



Atlantic forest and leaf traits: an overview

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Abstract

Key message Leaf traits in Atlantic forest are modulated by environmental filters and biotic interactions. More information about leaf traits and nutrient are needed.

Abstract Categorizing tree species according to their relationships with ecosystem processes in the Atlantic forest (AF) biome is fundamental to better understand their functionality in this high biodiversity hotspot. For categorizing vegetation, leaf traits are extremely useful and this is the first compilation of leaf traits focusing on photosynthesis, water relations, nutrients, and functional diversity across major AF vegetation types: (1) rainforest (ombrophilous dense and mixed ombrophilous *Araucaria* forest), (2) seasonal semi-deciduous forest, (3) deciduous forests, and (4) coastal plain forests (*restingas*). Species showed high plasticity of photosynthetic traits from early developmental stages, including adjustments in Rubisco carboxylation capacity, maximum photosynthetic capacity, photochemical and non-photochemical quenching, specific leaf area (SLA), and chlorophyll and spongy parenchyma thickness. Montane rainforest tree species showed lower SLA and longer leaf lifespan in comparison to lowland rainforest species. Tree communities are structured by environmental filtering leading to trait convergence in early successional stages or in stressful ecosystems such as *restingas*, and by biotic interactions leading to trait divergence in later stages. Altitudinal gradients in litter production and below/aboveground biomass stocks in AF show contrasting patterns in comparison to other tropical forests, with important consequences for responding to climate change. However, the identity of limiting elements to growth still represents a critical gap in leaf trait data for AF species. Other gaps in knowledge of AF leaf traits are highlighted for consideration in future studies.

Keywords Photosynthesis · Water relations · Leaf nutrients · Functional diversity · Brazilian biome

Introduction

The *Mata Atlântica* or Atlantic forest (AF) biome is located in South America and has been identified as one of the world's hotspots of biodiversity (Myers et al. 2000). Brazil houses 92% of its original AF area, from the Rio Grande do Norte to the Rio Grande do Sul states, extending over 4000 km from 6°N to 30°S latitudes. Originally, a continuous forest covered 1,300,000 km² along the Brazilian coast, but currently it has been reduced to only 9–12% of its original vegetation (Ribeiro et al. 2009). In some parts of the northeast and southeast regions, AF extends from the Brazilian coast up to 700 km into the continent. The remaining area extends east to Paraguay and northeastern Argentina (Oliveira-Filho and Fontes 2000; Ribeiro et al. 2009; PBMC 2014). Due to its wide geographical extension (Oliveira-Filho and Fontes 2000), the AF comprises different vegetation types or forest formations distributed in tropical and subtropical areas, including Atlantic rainforest

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(ombrophilous dense forest, and mixed ombrophilous *Araucaria* forest), seasonally dry semi-deciduous and deciduous forests, coastal plain forests (*restingas*), swamp forests, mangroves and dunes as well as high altitude grasslands and rocky outcrop vegetation (Table 1) (IBGE 2012; Marques et al. 2015; Scarano 2002). Temperature changes seasonally and spatially in AF, with ecosystems such as the high latitude subtropical *Araucaria* forest of south Brazil, ranging in annual mean temperature from 12 to 22 °C throughout the year, to tropical latitude AF, ranging in annual mean temperatures from 22 to 25 °C (Colombo and Joly 2010). In general, mean annual daytime temperature in AF broadly ranges from 15 to 35 °C during the whole year with freezing temperatures uncommon in AF, especially during the day, but occurring in the south or highlands. Due to high biodiversity, studies of the flora, conservation, fragmentation, and loss of biodiversity in AF are well documented by reviews discussing the past and future of this biome (Morellato and Haddad 2000; Myers et al. 2000; Oliveira-Filho and Fontes 2000; Santos et al. 2008; Ribeiro et al. 2009; Colombo and Joly 2010; Couto et al. 2011; Couto-Santos et al. 2015; Scarano and Ceotto 2015; Neves et al. 2017). Recently, AF has been described as one of the three most vulnerable biodiversity hotspots to global change (Bellard et al. 2014).

In a highly diverse biome such as the AF, it is important to establish patterns among species to better understand their functionality and to predict vegetation responses to environmental change. This strategy allows us to group species according to a common function in the ecosystem, reducing the number of units to be studied. In this sense, traits are useful for giving ecological information, and can represent more complex syndromes involving trade-offs and synergies (Herben et al. 2012). Leaf traits have been defined by Violle et al. (2007) as a “surrogate of organismal performance”. Due to biodiversity and conservation concerns, leaf traits of AF species have been receiving more attention in the last decade.

