer to them as the eastern and western SADDs, respectively (i.e., eSADD and wSADD). The first mention of any of these diagonals in the literature appears to come from Martonne (1935) who referred to the wSADD (Abraham et al. 2020). The eSADD was probably first mentioned by Vanzolini (1963; see Ab'Sáber 1977, Werneck 2011). There seems to be few integrative studies addressing the biogeography of these two diagonals. Apparently, Ab'Sáber (1977) was the first to recognize the existence and notice the structuring role of the two dry diagonals on South American biogeographical patterns. In this communication I selectively review the literature and compare these diagonals in terms of climatic conditions, possible origins and biogeograhical patterns. Based on this review, I address the question of whether these two

diagonals are biogeographically related or whether they do correspond to distinct evolutionary arenas thus justifying the apparent lack of connection observed in the literature.

Climatic conditions of the dry diagonals

Most climatologists have defined aridity or dryness in terms of water balance (see Ward 2009), i.e., the ability of precipitation (P) to compensate water loss through evapotranspiration (ETP). Thus, one of the most widely used indices is the Aridity Index (AI), corresponding to the P/ETP ratio (Kimura and Moriyama 2019). The annual AI in South America shows that drylands are located both east and west of the Central Andes (Atacama and Peruvian Deserts, dry Puna, Chaco and Monte), east of the southern Andes (Patagonia and Prepuna), in the Brazilian Nordeste (Caatinga) and in the Caribbean coast (Fig. 2). The South American dry diagonals include all of these regions except for the Caribbean coast. They also exclude areas typically considered as dry, such as central Chile under Mediterranean-type climate or the dry inner-Andean valleys and includes the Cerrado, located between the Caatinga and Chaco in the eSADD (Fig. 1). The wSADD can be classified as either arid or hyperarid (AI<0.2; Fig. 2A). It thus appears that the denomination
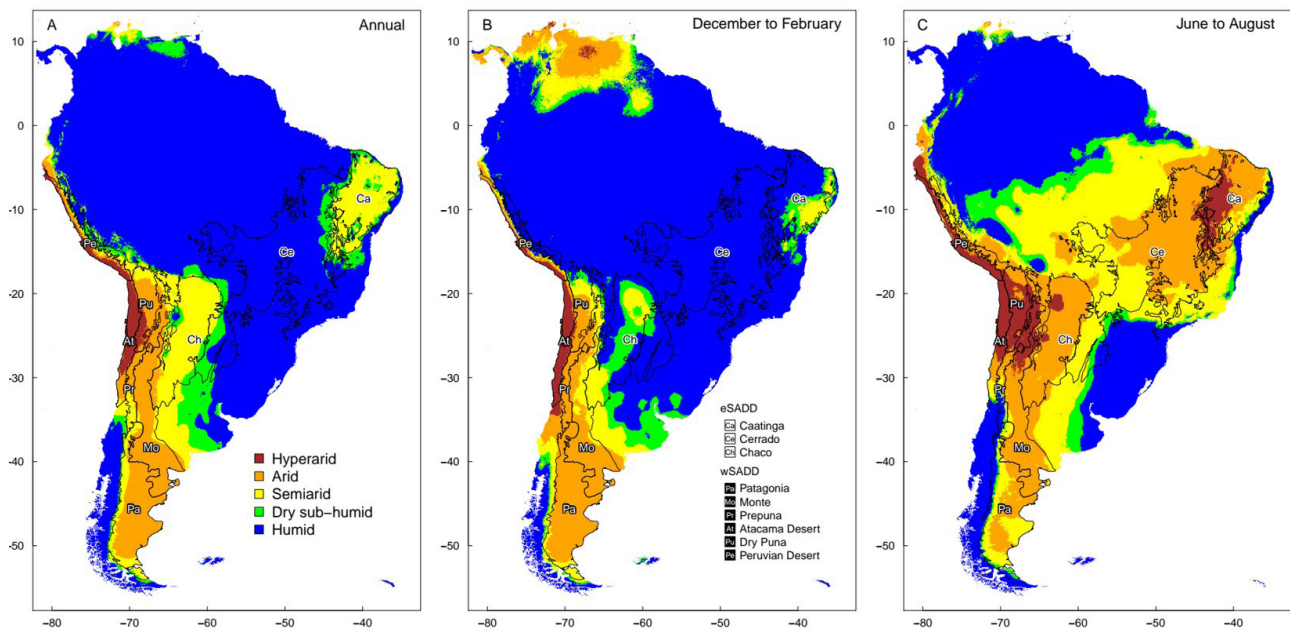
Figure 2. Distribution of the Aridity Index (AI) in South America calculated for annual values (A) and for the austral summer (B) and winter (C). Data was directly obtained from Trabucco and Zomer (2018) for A and from Trabucco and Zomer (2018) and Fick and Hijmans (2017) for calculating B and C. Categories of aridity are those of Middleton and Thomas (1997): Hyperarid (AI<0.03), Arid (0.03<AI<0.2), Semiarid (0.2<AI<0.5), Dry sub-humid (0.5<AI<0.65) and Humid (AI>0.65). Lines and letters correspond to the boundaries of the regions comprising the SADDs depicted in Figure 1.

