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TECHNICAL COMMENT

On the risks of using dendrograms to measure functional diversity and multidimensional spaces to measure phylogenetic diversity: a comment on Sobral *et al.* (2016)

Sébastien Villéger,* Eva Maire and Fabien Leprieur

Abstract

Sobral *et al.* (Ecology Letters, 19, 2016, 1091) reported that the loss of bird functional and phylogenetic diversity due to species extinctions was not compensated by exotic species introductions. Here, we demonstrate that the reported changes in biodiversity were underestimated because of methodological pitfalls.

Keywords

cophenetic distance, dendrogram, Euclidean space, functional diversity, functional space, phylogenetic diversity.

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Sobral *et al.* (2016) proposed a framework to test whether introductions of exotic species can compensate for the loss of functional and phylogenetic diversity due to extinctions of native species. They applied this framework on island bird communities and did not find compensation for the functional and phylogenetic components of biodiversity. However, their analyses were biased by three methodological choices.

First, Sobral *et al.* built a PCoA-based functional space for each island, separately, to assess temporal changes in functional diversity after species extinction and/or introductions. However, Gower's distance computed before PCoA accounts for the range of values present among species (Pavoine *et al.* 2009), which implies that each functional space constructed had different total inertia and that distances between the same species vary between islands (Fig. 1a). Consequently, changes in functional diversity measured by Sobral *et al.* differed from those measured using a single Gower's distance matrix computed according to trait values of all the species present in the assemblages (Fig. 1b). More importantly, Sobral *et al.* computed functional richness (FRic), that is, volume of functional space filled by species, in 2- to 5-dimensional spaces (because 'dbFD' function from Laliberté & Legendre 2010 reduced the number of PCoA axes for islands with low species richness; Appendix S1). This was therefore incorrect to compute statistical tests on FRic values having different units (i.e. area vs. five-dimensional volume). When comparing functional diversity between assemblages, a single functional space should be computed (Mouillot *et al.* 2013), which is exactly what is done when computing phylogenetic diversity using a single tree. Contrary to the results from the island-by-island approach, we found that FRic significantly decreased after extinctions and that FRic significantly

increased for islands that experienced only introductions (Table 1). In addition, we also revealed that functional dispersion (FDis), mean pairwise functional distance between species (MPD_{FD}) and mean nearest taxon distance (MNTD_{FD}) significantly decreased after both species extinctions and introductions (Table 1).

Second, Sobral *et al.* computed phylogenetic richness index (PRic) based on species position in a five-dimensional phylogenetic space. To build this multidimensional space they applied a PCoA to the cophenetic distance matrix derived from the phylogenetic tree. To our knowledge, this is the first time that such an approach was used to quantify phylogenetic richness. Indeed, all previous studies used the Faith's PD index that is based on branch lengths on a phylogenetic tree (Tucker *et al.* 2017). We found that Faith's PD was not significantly correlated with the PRic index for both past and present scenarios (Fig 1c and d). Indeed, the 5D phylogenetic space did not faithfully represent actual phylogenetic distances between species (Fig 1e). We found similar mismatch using simulated phylogenetic trees and communities with varying species richness (Fig. S1, Appendix S1). Contrary to PRic, Faith's PD significantly decreased after extinctions and Faith's PD significantly increased for islands that experienced only introductions (Table 1).

Third, functional and phylogenetic similarities between native and extinct or introduced species were both assessed using indices accounting for the length of shared branches on dendrograms. This tree-based approach is relevant and commonly used for assessing phylogenetic beta-diversity since a tree representation is logical to describe the evolutionary processes (such as speciation and extinctions events) that resulted in current phylogenetic relatedness between a set of species. However, there is no rationale behind representing functional

relatedness between species using a dendrogram (i.e. assuming hierarchical differences; Petchey & Gaston 2006). In addition, Maire *et al.* (2015) demonstrated that using a dendrogram-based approach artificially increases the functional distance between species that have actually similar trait values (Maire *et al.* 2015). To quantify this bias, they proposed the 'mSD' metric that measures the average squared deviation between the initial Gower's distances and the cophenetic distances on the functional dendrogram. Twenty-seven dendrograms out of 32 computed by Sobral *et al.* had a low quality (i.e. mSD > 0.01, which means that average absolute deviation between Gower's distance and cophenetic distance is > 10%, Fig. 1f), which ultimately biased the quantification of functional beta-

diversity. We indeed found that beta-diversity values computed based on overlap between species pools in a single multidimensional space (Villéger *et al.* 2013 and R library *betapart*, Baselga *et al.* 2013) were not significantly correlated with values computed using dendrograms ($n = 9$, $r = 0.305$, $P > 0.05$). More importantly, functional dissimilarity between native and exotic species pools was on average 1.13 times higher than the one calculated using the dendrogram-based approach ($t = -7.09$, d.f. = 8, $P < 0.001$; Appendix S1).