Meta-analysis in plant ecology has been useful for compiling results, testing predictions of hypotheses and

theories, and assessing impacts of major environmental drivers (Koricheva and Gurevitch, 2014). In this review, we synthesized results from selected published studies of leaf traits in species from the AF biome. We searched scientific digital repositories at international (Web of Science, Google Scholar, Scielo) and national (Brazilian repositories of theses and dissertations) levels for studies using the following keywords: leaf trait, Atlantic forest, *restinga*, ecophysiology, photosynthesis, leaf nutrient, water-use efficiency, and functional diversity. These words were combined using: (1) “Atlantic forest” AND all the other words; (2) “*restinga*” AND all the other words; (3) “Atlantic forest” OR “*restinga*” AND “photosynthesis” AND “leaf nutrient”; (4) “Atlantic forest” OR “*restinga*” AND “functional diversity” AND “leaf trait”; (5) “Atlantic forest” OR “*restinga*” AND “water use efficiency” AND “leaf trait”. Thus, we compiled data from nearly 220 selected references including manuscripts, technical reports, theses, dissertations and meeting abstracts performed in AF and general manuscripts about leaf traits and tropical forests to provide a synthesis and context of leaf traits from AF species, with a focus on Brazil, emphasizing photosynthesis, water relations, nutrients, and functional diversity. Our main goals were to compile results to establish a framework of the current knowledge as well as identify research gaps in these topics in AF. In addition, comparisons with other tropical forests and contextualization with current scenarios of global climate change were also included.

Photosynthesis: irradiance, seasonality and the leaf economic spectrum (LES)

Species of the AF are distributed across a broad range of light environments, from open *restingas* to ombrophilous dense forest, with many abundant species showing high plasticity to variation in irradiance from early ontogenetic stages (Mattos et al. 1997; Geßler et al. 2005; Santos et al. 2008; Mielke and Schaffer 2010; Goulart et al. 2011; Barros et al. 2012; Luttge et al. 2015; Scarano and Ceotto 2015; Vieira et al. 2015; Melo Junior and Boeger 2016). Photosynthetic

Table 1 General characteristics of major Atlantic forest vegetation types Adapted from IBGE (2012), Oliveira-Filho and Fontes (2000) and Marques et al. (2015)

Vegetation type	Altitudinal variation (m asl)	Seasonality
Rainforest (ombrophilous dense, and mixed ombrophilous <i>Araucaria</i> forest)	Lowland (< 300); submontane (300–700); montane (700–1100); upper montane (> 1100)	Up to 2 months with < 100 mm pp
Seasonal semi-deciduous forest	Lowland (< 300); submontane (300–700); montane (700–1100); upper montane (> 1100)	2–5 months with < 100 mm pp
Seasonal deciduous forests	Lowland (< 300); submontane (300–700); montane (700–1000)	5–6 months with < 100 mm pp
Coastal plain forests (<i>restingas</i>)	Lowland, periodically flooded sites along the south and southern coast of Brazil	Up to 2 months with < 100 mm pp

asl at sea level

plasticity is a multivariate response achieved through many correlated physiological and morphological variables. AF species present higher photosynthetic plasticity than *cer-rado* (Brazilian savanna) species, where the shorter height of individuals promotes less shading and whose morphological features are more related to the stress resistance syndrome, mainly to water constraints, nutritionally poor acid soils, and fire events (Bustamante et al. 2004; Franco et al. 2005; Hoffmann et al. 2005; Lemos Filho et al. 2008; Goulart et al. 2011; Barros et al. 2012; Rossatto et al. 2013). The response of AF species to irradiance can be interpreted as habitat-based selection for plasticity and shows more efficiency for individuals exploiting this limiting resource. By monitoring seedlings from five tropical AF species (early and late secondary succession) under different irradiance conditions, Dos Anjos et al. (2015) showed that the traits that best explain photosynthetic plasticity were: dark respiration rate (Rd; see Table 2 for list of symbols), Rubisco carboxylation capacity (V_{cmax}), total chlorophyll content, contribution of spongy parenchyma, contribution of leaf collenchyma tissue, chlorophyll parenchyma thickness and specific leaf area (SLA). The AF species in that study included the early secondary trees *Schinus terebinthifolius*, *Pseudobombax grandiflorum*, and *Joannesia princeps*, and

the late secondary trees *Lecythis pisonis*, and *Hymenaea courbaril*, which are commonly used in forest restoration programs in Brazil. Dos Anjos et al. (2015) did not find any significant correlation between photoplasticity and successional classification, indicating that successional status is not necessarily a predictor of photosynthetic plasticity. This highlights the importance of including physiological features related to irradiance tolerance in successional classifications of tree species in AF (Dos Anjos et al. 2015). Indeed, significant relationships between successional stage and photoplasticity have been described for more extreme conditions within natural forests, such as gap openings (Rabelo et al. 2013; Teixeira et al. 2018). In gap environments of Atlantic semi-deciduous forests in southeast Brazil, the pioneer, *S. terebinthifolius*, and early successional species *Actinostemon verticillatus* presented higher values for leaf thickness (TH), succulence (SUC) and leaf mass area (LMA) than the late successional species *Metrodorea brevifolia*, which showed less leaf morphological plasticity within gaps but compensated for high irradiance with increases in photochemical and non-photochemical quenching (NPQ and qP, respectively) and ultrastructural changes such as increases in stroma volume in chloroplasts, oil droplets, and plastoglobuli (Rabelo et al. 2013). Chloroplast ultrastructural changes have also been shown to help avoid photochemical stress after forest management increases incoming irradiance in AF (Teixeira et al. 2018).

