The potential of trait-based approaches to contribute to marine conservation

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The value of diversity metrics to represent ecological communities and inform broad-scale conservation objectives and policy has often been subject to debate and uncertainty[1,2]. In practice, diversity metrics are important in setting management and conservation priorities, just as economic indices contribute to global monetary and financial policies. Thus, key challenges for ecologists are to identify new ways to view and summarise patterns in biodiversity and improve on the metrics available for management purposes. In a recent paper on functional diversity patterns in reef fishes[3], we highlighted the potential of new insights gained from functional trait-based approaches to inform marine management, stressing the need to develop and refine biodiversity measures that are linked to ecology (rather than taxonomy). We used a unique, fisheries-independent reef fish identity and abundance dataset, collected using standardised methods from equatorial to high latitude regions all over the world, to provide the first global view of the distribution of individuals amongst species (including a measure of evenness) and functional traits amongst marine communities. A recent paper by Robinson et al.[4] published in *Marine Policy* criticised the use of our evenness index as a measure of biodiversity, and questioned the use of functional trait-based metrics derived from surveys of standardised areas for decisions relating to broad-scale management of marine systems. In this paper we respond to Robinson et al. and rebut their claims related to sampling bias and broad-scale applicability of trait-based approaches.

Firstly, we agree with the point of Robinson et al. that the use of evenness as a measure of diversity is of limited value for prioritisation of conservation efforts, and this was not implied in our paper. Rather, as we outline below, the evenness patterns were presented to provide context to assist with interpreting functional diversity patterns, and we maintain that detailed exploration of these patterns will provide valuable ecological insight. We also agree with Robinson et al. that reliance on particular individual diversity metrics for global conservation prioritisation is unwise, regardless of whether taxonomic or trait-based. Nevertheless, the services provided by functioning ecosystems represent one of several central motivations for conserving them. Thus we reiterate our conservation-related conclusions from our paper that metrics based on functional traits can provide an important additional input into management for conservation, bearing in mind that they complement rather than replace other approaches. Our paper contributes to the emerging body of research needed to develop and refine such approaches for marine systems.

The simulations provided by Robinson et al.[4] summarised several characteristics of evenness measures, including the one we used (the inverse Simpson diversity index divided by species richness), noting that they are inherently dependent on species richness (S) and total abundance (N). These properties are well-known; in fact, one co-author, amongst others, published a paper over thirty years ago in which he highlighted mathematical artefacts associated with sample size for some evenness measures[5]. As stated above, the inclusion of an evenness measure in our results was not intended to inform primary conclusions or conservation decisions, but to provide context to the abundance-related aspects of functional diversity. We used a common calculation for evenness, which was recommended in the most recent review of the subject[6], to portray spatial patterns in species dominance that are, by definition, intimately associated with local richness. Thus, communities typical of tropical latitudes with a few highly abundant species and many rare species were scored, at the scale of our 500 m^2 transects, as being less even than communities with fewer

species and a more similar distribution of individuals amongst those species – a result which is both intuitive and in line with the extensive collective field experience of the authorship team.

The trends shown by the simulations in Robinson et al. are certainly valid and long-known, in their most general form, but were exaggerated by the inclusion of impossible scenarios in their Figure 1 where the number of species exceeded the number of individuals (the upper lines and any situation where S > N should have been excluded from their simulations). But more importantly, beyond demonstrating mathematical relationships between diversity metrics, these simulations provide little useful inference for real world situations due to a critical assumption: that the species abundance distribution (SAD) shape is universally consistent (i.e. across all latitudes, regions, assemblages). Although they tried different SAD shapes in different sets of simulations, Robinson et al. held the SAD shape constant within each set of simulations (e.g., the log-normal was presented in their Figure 1).

Numerous hypotheses have been proposed to relate differences in local SAD shape to factors such as habitat, regional richness, productivity, phylogenetic background of species present, and importantly, spatial scale (many well discussed by McGill, et al. [7]). While most of these potential relationships are yet to be empirically tested, it has long been known that tropical communities typically contain disproportionately more rare species and more curvilinear SADs (when ranked abundances are expressed logarithmically) than do temperate communities[8].

While the general 'hollow curve' of the SAD is said to be a universal phenomenon (and is responsible for the simulation results of Robinson et al.), variation in the form of SAD observed locally is what prompted McGill et al. to urge ecologists to 'move beyond treating the SAD in isolation and to integrate the SAD into its ecological context'. Clearly, such patterns are of great interest to ecologists, including recent investigations that link species rarity to uncommon sets of traits[9]. Further research is certainly needed that integrates theory and broad-scale empirical data to assess where (and why) predictable differences occur in the finer-scale structure of SADs, and beyond that, what the ecological consequences of this are. But for now, assuming a universally constant form of SAD forms a poor basis for assessing the behaviour of locally-derived field estimates of any diversity metric.