of "Arid Diagonal" (see above) and the exclusion of central Chile and the dry inner-Andean valleys from it is appropriate. Though not customary in the literature (see Abraham et al. 2020), including central Chile and the dry inner-Andean valleys in the wSADD would make it geographically larger and climatically broader (i.e., incorporating semi-arid zones), but would not affect its approximate geographical location. To understand the eSADD, seasonality needs to be taken into account. While Caatinga and Chaco prevail semiarid throughout the year (0.2<AI<0.5; Fig. 2A) most of the Cerrado can be classified as humid (AI>0.65). This pattern also holds if only sites of dry formations are considered (i.e., the local climate of specific sites with xeromorphic vegetation; Neves et al. 2015). However, the Cerrado becomes arid to semiarid during the austral winter (Fig. 2C). Partially due to this lack of climatic identity, de Queiroz et al. (2017) argued that the term "Dry Diagonal" is conceptually equivocal to designate the eSADD. While most references cited above refer to the eSADD as composed of the Catinga, Cerrado and Chaco domains, Neves et al. (2015) also included the Pantanal, a seasonally flooded savanna formation located between Cerrado and Chaco (Junk and Nune da Cunha 2016) and the Chiquitania, a mosaic of savanna, savanna wetland and dry forests in eastern Bolivia (Killeen et al. 1990), in their assessment of the eSADD.

Climatic controls and possible origins

There is no single factor that can explain aridity throughout the continent. Therefore, there are likely multiple origins of aridity responding to different combinations of factors. Aridity of the wSADD forms in a zone where the influence of both austral winter and summer rainfall is marginal. Winter rainfall is caused by the Pacific westerlies (air masses originating in the Pacific Ocean and reaching southwestern South America from the west), while summer rainfall is caused by air masses from the Amazon moving southwards due to the summer formation of the continental low (a low-pressure system situated over the Chaco region) (Garreaud et al. 2009). Patagonian aridity is largely the consequence of the rain-shadow effect of the austral Andes that prevents the Pacific westerlies to reach eastern locations (Garreaud et al. 2013). On the other extreme, aridity in the Atacama and Peruvian deserts is largely controlled by the position the Pacific Anticyclone, which prevents northward penetration of the westerlies (Garreaud and Aceituno 2007). This is reinforced by the effect of the Humboldt current and central Andean rain-shadow with respect to the influence of tropical air masses from the Amazon basin (Houston and Hartley 2003).

