Capturing richness-independent phylogenetic diversity and testing surrogates in woody plant communities

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Phylogenetic diversity (PD) indices quantify the evolutionary history of a community. Studies have shown how decoupling between taxon richness (TR) and PD provides useful insights into biodiversity. The present study on three dry deciduous forest patches (Nandi, Savandurga and Devarayandurga) shows such decoupling patterns. Our analysis of unique (endemic) taxa revealed that whereas the high PD in Nandi was contributed largely by its unique taxa which were composed of different evolutionary lineages, unique taxa in Savandurga contributed negatively due to highly shared lineages. Also, the use of higher-level TR did not provide an adequate surrogate for PD. We, therefore, propose the use of an integrative approach (both TR and PD) to quantify biodiversity for gaining better insights into the composition and evolutionary history of a community.

Keywords: Biodiversity, community phylogenetics, conservation, deciduous forest.

'BIODIVERSITY' – a portmanteau of 'biological diversity' – was a term first coined by Walter G. Rosen and loosely defined to represent the topics under discussion during the 1986 'National Forum on BioDiversity'[1]. A more modern definition of biodiversity comes from United Nations Environment Programme (UNEP)[2] which states: 'Biodiversity is the variety of life on Earth, it includes all organisms, species, and populations; the genetic variation among these; and their complex assemblages of communities and ecosystems.'

Biodiversity studies have taken a forefront in recent years and an increasing number of studies are being undertaken to analyse and understand the diversity for current and long-term conservation efforts[3]. Coupled with the diverse contexts in which the term 'biodiversity' has been used[4], this has resulted in the development of several diversity indices that provide varying degrees of information[5–8].

Species richness or taxon richness (TR) is the most intuitive and simplest index, defined as the total number of species present in a community, region or plot[9]. Its simplicity and quantitative nature, however, indicate that its ability to capture complicated patterns and qualitative information is highly limited[10]. For example, a mammal community consisting of slow loris, rhinoceros, deer, tiger and jackal would be unequivocally considered more diverse than one that consists of macaque, langur, gibbon, wild boar and tiger despite having the same richness (TR = 5). The presence, in this case, of the loris and rhinoceros contributes to greater diversity which cannot be evaluated by TR alone. To evaluate such qualitative differences, ecologists began looking at other forms of diversity (such as functional diversity) by quantitatively measuring morphological, behavioural and physiological characters[11,12]. These can be difficult characters to measure unambiguously; however, they are reflected in the evolutionary history of the species and can thus be quantified from the phylogenetic relationships of the species[13]. This form of diversity, termed phylogenetic diversity (PD), has the ability to quantify these qualitative differences using unambiguous and discrete data points (molecular sequence data) that can be compared across a wide taxonomic range.

One of the first indices of PD was proposed by Faith[8], and henceforth called Faith's PD (F-PD). This is calculated as the sum of all branch lengths in the minimum spanning path on the phylogeny that includes the subset of taxa found in a community/plot within the study region (Figure 1). Since its inception, it has been used in numerous studies and is now extensively used in community phylogenetics[14]. Initial studies showed that TR and F-PD are highly correlated[15]. However, Rodrigues and Gaston[16] caution against this expectation in certain scenarios. Indeed, there were other studies that showed PD patterns decoupled with that of TR[17–19]. In the Cape of South Africa, for example, Forest *et al.*[19] showed that despite having higher generic richness, the western region flora showed significantly lower PD. Patterns of decoupling have also been examined at a global scale, such as a study of mammals[20] that showed Africa and the Indian subcontinent to have the highest PD, whereas South America, which had high species richness, exhibited very low PD values.

