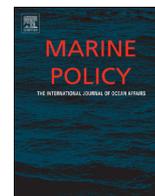




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Short communication

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 marine ecosystems. A recent Nature publication claims to have uncovered new latitudinal gradients in the evenness of reef communities and new reef hotspots based on functional diversity. Simulation models show that the purported evenness gradient is a mathematical inevitability of differences in species richness and detectability between vastly different marine ecosystems, namely 'reefs' in tropical, temperate, and polar regions. Constraints on evenness, along with disparity amongst communities in possible functional traits, cast doubt on the utility of global functional diversity comparisons for management of marine systems.

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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 recognised 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 tropical, temperate, and polar '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 by the number of individuals observed, N [5,6]. It will be high whenever a small number of species or individuals are 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: $\{N=1$: species detected (SD)=1, $E=1$; $N=2$: $SD=1$ or 2, $E=1$ in both cases; $N=3$: $SD=3$, 2, or 1 $E=1$,

0.9 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 richnesses (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

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

where p_i is the proportional abundance of species i , divided by species richness, N (Eq. (1)). Abundances, reflecting the number of individuals detected in a single sample were generated with a species abundance distribution (SAD) across the range of richness values. Detectability of each species was simply a reflection of the SAD, where dominant species were detected more frequently than rare species. 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

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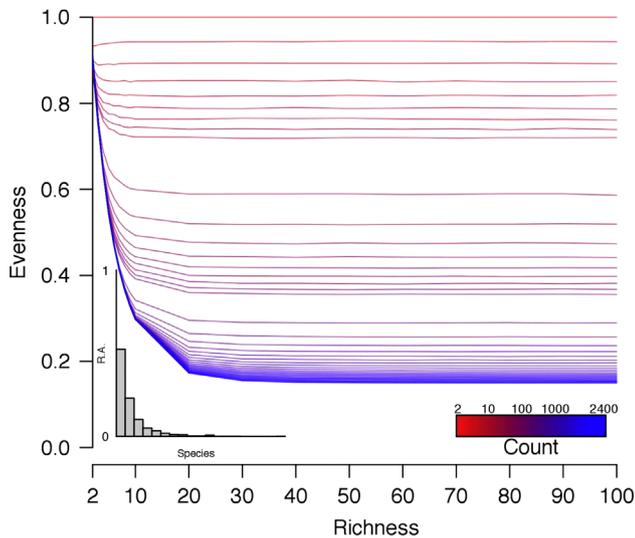


Fig. 1. Evenness as a function of species richness for communities with a classic 'hollow curve' species abundance distribution (SAD; sampled here from a lognormal distribution with mean=0.01), across a range of individuals counted. Histogram inset shows an example of the sampled SAD; R.A. is relative abundance. (Selected count values are annotated to the right of each line.)

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; [9]). 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, tested using the aforementioned probability distributions and shape parameters [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 (i.e., those with at least several hundred individuals counted, as in the bottom set of numbers in Fig. 1) 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].

We posit that 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 and different community richness values, such as tropical coral reefs and temperate rocky reefs are compared [11,12]. Failure to detect rare or cryptic species in low visibility temperate and polar waters that already support a smaller species pool 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 sit below the 'threshold', constraining their evenness estimates. 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]. In tropical reef systems, visibility is generally much higher, and although some rare or cryptic species may go undetected because of habitat complexity, the

greater underlying community richness ensures that samples sit above the threshold. Without confident detection of rare species, evenness estimates of any low diversity system are subject to the mathematical constraints outlined here (Fig. 1) and are likely not reflective of 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]. Determining precisely how such biases affect functional diversity metrics is an important next step in diversity research. With respect to Stuart-Smith et al.'s results, although much has been made of the 'new hotspots of functional diversity' for marine fishes [18], we note 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 the 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 to 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 prioritisation schemes.

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