Rainfall occurs during winter over the western coast of subtropical South America (Fig. 3; Schulz et al. 2011), when the Pacific anticyclone reaches its northernmost position (Montecinos and Aceituno 2003). North of Patagonia, on the Monte region, the influence of the westerlies declines both because of distance and increasing elevation of the Andes, but the effect of the Pacific Anticyclone is also weak. Tropical air masses from the Amazon exert marginal seasonal influence over this region, causing a slight
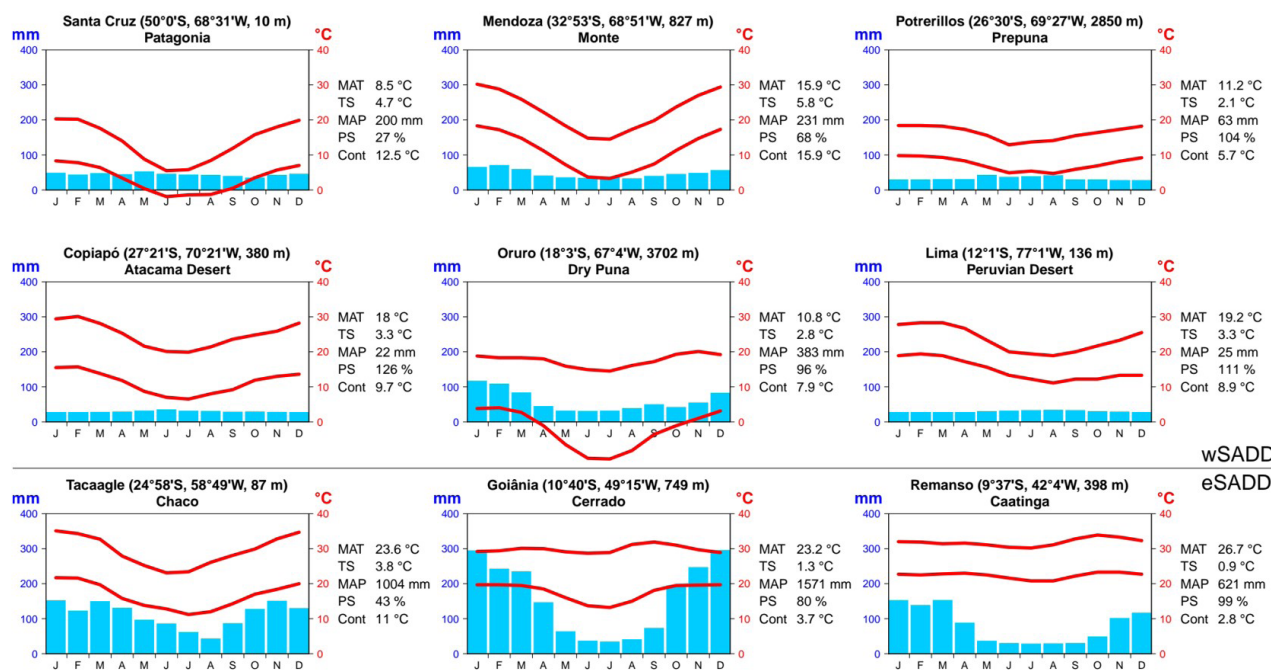
Figure 3. Climate diagrams of representative meteorological stations of each domain of the two South American dry diagonals. The horizontal line divides the diagrams of the wSAAD (above the line) and the eSADD (below the line). Bars correspond to mean monthly precipitation. Red lines correspond to mean maximum and minimum monthly temperature. MAT: Mean annual temperature; TS: Temperature seasonality (standard deviation of mean monthly temperatures); MAP: Mean annual precipitation; PS: Precipitation seasonality (coefficient of variation of mean monthly precipitation); Cont: Continentality (difference between mean monthly temperature of the warmest and coldest months). Diagrams built following Mucina et al. (2006). Data obtained from FAO (2001) except for Cerrado and Caatinga, obtained from Banco de Dados Meteorológicos do INMET (https://bdmep.inmet.gov.br, accessed 7 September 2020).

increase of summer rainfall, the same being true for the dry Puna (Fig. 3), when the Intertropical Convergence Zone (ITCZ) reaches its southernmost position (Garreaud et al. 2009). This trend intensifies northward and is responsible for summer rainfall over the Chaco and Cerrado (Fig. 3). Year-round greater aridity of the Caatinga appears to be the consequence of the combination of the local intensification of the Hadley cell (Garreaud et al. 2009) associated with African teleconnections (the influence of heating over Africa on South American precipitation patterns), the latter inducing considerable suppression of summer rainfall over northeastern Brazil (Cook et al. 2004).

