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Functional Traits of Trees From Dry Deciduous "Forests" of Southern India Suggest Seasonal Drought and Fire Are Important Drivers

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Two dominant biomes that occur across the southern Indian peninsula are dry deciduous "forests" and evergreen forests, with the former occurring in drier regions and the latter in wetter regions, sometimes in close proximity to each other. Here we compare stem and leaf traits of trees from multiple sites across these biomes to show that dry deciduous "forest" species have, on average, lower height: diameter ratios, lower specific leaf areas, higher wood densities and higher relative bark thickness, than evergreen forest species. These traits are diagnostic of these dry deciduous "forests" as open, well-lit, drought-, and fire-prone habitats where trees are conservative in their growth strategies and invest heavily in protective bark tissue. These tree traits together with the occurrence of a C_4 grass-dominated understory, diverse mammalian grazers, and frequent fires indicate that large tracts of dry deciduous "forests" of southern India are more accurately classified as mesic deciduous "savannas."

Keywords: functional traits, fire, savnnas, forests, southern India

INTRODUCTION

Ecologists have long organized earth's vegetation into biomes or vegetation types that occur predictably under certain combinations of precipitation and temperature (Schimper, 1903; Holdridge, 1947; Walter, 1973; Whittaker, 1975). However, Whittaker (1975); recognized that there were certain climatic zones where vegetation was unpredictable; this zone of "ecosystems uncertain" includes large parts of the tropics where vegetation can be tropical forest, savanna, shrubland, or grassland, depending on seasonality, drought, and other disturbances (Whittaker, 1975; Bond et al., 2005; Bond, 2013). It is also now widely agreed that while temperature and precipitation together define the major biomes at continental scales, local scale turnover in vegetation types can be driven by sharp differences in underlying topographic and edaphic conditions (Ratter, 1992; Esler et al., 2015; Moncrieff et al., 2016; Miatto and Batalha, 2017) but more often by vegetation-disturbance feedbacks that can result in very different ecosystems within comparable climatic conditions (Bond et al., 2005; Staver et al., 2011; Hoffmann et al., 2012; Dantas Vde et al., 2013, 2016; Charles-Dominique et al., 2015; Pausas and Dantas, 2017).

Across the mesic tropics, where both wooded savannas and forests occur, sometimes in close proximity within a landscape, recent evidence clearly establishes a critical role for vegetation-fire feedbacks in maintaining these savanna-forest transitions (Hoffmann et al., 2012; Dantas Vde et al., 2013; Charles-Dominique et al., 2015; Gray and Bond, 2015). Specifically, open lighted environments and frequent grass-fuelled fires are associated with the savanna state, while closed, shaded environments and rare fires are associated with the forest state (Bond and Parr, 2010; Hoffmann et al., 2012). Reflecting these differences, the woody species that are characteristic of these different ecosystems are expected to vary in their morphological and physiological traits in ways that are adapted to their distinctive disturbance-environment regimes (Ratnam et al., 2011; Hoffmann et al., 2012; Dantas Vde et al., 2013).

Forest trees, which rarely encounter fire and are under selection to out-shade competitors are predicted to grow taller and develop wider canopies for a given diameter, and invest little in protective bark tissue (Ratnam et al., 2011). They may also have higher specific leaf area and lower wood density, which are supportive of rapid nutrient acquisition and growth (Poorter and Bongers, 2006; Chave et al., 2009; Miatto and Batalha, 2017). In contrast, savanna trees that grow in fire-prone environments are expected to invest heavily in thick bark that protects them from fire (Gignoux et al., 1997; Hoffmann et al., 2012; Dantas Vde et al., 2013). They may store much of their biomass in belowground tissue that is safe from fire, and aboveground, they may be shorter and have narrower canopies for a given diameter (Ratnam et al., 2011). They may also be expected to have lower specific leaf area and higher wood densities that support the more conservative growth strategies that are favored in their open and desiccating environments (Miatto and Batalha, 2017).

Here, we consider the functional traits of woody trees across different vegetation types in the southern Indian peninsula. Much of this region falls within the zone of "ecosystems uncertain" in the seasonal tropics (Bond, 2013, Figure 16.1); it supports a diversity of vegetation formations ranging from open thorn scrub to wooded grasslands to closed forests. However, a historical problem with the vegetation nomenclature in this region is that all the vegetation formations with some degree of woody cover are classified as "forests" (see Champion and Seth, 1968; Ratnam et al., 2016). Thus, both open and closed woody formations fall within this nomenclature such that savannas are not distinguished from forests. In past work, we have argued that large tracts of the vegetation type in this region classified as "dry deciduous forest" that are characterized by relatively open tree canopies in grassy understories are more correctly viewed as mesic savannas, while vegetation types with dense tree cover and non-grassy understories are true forest formations (Ratnam et al., 2011, 2016; Sankaran and Ratnam, 2013). Here, we extend these arguments to an examination of the traits of tree species in these habitats. If, as we argue, many of the dry deciduous "forests" in southern India are in fact deciduous "savannas" that are adapted to seasonal water-stress and frequent grass-fuelled fires (Ratnam et al., 2016), which is not the case for true forests, we expect traits of tree species characteristic of these habitats to reflect this difference.