The plasticity of photosynthetic traits has specifically been studied in seedlings of AF species to determine candidate species for reforestation. These studies suggest that the palm *Euterpe edulis* (Dos Anjos et al. 2012), and trees *L. pisonis* (Dos Anjos et al. 2015), *Brosimum guianense* (Souza et al. 2010), and *Tabebuia chrysostricha* (Endres et al. 2010) are suitable for planting in low light conditions, which minimizes photoinhibition and improves early growth. Otherwise, species suitable for planting in high irradiance conditions are: *S. terebinthifolius*, *Eugenia uniflora*, *Siparuna guianensis*, *Xylopia sericea*, *Byrsonima sericea* (Dos Anjos et al. 2015; Teixeira et al. 2015; Vitoria et al. 2016; Teixeira et al. 2018) and *Inga* sp. (Souza et al. 2010). Other species able to support diversified irradiance conditions include *Cinnamomum zeylancium*, *Tapirira guianensis* (Souza et al. 2010), *P. grandiflorum*, *J. princeps*, and *H. courbaril* (Dos Anjos et al. 2015). For *S. guianensis*, increased irradiance facilitated photosynthetic performance independently of developmental stage. However, different traits conferred photoplasticity in each developmental stage: for seedlings, morphological (height investment), anatomical (thinning of spongy parenchyma), and biochemical (V_{cmax} , maximum photosynthetic capacity) traits showed more photoplasticity, whereas for saplings, photochemical (effective quantum yield) and biochemical (V_{cmax}) traits were the most plastic (Vieira et al. 2015). The sudden exposure to high irradiance

Table 2 List of leaf traits, symbols, and units, for leaf-level parameters used in the text

Trait	Symbol	Units
Photosynthetic CO ₂ assimilation rate	A	μmol CO ₂ m ⁻² s ⁻¹
Intercellular CO ₂ concentration	C _i	ppm
Leaf density	DEN	g mm ⁻³
Transpiration rate	E	mmol H ₂ O m ⁻² s ⁻¹
Bulk modulus of elasticity	ε	MPa
Maximum quantum yield of PSII	F _v /F _m	unitless
Stomatal conductance to water vapour	g _s	mol H ₂ O m ⁻² s ⁻¹
Leaf-specific hydraulic conductance	K _L	kg m ⁻¹ s ⁻¹ MPa ⁻¹
Leaf:sapwood area ratio	LA/SA	cm ² m ⁻²
Leaf life span	LL	days
Leaf mass per area	LMA	g m ⁻²
Non-photosynthetic quenching	NPQ	unitless
Leaf water potential at turgor loss point	Ψ _{TLP}	MPa
Leaf water potential	Ψ _w	MPa
Photosynthetic quenching	qP	unitless
Dark respiration rate	Rd	μmol CO ₂ m ⁻² s ⁻¹
Specific leaf area	SLA	cm ² g ⁻¹
Leaf succulence	SUC	g m ⁻²
Leaf thickness	TH	mm
Rubisco carboxylation capacity	V _{cmax}	μmol CO ₂ m ⁻² s ⁻¹
Water-use efficiency	WUE	μmol CO ₂ mol H ₂ O ⁻¹

in shade-acclimated seedlings of *E. edulis* induced fast dynamic photoinhibition as observed by a decline in maximal quantum yield of PSII (F_v/F_m), low Rd and fast stomatal opening in response to intermittent occurrence of sunflecks, demonstrating the photoacclimation capacity of this species and highlighting the importance of sunflecks to understory photosynthesis (Lavinsky et al. 2014).

Water limitation is another factor that can limit photosynthetic activity of AF species. Young and adult individuals of *Anthurium scandens*, an epiphytic Araceae, showed great stomatal sensitivity, fast stomatal closure under water stress and a strong dependence on water availability at the root level for both ontogenetic phases according to seasonality (Lorenzo et al. 2010). However, seedlings of *A. scandens* showed higher epidermal conductance to water loss and had significantly less succulent and sclerophyllous leaves than young and adult individuals, explaining the mesic microsite canopy occurrence of this species (Lorenzo et al. 2010). Water is especially important in the *restingas*, the seasonally semi-deciduous and deciduous vegetation types that are the driest type of AF. During the dry season, *restinga* plants may experience up to 6 months with no rain. Strong seasonal alterations in phenology and morphological leaf traits have been described in the dry season mainly due to soil water constraints (Rosado and De Mattos 2007; Miranda et al. 2011). Deciduous species in semi-deciduous and deciduous AF are more abundant than in the other AF vegetation types, changing the irradiance regime in the understory. In this sense, high irradiance in the forest understory beneath the crowns of dry season deciduous canopy trees when they are leafless can be thought of as “gaps of deciduousness”, and can function as high light opportunities for plants in the normally shaded understory (Gandolfi et al. 2009).

Water availability may modulate photosynthesis due to seasonal variation in vapor pressure deficit (VPD) in Atlantic rainforest, where evergreen species are the majority and in general no water constraint is related to soil (Braga et al. 2016). Decreases in the photosynthetic rate in the dry season due to increased VPD and a consequent decrease of transpiration (E), stomatal conductance (g_s), and intercellular CO₂ concentration (C_i) have been described for tree species in an Atlantic rainforest from southeast Brazil, even with a significantly higher concentration of photosynthetic pigments than in the wet season (Silva et al. 2010; Lage-Pinto et al. 2012, 2015; Teixeira et al. 2018). The increase in leaf pigment concentration in the dry season is probably due to the lower relative water content in leaf cells in the dry season (Silva et al. 2010). Therefore, increases in NPQ and decreases in the total chlorophyll/carotenoid ratio in the dry season can be considered as an important strategy to avoid potential photoinhibition due to reduced water availability (Lage-Pinto et al. 2012). Beyond water, increases in photosynthetic rate in AF plants during the rainy season could also be supported

by the higher growth temperature and greater sink strength within the plant resulting from increased growth during this period (Lage-Pinto et al. 2012).

