

Functional Dispersion and Variation in Above-Ground Traits in Tropical Dry Deciduous Forests of Central India

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ABSTRACT

Plants are adapted to their environment through a suite of anatomical, morphological, and physiological traits. These functional traits are commonly thought to determine the plant's tolerance to environmental conditions. Functional diversity quantifies diversity of species traits which reflects the kind of species functions and acts as a key driver of ecosystem processes and services. The objective of the present study is to quantify the intraspecific functional distance among species in terms of their traits within two selected tropical dry deciduous forest communities in Central India. Six key functional traits namely, specific leaf area, leaf dry matter content, leaf size, height, basal area and circumference, were considered for their significant ecological functions. The interspecific functional distances ranged from 2 to 52 in Garpehra forest community while it was 0 to 50 in the Jaruakhera forest community. The average functional distance recorded within two communities were 21.43 and 14.42 respectively. Most similar species pairs were *Hollarhena antidysenterica* - *Aegle marmelos*, *Hollarhena antidysenterica* - *Lagerstroemia parviflora*, *Holoptelea integrifolia* - *Miliusa tomentosa* in the Garpehra forest whereas in Jaruakhera species pairs namely, *Madhuca indica* - *Diospyros melanoxylon*, *Ficus glomerata* - *Eugenia heyneana* indicates high similarity for functional attributes. Being similar they are most redundant to each other. Few species pairs were highly dissimilar under functional trait space in Garpehra forest namely, *Miliusa tomentosa* - *Sterculia urens*, *Holoptelea integrifolia* - *Sterculia urens* and *Helicteres isora* - *Boswellia serrata* while in Jaruakhera, highly dissimilar species pairs were *Ficus religiosa* - *Ziziphus xylopyrus* and *Helicteres isora* - *Ficus religiosa*. Being dissimilar, they show complementarity to each other. The study depicts the functional structure of community and the redundant and complementary species pairs for predicting resilience, resistance, invasibility and conservation.

Key words: Functional trait, functional distance, functional space, redundancy, resilience.

INTRODUCTION

Organisms are peculiar in their adaptation to the environment's abiotic and biotic components. These adaptations are referred to as "functional traits" which are measurable characteristics that determine a species' performance in a particular habitat, and are significant for community assembly and dynamics, and determine biodiversity patterns at global, regional, and local scales (Garnier et al. 2004, McGill et al. 2006, Violle et al. 2007, Chelli et al. 2019). Functional traits are useful to understand species tolerance, resource utilization as well as competition with co-existing species (McGill et al. 2006). The use of functional trait assessment to analyse ecosystem alterations in response to changing habitat circumstances is a strong tool in community ecology (Wright et al. 2004, Ackerly and

Cornwell 2007, Kleyer et al. 2008, Suding et al. 2008). During the past two decades, a number of studies were done on functional traits, to understand plant life-history strategies and ecological differences across species (Wright et al. 2004, wright et al. 2010, Adler et al. 2013, Diaz et al. 2015). New trends in ecological research that focus on functional traits might help to better understand how natural ecosystems respond to ongoing anthropogenic global change (Laliberté and Legendre 2010).

One of the key issues of modern ecology is determining the composition and variety of functional traits at the community level (Grime 2006, Cornwell and Ackerly 2009, Myers-Smith et al. 2019). Conceptually, differences in these functional traits may account for the co-existence of species if variations enable them to allocate resources to restrict competition and prevent competitive exclusion

(Tilman 1982, Adler et al. 2013). It is still uncertain how diversity in functional traits among species affect competition and, as a result, competitive exclusion (Adler et al. 2013, Chen et al. 2019). Quantifying the degree to which coexisting species differ in their functional attributes is the first step in determining how functional traits may explain species coexistence. Differences in functional traits across co-occurring species have been observed in various studies (McGill et al. 2006, Shipley 2006, Violle et al. 2007, Wright et al. 2010, Diaz et al. 2015). It has been reported that tropical trees differ significantly in functional attributes, with some variables, such as wood density, indicating substantial variations in species life history strategies (Wright et al. 2010). Plant life–history strategies can also be predicted by functional traits linked to leaf tissue formation as more efforts into leaf formation, results in slower growth rates (Shipley 2006).

Tropical deciduous forests (TDFs) are characterised by significant seasonality of rainfall distribution as well as several months of drought (Mooney et al. 1995). Pennington et al. (2009) use a broader explanation of TDF that includes vegetation with a minimum dry season of 5-6 months, leading to highly seasonal processes and ecological functions. During dry season, plant species in TDFs are exposed to water stress (Eamus 1999) and the duration of the dry season is a limiting factor in vegetation structure and trends (Gritti et al. 2010). There is a lot of inter-specific and intra-specific variation in the attributes among tree species due to the characteristics such as rooting depth and the degree of dryness experienced by the trees (Van Schaik et al. 1993).

Leaves play a key role in sharing energy and nutrients with the environment, therefore, much attention has been given to the interspecific variation to this floristic traits (Wright et al. 2004). As leaves are exposed and sensitive to the environmental variations, the response of leaf functional traits to such changes may allow plants to thrive in a wide range of environmental conditions (Poorter et al. 2009, Campitelli and Stinchcombe 2013) and can serve as a connection between environmental influences and leaf function (Legner et al. 2014, Xiao et al. 2015, Wang et al. 2016). Plant height and leaf traits are well known indicators of ecological functioning at the community level (Diaz et al. 2004,

de Bello et al. 2010). The spatial patterns of commonly measured plant attributes (e.g., plant maximum height (PMH), specific leaf area (SLA), and leaf dry matter content (LDMC) frequently address the underlying variation in environmental conditions (Hodgson et al. 2011; Bjorkman et al. 2018). SLA and Leaf Area (LA) are leaf metrics that are used to compare relative growth rates between species. Photosynthetic rate, leaf life span, nutrient content (nitrogen and carbon), and species assembly over gradients of light and water availability are all linked to the LA (Poorter 2009). LDMC is related with resistance to physical hazards and litter decomposition as well as soil fertility. However, in-depth studies examining the above-ground traits related to the growth of mature trees under natural conditions, particularly in tropical dry deciduous forests, are scarce. Although species identity offers crucial ecological and evolutionary information, further study is required to better understand how floristic changes are linked to functional trait composition and diversity.

