

The limitations of diversity metrics in directing global marine conservation

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ABSTRACT

Biodiversity hotspots have been used extensively in setting conservation priorities for reef ecosystems. A recent Nature publication claims to have uncovered new hotspots based on global comparisons of functional diversity. Simulation models show that the purported novel evenness pattern is a mathematical inevitability of differences in species richness, as well as an artefact of differences in detectability between vastly different marine ecosystems. Constraints on evenness, along with disparity among communities in possible functional traits, cast doubt on the utility of global functional diversity comparisons for management of marine systems.

Keywords: conservation; diversity hotspots; evenness; functional diversity; marine fish; reef ecosystems

Global conservation priorities often centre on threatened species-rich areas known as ‘hotspots’ [1]. Much ocean conservation effort is, for example, directed to the Indo-Pacific Coral Triangle [2-3]. Although it is widely recognized that this focus on species richness overlooks the contributions of species abundances and trait diversity to ecosystem functioning, documenting global patterns in these metrics has been hindered by a paucity of data. In a recent paper published in *Nature*, Stuart-Smith *et al.* [4] claim to make a significant step forward in this regard. Using standardized reef fish surveys from temperate and tropical reefs around the world, the authors describe a hitherto unnoticed latitudinal gradient in community evenness – a measure of species’ relative abundances – which contributes to the identification of new functional diversity hotspots [4]. Neither of these findings withstands scrutiny.

Evenness, E , has previously been shown to be constrained both by species richness, S , and number of individuals observed, N [5,6]. It will be high whenever a small number of species or individuals is observed. For example, the evenness of a community with three species, in which only 1, 2, or 3 individuals are counted, is either 0.9 or 1: $\{N=1: \text{Species Detected (SD)}=1, E=1; N=2: SD=1 \text{ or } 2, E=1 \text{ in both cases}; N=3: SD=3, 2, \text{ or } 1 E=1, 0.9 \text{ or } 1\}$. More broadly, it has been shown that, over a range of evenness indices, evenness is not independent of species richness [5,6].

Here, the extent of these constraints, and their impact on Stuart-Smith *et al.*’s [4] findings, were tested by examining how evenness varies across combinations of S and N in simulated communities. Evenness was calculated over the feasible set of richness (1-1200) and number of individuals counted (1-2400) observed in Stuart-Smith *et al.*’s [4] surveys, using their evenness metric, the inverse Simpson diversity index divided by species richness. In this measure of evenness:

$$E = \frac{(\sum_{i=1}^N p_i^2)^{-1}}{N} \quad \text{Equation 1}$$

where p_i is the proportional abundance of species i , divided by species richness, N (Equation 1). Abundances were generated with a species abundance distribution (SAD) across the range of richness values. Truncated forms of the lognormal, gamma, and exponential distributions [7] were examined, and the shape parameters of each distribution varied to test SADs ranging from the classic hollow curve (*i.e.* few dominant species and many rare species) [8] to approximately even communities (*i.e.* species have nearly equal abundances). Simulations for each distribution form were repeated for 9999 replicates.

These simulations reveal that evenness is mathematically constrained to be high whenever species richness is low (<10-40 species, the exact threshold depending on the underlying SAD) and to be low whenever species richness is high (*i.e.* exceeding the threshold of <10-40, depending on the underlying SAD; Fig. 1). Moreover, variability in estimated evenness is highest below the richness threshold [9]. Irrespective of richness, evenness also is constrained to be high when N is low (Fig. 1). These results are robust across the entire range of plausible SADs [9]. Thus, high evenness can arise in only three ways: 1) in a truly depauperate community, 2) as a statistical artefact of poor detectability (*i.e.* low observed S), or 3) as a statistical artefact of undersampling (*i.e.* low N). Indeed, for all well-sampled communities above the species richness threshold, evenness was always between 0.15 and 0.47 (Fig. 1 and simulations presented in [9]). Uneven community values should not be surprising: they are a direct consequence of the ‘hollow curve’, which some have called a universal law [8,10].

Stuart-Smith *et al.*’s latitudinal evenness gradient is largely a statistical artefact of poor detectability [4]. Imperfect species detectability is a given with any underwater visual census.

Problems arise, however, when communities with significantly different detectabilities, such as tropical coral reefs and temperate rocky reefs, are compared [11,12]. Failure to detect rare and cryptic species in low visibility temperate waters can push these communities below the richness ‘threshold’, and lead to artificially inflated evenness estimates. Stuart-Smith *et al.*’s [4] low diversity estimates for temperate and polar regions suggest this was the case. Independent estimates of local richness using underwater video or enhanced survey effort at comparable sites vault temperate marine fish communities closer to or above the richness threshold [11, 13-17]. Without confident detection of rare species, evenness estimates of any low diversity system is subject to the mathematical constraints outlined here (Figure 1) and are likely not reflective of the true community diversity. In short, such diversity indicators are biased and misleading.

These biases also call into question the validity of the presented functional diversity patterns [4]. Although much has been made of the ‘new hotspots of functional diversity’ for marine fishes [18], it should be noted that neither of the two ‘temperate hotspots’, the Benguela Current and the Humboldt Current, has any data underlying them [4]. Both are purely unvalidated model predictions. Caution also should have been taken in comparing functional diversity across vastly different marine ecosystems. Fundamental differences in trophic structure (herbivorous fishes and corallivores help to maintain tropical reef structure [19], and yet are largely absent on temperate reefs), oceanographic processes, patterns of species distribution and diel behaviour patterns [11] indicate that comparisons of tropical and temperate reef functions in fact require distinct approaches, without which global comparisons are meaningless.

In sum, the mathematical constraints of evenness and disparity of functional traits confound global comparisons of ecosystems and produce misleading diversity patterns. No ecological mechanism need be invoked to explain Stuart-Smith *et al.*’s [4] latitudinal evenness gradient;

rather, it is a mathematical inevitability of low species detectability in temperate regions. Additionally, functional traits are generally specific to one ecosystem type and cannot meaningfully be compared across fundamentally different ecosystems. Used correctly and alongside other ecological criteria, biodiversity metrics can help direct marine conservation priorities [20,21]. However, the simulations presented here indicate that Stuart-Smith *et al.*'s [4] diversity patterns are misleading. Interpretations of evenness estimates as indicators of ecosystem properties should be treated with caution, particularly in cross-ecosystem comparisons. Explicit consideration of the limitations of diversity metrics is paramount to the development of successful marine conservation prioritization schemes.

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Figure 1 | Evenness as a function of species richness for communities with a classic ‘hollow curve’ species abundance distribution (SAD; sampled here from a lognormal distribution with mean = 0.01), across a range of individuals counted. Histogram inset shows an example of the sampled SAD; R.A. is relative abundance.