

Functional endemism captures hotspots of unique phenotypes and restricted ranges

Endemism is a measure of geographic range restriction which is used to highlight regions with unique biota, found nowhere else on earth. Several metrics have been developed to capture the degree to which regions harbour a high degree of endemic species richness [1] or endemic evolutionary history [2], however trait-based approaches have been largely neglected [3]. Here, we develop a trait-based metric for a functional approach to endemism studies - functional endemism (FE) - and explore global FE patterns in birds.

Endemism metrics capture continuous spatial patterns of range restriction. One of the most commonly used metrics, weighted endemism (WE), is the sum of species in a site (species richness) inversely weighted by each species geographic range size, such that narrowly distributed species contribute more to the value [1]. Phylogenetic endemism (PE) extends this concept using the sum of phylogenetic branch lengths from molecular phylogenies (phylogenetic diversity), instead of species richness. Therefore, PE captures regions with many narrowly distributed and evolutionarily distinct species [2]. Emphasising evolutionary history instead of a raw species counts means lineages separated by a longer period of evolutionary time contribute more to the measure. These lineages may be of a high conservation priority because they represent unique evolutionary history and are predicted to exhibit distinct ecological features [2]. While PE is widely used in biogeographic studies to predict hotspots of high conservation value [4], it remains unclear whether evolutionary history indeed captures intended ecological feature diversity [5], which is crucial for understanding ecosystem functioning and resilience in the face of global change. While feature diversity itself is an amorphous concept in ecology [6], a related and more tractable concept is functional diversity, which describes variation in measurable traits which are understood to define ecological roles of organisms [7]. In this study, we propose a new metric, functional endemism (FE), which combines information on functional traits with geographic range size, to extend the measure of endemism for functional diversity in the same way that phylogenetic endemism extends the measure for phylogenetic diversity. In this way, FE is intended to identify regions with a high proportion of ecologically distinct yet narrowly distributed species.

To quantify FE, we compiled data on 11 functional traits for 8074 bird species globally using a comprehensive morphological traits database; Avonet [8]. These traits included measures of body size, wing shape, beak size, and tarsus length. We performed a principle component analysis on the 11 traits and estimated pairwise Euclidean distances of the principle components between species. We then performed hierarchical clustering on this distance matrix to obtain a dendrogram representing a hierarchy of functional distinctiveness among species. We obtained spatial information on the distribution of the 8074 bird species in 110 km x 110 km grid cells globally from [9]. Geographic range size was estimated as the number of unique grid cells a species is found in. Similarly to PE, FE is calculated as the sum of the unique branch lengths of the dendrogram separating species in a site, divided by the inverse of their geographic range size. However, unlike PE, the branch lengths of FE represent functional distinctiveness rather than evolutionary distinctiveness. WE was calculated following the method of [1] and PE was calculated following the method of [2] using a single tree from the posterior distribution of [9] containing all 8074 species. We explored how patterns of FE differ to PE and WE using linear regression. We found that WE and PE were colinear using variable inflation factors and so we selected PE as a single predictor variable.

Our global analysis revealed that FE is highest in the tropical mountain ranges of the Andes, African Rift, Himalaya-Hengduan, and New Guinea, while FE is lowest in arid regions of central Australia,