In view of the above, the present study aims to assess the functional composition and above-ground traits at the community level in dry deciduous forests of Central India. In particular, we mainly addressed the following: (1) How are the functional attributes of the dominant tree species of tropical dry deciduous forests distributed in communities? (ii) Role of functional structure and dispersion of species in species coexistence (iii) Do the leaf traits reveal significant differences in resource use strategies (conservative vs. acquisitive) within two plant communities?

The findings may assist to understand which plant functional features and resource use strategies are preferred in tropical dry deciduous ecosystems in a warmer climate, since the trait-based approach may assist to understand ecosystem functioning and its susceptibility to environmental changes (Matteodo et al. 2013).

MATERIAL AND METHODS

Study area and vegetation

Present study was carried out selecting two tropical dry deciduous forests in Central India in Sagar district, Madhya Pradesh located between 23° 05' and 24° 27'N latitude and between 78° 04' and 79° 21'E longitude, having total geographical area of

10252 km². It is 620 m above sea level. Average monthly temperature ranges from 11 to 25°C with maximum temperature of 45°C during the month of May and June.

The climate of study area is typically monsoonal with total annual rainfall of 1240 mm, mostly received during rainy season i.e. from late June to late September. The first site namely Garpehra is situated 10 kilometers north of Sagar at 23° 55' N latitude and 78° 42' E longitude. Altitude ranges from 520 to 560 m. Geologically the soil is derived from sedimentary deposits of Vindhyan sandstone. Due to dry conditions, its flora differs from other neighbouring forest communities. Vegetation is dominated by *Anogeissus latifolia*, *Lannea coromandelica*, *Diospyros melanoxylon*, *Aegle marmelos*, *Lagerstroemia parviflora* and *Wrightia tinctoria*.

The second site namely Jaruakheda, is situated 36 kilometers in north-east direction of Sagar, consist of basalt hills rising to an average height of 533 meters with altitude ranging from 460 to 560 m. It lies at 24° 01' N latitude and 78° 27' E longitude. Vegetation is fairly dense, dominated by *Tectona grandis* and *Diospyros melanoxylon*. *Butea*

monosperma and *Acacia leucophloea* are found as associates. Barring a few large trees of *Diospyros melanoxylon*, a large population of this species forced to remain as coppice and sucker stage due to regular harvesting of leaves for making country cigarettes.

Functional Traits

Thirty tree species common to both sites were selected for measurements of functional traits. For each species, six above-ground functional traits namely, Specific leaf area (SLA), Leaf dry matter content (LDMC), Leaf size (LS), Basal Area (BA), Height (H) and Circumference (C) were measured following standard protocols given by Cornelissen et al. (2003) (Table 1). Healthy and robust trees, were selected for trait measurements. Traits were measured considering ten individuals per species and mean values were used for further analysis. All the set of measured taxa included 30 species for which the above plant functional traits were measured (Westoby 1998, Wright et al. 2004). SLA is the one-sided area of a fresh leaf divided by its oven-dry weight expressed in mm²/mg. It is positively correlated with potential relative growth rate or photosynthetic rate, leaf nitrogen (N) concentration and negatively with

Table 1. List of measured plant traits, with associated ecological function and references

Trait	Description	Plant function	References
Plant height (H)	The distance between the upper boundary of the main photosynthetic tissues on plant and the ground level (in cm)	Competitive ability, dispersal capacity	Diaz et al. (2016); Perez-Harguindeguy et al. (2013)
Specific leaf area (SLA)	The ratio between leaf area (mm ²) and dry weight (mg).	Resource exploitation and conservation; protection against hazard, photosynthetic capacity	Perez-Harguindeguy et al. (2013); Garnier et al. (2001); Shipley et al. (2005)
Leaf dry matter content (LDMC)	The ratio between leaf dry weight(mg) and the respective fresh weight(g)	Resource exploitation and conservation; protection against hazard, leaf lifetime	Perez-Harguindeguy et al. (2013); Garnier et al. (2001)
Leaf size(LS)	The leaf size is the one-sided projected surface area of a leaf, expressed in mm ² .	Leaf energy and water balance. Ecological strategy with respect to environmental nutrient stress and disturbances.	Cornelissen (1999); Moles and Westoby (2000)
Basal area (BA)	It is the cross sectional area of trunk of tree expressed in cm ² .	Above ground biomass and carbon sequestration potential	
Circumference(C) / GBH	It is the stem girth at breast height measured in cm.	Stability, defence, architecture, carbon gain and growth potential	

leaf longevity. It also affects primary production, carbon and nutrient cycling and litter decomposition (Poorter et al. 2009). Species in resource-rich environments tend to have larger SLA than those in environments with resource stress. Petiole or rachis and all veins are considered part of the leaf for standardized SLA measurement. LDMC is the oven-dry weight of a leaf, divided by its water-saturated fresh weight, expressed in mg g^{-1} . LDMC is related to the average density of the leaf tissue. It has been shown to correlate negatively with potential relative growth rate and positively with leaf life span. Leaf size is the one-sided projected surface area of a leaf expressed in cm^2 . Leaf size has important consequences for the leaf energy and water balance. Inter-specific variation in leaf size has been connected with climatic variation, geology, altitude or latitude, where heat stress, cold stress, drought stress and high-radiation stress all tend to select for relatively small leaves. Within climatic zones, leaf size variation can also be linked to allometric factors (plant size, twig size, anatomy and architecture) and ecological strategy, with respect to environmental nutrient stress and disturbances, while phylogenetic factors can also play an important role. Plant maximum height (H) is the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level, expressed in meters. Plant height is associated with competitive vigor and whole plant fecundity. There are also important trade-offs between plant height and tolerance or avoidance of environmental (climatic, nutrient) stress. Even, some tall plants can successfully avoid fire reaching the green parts and meristems in the canopy. Height tends to correlate allometrically with other size traits in broad interspecific comparisons, for instance aboveground biomass, rooting depth, lateral spread.