Physiological variation among AF tree species can also be understood through axes of ecological strategy variation, such as the leaf economics spectrum and coordination with hydraulic supply to support photosynthetic activity in leaves (Santiago et al. 2004; Wright et al. 2004; Reich 2014). The leaf economics spectrum represents variation in photosynthetic traits from species with high photosynthetic CO₂ assimilation rate (A), leaf N concentration, SLA and short leaf life spans (LL) on one end of the spectrum and opposite traits at the other (Reich et al. 1997; Wright et al. 2004). The stem economics spectrum is defined as the balance between dense wood versus high water content and thick bark (Baraloto et al. 2010). To maximize photosynthesis and maintain hydraulic safety, plants may use strategies of functional integration between organs, such as leaf and stem (Ishida et al. 2008; Méndez-Alonzo et al. 2012; Pivovarov et al. 2014). However, for tropical forests including Atlantic rainforest, some species show decoupled leaf and stem economic performance (Baraloto et al. 2010; Braga et al. 2016). For example, LL is a major trait related to leaf lifetime C gain and its economic return, with the proportion of deciduousness species increasing as the unfavorable period for growth increases (Kikuzawa 1991). Weak relationships between deciduousness and water regulation have been suggested for an Atlantic rainforest in southeast Brazil (Braga et al. 2016). On the other hand, in biomes under extreme water and nutrient constraints, such as *cerrado* and *campo rupestre* (a distinct vegetation type comprising numerous microhabitats on rocky mountain tops with varying conditions of water restrictions, soil nutrients, and soil depths), some studies have shown higher LL and LMA than in rainforests (Hoffmann et al. 2005; Rossatto et al. 2013; Moraes et al. 2017). For tree species from subtropical AF in Argentina, Villagra et al. (2013a) observed a C cost associated with increased water transport that is compensated by a longer LL. Leaves from resource-poor environments have been shown to have high LMA, high wood density, longer LL, more resistance to herbivory or physical damage and low growth rate, consistent with the conservative resource use (Westoby et al. 2002).

Water relations

Spatio-temporal variation in water availability is described for AF, imposing physiological constraints and involving seasonal changes in leaf traits related to C gain and hydraulic performance (Lemos Filho and Mendonça Filho 2000; Scarano et al. 2001, 2004; Duarte et al. 2005; Rosado and De Mattos 2007; Miranda et al. 2011; Eller et al. 2013, 2015; Rosado et al. 2013, 2016; Vitória et al. 2018). In general,

during drought or in sites with water constraints, plants can reduce water loss by shedding their leaves or closing their stomata to maintain plant water potential (Ψ_w) and avoid the risk of drought-induced xylem cavitation.

Tree species from *Restinga* forests possess life history attributes to deal with low water and nutrient availability to survive (Scarano et al. 2004; Duarte et al. 2005; Rosado et al. 2010; Rosado and Mattos 2010). Trends pointing to higher leaf density (DEN), SUC, TH and LMA were observed in ten woody species during dry months in *Restinga* of Juruatiba National Park, southeast Brazil, independent of leaf phenological patterns and phylogeny (Rosado and De Mattos 2007). Chronic photoinhibition has been described for *restinga* species in the dry season based on midday F_v/F_m , possibly as a consequence of a marked decrease in stomatal conductance in periods of water shortage (Rosado and Mattos 2010). Functional traits such as bulk modulus of elasticity (ϵ), water potential at the turgor loss point (Ψ_{TLP}), midday Ψ_w and midday F_v/F_m showed important ecophysiological significance for *restinga* species in addition to leaf death rate, SUC, TH, and LMA (Rosado and Mattos 2010).

Seasonal water variation is also described for other AF vegetation types even where there are no soil water constraints, suggesting that VPD is the main factor driving daily changes in Ψ_w (Lemos Filho and Mendonça Filho 2000; Miranda et al. 2011; Braga et al. 2016). In general, the dry season is delimited by abiotic parameters such as VPD, soil water potential, rainfall amounts. However, other ecological aspects such as water availability differences in relation to altitude between lowland and montane rainforest could also be important as has been shown in Serra do Mar State Park, southeast Brazil (Rosado et al. 2010, 2016). In montane tropical forests, a lower partial pressure of atmospheric CO_2 at altitude requires an increase of stomatal conductance, thus imposing greater water loss for trees (Leuschner 2000). In montane Atlantic rainforest, species showed higher leaf water repellency and WUE than at the lowland site as a consequence of lower soil moisture, higher radiation and higher VPD in the dry season-winter (Rosado et al. 2010, 2012, 2016; Sousa Neto et al. 2011). The average volume of sap flow per individual showed spatial, instead of seasonal variation, with lowland forest ranging around ten times more in comparison to the montane forest (Rosado et al. 2016). In this sense, the montane forest species were under constant water constraints and showed more conservative water use throughout the year, associated with lower SLA, TH, total leaf area per sapwood cross-sectional area (LA/SA), crown conductance, and higher DEN than the lowland site (Rosado et al. 2016). It has been suggested that the higher DEN and lower SLA in the montane forest might be related to increases in LL, because increases in tissue durability occur with increases in fiber and sclereids, as observed for dry environments (Kikuzawa and Lechowicz 2011). On the other