Using unbiased methods, we found that both functional and phylogenetic richness significantly increased due to exotic species introductions on islands that did not experience extinctions, but did not significantly increase on islands that

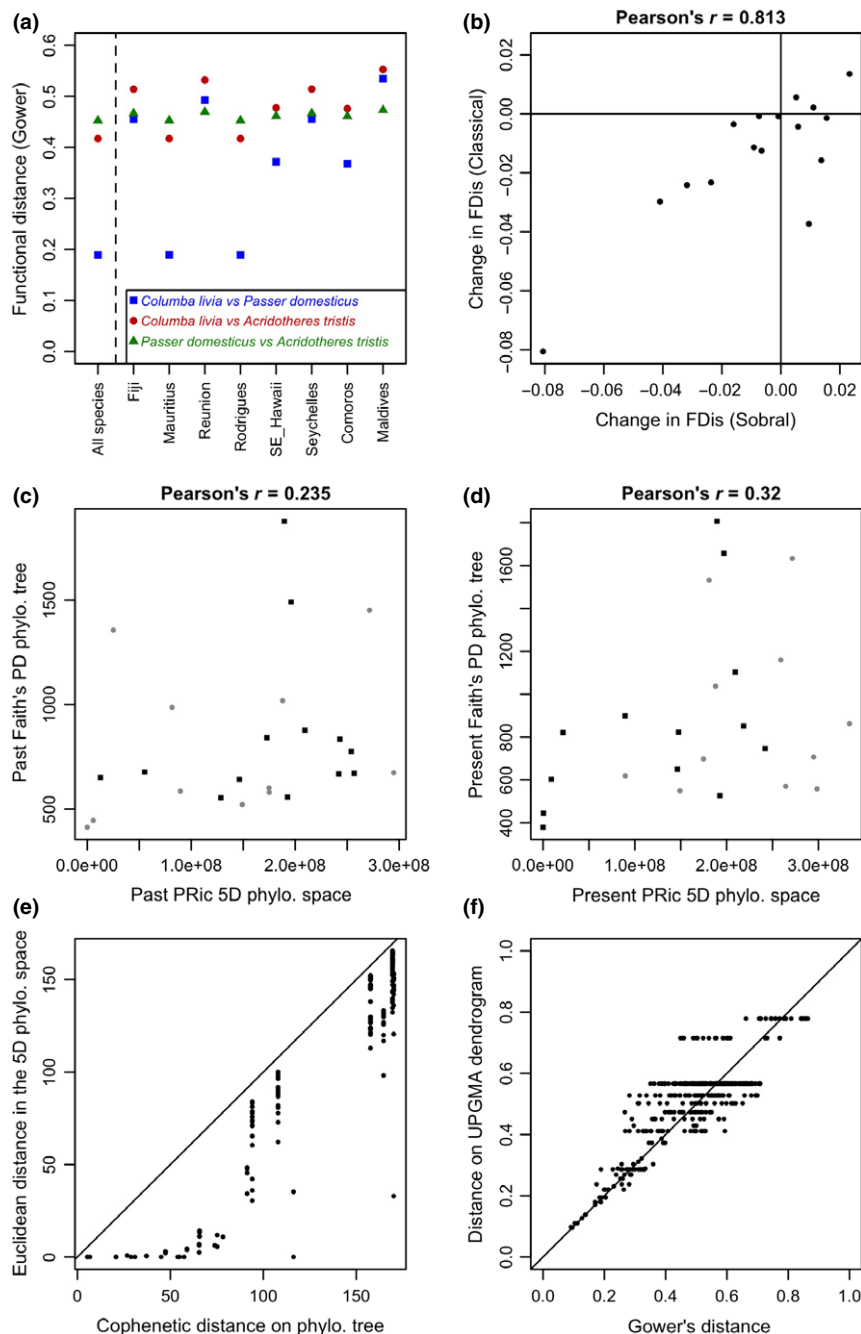


Figure 1 Illustration of biases when assessing changes in functional diversity in multiple functional spaces, when assessing phylogenetic diversity in a multidimensional space and when assessing functional beta-diversity on dendrograms. With Sobral *et al.* approach (i.e. Gower's distance computed accounting only for species present on an island), distance between a species pair can vary across islands as illustrated for three exotic species that have been introduced on eight islands (a), for example, distance between *Columba livia* and *Passer domesticus* on Mauritius is half of distance on Maldives islands. In addition, ranking of distances between species pairs also vary between islands, for example, *P. domesticus* is functionally closer to *Acridotheres tristis* than to *C. livia* on two (Reunion and Maldives) out of the eight islands where these three species have been introduced. More importantly, the Gower's distances computed with Sobral *et al.* island-by-island approach differ from Gower's distance computed with accounting for trait values of all species present on the 32 islands, for example, distance between *C. livia* and *P. domesticus*. As a consequence of this mismatch, changes in functional dispersion (FDis) from past to present situations computed with Sobral *et al.* approach (one Gower's distance matrix per island) deviate from changes in FDis computed using a single Gower's distance matrix (i.e. computed according to trait values of all species) among the 16 islands that experienced both extinctions and introductions (b). For instance, four islands showed a decrease in FDis only with the latter approach (right bottom of the plot). Phylogenetic richness assessed using PRic index computed in a 5D space is not correlated with Faith's PD index computed on the phylogenetic tree for both past (c) and present (d) situations (black squares: islands that experienced both introductions and extinction, grey points: islands that experienced only introductions; only islands with more than five species for both situations were considered). Mismatch between cophenetic distance on the phylogenetic tree and Euclidean distance in the five-dimensional space where PRic index was computed is high for most pairs of species from Mauritius island (e), with, for instance, very low Euclidean distance in the 5D space among species pairs that have a phylogenetic distance lower than 80. Average