Data analysis

We synthesize and compared the functional trait composition and dispersion of the species between Garpehra and Jarua khera forest community by using multi trait indices i.e. Functional Attribute Diversity (Walker et al. 1999). FAD is the sum of the standardised distance between all pairs of species in the functional space (Walker et al. 1999). It measures the dispersion of species in trait space and evaluates the average functional contribution of each species

to the total diversity of a community (Ricotta 2005, Mouchet et al. 2010). FAD is calculated using formula:

$$\text{FAD} = \sum_{i=1}^s \sum_{j>1}^s \text{ED}_{ij}$$

$$\text{ED}_{ij} = \sqrt{\sum_{t=1}^T (x_{tj} - x_{ti})^2}$$

where, FAD- Functional attribute diversity, S – total number of species, ED_{ij} – the ecological distance between two species i and j, T – total number of traits, x_{ti} and x_{tj} are the values of the t_{th} trait of species 'i' and 'j'.

Euclidean distance (functional or ecological distance) among species is calculated by the formula:

$$\text{ED}_{jk} = \left[\sum_{i=1}^I (A_{ij} - A_{ik})^2 \right]$$

Where, ED= Euclidean distance, A_{ij} and A_{ik} are the trait values of species j, k for attribute I, and I is the total number of attributes being considered.

Shannon-Weiner index (H) is a measure of the degree of uncertainty related to a random selection of individuals from the community (Shannon and Weiner 1949). It is calculated by the formula:

$$H = - \sum_{i=1}^s w_i \ln(w_i)$$

Where, w_i is the proportion of i^{th} species, \ln is a natural log, s is the number of species.

Simpson's index (D) is an index of diversity equals the probability of drawing without replacement two individuals of different type from a given collection (Simpson 1949).

After assessing different parameters for various traits, functional trait values for each traits were assigned (Table 2). To eliminate scale effects, a species-by-trait matrix was created, and characteristics were standardized on a five-point scale (Walker et al. 1999) to avoid scale effects (Tables 3 and 4). Functional distance (here, ED) was estimated for each species pair for these standardized traits. After determining the functional distances across species, a distance matrix termed as functional trait space was created. This distance matrix depicts the species distribution throughout the functional space as well as the functional distances between species pairings. The frequencies of functional

Table 2. Mean trait values of collected plant species

Species	Site1 (Garpehra)						Site 2 (Jaruakhera)					
	SLA (cm ² /g)	LDMC (mg/g)	LS (cm ²)	H (m)	BA (cm ²)	C (cm)	SLA (cm ² /g)	LDMC (mg/g)	LS (cm ²)	H (m)	BA (cm ²)	C (cm)
<i>Anogeissus latifolia</i>	169	355	52	5	780.33	99	-	-	-	-	-	-
<i>Lannea coromandelica</i>	49	309	389	7	435.99	74	187.3	257.83	462.7	10.5	832.41	102.2
<i>Diospyros melanoxylon</i>	105	456	139	4	109	37	105.7	394.62	93.00	7.43	377.49	68.8
<i>Aegle marmelos</i>	166	430	86	4	25.8	18	118.2	335.37	65.0	2.50	25.80	18.0
<i>Lagerstroemia parviflora</i>	79	272	96	3	35.11	21	-	-	-	-	-	-
<i>Tectona grandis</i>	-	-	-	-	-	-	210	216.52	682.6	18.25	1001.2	112.1
<i>Butea monosperma</i>	-	-	-	-	-	-	53.95	565.05	232.0	7.33	366.35	67.83
<i>Elaeodendron glaucum</i>	-	-	-	-	-	-	101.1	522.73	23.25	5.0	13.46	13.0
<i>Terminalia tomentosa</i>	-	-	-	-	-	-	125.8	285.71	181.1	15.5	1077.5	116.3
<i>Miliusa tomentosa</i>	-	-	-	-	-	-	165.9	331.71	112.8	14.5	1053	115.0
<i>Ficus religiosa</i>	-	-	-	-	-	-	80.15	349.49	109.8	26.0	4779.1	245.0
<i>Hollarhena antidysenterica</i>	-	-	-	-	-	-	146.4	308.72	134.7	2.50	14.51	13.5
<i>Wrightia tinctoria</i>	137	332	112	2	17.91	15	-	-	-	-	-	-
<i>Sterculia urens</i>	107	359	515	7	780.33	99	-	-	-	-	-	-
<i>Boswellia serrata</i>	77	390	108	7	733.76	96	-	-	-	-	-	-
<i>Schleichera oleosa</i>	79	427	424	2	183.44	48	-	-	-	-	-	-
<i>Ziziphus xylopyrus</i>	89	440	19	2	97.53	35	124.8	392.86	41.17	3.50	31.85	20.0
<i>Bauhinia retusa</i>	124	81	17	3	133.84	41	-	-	-	-	-	-
<i>Mitragyna parvifolia</i>	116	386	334	4	1052.95	115	153.0	307.32	96.38	13.0	644.90	90.0
<i>Acacia catechu</i>	95	529	33	5	42.12	23	-	-	-	-	-	-
<i>Cassia fistula</i>	83	450	406	2	31.85	20	270.1	300.23	702.5	4.0	68.12	29.25
<i>Madhuca indica</i>	-	-	-	-	-	-	81.45	416.67	134.4	9.75	341.58	65.50
<i>Buchanania lanzan</i>	-	-	-	-	-	-	104.5	393.08	130.7	11.5	127.39	40.0
<i>Acacia leucophloea</i>	-	-	-	-	-	-	83.85	490.57	21.80	6.5	350.33	66.33
<i>Ficus glomerata</i>	-	-	-	-	-	-	98.75	402.88	55.30	4.5	191.16	49.0
<i>Terminalia arjuna</i>	-	-	-	-	-	-	103.9	329.11	54.00	13.0	103.18	37.0
<i>Helictris isora</i>	250	196	207	2	15.61	14	251.4	286.22	203.6	3.75	17.91	15.0
<i>Eugenia heyneana</i>	-	-	-	-	-	-	105.4	397.26	30.56	3.5	109.0	36.0
<i>Holoptelia integrifolia</i>	126	368	84	3	31.85	20	-	-	-	-	-	-
<i>Cordia myxa</i>	80	372	100	6	644.9	90	-	-	-	-	-	-