hand, leaf traits in the lowland forest showed less uniform responses through the year, with leaf traits changing in the dry season to maintain water storage (Rosado et al. 2016). Some of the altitudinal variations described by Rosado et al. (2016) were corroborated by one study comparing *Myrcia amazonica* populations from gallery AF (around 400 m) and *campo rupestre* (around 1000 m) (Moraes et al. 2017). *Myrcia amazonica* from *campo rupestre* sites showed higher LMA, WUE, g_s , A , and E than gallery AF sites. However, DEN and TH showed opposite behavior according to altitude in these studies (Rosado et al. 2016; Moraes et al. 2017). Studies in AF and other forests around the world suggest that montane sites may be more vulnerable to climate changes than lowland sites, because reductions in fog and mist events—an important water source—associated with others abiotic factors, constrain the water availability in montane forests (Pounds et al. 1999; Lemos Filho and Mendonça Filho 2000; Rosado et al. 2010, 2012, 2016; Sousa Neto et al. 2011; Eller et al. 2015).

Under the current scenario of global climate change, the occurrence of extreme and episodic drought events—strongly impacting water availability, triggering fire events and rates of attack agents—is expected to exacerbate tree death via severe loss of hydraulic function and C starvation (McDowell et al. 2011, 2018). Rising temperatures and elevated VPD are considered driving forces associated with tree mortality rates across large forest areas as both drivers increase the risk of C starvation via greater stomatal closure and hydraulic failure via increased evaporative demand (McDowell and Allen 2015; Hartmann et al. 2018; McDowell et al. 2018). Empirical and experimental studies have indicated a positive relationship between drought severity and mortality rates in Neotropical forests, especially of large trees (Nepstad et al. 2007; da Costa et al. 2010; Phillips et al. 2010; Meakem et al. 2018). This greater sensitivity of large tropical trees potentially reflects a combination of increased risk of xylem embolism associated with a higher evaporative demand of more exposed canopies (Meakem et al. 2018). Although strong climatic anomalies have impacted tropical South America in the recent decade (Erfanian et al. 2017), drought effects on AF tree mortality rates and associated mechanisms are unknown relative to other tropical regions.

Nutritional aspects

An important pathway for internal recycling in forest ecosystems is nutrient uptake from decomposing organic material on the forest floor (Villega et al. 2006; PBMC 2014). Nutrient inputs from litterfall in AF are highly seasonal (Villega et al. 2006; Martinelli et al. 2017). In general, in Atlantic rainforest peak litterfall occurs in the rainy season due to storms, while in Atlantic seasonal semi-deciduous and deciduous forest, peak litterfall occurs in the dry season

due to phenology (Villela et al. 1998, 2006, 2012; Moraes et al. 1999; Ferreira et al. 2014; Sousa Neto et al. 2017). This is a typical tropical forest pattern and shows rainfall seasonality as one of the main factors driving leaf litterfall and its nutrient fluxes within these ecosystems (Brando et al. 2008; Chave et al. 2010; Villela et al. 2012). Beyond seasonality, other factors may influence litterfall production, including nutrient availability, the presence of deciduous species, forest management (Borém and Ramos 2002; Villela et al. 2006; Souza 2012; Lage-Pinto et al. 2015), forest successional stage (Boeger et al. 2005, Martinelli et al. 2017), mean annual temperature (Martinelli et al. 2017), and fragment size and edge effects (Portela and Santos 2007; Vidal et al. 2007; Schessl et al. 2008; Lima 2009; Silva and Villela 2015). Five years of plant litter removal in an abandoned *Corymbia citriodora* plantation in a regenerating fragment of Atlantic rainforest from southeast Brazil caused decreases in C, P, K, Ca, Mg, Cu, Fe, Mn and Zn in leaves of the main species, although the litter removal also promoted the regeneration of native species in this regenerating fragment (Souza 2012). In this same experiment, no effects of the removal of plant litter was observed on intrinsic WUE, leaf photosynthetic gas exchanges or photosynthetic pigment concentration of the native species (Lage-Pinto et al. 2015). Leaf nutrient content (N, P, Mg and K) increased with successional stages in an Atlantic lowland rainforest from south Brazil, with Mg being the only nutrient decreasing as succession progressed (Boeger et al. 2005). In Atlantic rainforest from southeast Brazil, small forest fragments showed less leaf litterfall mass than bigger forest fragments (Portela and Santos 2007; Vidal et al. 2007; Silva 2009; Silva and Villela 2015). However, the total litter standing stock and Ca, Mg, K, Na, C, and N concentrations in superficial soil in this vegetation did not change according to the fragment size (Oliveira et al. 2008; Silva 2009). Fragment size did not influence N, P and K retranslocation in *Guarea guidonia* (Silva 2009). On the other hand, Mg showed higher concentration in fresh leaves of *G. guidonia* and *Cupania oblongifolia* in small fragments (Silva and Villela 2015). Comparison between edge and interior sites of forest fragments showed contrasting data to litterfall production in AF, probably due to other factors such as the age of the edge, vegetation type, and landscape structure (Nascimento 2005; Portela and Santos 2007; Vidal et al. 2007; Schessl et al. 2008).