The observed correlation between TR and F-PD exists because F-PD is a 'total index'[21], i.e. one that is a summation of individual values. Since F-PD is a summation

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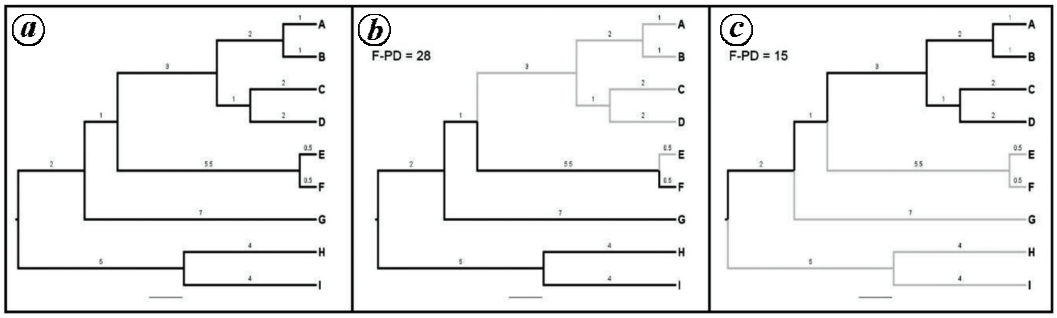

Figure 1. ***a***, Phylogenetic relationship of a group of taxa A–I. Branch lengths represent time. ***b***, Calculation of Faith's phylogenetic diversity (F-PD) for a community consisting of species F–I. Minimum spanning path branches are shown in black. Branch lengths are summed up to get F-PD. ***c***, F-PD of a community consisting of species A–D. Note the vast difference in F-PD values for these two communities in the two panels (***b***) and (***c***) despite having the same taxon richness (TR = 4).

of all branch lengths, each additional species will contribute an additional value, however small, that will increase the value of F-PD for that community. Schweiger *et al.*[21] showed that 'average indices' for PD can be used to study such decoupling between PD and TR. Average indices correct for dependency on TR by averaging the values across data points. One such measure is the mean phylogenetic distance (MPD), which is the average phylogenetic distance of any random species pair within a community[22]. This index is independent of TR and is thus ideal to identify decoupling between TR and PD.

A majority of studies that have investigated decoupling patterns have been undertaken in biodiversity hotspots. Simulations showed that such decoupling most likely occurs due to specific phylogenetic structure that is usually seen in areas of high diversity and endemic radiation[23]. However, it is to be noted that the underlying structure of the phylogeny is what causes this decoupling and not the endemism itself. We therefore believe that areas of low diversity could nevertheless exhibit a decoupling pattern which has largely remained unexplored. This is especially true in the Indian scenario, where most studies focus on the Western Ghats which is a biodiversity hotspot, while its adjacent drier areas are less explored. The dry forests are mostly deciduous and scrub jungles, spanning from the eastern slopes of the Western Ghats to most of peninsular India. These dry forests have been categorized into large, relatively homogenous forest types with relatively lesser number of species than their evergreen counterparts[24]. Owing to lands being converted for agriculture and urbanization, many of these forests are now restricted to small pockets[25]. While some of them, usually those that have high taxon richness, are part of protection schemes, other patches that have low taxon richness are usually not considered for protection[26]. These forest patches are thus ideally suited to test decoupling between TR and PD, and obtain a new axis of biodiversity information which may prove pivotal to understanding the biogeographic history of these forests.

Investigating the PD of these forests could also have conservation implications[18]. Endemic taxa are usually targeted for conservation priority and areas under protection tend to be chosen to maximize the number of endemic and/or threatened taxa[27]. However, as with the insufficiencies of using TR to quantify biodiversity, merely maximizing the number of endemic taxa might not always be the path to conservation prioritization. A careful examination of the endemic taxa and the extent of their endemism is required to make more meaningful assessments. Although PD in itself is more powerful than TR, analysing the PD of endemics alone might not be meaningful because the endemics need to be evaluated in the context of the larger community that includes other well-distributed taxa. One way to assess this would be to evaluate how much PD of that community is contributed by its set of endemic taxa. Excluding the endemic taxa from the analysis and comparing the resultant PD with the original value (after correcting for TR variation) gives a measure of this relative endemic PD. If PD decreases in the absence of endemics, it indicates that the endemic taxa are distantly related to the other taxa in that community and are positively contributing towards overall diversity. If the PD increases, it indicates that the endemic taxa are very closely related (not evolutionarily distinct) to the other taxa and are thus negatively contributing to the overall diversity[21]. In the present study we evaluate this by excluding taxa that are unique to a location (we avoid the term 'endemic' due to the limited geographical range of this study and that no taxon is a known point-endemic within these locations), and analysing both the degree and direction of change in PD values.