absolute deviation between the 2 distances among all species pairs was of 23 million years (i.e. 27% of phylogenetic tree depth). Similarly, distances on the functional dendrogram do not faithfully represent Gower's distances for many species pairs (f). For instance, *Raphus cucullatus* is at almost the same distance (0.72–0.79) to all other species on the dendrogram while its Gower's distance to these species range from 0.45 to 0.77. Mean squared deviation index (mSD) for Mauritius dendrogram is > 0.01, which means that average absolute deviation between Gower's distance and cophenetic distance is > 10%.

Table 1 Changes in the functional and phylogenetic diversity of island bird assemblages

Change in species composition	Diversity	Measures	Scenarios			Repeated measures ANOVA (<i>P</i> -value)		Pairwise <i>t</i> -test (<i>P</i> -value)		
			Past scenario (S1)	Extant native scenario (S2)	Present scenario (S3)	d.f.	<i>F</i>	S1–S2	S2–S3	S1–S3
Extirpations and introductions	Functional	FRic	0.115 (0.111)	0.070 (0.112)	0.118 (0.142)	2	4.38	3.05	−2.41	−0.16
		FDis	0.346 (0.033)	0.317 (0.050)	0.332 (0.038)	2	6.79	2.65	−2.54	2.50
		MPD _{FD}	0.508 (0.046)	0.479 (0.051)	0.478 (0.051)	2	6.26	2.45	0.01	2.93
		MNTD _{FD}	0.261 (0.079)	0.275 (0.088)	0.234 (0.069)	2	7.56	−1.23	3.68	2.87
Only introductions	Phylogenetic	Faith PD	770 (419)	607 (449)	830 (468)	2	8.78	3.69	−3.31	−1.17
	Functional	FRic	0.098 (0.122)		0.116 (0.134)					−3.69
		FDis	0.335 (0.058)		0.339 (0.039)					−0.51
		MPD _{FD}	0.531 (0.121)		0.507 (0.0767)					1.35
		MNTD _{FD}	0.335 (0.210)		0.271 (0.139)					2.34
	Phylogenetic	Faith PD	600 (410)		721 (427)					−5.60

Outputs of statistical analyses as the ones reported in tables 1 and 2 from Sobral *et al.* (2016), but using functional diversity computed in a single functional space for all islands (instead of one space per island) and phylogenetic richness computed with Faith's PD index (instead of PRic index). Significant differences ($P < 0.05$) from ANOVA or *t*-test are in bold. Statistical tests that are significant with our approach but not with Sobral *et al.* approach are in italics (note that all the significant results found by Sobral *et al.* remain significant with our reanalyses).

experienced extinctions. We also found that the functional distance between species (as measured by FDis, MPD and MNTD indices) decreased on islands that experienced both extinctions and introductions, hence testifying for an increased functional redundancy between species. These findings highlight the strengths of Sobral *et al.* framework to assess the combined effects of extinctions and introductions on biodiversity.

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