Table 3. Functional trait value assigned to tree species of two different plant communities

Functional trait value	Site 1 (Garpehra)						Site 2 (Jaruakhera)					
	SLA (cm ² /g)	LDMC (mg/g)	LS (cm ²)	H (m)	BA (cm ²)	C (cm)	SLA (cm ² /g)	LDMC (mg/g)	LS (cm ²)	H (m)	BA (cm ²)	C (cm)
1	<50	<105	<103	<1.5	<210	<23	<54	<113	<140	<5	<955	<49
2	50-100	105-210	103-206	1.5-3	210-420	23-46	54-108	113-226	140-280	05-10	955-1910	49-98
3	100-150	210-315	206-309	3-4.5	420-630	46-69	108-162	226-339	280-420	10-15	1910-2865	98-147
4	150-200	315-420	309-412	4.5-6	630-840	69-92	162-216	339-452	420-560	15-20	2865-3820	147-196
5	>200	>420	>412	>6	>840	>92	>216	>452	>560	>20	>3820	>196

distances in the given species assemblage is shown in the histogram prepared from this matrix (Fig 1).

RESULTS

Similarity index for floristic comparison of the selected forest communities revealed differences,

primarily due to differences in species abundance, with 41 percent of the species common in both plant communities. The most recurrent species in both plant communities are, *Diospyros melanoxylon*, *Lannea coromandelica*, *Aegle marmelos*, *Miliusa tomentosa*, *Hollarhena antidysenterica*, *Ziziphus xylopyrus*, *Mitragyna parvifolia*, *Cassia fistula* and