METHODS

We sampled dry deciduous and evergreen forests across seven sites in southern India (see inset in **Figure 1**). Rainfall across our sampling points in dry deciduous forests ranged from 516 to 1,260 mm, while rainfall across sampling points in evergreen forests ranged from 1,078 to 5,660 mm. Rainfall across this entire region is monsoonal such that all sites experience long dry seasons of 5–8 months per year (**Figure 1**).

We collected functional trait data from 1,350 individual trees of 75 dry deciduous "forest" (DD) species and 92 (EG) evergreen forest species (**Supplementary Table 1**), with 9 species common to both habitats. Specifically, we measured specific leaf area (SLA), tree height, girth at breast height (GBH), wood density, and bark thickness. For each species, in each habitat, we collected traits from multiple individuals (3–25, depending on the commonness of the species).

For SLA, five mature sun leaves were collected from the canopy of each individual and scanned in a flat-bed scanner on the same day. Leaf areas of scanned leaves were calculated using either Blackspot (Varma and Osuri, 2013) or Image J software (Rasband, 2014). Leaves were then oven-dried and dry weights measured in a precision balance. SLA was calculated as leaf area per unit dry weight. GBH was measured with a tape-measure, 1.3 m above the ground. Tree heights were measured using a clinometer or, alternately, a laser range-finder when the observer could stand at the base of the trunk and sight the top of the tree with the laser beam. Wood cores were collected using an increment borer, and placed into sealed plastic bags with moist cotton. Back in the field station, they rehydrated in water for 1 h. Fresh wood volume was estimated by water displacement, following which samples were oven-dried at 65°C for 72 h and weighed, and wood density estimated as oven-dried weight divided by fresh volume (Chave, 2005). Bark thickness was measured at breast height on the trunk, using a bark gauge. Using the sharp end of the gauge, we gently gouged through the outer layers of bark until it gave way to the thick inner wood which was visibly different tissue, and measured bark thickness to this point. Relative bark thickness was calculated as: (Bark thickness*2/Diameter)*100.

We used Generalized Linear Mixed Models (GLMM) to look at how traits differed between the two vegetation types. Vegetation type (DD, EG) was included as a fixed effect, with species nested within sites as the random effect. Analyses were carried out using the "*lme4*" package, and the "*car*" package was used to conduct Type II Wald Chi square tests to assess statistical significance of the fixed effects (Bates et al., 2017). Values for SLA, H:D, and relative bark thickness were log transformed to meet model assumptions.

RESULTS

Consistent with our expectations, dry deciduous "forest" species differed significantly from evergreen forest species for the four traits measured. DD species had, on average, lower