All these methods, however, require that one has an adequately accurate phylogeny, preferably a dated phylogeny, for all the taxa included in the study. Obtaining full phylogenetic information of the study taxa is somewhat of a challenge because it is only in the recent past that dependable techniques and methods of generating adequately accurate phylogenies have been developed. In many cases a confident tree topology (from multiple studies) is available, but sequence data across all species are not available, which are essential to obtain branch length information. In such cases, higher-level-taxon richness

was proposed as a promising surrogate owing both to its ease of data collection as well as reduced taxonomic ambiguities[28]. Higher-level-taxon richness is the richness at higher taxonomic ranks such as number of genera, families or orders, and is suggested to adequately represent diversity for conservation efforts and protected area management[29]. We are not aware of any study that has explicitly tested this, although one study on South African flora showed a strong correlation between functional diversity (attributes such as seed dispersal properties) and higher-level-taxon richness[30]. Additionally, these high-level rankings are neither natural units (may not be monophyletic), nor are they comparable (class Mammalia is orders of magnitude younger than class Insecta)[31]. We thus argue that these indices have the same shortcomings of using TR – a given set of orders or families may be more closely related to one another than a set of distantly related orders or families.

The results of the present small-scale study, would help us undertake phylogenetic diversity analysis at a larger scale for the entire Western Ghats and its adjacent drier areas. The goal of this study, therefore, is threefold: (a) To analyse decoupling of TR with PD in areas of low diversity; (b) to identify the contribution of unique (endemic) taxa towards overall PD; and (c) to test the utility of higher-level-taxon richness as a surrogate for PD. To do this we collected data on woody plant taxa, generated a phylogeny using sequence information, resolved the same, and finally calculated the various indices of diversity.

Methods

Location and sampling

The study area is located in the dry zone of peninsular India with mostly patchy dry deciduous to scrub forests. Three forest patches, namely Devarayanadurga (Dev), Nandi Hills (Nandi) and Savandurga (Sav) were chosen based on forest cover and isolation from each other. The locations are separated by 50–60 km, are surrounded by villages and suburban areas, and present on/around rocky outcrops surrounding the major city of Bengaluru, Karnataka, India.

We collected presence data on all woody plants with a girth of 20 cm at breast height (GBH). As plants have fixed positions, we employed a plotless sampling strategy wherein a path is chosen and as one walks along, any new taxon in view is collected. We undertook 2–4 days of data collection for each location ensuring that the walk paths covered the elevation range at each location. Sav required the least number of days (two) as a large portion of it is a rock monolith with no trees found in the region, while Dev required the most (4 days) given that it has a wider spread of forested area. The walk paths were approximately 11, 12 and 15 km for Sav, Nandi and Dev respectively. Taxa were identified using field guides and by photographing them on site, collecting representative samples and consulting with botanists. We collated these data with existing flora lists for each location to obtain a more complete list of taxa found in these regions[32–34]. Given that the PD index we use can effectively capture PD with as little as 60% taxa representation across varied sampling efforts[21], data collation with existing records would provide an adequate representation of diversity for this study. Exotic taxa were identified using species ranges from the published literature and regional floras, and were excluded as they do not reflect native diversity. We used genus-level data, which are adequate surrogate for species numbers, due to difficulty in species-level identification and possible nomenclature ambiguity in the lists[35]. We recorded a total of 129 genera across all three locations (Table 1).