Since global atmospheric circulation does not appear to depend on the regional distribution of land and sea, it is likely that the major features of anticyclonic aridity have not dramatically changed throughout the Cenozoic (Hartley 2003). However, the well-documented global cooling since the Mid Miocene (Zachos et al. 2001) and the subsequent decrease of sea surface temperature and changes in oceanic circulation due to a long-term trend in expansion of the Antarctic ice sheet during the late Pliocene compared to previous times (McKay et al. 2012) have probably led to increasing subtropical aridity (Herbert et al. 2016). The expansion of the Antarctic ice sheet may have also pushed the ITCZ northward

(Chiang and Bitz 2005; Hyeong et al. 2016), giving rise to present-day rainfall seasonality over subtropical latitudes of the eSADD. This is also well correlated to the Miocene expansion of C4 taxa (Latorre et al. 1997), the origin of fire-adapted plants of the Cerrado (Simon et al. 2009), the expansion of seasonally dry tropical forests of the Caatinga (Almeida et al. 2018) and other arid-adapted plant groups (Arakaki et al. 2011). In Patagonia, the rain-shadow effect of the Andes can be traced back to its uplift that also took place during the Mid Miocene (Blisniuk et al. 2005), which along with the cooling trend may have led to the formation of xeromorphic vegetation towards the late Miocene (Palazzesi et al. 2014). The fossil record of Patagonia further supports the idea of late Miocene aridification in southeastern South America (Barreda and Palazzesi 2007, Palazzesi et al. 2014). The onset of aridity in the Atacama Desert probably took place during the late Oligocene (Dunai et al. 2005) and intensified during the Miocene due to increasing rain-shadow associated with positive feedbacks with central Andean uplift (Lamb and Davis 2003) as well as with the development of the Humboldt current (Sepulchre et al. 2009). Miocene intensification of aridity in the Atacama Desert is further supported by cosmogenic nuclide exposure dating (Ritter et al. 2018). This is coincident with Miocene-to-Pliocene divergence time estimates

for the origin and diversification of several plant taxa of the Atacama Desert (e.g., Luebert and Wen 2008, Heibl and Renner 2012, Böhnert et al. 2019).

Biogeographic patterns within and around the dry diagonals

Both SADDs may be seen as structuring a number of South American biogeographical patterns. On the one hand, both constitute environments for colonization and diversification of arid-adapted lineages. On the other hand, they act as a barrier for lineages that are not capable to survive in such arid environments and have been suggested to be responsible for biogeographical disjunctions on both sides of the diagonals. However, little has been documented about potential biogeographical connections between them. As shown below, this is possibly due to the fact that they actually have little in common.

The eSADD separates the Amazon and Atlantic Forest, two domains dominated by tropical rain forests. The Amazon-Atlantic Forest disjunction is one of the biogeographical patterns identified by Fiaschi and Pirani (2009). Atlantic Forest shows a stronger floristic connection to the Amazon at the species level than to any other Neotropical evergreen forest (Cupertino-Eisenlohr et al. 2021), suggesting recent floristic exchanges between Atlantic Forest and the Amazon (Antonelli et al. 2018). These exchanges have been suggested to be most intensive through the western portion of both Atlantic Forest and the Amazon (Batalha-Filho et al. 2013, Thode et al. 2019), though evidence also suggests that this route may have been continuously used by vertebrates since the Oligocene (Fouquet et al. 2014; Ledo and Colli 2017, Antonelli et al. 2018). The formation of the Pantanal during the late Pliocene (Ussami et al. 1999), and Pleistocene climatic cycles (Sobral-Souza et al. 2015) may have contributed to the intensification of these exchanges. Even more recent exchanges have been suggested for vertebrates through the coastal region of the Caatinga on the eastern portion of both rainforests, possibly associated with Pleistocene climatic cycles (Ledo and Colli 2017). These studies, however, underscore the importance of the eSADD as a barrier between Amazon and Atlantic Forest, which may explain early vicariant events in both vascular plants and vertebrates (e.g., Fouquet et al. 2012, Batalha-Filho et al. 2013, Thode et al. 2019, Almeida and van den Berg 2020; Masa-Iranzo et al. 2021) as a consequence of the formation of these dry environments during the Miocene (see above).