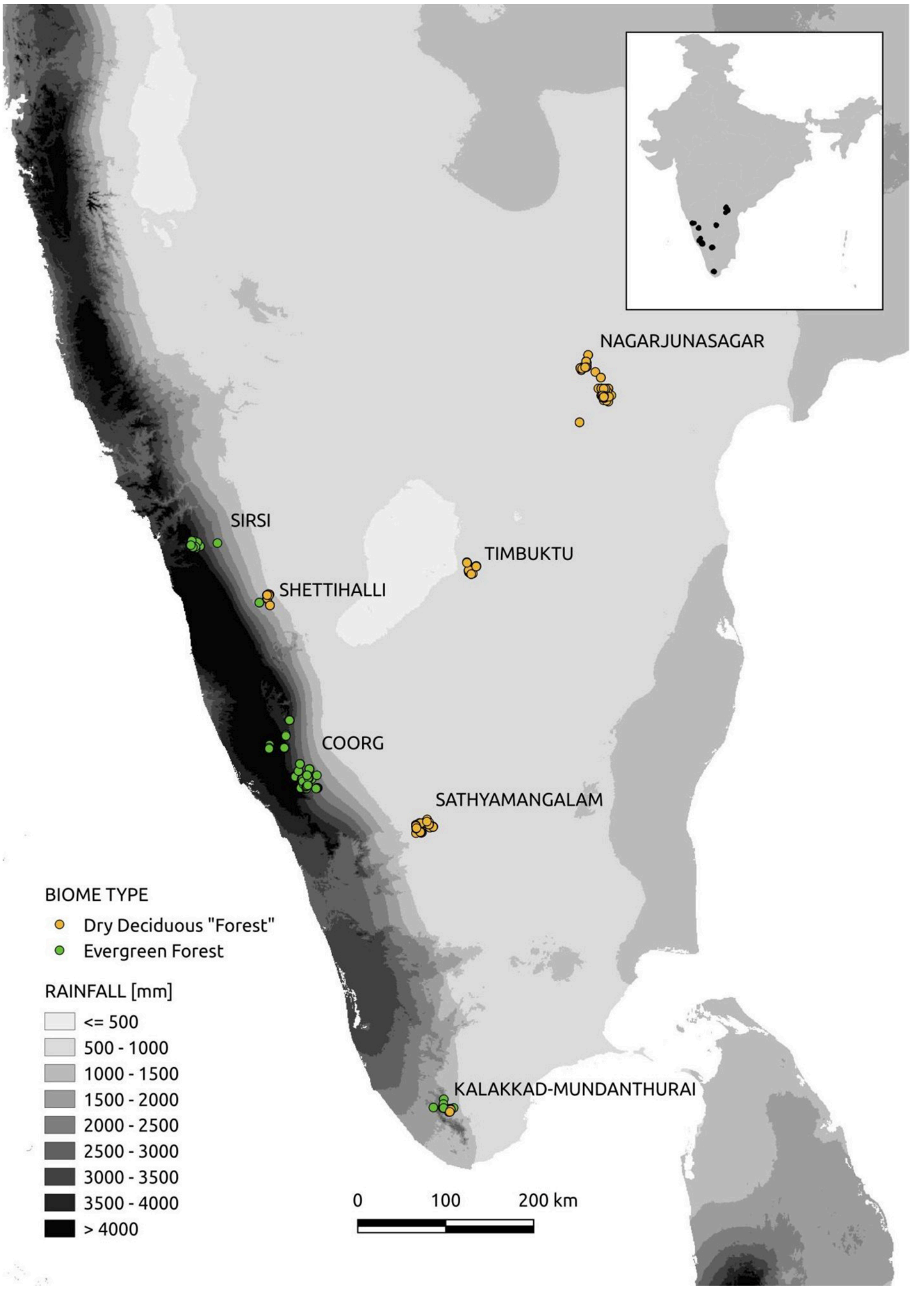

FIGURE 1 | Sampling sites across Southern India. Sites span a rainfall gradient from a little over 500 mm to over 4,000 mm per year. Rainfall is seasonal and all sites have long dry seasons ranging from 5 to 8 months.

height: diameter ratios (Mean ± SE, DD: 0.360 ± 0.01, EG: 0.576 ± 0.017, $\chi^2 = 184.71$, df = 1, $p < 0.0001$) higher relative bark thickness (DD:8.75 ± 0.47%, EG:4.26 ± 0.26%, $\chi^2 = 50.03$, df = 1, $p < 0.0001$), lower SLA (DD: 94.58 ± 2.42 g/cm^2, EG:106.31 ± 2.96 g/cm^2, $\chi^2 = 5.801$, df = 1, $p = 0.016$), and marginally higher wood densities (DD: 0.619 ± 0.015 g/cm^3, EG:0.603 ± 0.011 g/cm^3, $\chi^2 = 5.87$, df = 1, $p = 0.015$) than EG species (**Figure 2**).

DISCUSSION

Our cross-site comparison of the functional traits of tree species from dry deciduous and evergreen forests of southern India indicate that dry deciduous "forests" are fundamentally different in the environments and species traits that they support than are evergreen forests, even though they occur in close proximity in many regions. Dry deciduous "forest" trees have lower height to diameter ratios, produce leaves with lower specific leaf areas, and

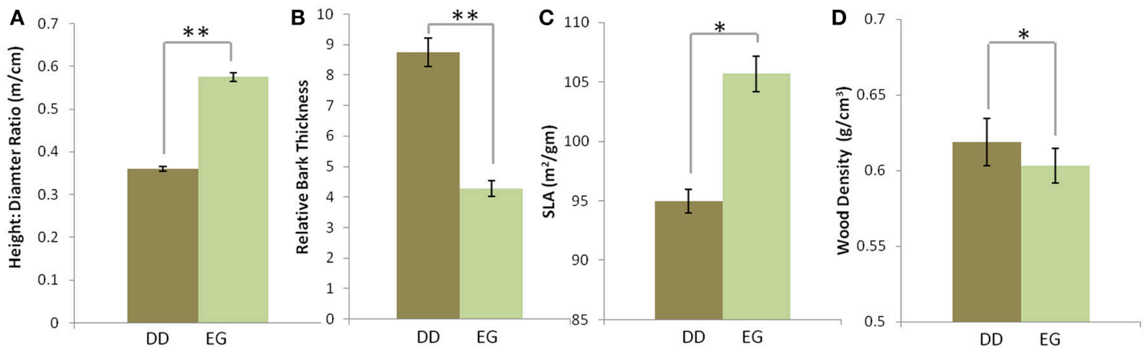

FIGURE 2 | Comparisons of functional traits of trees from dry deciduous "forest" (DD; 79 species) and evergreen forest (EG; 92 species) across seven sites in Southern India. The data shown (Mean ± SE) are for **(A)** height: diameter ratios, **(B)** relative bark thickness, **(C)** specific leaf area, and **(D)** wood density. Asterisks indicate significant differences between mean trait values in DD and EG habitats (*$p < 0.05$, **$p < 0.001$).