Phylogeny

We used silica-dried leaf samples to extract and sequence DNA for as many genera as possible. For the remaining genera, sequences were obtained from GenBank (http://www.ncbi.nlm.nih.gov/nuccore/). DNA was extracted using Quiagen DNeasy Plant Kit and Macherey-Nagel Nucleospin Plant Kit. Owing to the wide taxonomic range of this study, we chose a marker that shows adequate informative variation across different orders. The chloroplast marker maturase K (matK) is one such marker that has been widely used for DNA barcoding in plants[36,37] and for which universal primers have been designed[38], thus allowing us to generate and obtain comparable sequences for a wide range of taxa. We used the primers matK390F and matK1326R which generated ~930 bp section of the gene[39].

The PCR reaction mix consisted of 1× Buffer, 2 mM $MgCl_2$, 1.5 mM of each dNTP, 0.06 U/ml *Taq* polymerase, 0.4 µM of each primer and 20–30 ng of template DNA. Thermal cycling conditions were as follows: 95°C for 120 s followed by 40 cycles of 95°C for 25 s, 48°C for 30 s, 72°C for 60 s and a final extension at 72°C for 5 min. The amplified products were sent to Amnion Biosciences Pvt Ltd for purification and sequencing (Sanger capillary sequencing). The forward and repeat reads were analysed in FinchTV (http://www.geospiza.com/Products/finchtv.shtml) for any errors. Each sequence was BLASTed to ensure it matched with the gene of interest. Sequences obtained from GenBank and those generated were consolidated and aligned using ClustalW on MEGA 5.2 (http://www.megasoftware.net/)[40].

To build a phylogeny with branch length information, we first generated a cladogram which was then used as a constraint to generate branch lengths from our sequence alignment. The genus-level cladogram was generated from known angiosperm phylogenies[41–43]. However, 12

Table 1. List of genera and sequence data used in this study

Order	Family	Genus	Dev	Nandi	Sav	Accession no.
Apiales	Araliaceae	*Schefflera*	*	*	*	MG737444
	Pittosporaceae	*Pittosporum*		*		MG737442
Boraginaceae	Boraginaceae	*Cordia*	*	*		EU599652.1
		Ehretia	*	*	*	MG737418
Brassicales	Capparaceae	*Cadaba*		*	*	EU371753.1
	Moringaceae	*Moringa*	*			JX092021.1
Celastrales	Celastraceae	*Cassine*	*	*	*	MG737424
		Celastrus	*	*	*	EU328944.1
		Maytenus	*			EF135566.1
Cornales	Cornaceae	*Alangium*	*		*	JF308672.1
Ericales	Ebenaceae	*Diospyros*	*	*	*	MG737417
	Lecythidaceae	*Careya*	*		*	DQ924096.1
	Sapotaceae	*Madhuca*	*	*		DQ924091.1
		Manilkara	*	*		DQ924092.1
Fabales	Fabaceae	*Acacia*	*	*	*	MG737427
		Adenanthera	*			AF521808.1
		Albizia	*	*	*	MG737431
		Bauhinia	*	*	*	JN881391.1
		Butea	*	*	*	MG737430
		Caesalpinia	*		*	EU361906.1
		Cassia	*	*	*	MG737426
		Dalbergia	*	*	*	JX506655.1
		Erythrina	*			AY386869.1
		Hardwickia	*			EU361967.1
		Mundulea	*			AF142713.1
		Pithecellobium		*		HM020740.1
		Pongamia	*	*	*	MG737447
		Prosopis	*		*	HM020741.1
		Pterocarpus	*		*	JN083553.1
		Pterolobium	*			EU362032.1
		Tamarindus	*		*	MG737446
Gentianales	Apocynaceae	*Carissa*	*	*		MG737443
		Ichnocarpus	*	*	*	EF456267.1
		Tabernaemontana		*		GU973934.1
		Wrightia	*		*	DQ660555.1
	Loganiaceae	*Strychnos*	*		*	JF270953.1
	Rubiaceae	*Canthium*	*		*	HQ415390.1
		Catunaregam	*	*	*	MG737438
		Gardenia	*	*	*	MG737420
		Haldina^{+}	*		*	GQ434176.1
		Ixora	*	*		AM412468.1
		Mitragyna	*			AY538390.1
		Morinda	*			GQ130297.1
		Psydrax		*		MG737435
		Tarenna		*	*	HQ415401.1
		Wendlandia	*	*		MG737439
Lamiales	Acanthaceae	*Justicia*	*		*	JQ586385.1
	Bignoniaceae	*Dolichandrone*		*		MG737421
		Radermachera		*		MG737423
		Sterospermum	*			JN183984.1
	Lamiaceae	*Gmelina*	*		*	JX495721.1
		Premna	*	*	*	HQ427331.1
		Tectona	*	*	*	442742942:2051-3595
		Vitex	*	*	*	166788482
	Oleaceae	*Chionanthus*		*		MG737436
		Jasminum	*			EU281182.1
		Ligustrum		*		JF830531.1