Higher C and N stocks were found belowground than aboveground in lowland and montane Atlantic rainforest in southeast Brazil (Vieira et al. 2011; Villela et al. 2012), whereas in other lowland tropical forests, C is preferentially allocated aboveground (Kitayama and Aiba 2002; Raich et al. 2006; Girardin et al. 2010). Both above- and belowground C and N increased significantly with elevation, and it was proposed that an increase of 1 °C in soil temperature

decreases stocks by approximately 17 Mg ha⁻¹ for C and 1 Mg ha⁻¹ for N (Vieira et al. 2011). The loss of N by gas emission includes losses by volatilization (NH₃) and denitrification (N₂ and N₂O). In this sense, higher N₂O emissions in AF were observed in lowlands (around 100 m) than in higher altitudes (around 1000 m) possibly due to higher litterfall inputs in lowland than in highland sites (8.40 and 5.50 Mg ha⁻¹, respectively) and to the higher air and soil temperatures in lowland sites, affecting the decomposition rate (Sousa Neto et al. 2011). Atlantic forest showed higher C and N soil stocks to 1 m soil depth than any other Brazilian biome (PBMC 2014). However, N as well as P were described as limiting factors to AF and for most tropical forests (Boeger et al. 2005; Villagra et al. 2013b; Goldstein and Santiago 2016). On the other hand, strong altitudinal controls over nutrient cycling have been observed and higher litterfall N and P fluxes in lowland than in other AF types are described. Therefore, in lowland sites, lower nitrogen-use efficiency and litter nitrogen stable isotopic composition support the idea of no N constraints to productivity in lowland sites of the south-eastern AF (Sousa Neto et al. 2017). Nitrogen and P are linked to photosynthesis and Rd demand because they are related to the enzyme and chlorophyll content (Duursma and Marshall 2006). In general, P limitation of photosynthesis in tropical forest has been considered more drastic than N limitation (Alvarez-Clare et al. 2013; Santiago and Goldstein 2016; Rowland et al. 2017). On the other hand, Rd has shown more sensitivity than photosynthesis to low P levels in tropical forests (Rowland et al. 2017). In an experiment in Panama, P addition increased leaf-specific hydraulic conductance (K_L) when a species with an affinity for high P soils (*Hura crepitans*) was grown under high P conditions (Dalling et al. 2016). Some morphological traits have been suggested to increase K_L under high P, such as the increase in xylem vessel diameter and the reduction in wood density (Goldstein et al. 2013). These results suggest an influence of P in ecosystem water balance and may help understand the strong effect of this element on photosynthesis. However, no responses to fertilization (N + P) were observed in K_L of five species in a nutrient addition experiment in a semi-deciduous subtropical Atlantic forest in northeastern Argentina (Villagra et al. 2013a). Deciduousness is probably the main strategy to deal with water constraints for these species and leaf hydraulic control may not be crucial in the adaptation to environments with contrasting soil nutrient availability (Villagra et al. 2013a). The addition of N + P affected traits related to the leaf economic spectrum (decreased LL and increased LMA), and both showed negative correlation with K_L on a mass basis (Villagra et al. 2013a). On the other hand, the same species become less vulnerable to cavitation and are able to avoid hydraulic dysfunction under the same N + P supply during the initial phase of establishment in gaps, suggesting that

when light is not limiting, N and P are important limiting resources for this AF species (Villagra et al. 2013b).

Functional diversity

Functional diversity is the degree of dissimilarity in trait values between coexisting species (Dias et al. 2013) and has been postulated to be critical for the maintenance of ecosystem processes and properties. Several forces influence functional diversity, particularly species interactions and habitat filtering (Grime 2006). Trait functional diversity data can be useful for explaining why certain species are absent from positions along resource gradients, if relationships between the traits and environmental performance are well known. However, it can be difficult to infer some community assembly processes based on trait functional diversity data alone because various assembly processes can lead to the same pattern of trait dispersion and similar processes can lead to contrasting patterns of dispersion (Herben and Goldberg 2014).

Functional diversity in AF species has been studied to make inferences about the consequences of fragmentation (Metzger 2000; Tabarelli and Peres 2002; Girão et al. 2007; Magnago et al. 2014), species coexistence and diversity (Muelbert 2012), fire disturbance (Müller et al. 2007), regeneration and succession (Koch et al. 2013; Marcílio-Silva et al. 2016; Warring et al. 2016), resource availability and/or environmental conditions (Rosado and De Mattos 2007; Rosado and Mattos 2010; de Paula et al. 2015; Silveira et al. 2015), and others to better understand how species influence forest function and respond to environmental change (Laureto et al. 2015). Leaf traits showing convergent responses related to surviving temporal heterogeneity of water availability have been described for *restinga* species (Rosado and De Mattos 2007; Rosado et al. 2013). In this sense, several *restinga* species showed convergent trends of increases in LMA, SUC, TH and DEN in dry season, enabling plants to cope with water shortage during rainless periods (Rosado and De Mattos 2007). Convergent leaf traits have also been described for the majority of 57 woody species in an Atlantic rainforest sites with mixed ombrophilous *Araucaria* forest in southeast Brazil. In these closed canopy forests, low irradiance is the environmental filter related to high SLA and thinning of the leaf blade with the mesophyll composed of only one layer of palisade parenchyma and few layers of spongy parenchyma to improve irradiance interception (Silveira et al. 2015). Four functional groups related to survival and growth strategies were identified using SLA, maximum height, mortality rate, wood density, seed shape and growth rate for 47 woody species in AF in northeastern Brazil (Monteiro et al. 2017). Strong evidence suggests a role of environmental filters in structuring native and exotic species in plant communities of semi-deciduous seasonal