Biotic connections within the eSADD have been widely documented. High floristic similarity and numerous examples of species and higher taxa distributed across the Caatinga, Cerrado and Chaco are available for vascular plants (Prado and Gibbs 1993, DRYFLOR et al. 2016), though many of them are presently absent in the Cerrado. Prado (2000) suggested that observed distribution patterns indicate that areas of the Cerrado had been inhabited by taxa currently distributed only in the Caatinga and Chaco

domains in the recent geological past. Current absence of taxa in the Cerrado may thus be due to more humid conditions and more pronounced rainfall seasonality (Neves et al. 2015; see Figs. 2 and 3) that also favor the occurrence of fires (Miranda et al. 2009), but general climate of the area currently occupied by Cerrado appears to have been drier during Quaternary glacial periods (Collevatti et al. 2020, Oliveira et al. 2020). Examples of other species distributed across the eSADD are also available for anurans (Santos et al. 2009; Vasconcelos et al. 2019), geckos (Werneck et al. 2012), lizards (Fonseca et al. 2018; Ledo et al. 2020), birds (Rocha et al. 2020), and arthropods (Zanella 2011, Bartoleti et al. 2018), though many of these groups show connections to the neighboring domains, especially the Atlantic Forest.

Similar to what has been proposed for the eSADD, the wSADD has been considered as a vicariant barrier that had shaped disjunctions, especially in plants (Villagrán and Hinojosa 1997, 2005, Moreira-Muñoz 2011). Evidence for the formation of vicariant disjunct patterns has been found in plant groups disjunctly distributed in the southern Andes (Mediterranean woodlands and temperate rainforests domains) and southern Brazil (mainly Atlantic Forest domain) that split during the Miocene (Chacón et al. 2012, Murillo et al. 2016, Luebert et al. 2020, Moreira-Muñoz et al. 2020), though not all groups sharing this disjunction can be explained by the origin of the wSADD, with some groups probably having dispersed more recently across already formed arid environments (Luebert et al. 2020). A disjunct distribution pattern between the southern and the tropical Andes with a distribution gap at the arid zones of Atacama and Peruvian deserts has also been documented in several plant groups (reviewed in Lörch et al. 2021). Some of them have been shown to have also split during the Miocene, coinciding with the formation of the Atacama and Peruvian deserts (Drew and Sytsma, 2013, Renner et al. 2020, Lörch et al. 2021). This arid barrier has also been suggested to limit north-south dispersal in wild South American camelids (Marín et al. 2013, Casey et al. 2018) and appears to split the distribution of Neotropical snakes on the western side of the Andes (Azevedo et al. 2020b).

On the other hand, Palma et al. (2005) suggested that the formation of the wSADD "provided new environments for the differentiation of local biota". There appears to be only few groups distributed along the entire wSADD. Kelt et al. (2000) showed high similarity of small mammal faunas within the wSADD, though no species were shared between the geographically extreme areas of the Atacama Desert and Patagonia, perhaps because the Andes act as a geographical barrier within the wSADD (see Ab'Sáber 1977, Luebert and Weigend 2014). While most of the endemisms are restricted to portions of it, several plant groups that occupy the entire wSADD are also present in other neighboring regions, such as *Ephedra*, (Ephedraceae; Ickert-Bond et al. 2009), *Leucheria* (Asteraceae; Jara-Arancio et al. 2017), *Montiopsis* (Montiaceae; Hershkovitz 2019),

Nassauvia (Asteraceae; Grossi et al. 2017) and *Proustia* (Asteraceae; Sancho et al. 2018). Unlike the eSADD, it is questionable that the wSADD has acted as a corridor for arid adapted taxa. Rather, it has probably functioned as a receptor area for immigration and, in some cases, subsequent local diversification (e.g., Katinas and Crisci 2000, Gengler-Nowak 2002, Luebert and Wen 2008, Dillon et al. 2009, Luebert et al. 2009, Heibl and Renner 2012). Still, there are some examples of plant groups that appear to be distributed along the wSADD, such as *Atriplex* South American clade 2 (Chenopodicaceae; Brignone et al. 2019), *Cristaria+Lecanophora* (Malvaceae; Böhnert et al. 2019), *Eulychnia+Austrocactus* (Cactaceae; Merklinger et al. 2021), and *Monttea* (Plantaginaceae; Baranzelli et al. 2014).