(*Contd*)

Table 1. (*Contd*)

Order	Family	Genus	Dev	Nandi	Sav	Accession no.
		Olea	*		*	365823312:2124-3701
		Schrebera	*			JX517454.1
Laurales	Lauraceae	*Cinnamomum*		*		AJ247154.2
		Neolitsea		*		MG737437
		Phoebe		*		AJ247184.1
Magnoliales	Annonaceae	*Annona*	*	*	*	GQ139717.1
		Polyalthia	*		*	AY518854.1
	Magnoliaceae	*Magnolia*	*			AY008988.1
Malpighiales	Erythroxylaceae	*Erythroxylon*	*	*	*	MG737440
	Euphorbiaceae	*Euphorbia*	*			JQ952104.1
		Givotia^{+}	*			GQ434082.1
		Mallotus	*	*		MG737432
		Ricinus	*			AB233767.1
	Malpighiaceae	*Hiptage*		*		MG737445
	Ochnaceae	*Ochna*	*	*		EF135572.1
	Phyllanthaceae	*Bridelia*	*	*	*	AY552421.1
		Phyllanthus	*	*	*	AY936594.1
		Flueggea			*	AY552426.1
	Salicaceae	*Flacourtia*	*	*		AB233829.1
Malvales	Bixaceae	*Cochlospermum*	*			JQ587262.1
	Dipterocarpaceae	*Shorea*	*	*		MG737433
	Malvaceae	*Bombax*	*		*	HQ696690.1
		Firmiana^{+}			*	JX088700.1
		Grewia	*	*		AY321193.1
		Helicteres	*	*	*	AY321186.1
		Kavalama	*		*	AY321178.1
		Thespesia	*			GU135012.1
Myrtales	Combretaceae	*Anogeissus*	*	*	*	MG737425
		Terminalia	*	*	*	MG737419
	Lythraceae	*Lagerstroemia*	*	*		MG737422
	Melastomataceae	*Memecylon*		*		AF368211.1
	Myrtaceae	*Callistemon*	*			AF184705.3
		Psidium	*	*		AB354958.1
		Syzygium	*	*	*	MG737434
Ranunculales	Menispermaceae	*Tinospora*	*		*	EF143855.1
Rosales	Cannabaceae	*Trema*	*	*		JX518199.1
	Moraceae	*Artocarpus*		*		HQ415243.1
		Ficus	*	*	*	MG737428
		Strebulus	*		*	GQ434235.1
	Rhamnaceae	*Ziziphus*	*	*	*	MG737441
	Rhamnaceae	*Scutia*	*			JX517733.1
	Rosaceae	*Eriobotrya*		*		DQ860462.1
	Ulmaceae	*Holoptelea*	*	*	*	MG737429
Santalales	Opiliaceae	*Cansjera*			*	DQ790167.1
	Santalaceae	*Santalum*	*	*	*	AY042650.1
Sapindales	Anacardiaceae	*Anacardium*	*	*		AY594459.1
		Buchanania^{+}	*		*	HQ427343.1
		Lannea	*		*	JX518185.1
		Mangifera	*	*		AY594472.1
		Semecarpus	*	*		AY594479.1
		Spondias	*			AY594480.1
	Burseraceae	*Boswellia*	*		*	AY594461.1
		Garuga^{+}			*	AY594475.1
	Meliaceae	*Aglaia*	*			AY128177.1
		Azadirachta	*		*	AY128179.1
		Cipadessa	*			EF489116.1
		Soymida^{+}	*			EF489117.1
		Swietenia	*			EU042835.1