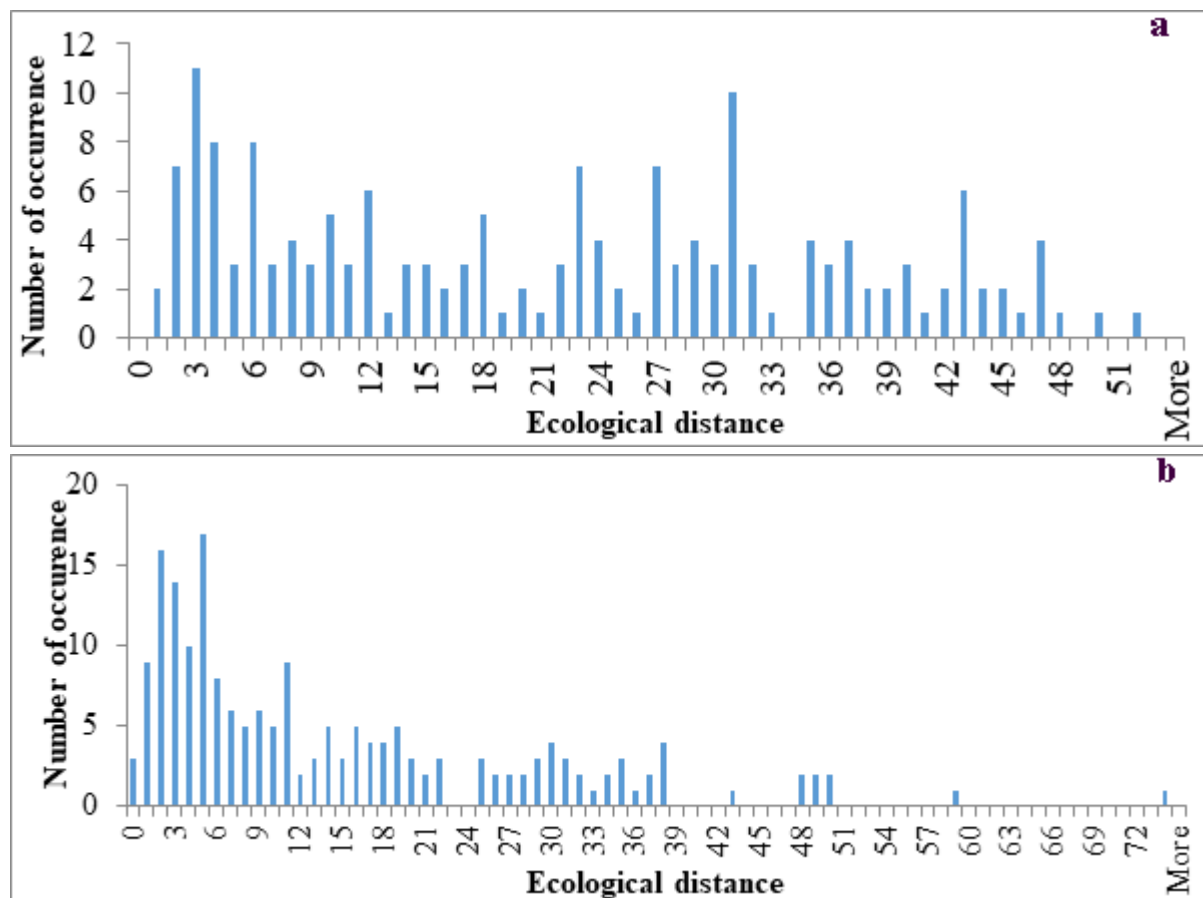


Figure 1. Comparison of ecological distances between species across functional trait space within Garpehra site (a) and Jaruakhera site (b)

Helicteres isora. Tree species exclusive to the site Garpehra are *Anogeissus latifolia*, *Lagerstroemia parviflora*, *Wrightia tinctoria*, *Sterculia urens*, *Boswellia serrata*, *Schleichera oleosa*, *Bauhinia retusa*, *Acacia catechu*, *Cordia myxa* and *Holoptelea integrifolia*. The Jaruakhera forest community has a high abundance of *Tectona grandis*, *Butea monosperma*, *Eleodendron glaucum*, *Terminalia tomentosa*, *Ficus religiosa*, *Madhuca indica*, *Buchanania lanzan*, *Acacia leucophloea*, *Ficus glomerata* and *Terminalia arjuna*. In terms of species trait values of Jaruakhera forest, the mean plant maximum height for *Tectona grandis* and *Ficus religiosa* were highest (18.25 and 26.0 m, respectively), while it was lowest (2.50) for *Aegle marmelos* and *Hollarhena antidysenterica*. On the contrary, the trees species of Garpehra such as *Lannea coromandelica*, *Sterculia urens* and *Boswellia serrata* showed maximum mean height values (7m) whereas *Wrightia tinctoria*, *Miliusa*

tomentosa, *Schleichera oleosa*, *Ziziphus xylopyrus*, *Cassia fistula* and *Helicteres isora* showed the lowest values (2 m). High SLA values were found for tree species such as *Helicteres isora* (251.4 cm² g⁻¹) and *Cassia fistula* (270.19 cm² g⁻¹) in Jaruakhera forest as compared to Garpehra where it was 250 and 83 cm² g⁻¹, respectively. Similarly, tree species at Jaruakhera forest such as *Butea monosperma*, *A. catechu*, and *Eleodendron glaucum* had the highest mean LDMC values (565.05, 529 and 522.73 mg g⁻¹), while at Garpehra, *Bauhinia retusa* (81 mg g⁻¹), and *Helicteres isora* (196 mg g⁻¹) had the lowest values. Further, the mean LS values were particularly high for *Tectona grandis* (682.6 cm²) and low for *Acacia leucophloea* (21.80 cm²) at Jaruakhera site. At Garpehra, it was 515cm² (*Sterculia urens*) as maximum and 17cm² (*Bauhinia retusa*) as minimum. The highest and lowest mean BA was recorded in *Ficus religiosa* (4779.1 cm²) and *Elaeodendron glaucum* (13.46 cm²), respectively, at Jaruakhera

Table 4. Standardized data for tree species in distinct plant communities at five point scale

S. No.	Species	Site1 (Garpehra)						Site2 (Jarua khera)					
		SLA	LDMC	LS	H	BA	C	SLA	LDMC	LS	H	BA	C
1	<i>Anogeissus latifolia</i>	4	4	1	4	4	5	-	-	-	-	-	-
2	<i>Lannea coromandelica</i>	1	3	4	5	3	4	4	3	4	3	1	3
3	<i>Diospyros melanoxylon</i>	3	5	2	3	1	2	2	4	1	2	1	2
4	<i>Aegle marmelos</i>	4	5	1	3	1	1	3	3	1	1	1	1
5	<i>Lagerstroemia parviflora</i>	2	3	1	3	1	1	-	-	-	-	-	-
6	<i>Tectona grandis</i>	-	-	-	-	-	-	4	2	5	4	2	3
7	<i>Butea monosperma</i>	-	-	-	-	-	-	1	5	2	2	1	2
8	<i>Elaeodendron glaucum</i>	-	-	-	-	-	-	2	5	1	1	1	1
9	<i>Terminalia tomentosa</i>	-	-	-	-	-	-	3	3	2	4	2	3
10	<i>Miliusa tomentosa</i>	4	3	1	2	1	1	3	3	1	3	2	3
11	<i>Ficus religiosa</i>	-	-	-	-	-	-	2	4	1	5	5	5
12	<i>Hollarhena antidysenterica</i>	3	4	1	3	1	1	3	3	1	1	1	1
13	<i>Wrightia tinctoria</i>	3	4	2	2	1	1	-	-	-	-	-	-
14	<i>Sterculia urens</i>	3	4	5	5	4	5	-	-	-	-	-	-
15	<i>Boswellia serrata</i>	2	4	2	5	4	5	-	-	-	-	-	-
16	<i>Schleichera oleosa</i>	2	5	5	2	1	3	-	-	-	-	-	-
17	<i>Helictis isora</i>	5	2	3	2	1	1	5	3	2	1	1	1
18	<i>Eugenia heyneana</i>	-	-	-	-	-	-	2	4	1	1	1	1
19	<i>Holoptelia integrifolia</i>	3	4	1	2	1	1	-	-	-	-	-	-
20	<i>Cordia myxa</i>	2	4	1	5	4	4	-	-	-	-	-	-
21	<i>Ziziphus xylopyrus</i>	2	5	1	2	1	2	3	4	1	1	1	1
22	<i>Bauhinia retusa</i>	3	1	1	3	1	2	-	-	-	-	-	-
23	<i>Mitragyna parvifolia</i>	3	4	4	3	5	5	3	3	1	3	1	2
24	<i>Acacia catechu</i>	2	5	1	3	1	1	-	-	-	-	-	-
25	<i>Cassia fistula</i>	2	5	4	2	1	1	5	3	5	1	1	1
26	<i>Madhuca indica</i>	-	-	-	-	-	-	2	4	1	2	1	2
27	<i>Buchanania lanzan</i>	-	-	-	-	-	-	2	4	1	3	1	1
28	<i>Acacia leucophloea</i>	-	-	-	-	-	-	2	5	1	2	1	2
29	<i>Terminalia arjuna</i>	-	-	-	-	-	-	2	3	1	3	1	1
30	<i>Ficus glomerata</i>	-	-	-	-	-	-	2	4	1	1	1	1