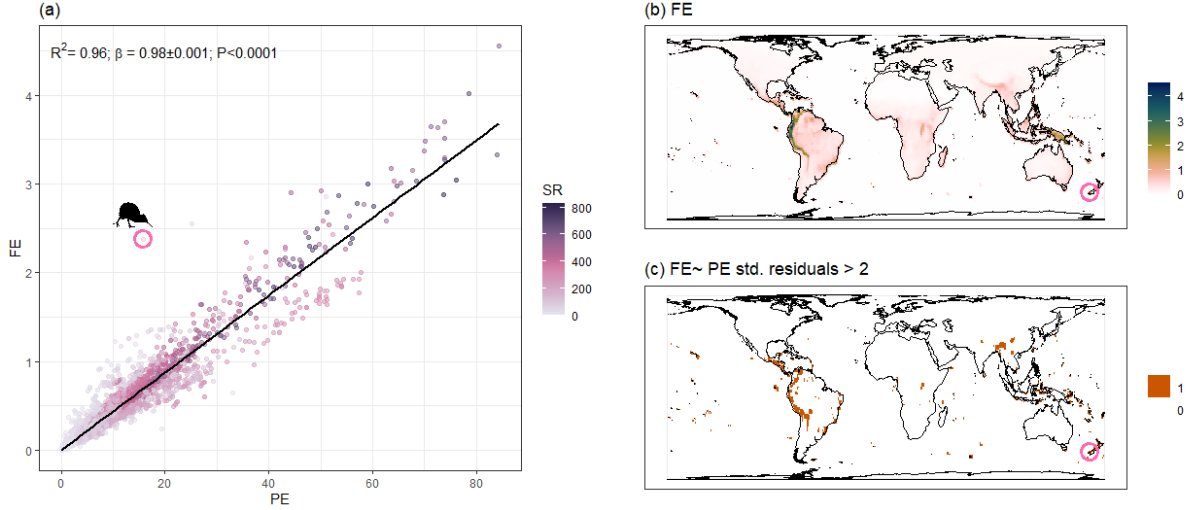


Figure 1: (a) Linear relationship between functional endemism (FE) and phylogenetic endemism (PE), (b) the global distribution of FE, and (c) the global distribution of standardised residuals greater than 2 from a linear regression between FE and PE. A site with very high residuals in southwest Aotearoa, which contains the Fjordland region and Tau Moana, is highlighted in panels a-c. This site contains species with very high functional divergence and small geographic ranges, such as the kiki (*Apteryx australis*), Fjordland penguin (*Eudyptes pachyrhynchus*), and Takahe (*Porphyrio hochstetteri*). Maps are displayed with a Behrmann equal area projection with a spatial resolution of 110 km x 110 km.

the Sahara, the Arabian Peninsular, and Tibetan plateaus, and the northern Boreal region (Fig. 1b). Most sites had similar FE to what we expected based on PE, and there is a strong positive relationship between the two metrics ($R^2 = 0.96$; $\beta = 0.98 \pm 0.001$; $df = 40678$, $p < 0.0001$; Fig. 1a). However, exploration of the model residuals showed that some spatially restricted regions exhibited higher levels of FE than is predicted based on PE. Notably, the tropical Andes, African Rift, and Hengduan mountain ranges, as well as many of the world's islands including Aotearoa (New Zealand), Galapagos, Canaries, Melanesia, Polynesia, Wallacea, and Comoros, had much higher FE than predicted (standardised residuals > 2 ; Fig. 1c). Our results suggest that mountains and islands are hotspots of functional endemism and similar regions have been highlighted as hotspots of ecologically rare species using a different approach [10].

Greater than expected FE of mountain and island regions may be driven by analogous processes. Mountains and islands harbour many narrow-range endemics, separated by dispersal barriers of ocean and topography which can prevent geographic range expansion and may drive allopatric speciation ([11]). Further, these regions also harbour functionally distinct species which may be the outcome of selection to unique montane environments (such as in Alpine Kea parrot, *Nestor notabilis*), or driven by the unique ecological conditions provided by the relative isolation of islands (such as Kiwis, *Apteryx sp.*, filling typically mammalian niches in Aotearoa [12]). Highlighting hotspots of FE provides an exploratory step in understanding regions which might harbour ecologically distinct species, essential to ecosystem functioning, that are additionally highly vulnerable to global change due to their restricted distributions.

FE is closely related, and provides a complementary approach, to existing measures of endemism, such as WE and PE. Where patterns of FE deviate from expected patterns provides the opportunity to explore the ecological and evolutionary processes that shape functional biogeographic patterns, while highlighting regions that may contain particularly vulnerable species that could be overlooked using other measures. There are several examples of studies using endemism metrics to inform conservation targets (e.g. [13, 14]) and recent studies have predicted heavy losses to functional diversity across taxa due to ongoing global change [15]. Therefore, new ways to document and describe spatial patterns of functional diversity, particularly in vulnerable range-restricted species, is an urgent necessity. Here,

we develop and advocate for a trait-based approach to the study of patterns of endemism that should be assessed in concert with other facets of endemism in future studies.

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