Following their criticism of the evenness measure, Robinson et al. went much further in also suggesting that global patterns described in our paper are flawed due to poor detectability of fishes in temperate zones (and thus underestimated species richness in these areas). They provided no clear evidence to support this conjecture.

(1) First, they attempted to compare species richness estimates from temperate regions in our study with those from other studies in the same or similar regions. The studies they drew comparison with mostly described species richness at different scales to that reported in our study (which was standardised within 500 m^2 transects, as a measure of local, or alpha, diversity), making comparison difficult. For example, one study they cited described accumulated richness of fishes from the coast to the continental shelf margin of South Africa in 52 km blocks[10]. It is not possible to compare species richness from this with our study - not only was it at a much coarser spatial resolution than in our study, but it also encompassed a much broader range of depths and habitats. Further, it was based on overlaid distribution maps of species (rather than point observations), an approach known to overestimate local species richness at any site within the region[11], as species do not occur

at every site within their range. The only references cited by Robinson et al. from which local richness estimates per unit area can be roughly compared to those reported in our study actually support our results, rather than suggesting numerous species were missed in our surveys of these regions, and were studies by authors who contributed to our dataset for these regions[12,13].

(2) In recognising biases associated with visual census methods, Robinson et al. also claimed that video survey methods in the same areas 'vault' temperate richness values above those we reported. In contrast to this claim, rigorous comparisons have suggested that video methods tend to underestimate richness in comparison to visual census[14] by missing more small and cryptic species[15] or through poorer coverage of non-carnivorous species (in the case of baited video[14]). This tendency is confirmed by comparing the total number of species recorded in the video study Robinson et al. cited[16] (total 54 species from three video methods, 18,000 m^2 surveyed) to the visual census data used in our study from the same southwest Australian region (78 species, 12,000 m^2) (in the same habitat type and presumably similar depths). In our paper we acknowledged known biases in visual census methodology, which are common to all census methods, but argue that no other type of method for estimating local fish species richness, short of destructive sampling, would provide a less biased assessment of global reef fish richness patterns.

Rather, the claims of Robinson et al. seem instead to reflect a lack of understanding of true patterns in local species richness and fish density on high latitude reefs. Should one expect all well-sampled communities to sit above the 'threshold' of 10-40 species that their simulations identify? A study in southern Chile (not referenced by Robinson et al.) which used a combination of visual and capture sampling methods and covered a range of depths over four seasonal surveys of two weeks each (including 240 hours of SCUBA effort), accumulated a total of 18 fish species[17]. Whether this would surpass the richness 'threshold' suggested by Robinson et al. would depend on the local form of the SAD. The richness within a single transect in this location on a single occasion will of course be much lower and less likely to reach the threshold, even if every species present was sighted (i.e. zero influence of detectability). We suggest that this threshold will not be reached on reefs without surveying increasingly larger areas of reef with distance from the equator. It is in fact likely impossible for some fish communities associated with rocky reefs at high latitudes to reach such a threshold within an area that is logistically possible to sample. Rather than being driven by methodological biases, the evenness patterns questioned by Robinson et al. simply highlight the stark differences in densities of fish species and individuals from tropical and temperate marine systems in nature.

Importantly, comparison of our global maps of evenness and functional diversity clearly shows that the major functional diversity hotspots, and thus our primary conclusions[3], were not biased towards regions with highest evenness or lowest richness. Surveys with <3 species were omitted from predictive modelling, and predicted functional diversity hotspots occur at mid- to low latitudes with moderate richness. They are thus not invalidated by richness constraints on evenness, nor by methodological bias that affects local richness (as discussed above). We agree with Robinson et al. that a lack of data from the Benguela and Humboldt systems requires further study, as do other unsurveyed regions. Our maps represent predictive hypotheses that align well with current

knowledge. Major gaps in the global distribution of survey effort clearly represent priorities for investigation, with new data allowing predictions to be refined through the future.

Finally, by suggesting that functional traits are system-specific and cannot be fairly compared across large scales, Robinson et al. have apparently missed one of the key advantages of trait-based approaches: while species themselves differ between regions and can only be compared in traditional taxonomic measures when considered as equal units, many ecologically-relevant characteristics of species can be directly compared across large-scales and assemblage types, and can ultimately prove extremely informative. There are many considerations associated with the selection of traits that have been discussed elsewhere[18], but an important consideration in this context, as in our study, is that traits chosen should not be geographically-constrained, in the sense that any value should be conceivably possible for species at any site. Much more work still needs to be done, however, to determine which traits are the most informative for particular ecosystem functions and community types, and in relation to particular threats to biodiversity.

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