AF from southeast Brazil on *inselbergs*, isolated granitic and gneiss rocks that rise sharply above the lowland surrounding forests (de Paula et al. 2015). In these *inselbergs*, flatter sites showed species with higher SLA and less leaf toughness, demonstrating that the diversity in functional traits reflects the response of *inselberg* communities to resource availability. The invasive grass species, *Melinis repens*, was functionally distinct from native communities and although it was positioned near the center of the trait space (according to Grime 1977), it showed traits associated with a ruderal plant strategy (de Paula et al. 2015). Tree communities of 23 Atlantic ombrophilous dense rainforest fragments from south and southeast Brazil in different successional stages were mainly structured by environmental filtering leading to trait convergence in the early stages and by biotic filtering leading to trait divergence in the later stages of succession (Marcílio-Silva et al. 2016). The trait convergence assembly patterns related to the successional gradient was canopy versus understory position, and the presence of compound leaves, both constrained by environmental filters such as higher temperature, and lower air relative humidity in early succession. The trait divergence assembly patterns were leaf width, leaf area, and pollination by vertebrates, possibly resulting from species competition for irradiance, space and pollinators. Tree versus shrub form and pollination by entomophilous generalists were traits maximizing both convergence and divergence patterns related to successional age. In the early successional phase, there are a few species of shrubs and trees with an early and abundant production of seeds with long-distance dispersal that can colonize initial stage patches (Bazzaz and Pickett 1980). This can lead to a homogenization of trees and shrubs among communities, converging early in succession and increasingly diverging as succession proceeds. In a recently disturbed environment, the entomophilous generalist pollination syndrome can facilitate the reproduction of plants, however, the dependency of a more specialized pollination syndrome tends to appear late in succession. Leaf width and animal dispersal increase according to increases in succession stage, whereas the opposite has been observed for trees. No phylogenetic signal was found in this study (Marcílio-Silva et al. 2016).

Concluding remarks and future directions

The majority of the leaf trait data for AF found when we focused on photosynthesis, water relations and leaf nutrients were related to irradiance, water use, and spatio-temporal variation, respectively. We do not discard the possibility that the order of our search terms emphasized some of these results. Yet, most studies in this review were developed in coastal and sub-coastal forest areas located in southeast Brazil, and have led us to a body of current knowledge focused

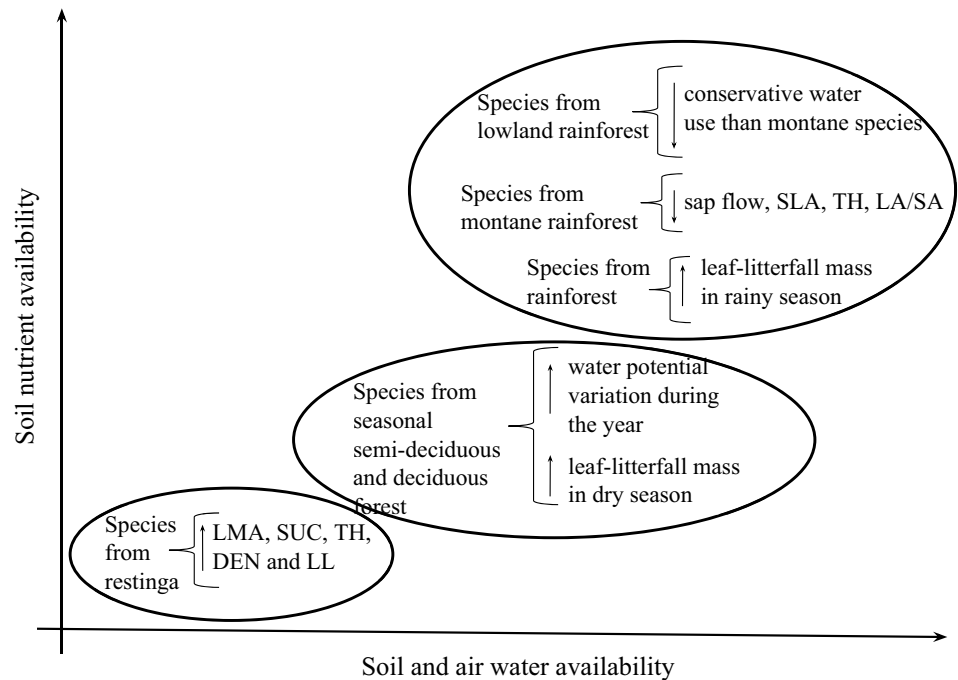
on the most studied AF vegetation types. Therefore, we propose an ordination between environmental water and nutrient gradients, highlighting the main leaf traits and characteristics of the majority of species of these AF vegetation types (Fig. 1).