(*Contd*)

Table 1. (*Contd*)

Order	Family	Genus	Dev	Nandi	Sav	Accession no.
	Rutaceae	*Aegle*	*	*		AB762358.1
		Chloroxylon[+]	*		*	EF489044.1
		Citrus		*		AB626785.1
		Glycosmis	*			AB762391.1
		Limonia	*		*	AB762356.1
		Murraya		*	*	AB762390.1
		Naringi	*		*	AB762385.1
		Paramignya			*	AB762387.1
		Toddalia	*	*	*	FJ716738.1
	Sapindaceae	*Dimocarpus*		*		AY724286.1
		Sapindus	*	*		AY724324.1
		Schleichera	*			AY724329.1
	Simaroubaceae	*Ailanthus*	*			EF489112.1
Solanales	Solanaceae	*Solanum*	*			HQ593448.1

[+]Due to unavailability of sequence, the phylogenetically closest genus sequence was considered.
Dev, Devarayanadurga; Nandi, Nandi Hills; Sav, Savandurga.

Figure 2. Combined phylogeny of 129 genera used in this study. Branch lengths (not shown here) are calculated using maximum parsimony on a constrained cladogram constructed from known angiosperm phylogeny (see text for details).

families had genera that were not represented in these studies, thus we resolved them individually from our sequence alignment using PAUP* 4.0 (http://paup.csit.fsu.edu/)[40]. This final cladogram was then used as the backbone constraint along with the complete sequence alignment to generate a phylogeny with branch lengths (Figure 2) under maximum parsimony criteria in PAUP* 4.0.

Diversity indices

Taxon richness was calculated simply by counting the number of genera (families and orders for higher-level-taxon surrogates) present in a given location. F-PD was calculated as the sum of all branch lengths in the minimum spanning path of the phylogeny incorporating all genera found in a given location. MPD was calculated

Table 2. Comparison of diversity measures across the three study areas

Study site	Genera richness	Mean phylogenetic distance	Faith's phylogenetic diversity	Non-unique genera	$MPD_{non\text{-}uniq}$
Devarayanadurga	104	232.68	4242	75	233.16
Nandi	70	239.36	3500	53	236.05
Savandurga	64	227.91	3121	59	238.24

from the tree-based distance matrix using the following formula

$$\text{MDP} = \frac{\sum d_{i,j}}{s^2},$$

where s is the number of genera and $d_{i,j}$ is the phylogenetic distance between two genera in a given location. To determine the contribution of unique taxa, $MPD_{non\text{-}unique}$ was calculated using the same formula as MPD, except that the taxa composition of each location excluded those which were unique to that region. All calculations were done using R[45] on R.Studio[46] with functions from packages ape[47], geiger[48] and picante[49].

Results and discussion

Decoupling richness and PD

Table 2 shows the TR, F-PD and MPD of the three study areas – Nandi, Sav and Dev. There is an overall positive correlation between TR and F-PD: Sav shows the lowest values (TR = 64, F-PD = 3121) and Dev has the highest values (TR = 104, F-PD = 4242), while Nandi has intermediate values (TR = 70, F-PD = 3500). However, when PD is corrected for TR variation we observe patterns of decoupling between PD and TR. It has been suggested that such decoupling is most likely to occur in biodiversity hotspots largely in part due to the high endemism[19]. Our results, however, show such decoupling to also be present in areas of relatively low endemism. Dev, for example, has the highest TR (104 genera), but intermediate PD (MPD = 232) (Table 2). Sav and Nandi have similar TR (64 and 70 genera respectively), yet show differences in their PD – Nandi being the most phylogenetically diverse (MPD = 239) and Sav being the least (MPD = 228). It is clear that Nandi has much more PD than might be predicted by its generic richness. Among our study sites, one might have focused on the diversity in Dev because it has much greater TR (about 60% more) than other sites. Adding the phylogenetic axis to evaluating its diversity has thus made it possible to consider that Nandi, despite having lower TR, harbours a more diverse set of flora. It is thus quite evident that we must include this additional axis to diversity studies not only in biodiversity hotspots, but also when studying lesser diverse regions.