have higher wood densities. Taken together, this suite of traits is suggestive of slower and more conservative growth strategies in these trees than in their evergreen forest counterparts (Poorter and Bongers, 2006; Chave et al., 2009; Miatto and Batalha, 2017). Such strategies may indicate either relatively lower resource environments, or less competitive ones (Miatto and Batalha, 2017). Clearly, dry deciduous "forests" occur in areas with less rainfall than evergreen forests, although the two forest types overlap at the wetter end of the dry deciduous zone. Seasonal water stress is thus likely to be more pronounced in these habitats. With relatively lower tree densities, dry deciduous "forests" may also be both more desiccating, and less competitive environments for adult trees that grow in them.

Critically, dry deciduous "forest" trees have dramatically higher investment in bark, producing, on average, almost twice as much bark for a given diameter as evergreen forest trees. Thick barks are known to serve multiple protective functions including drought resistance, fire resistance, and prevention of stem damage (Poorter et al., 2014; Schafer et al., 2015). For fire-prone environments, there is overwhelming evidence for a primary role of thick barks in enabling trees to persist through fires (Lawes et al., 2011; Hoffmann et al., 2012; Pausas, 2015; Pellegrini et al., 2017) and several recent analyses across the globe have shown that fire-resistant savanna trees are characterized by thicker bark than fire-sensitive forest trees (Hoffmann et al., 2012; Dantas Vde et al., 2013; Lawes et al., 2013; Pellegrini et al., 2017). Thicker barks may also increase drought resistance in drier environments (Poorter et al., 2014; Schafer et al., 2015) as in these dry deciduous "forests," but this function may be secondary to a strategy of deciduousness where species avoid drought by being leafless in the dry season.

Several analyses of contemporary fire regimes in the subcontinent confirm that dry deciduous "forests" burn much more frequently (fire return intervals range from 1 to 6 years) and extensively (10–50% of these landscapes burn annually) than do other forest types (Kodandapani et al., 2008; Kodandapani, 2013; Srivastava and Garg, 2013; Mondal and Sukumar, 2016; Reddy et al., 2017). Together with the trait comparisons we report in this study, which are consistent with predicted trait differences between mesic savanna and forest species (Ratnam et al., 2011), these data suggest that large tracts of dry deciduous "forests" in this region, characterized by trees in grass-dominated understories, are in fact deciduous "savannas," where seasonal water-stress and fire are important drivers. Further, these habitats are also home to an ancient and diverse mammalian herbivore assemblage, ranging from smaller-bodied spotted deer to large-bodied mega-herbivores like the Asian bison and elephant (Bibi and Métais, 2016; Sankaran and Ahrestani, 2016). Large mammalian grazers, which are supported by the forage in grass-dominated understories are characteristic of savannas globally, additional evidence that these "forests" are indeed "savannas."

These confirmatory findings have important implications for how fire is managed in these ecosystems. At the current time, these habitats are managed under a blanket policy of fire exclusion and suppression and fire-setting is a punishable offense according to the Indian Forest Act (Ratnam et al., 2016; Thekaekara et al., 2017). These policies, which stem from a historical misreading of these ecosystems as "forests" are inimical to the conservation and sustainable management of these savannas (Lehmann and Parr, 2016; Griffith et al., 2017). First, the notion that fires are always undesirable disturbances in these ecosystems, widespread amongst both managers and vegetation scholars, prevents nuanced understanding, and appropriate research on the ecology of these systems. Second, these policies preclude the use of fire as a management tool, an opportunity lost in many areas where fire exclusion has been associated with severe non-native shrub invasions (Sundaram et al., 2012) and associated losses of native biodiversity (Ramaswami and Sukumar, 2011; Sundaram and Hiremath, 2012). Official recognition of these tree-grass ecosystems as drought- and fire-driven mesic savannas will provide multiple opportunities for vital research and effective management.

AUTHOR CONTRIBUTIONS

JR led and wrote the paper. MS and JR planned the trait comparisons. SKC, SJM, NN, AMO, JR, and MS collected data. All authors commented on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00008/full#supplementary-material

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