Table 5. Functional trait matrix showing functional distance between species in Garpehra site.

Species	Al																		
<i>Anogeissus latifolia</i>	x	Lc																	
<i>Lannea coromandelica</i>	22	x	Dm																
<i>Diospyros melanoxylon</i>	22	24	x	Am															
<i>Aegle marmelos</i>	27	39	3	x	Lp														
<i>Lagerstroemia parviflora</i>	31	27	7	8	x	Wt													
<i>Wrightia tinctoria</i>	31	31	3	4	4	x	Su												
<i>Sterculiaurens</i>	18	8	32	47	47	43	x	Mt											
<i>Miliusa tomentosa</i>	30	40	8	5	5	3	52	x	Hu										
<i>Hollarhena antidysenterica</i>	27	31	3	2	2	2	45	3	x	Bs									
<i>Boswellia serrata</i>	6	8	24	35	31	35	10	40	31	x	So								
<i>Schleichera oleosa</i>	38	20	12	25	25	15	24	28	23	32	x	Zx							
<i>Ziziphus xylopyrus</i>	27	31	3	6	6	4	45	9	4	29	17	x	Br						
<i>Bauhinia retusa</i>	29	29	17	18	6	12	47	7	10	33	35	18	x	Mp					
<i>Mitragyna parvifolia</i>	12	14	30	43	43	37	6	44	41	10	24	37	43	x	Ac				
<i>Acacia catechu</i>	31	31	3	4	4	4	47	9	2	31	21	2	18	43	x	Cf			
<i>Cassia fistula</i>	43	27	7	14	14	6	37	17	12	39	5	10	28	35	10	x	Cm		
<i>Cordia myxa</i>	6	12	20	27	23	29	18	32	23	2	36	23	27	16	23	37	x	Hoi	
<i>Holoptelea integrifolia</i>	30	36	4	3	3	1	50	2	1	36	22	3	11	42	3	11	28	x	Hi
<i>Helicteres isora</i>	38	40	16	15	15	9	46	6	13	48	26	23	11	42	23	19	44	12	x

Table 6. Functional trait matrix showing functional distance between species in Jaruakhera site.

Species	Tg																			
<i>Tectona grandis</i>	x	Dm																		
<i>Diospyros melanoxylon</i>	30	x	Bm																	
<i>Butea monosperma</i>	33	3	x	Ac																
<i>Acacia leucophloea</i>	35	1	2	x	Ha															
<i>Hollarhena antidysenterica</i>	32	4	11	7	x	Mt														
<i>Miliusa tomentosa</i>	19	5	12	8	9	x	Cf													
<i>Cassia fistula</i>	16	28	31	31	20	29	x	Zx												
<i>Ziziphus xylopyrus</i>	35	3	8	4	1	10	21	x	Lc											
<i>Lannea coromandelica</i>	4	16	19	19	18	11	10	19	x	Eg										
<i>Elaeodendron glaucum</i>	43	3	4	2	5	14	29	2	25	x	Tt									
<i>Terminalia tomentosa</i>	11	9	14	12	15	2	27	16	7	20	x	Fr								
<i>Ficus religiosa</i>	38	34	37	35	50	19	74	49	38	49	17	x	Mi							
<i>Madhuca indica</i>	30	0	3	1	4	5	28	3	16	3	9	34	x	Hi						
<i>Helicteris isora</i>	25	13	22	16	5	14	9	6	13	14	18	59	13	x	Bl					
<i>Buchanania lanzan</i>	30	2	5	3	6	7	30	5	18	5	9	36	2	15	x	Mp				
<i>Mitragyna parvifolia</i>	21	3	10	6	5	2	25	6	11	10	4	31	3	10	3	x	Am			
<i>Aegle marmelos</i>	32	4	11	7	0	9	20	1	18	5	15	50	4	5	6	5	x	Fg		
<i>Ficus glomerata</i>	38	2	5	3	2	11	26	1	22	1	17	48	2	11	4	7	2	x	Ta	
<i>Terminalia arjuna</i>	27	3	8	6	5	6	29	6	17	8	8	37	3	14	1	2	5	5	x	

forest. Comparatively BA was less at Garpehra forest with highest as 1052.9 cm² in *Mitragyna parvifolia* and lowest (15.61 cm²) in *Helicteres isora*. Similarly, the mean circumference (C) values at Jaruakhera site was particularly high for *Ficus religiosa* (245.0 cm) and very low in *Elaeodendron glaucum* and *Hollarhena antidysenterica* (13 and 13.5 cm, respectively) at Garpehra forest.