While it is true that this additional axis of diversity could also be calculated from functional and morphological diversity, such as the avalanche index (AI)[12], we defend the use of PD considering that such indices need morphological and functional trait data which are: (a) difficult to collect unambiguously; (b) need a specialist for the study taxa, and (c) cannot span wide taxonomic ranges due to restriction in the number of comparable traits. Molecular phylogenetics overcomes this by using a large number of unambiguous discrete data points (DNA base pairs) as the source data, and a wide range of taxa can be meaningfully compared (by comparing orthologous loci). Morphological and functional diversity is also reflected in the divergence of DNA sequence through the course of evolution[13]. With the growing body of molecular data available, reduced sequencing costs and improved tree-building tools, molecular phylogenies provide informative data available at relative ease. Although these problems with AI restricted us from employing it in this study, it would be interesting to explicitly compare AI with PD measures.

We also corroborate the proposition of Schweiger *et al.*[21] that 'average indices' of PD should be used rather than 'total indices' when studying independent communities and such decoupling patterns. Due to a high dependence of F-PD on richness, the values increase with increasing richness – Dev has the highest TR (104 genera) and F-PD (F-PD = 4242), whereas Sav has the lowest TR (64 genera) as well as lowest F-PD (3121). The simplest way to counter this is to use a richness-independent index, such as MPD, as shown in the present study. MPD values by themselves are not informative about such decoupling; it is their relative values that aid in disentangling the pattern of TR and PD. Alternately, the residuals from a regression of F-PD against TR can be used to identify data points that deviate from the expectation[19,20]. A more robust method is to compare the observed values against a null distribution of possible range of values for a given TR[50]. These methods, however, are ideally useful for larger datasets with more number of data points than available in this study (three data points).

Unique taxa evaluation

The phylogenetic contribution of taxa unique to each community was determined by excluding them from PD

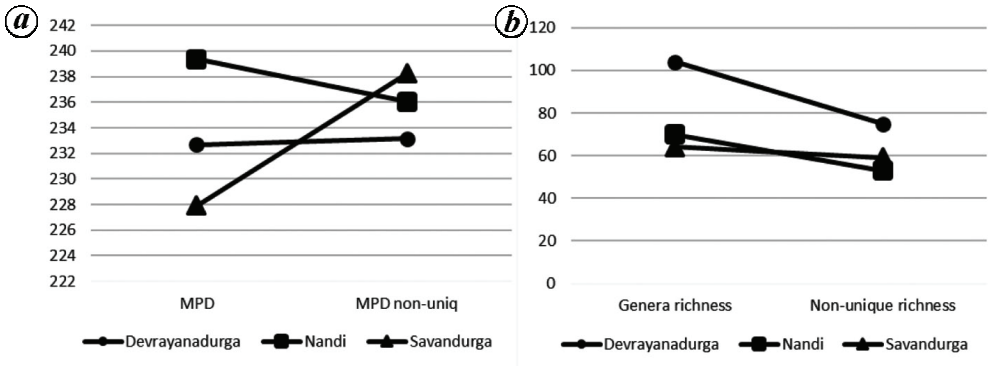

Figure 3. Change in (***a***) PD and (***b***) richness with exclusion of unique taxa.