Although photosynthesis and water relations studies are abundant compared to studies of leaf nutrients and functional diversity, there are relatively few studies in AF relating leaf functional traits and physiological processes such as photosynthesis and respiration rates. Another important but less studied topic is the relationship between photosynthesis and water relations for early ontogenetic stages such as seedlings. Seedling establishment tends to be the most vulnerable stage in the plant life cycle due to a less favorable water status in comparison to advanced ontogenetic phases once plant size increases and there are lower seedling surface/volume ratios (Winkler et al. 2005). Efforts for AF conservation include, preserving and connecting remnant patches through restored vegetation corridors, and habitat restoration using seedlings and young saplings. Thus, studies focusing on seedlings and their photoacclimation capacity and WUE, in response to global climatic changes are urgent for AF species. Actually, most studies on the ecophysiological traits of forest tree seedlings focus mainly on irradiance acclimation, but other functional ecology information is needed for AF conservation. Though water relations is considered one of the most studied ecophysiological topics, drought effects on AF trees is less known than in Amazonia, where field-based studies and long-term drought experiments have been carried out (Brando et al. 2008; Maréchaux et al. 2015; Rowland et al. 2015; Binks et al. 2016). The AF is the second

largest tropical moist forest area of South America, after the vast Amazonian domain (Oliveira-Filho and Fontes 2000). Atlantic rainforest presents higher biodiversity than Amazonia and shows higher floristic similarity with semi-deciduous AF than Amazonian forests (Oliveira-Filho and Fontes 2000). A remarkable difference in the geographical spread between both is, while Amazonian forest is mainly distributed longitudinally around the Equator, AF is distributed latitudinally throughout almost the entire Brazilian Atlantic coast, from tropical to subtropical regions exposing the vegetation to high variation in temperature and rainfall. This great latitudinal extension increases the temperature seasonality in the north–south direction, representing a major factor associated with floristic differentiation in AF (Neves et al. 2017). The temperature seasonality gradient is congruent with increasing leaf deciduousness, suggested by Oliveira-Filho et al. (2015) as a trait associated with frost-tolerance. Thus, great floristic differentiation according to latitude has been described for southeast Brazilian Atlantic rainforest and semi-deciduous forests (Oliveira-Filho and Fontes 2000). It is possible that there are different mechanisms related to drought survival in AF species in comparison to Amazonian forests and more research in this biome is required to better understand the diversity of tropical forest responses to global climatic change. Thus, long-term drought experiments and observational measurements will be key to improving our understanding of AF ecosystem responses to spatial and temporal variation in relation to moisture stress.

For marginal AF habitats associated with the harshest extremes, where 45% of all endemic species of the AF occur,

Fig. 1 Leaf traits and characteristics of some species from Atlantic forest (AF) vegetation types according to environmental water and nutrient availability. *SUC* succulence, *DEN* density, *LA/SA* the total leaf area per sapwood cross-sectional area, *LL* leaf lifespan, *LMA* leaf mass per area, *SLA* specific leaf area, *TH* leaf thickness, *WUE* water-use efficiency



limiting factors include temperature seasonality in high elevation and subtropical riverine forests in the south, flammability in scrub forests of rocky outcrops, high salinity in *restinga*, severe water deficit in semi-deciduous forests and waterlogged soils in tropical riverine forests (Neves et al. 2017).

Recent studies in Atlantic rainforest in southeast Brazil have focused on altitudinal gradients and their relationship with WUE, biomass production, and C and N stocks. These data show that montane species exhibit leaf traits related to conservative water use (Rosado et al. 2016). In addition, more C and N are stored below than aboveground in lowland and montane AF (Vieira et al. 2011; see also Alves et al. 2010), whereas there is a tendency for lowland tropical forests to allocate preferentially more C aboveground and montane forests to allocate more C belowground (Kitayama and Aiba 2002; Raich et al. 2006; Girardin et al. 2010). This shows a different pattern in AF in comparison with other tropical forests and has important consequences for global warming. This also shows the relevance of AF studies to help predictions about global warming, especially since this biome may be changing from an important C sink to C source with rising temperature.

Undoubtedly more efforts are needed to generate data from northeast Brazil and from mixed ombrophilous *Araucaria* forest in south Brazil, as well as data connecting nutrients and leaf traits. Currently, nutrient studies in AF focus on litterfall production, decomposition, and the effects of seasonality. Experimental data from nutrient addition experiments in AF are scarce, and just one thesis about nutrient retranslocation in AF species was found to address this critical topic in AF leaf traits. While limited data on leaf traits and natural resources in the AF show us the importance of being careful about making generalizations for this biome, they also serve as a warning about the lack of this information on larger scales, which could be used for its conservation and restoration.

We propose here to use long-term observations and experiments for improving our understanding of AF ecosystem responses to spatial and temporal variation in relation to moisture stress, nutrient availability and disturbance. Specifically, we highlight four priority research topics: (1) assessing changes in leaf traits and functional trait diversity under spatio-temporal variations of water availability, (2) the identity of limiting nutrients, (3) forest conditions (disturbance/land use), and (4) evaluating the role of leaf and hydraulic trait diversity on forest response and resilience to climate change.

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