Most of the species in Jaruakhera forest community had higher mean trait values of SLA, LS, H, BA, and C and low mean trait values of LDMC, whereas the Garpehra forest community had low mean trait values for these traits except for LDMC (Table 2). Garpehra forest community shows higher species diversity as compared to Jaruakhera forest community was (2.55 and 2.30) respectively, as H index. Functional diversity index in terms of FAD (Functional attribute diversity) value was 3664 in Garpehra community which represents the sum of all pair-wise functional distances among species pair under the functional space with average functional distance of 21.43. While in Jaruakhera community, FAD value and average functional distance were 2741 and 14.42 respectively. Trait matrices were used to calculate functional distances between species. The matrix depicts the distribution of functional distances and their frequencies across species in terms of their functional attributes in the Garpehra

and Jaruakhera community (Tables 5 and 6).

After comparing both plant communities, range of functional distances was found in between 2 to 52 in the Garpehra forest. The minimum functional distance of 2 was recorded among seven species pairs namely, *Hollarhena antidysenterica*- *Aegle marmelos*, *Hollarhena antidysenterica*- *Lagerstroemia parviflora*, *Hollarhena antidysenterica*- *Wrightia tinctoria*, *Holoptelea integrifolia*- *Milusa tomentosa*, *Acacia catechu*- *Hollarhena antidysenterica*, *Cordia myxa*- *Boswellia serrata* and *Acacia catechu* - *Ziziphus xylopyrus*, while maximum functional distance of 52 was recorded only for single species pair *Miliusa tomentosa*- *Sterculia urens*. No two species are exactly similar at Garpehra forest as zero distance was not recorded in the matrix. Results show that majority of the species are distributed in low to middle functional distances and a few species pair were recorded with high functional distances.

Few middle range functional distances of 23, 27 and 31 had high frequencies among different species pair as they are repeated for 7, 7 and 10 times respectively. The functional distance of 23 was observed among seven species pairs namely, *Cordia myxa*- *Lagerstroemia parviflora*, *Schleichera oleosa*- *Hollarhena antidysenterica*, *Cordia myxa*- *Hollarhena antidysenterica*, *Cordia myxa*- *Ziziphus*

xylopyrus and *Helicteres isora*-*Acacia catechu*. The functional distance of 27 was also found for seven species pair namely, *Aegle marmelos*-*Anogeissus latifolia*, *Hollarhena antidysenterica*-*Anogeissus latifolia*, *Ziziphus xylopyrus*-*Anogeissus latifolia*, *Lagerstroemia parviflora*-*Lannea coromandelica*, *Cassia fistula*-*Lannea coromandelica*, *Cordia myxa*-*Aegle marmelos*, and *Cordia myxa*-*Bauhinia retusa*. The functional distance of 31 was the second most commonly found functional distance in the forest community appeared ten times for ten species pairs. Higher functional distances were found to be associated with very low frequencies. Higher ecological distances of 48, 50 and 52 were found only once for species pairs i.e. *Helicteres isora*-*Boswellia serrata*, *Holoptelea integrifolia*-*Sterculia urens* and *Milusa tomentosa*-*Sterculia urens* respectively. Above results show that large number of species are distributed throughout the range of functional distances and a few species are distributed in higher distances.

The Jaruakhera forest community, shows a wide range of functional distances from 0 to 50. The minimum functional distance of 0 was recorded among 3 species pairs namely, *Madhuca indica*-*Diospyros melanoxylon*, *Aegle marmelos*-*Hollarhena antidysenterica*, *Ficus glomerata*-*Eugenia hylana* which indicate high similarity for functional attributes. Maximum functional distance of 74 was recorded only for one species pair namely *Ficus religiosa*-*Cassia fistula*. Some low ecological distances of 2, 3 and 5 show high frequencies and they were repeated 16, 14 and 15 times respectively. Functional distance of 2 showed highest frequency of 16, indicated its commonness among 16 species pairs namely, *Buchanania lanzan*-*Diospyros melanoxylon*, *Ficus glomerata*-*Diospyros melanoxylon*, *Eugenia heyneana*-*Diospyros melanoxylon*, *Acacia leucophloea*-*Butea monosperma*, *Elaeodendron glaucum*-*Acacia catechu*, *Ficus glomerata*-*Hollarhena antidysenterica*, *Eugenia heyneana* - *Hollarhena antidysenterica*, *Terminalia tomentosa*-*Milusa tomentosa*, *Mitragyna parvifolia*-*Milusa tomentosa*, *Elaeodendron glaucum* - *Ziziphus xylopyrus*, *Buchanania lanzan*-*Madhuca indica*, *Ficus glomerata*-*Madhuca indica*, *Eugenia heyneana*-*Madhuca indica*, *Ficus glomerata*-*Aegle marmelos*, *Eugenia heyneana*-*Aegle marmelos*. Higher functional distances were

associated with very low frequencies. Higher ecological distances of 48, 49, 50 were repeated for two times for species pair *Ficus glomerata*-*Ficus religiosa*, *Eugenia heyneana* - *Ficus religiosa*, *Ficus religiosa*-*Ziziphus xylopyrus*, *Ficus religiosa*-*Elaeodendron glaucum*, *Ficus religiosa*-*Hollarhena antidysenterica*, *Aegle marmelos*-*Ficus religiosa* and 59 were repeated only for one time for species pair *Helicteres isora*-*Ficus religiosa*. Above results show that large number of species are distributed in low to middle range of functional distances and very few species are distributed in higher distances.

DISCUSSION

Our findings revealed new insights on the above-ground resource use strategies of Garpehra and Jaruakhera forest communities in Central Indian dry deciduous forests. Variations were found in species functional composition and functional dispersion across a functional trait space. The differences in functional strategies of the compared communities are mainly driven by differences in species composition. In comparison to the Garpehra, Jaruakhera forest community showed higher values of above ground traits. *T. grandis*, *M. tomentosa*, *T. tomentosa* and *Buchanania lanzan* with height of more than 11 metres seem to be highly competitive in response to fire which is frequent during dry season, and tolerance or avoidance of environmental stress.