Table 3. Comparison of higher-level taxonomic richness with PD

Study site	Genera richness	Family richness	Order richness	MPD
Devarayanadurga	104	42	18	232.68
Nandi	70	27	16	239.36
Savandurga	64	30	17	227.91

calculations, and analysing the direction and extent of change compared with PD of the original community. This contribution is assessable because unlike richness, which can only decrease with the exclusion of taxa, MPD can either increase or decrease, and therefore be more informative about the excluded taxa. For example, after exclusion of unique taxa, Sav's richness decreased by 7% as opposed to its MPD which increased by 4.4%. Dev showed greatest decrease in richness, while Sav the least; however, the extent of shift in MPD showed the converse pattern: greatest shift for Sav and least for Dev (Figure 3). Both Sav and Dev showed an increase in MPD when unique taxa were excluded (albeit to different extents), indicating that though these species are taxonomically unique, they are phylogenetically redundant, being closely related to the commonly found taxa. Nandi, by contrast, showed a decrease in MPD when unique taxa were excluded, implying that these species are not only taxonomically unique, but also phylogenetically distinct, adding lineages not represented by the commonly found taxa to the diversity in these regions. On further analysing these taxa unique to Nandi, we found they were mostly evergreen elements (contrary to the majority of taxa in this study which are deciduous), which explains the diverse lineages that they add to the PD of Nandi. While one might argue that inclusion of such characters (functional diversity) would do just as well as PD, it is difficult to quantify these because functional differences almost always involve a complex array of traits; PD thus provides a better, easier and qualitatively superior measure of diversity[51]. Indeed, in some cases functional diversity shows a discordance with PD patterns[52]. It is thus essential to evaluate the importance of unique taxa from a phylogenetic perspective than merely by their numbers or unique traits.

Higher taxonomic level surrogates

The patterns of richness at family and order levels when compared with PD also suggest that these higher-level diversity measures do not capture the evolutionary history encompassed in these patches (Table 3). One extreme is exemplified by Nandi – the community with highest PD showing least richness at higher taxonomic levels. Conversely Sav, with the least PD, has more family and order richness compared to Nandi. This demonstrates that it is possible to obtain inflated values of richness at higher taxonomic levels which do not reflect high PD. Families and orders represented by a single taxon will add to the richness numbers, but not necessarily to PD because they can have very small branch lengths, while taxa belonging to the same family or order could add quite significantly to PD by having long branch lengths. The former case is exemplified by Magnoliaceae and Cannabaceae, both of which are families represented by one genus each in this study (Magnolia and Trema respectively) which have (small) terminal branch lengths of 19 and 14 units respectively. The latter case is exemplified by Dolichandrone and Holoptelea, both of which belong to families represented by multiple genera, which have (long) terminal branch lengths of 143 and 132 units respectively (Figure 2). Thus, whereas a community with Dolichandrone would not add to richness at higher taxonomic levels but add significantly to PD, one with Magnolia would add to richness at higher taxonomic levels but not

significantly to PD. These possible scenarios make it difficult to confidently use higher-level-taxon richness as an adequate surrogate for PD.

Conclusion

Our analysis demonstrates the advantage of using an average index of PD, namely MPD, to detect decoupling of richness and PD in fairly independent communities. Taxon richness is not reflective of PD – communities with high richness were not the ones with high PD. Communities with similar TR can exhibit extreme values of PD. Analysing the contribution of unique taxa also showed a decoupling pattern. Unique taxa can either be closely or distantly related to common taxa; in the latter case they significantly contribute towards the biodiversity of that community. These complex patterns and distribution of taxa in these seemingly uniform dry deciduous/scrub forests cannot be elucidated using richness numbers or even total indices of PD, such as F-PD.

Utility of surrogates for PD such as richness at higher taxonomic levels is highly limited. Although it is easier, less time-consuming and less expensive to gather such surrogate data, their disadvantages far outweigh their advantages. In certain cases, these surrogate indices lead to completely contrasting conclusions. These contrasting patterns become extremely important where sensitive issues are concerned, such as conservation prioritization, where over-representation of taxonomic diversity becomes a key issue[53]. With the development of phylogenetic tools and reduction in the cost of sequence generation, the disadvantages of using molecular data in phylogenetic analysis are diminishing rapidly. We recommend stopping the use of these surrogate measures for PD and suggest appropriate branch-length PD indices (average or total) depending on the nature of the study. An integrative approach to quantifying diversity incorporating multiple axes of measures will be more meaningful, and can aid in a better understanding of history and predicting changes in community composition.

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