Biogeographical relationships between the dry diagonals

The first attempt known to me to compare South American dry formations based on floristic similarity was undertook by Sarmiento (1975). While he included South American Caribbean drylands of Colombia and Venezuela in his analysis, Chaco and Cerrado were not considered, perhaps because they are evidently less arid than the other regions (see Fig. 2A), and due to the lack of knowledge about species composition of these areas up to that time. In his analysis, the Caatinga appears on one end, related to the Caribbean formations, which in turn are more related to the northern Andean dry valleys and the dry coastal lowlands of Ecuador and N Peru. On the other end, Patagonia, Monte, Prepuna, Central Chile, Puna and central high-Andean formations form a floristic group. The other formations (Central Andean dry valleys, Pacific Desert) are floristically intermediate between them. This network points to gradual north-to-south floristic transitions. Ab'Sáber (1977) pointed to the Chaco domain as the connecting area between the two SADDs. Subsequent studies have focused on the floristic connections between the seasonally dry tropical formations of the Caribbean, Caatinga, Cerrado, Chaco and the inter-Andean dry valleys (e.g., Prado & Gibbs 1993, Prado 2000, Linares-Palomino et al. 2003, 2011, 2015, Pennington et al. 2009; DRYFLOR et al. 2016), thus leaving the wSADD aside.

In another analysis, Roig-Juñent et al. (2006) studied arthropod assemblages of all South American dry plant formations except the Caribbean. They suggested that biogeographical relationships between both diagonals are weak. Indeed, Magalhaes et al. (2019) showed some connections between both SADDs in spiders, but Caatinga lineages seem to be more related to dry forest species from Mesoamerica and Colombia. For small mammals, Kelt et al. (2000) reported high faunistic similarity within regions of the wSADD, but no similarity of these with the Caatinga. This is also in line with phylogenetic differentiation of South American tropical and extra-tropical tree assemblages (Segovia et al. 2020). Furthermore, while modern worldwide biogeographical classifications tend to

group the whole of South America together (e.g., Cox 2001, Holt et al. 2013, though amphibians and mammalian faunas of each diagonal are not grouped together), biogeographical regionalizations of South America (e.g., Rivas-Martínez et al. 2011, Morrone 2014) consider the southern part of the wSADD outside the Neotropical region. Above the species level, however, some biogeographical connections have been reported between both SADDs. In plants, Luebert (2011) conducted a systematic review of phylogenies involving Atacama Desert taxa and showed that some groups may be related to the Chaco, forming a disjunction that was termed the "Trans-Andean element", representing nearly 13% of the analyzed taxa. One example of this disjunction is the genus *Bulnesia* (Zygophyllaceae), the origin of which has been suggested to be linked to the Andean uplift (Böhnert et al. 2020). The genus *Skytanthus* (Apocynaceae) is the only example of a plant taxon which is disjunctly distributed in the Caatinga and the wSADD. Although its monophyly is yet to be assessed, this genus comprises two species, one endemic to the seasonally dry tropical forests of the Caatinga domain and the other to the xeric scrubs of the Atacama Desert (Prado 2003). A similar pattern was documented for the South American representatives of the bee subfamily Rhophitinae (Zanella and Martins 2003).

Concluding Remarks

Researchers referring to the so-called South American dry diagonal actually refer to two different set of biogeographical regions, one corresponding to Caatinga + Cerrado + Chaco and the other to the Pacific deserts + dry Puna + Prepuna + Monte + Patagonia. The latter has also (and most commonly) been referred to as the South American arid diagonal. To avoid confusion, researchers could make a clear difference when talking about the South American dry diagonal, so that they are not wrongly cross-referenced (e.g., as in Chacón et al. 2012, Thode et al. 2019). Accordingly, the biogeoeographical literature on South American drylands can be separated into two clearly distinct bodies and only few studies have addressed all of them in an integrative fashion. These studies tend to show that biotic connections between both South American dry diagonals are scarce and weak, which may also explain the lack of unity in studies about them. Such weak connections are likely the result of both distinct climatic conditions and diverging biogeographical histories. Nonetheless, this might also be due to the isolation of the scientific communities in South America, which calls for more integrative biogeographical studies in this region.

Acknowledgments

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