The girth at breast height (gbh) of a tree is related to basal area, which is an essential property for quantifying vegetation structure and site quality (Suthari 2013). The basal area of tree species varies across the two sites in present study (ranged from 7.145 m² ha⁻¹ in Garpehra to 17.082 m² ha⁻¹ in Jaruakhera), indicating the stand structure. The range of basal area in the present study is similar to those reported in other studies conducted in similar types of tropical dry deciduous forests in the country (Jha and Singh 1990; Sahu et al. 2008; Bijalwan 2010; Panda et al. 2013; Sagar 2006). Basal area and tree density was more in Jaruakhera than in Garpehra forest indicating the intensity of biotic factors and soil nutrient status (Naidu and Kumar 2016). Leaf related functional traits like SLA, LA and LDMC are most extensively used traits which depicts three

major axes of leaf economics spectrum i.e. resource exploitation, competition ability and response to disturbance. (Grime 1977, Westoby 1998). Lower SLA and LDMC were observed in Garpehra forest as compared to Jaruakhera. Low SLA of trees may be due to the high photosynthetic capacity of their leaves at a given investment of N and phosphorus contents because their canopies can intercept more light than small individuals can (Liu et al. 2010). Previous studies reported that lower SLA has been linked to slower CO₂ intercellular diffusion (Parkhurst 1994, Hikosaka et al. 1998, Poorter and Evans 1998) or increased internal shading of chloroplasts due to attenuation of photons passing through the lamina (Terashima and Hikosaka 1995), both of which can reduce photosynthetic rate. Trait related variation in two sites may be attributed to variations in soil nutrient richness. Nutrient rich soil particularly N and P content, is the characteristic of soil derived from basalt at Jaruakhera site. Environmental filters select plant species with diverse traits and ecological strategies, as demonstrated by our findings.

Functional trait approach to plant community enable to understand interspecific functional distances among different species under the functional trait space (Kraft et al. 2014) and these interspecific functional distances depict the degree of functional similarity and dissimilarity among different species pairs to understand community assembly, species coexistence pattern, competition etc. (Walker et al. 1999). It influences community dynamics, resource dynamics, ecosystem functions and services, as well as the functional structure and composition of plant communities (Lasky et al. 2014). Low distances indicate functional similarity or trait convergence (Paine et al. 2011) whereas high distances indicate functional dissimilarity or trait divergence (Kraft et al. 2008). Similarity provided redundancy and resilience (Pillar et al. 2013) but dissimilarity provided complementarity or functional diversity resulting in higher ecological efficiency. Functional distances for various species combinations were found to be dispersed in the present study, ranging from low to high. Trait convergence is associated with habitat filtering, whereas trait divergence is associated with niche

differentiation as a filter of community assembly. At Garpehra site, species pair namely, *Hollarhena antidysenterica*-*Aegle marmelos*(2), *Hollarhena antidysenterica*-*Lagerstroemia parviflora*(2), *Hollarhena antidysenterica*-*Wrightia tinctoria*(2), *Holoptelia integrifolia*-*Miliusa tomentosa*(2), *Acacia catechu*-*Hollarhena antidysenterica*(2), *Cordia myxa*-*Boswellia serrata*(2) and *Acacia catechu*-*Ziziphus xylopyrus*(2) were found to have a low functional distance indicating that these species pairs were functionally more similar than others, hence, they are redundant to each other. Over a period of time when changes occur, one species substitutes for the role of the other species in such species pair, allowing for a better understanding of conservation strategies for particular species (Kahmen et al. 2002; Cadotte et al. 2011). Similarly, at Jaruakhera site in terms of functional distances, most functionally similar species pair are *Eugenia heyneana* - *Ficus glomerata* (0), *Acacia leucophloea* - *Diospyros melanoxylon* (1) and *Ziziphus xylopyrus* - *Hollarhena antidysenterica* (1), while functionally most dissimilar species pairs are *Ficus religiosa* - *Ziziphus xylopyrus* (74) and *Helicteres isora* - *Ficus religiosa*(59). Functional diversity provides the status of functional space filled by species traits. At this site, vacant distance may be occupied by the exotic, alien and other invasive species. Interspecific functional distances or differences help in predicting and facing invasibility (Funk et al. 2008, Van Kleunen et al. 2010). At Garpehra site, frequencies for very high functional distances were found relatively less, indicating occurrences of highly functional dissimilar species in plant community. The species pairs namely, *Helicteres isora*-*Boswellia serrata*(48), *Holoptelea integrifolia*-*Sterculia urens*(50) and *Miliusa tomentosa*-*Sterculia urens*(52) were found to be distributed in very high functional distances under functional space(species by trait matrix) with high dissimilarity under the effect of niche differentiation as a community assembly factor.

Although, the two dry deciduous communities did not show significant functional diversity attributes, but the Garpehra forest community has less functional space for invasion in future than the Jaruakhera forest community owing to higher functional distances.

ACKNOWLEDGEMENTS

First author (PK) is thankful to the University Grants Commission, India, for providing fellowship. Authors acknowledge the support of the Head, Department of Botany, Dr. Harisingh Gour Vishwavidyalaya, Sagar (M.P.) for permitting to access resources.

Conflict of Interest: The authors declare that they do not have any conflict of interest.

Authors' contributions: PK, BLC and PKK collected data, designed and drafted the manuscript. PKP contributed for arranging the data and MLK contributed to revision of first draft. No funding has been received for this study.

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Received: 10th July 2021

Accepted: 19th February 2022