

The use of taxonomic relationships among species in applied ecological research: Baseline, steps forward and future challenges

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Abstract Taxonomy is more than a mere exercise of nomenclature and classification of biological diversity: it profiles the identity of species by investigating their biological and ecological traits. Taxonomy is intimately related to ecology which, in turn, cannot be a mere exercise in describing ecological patterns, but instead requires deep knowledge of species' biological structures, roles, interactions and functions. Thus, the study of taxonomic and phylogenetic relatedness of species is of paramount importance in ecological research, enabling insights into potential evolutionary patterns and processes, allowing a more comprehensive view of biodiversity, and providing opportunities to improve the assessment and monitoring of ecological changes in time and space. The work of K. Robert ('Bob') Clarke forged new pathways in this direction, providing new ideas and statistical tools to include and exploit taxonomic relationships in applied marine ecological studies and beyond, also inspiring the next generation of ecologists. In this short review, we synthesise the application and development of these tools and concepts in marine biodiversity research over the last three decades and suggest future pathways in this evolving field.

Key words: marine biodiversity, species richness estimators, taxonomic distinctness, taxonomic sufficiency.

INTRODUCTION

The initial fundamental contribution of taxonomy and systematics to ecology was to name and classify units of living organisms, allowing ecologists critically to identify the objects of their research. For many years, taxonomy has been viewed as nothing more than an instrumental tool for ecological studies (Wilson 2004; Agnarsson & Kuntner 2007), largely overlooking the potential relevance of taxonomic relationships among species for achieving an understanding of the evolutionary and functional diversity of living organisms (Hooper *et al.* 2005; Wiens & Graham 2005). This led ecologists interested in biological diversity to focus almost exclusively on species richness and evenness (relative abundance) and on the ways in which natural and anthropogenic drivers could affect these metrics. As the human footprint on the planet has become greater and more intense, there has been an increased awareness that both natural factors and human activities can affect biodiversity beyond changes in the number of species or their

relative densities. This highlighted the need for a deeper understanding of species' responses to anthropogenic stressors, including changes in gene expression, metabolic pathways and physiological mechanisms (Gotelli *et al.* 2012; Jones *et al.* 2013), and a more comprehensive integrated assessment of human impacts and conservation measures on taxonomic, phylogenetic and functional diversity (Kim & Byrne 2006; Devictor *et al.* 2010; Mazel *et al.* 2018).

Taxonomic relatedness of species was first considered relevant in conservation studies as an aid to preserving evolutionary diversity (Faith 1992). However, as the effects of human activities can affect whole taxonomic groups of species (Warwick 1988a; Ferraro & Cole 1990), the assessment of changes in the structure of the taxonomic tree defined by a given community gained interest, as this can provide a deeper understanding of how human activities impact biodiversity in a broader sense. Moreover, increasing anthropogenic pressures on ecosystems worldwide require rapid and cost-effective monitoring and impact assessment, to enable timely responses to crucial environmental issues. A major difficulty in quantifying community patterns stems from the need to identify individual organisms as belonging to a

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specific taxon; species-level analysis is time-consuming and requires a high degree of taxonomic expertise, which is not always easily available (Wheeler 2004; Ebach 2011). This is particularly so for certain groups of organisms, such as invertebrates, and particularly in marine environments, where biodiversity is largely unknown and many taxa formally remain undescribed or are difficult to identify. The potential link between the taxonomic relatedness of species and their ecological similarity can help to ameliorate this problem. For example, the use of taxonomic levels higher than species (e.g. identifications to genera or families) in multivariate community analysis can be sufficient and effective in routine monitoring and impact assessment (Warwick 1993).

The statistical methodological developments of K. Robert Clarke, particularly as they embody also the biological and ecological intuitions of close colleagues and collaborators, such as Richard Warwick, led to pioneering concepts using taxonomic (or phylogenetic) relatedness in applied marine ecological research and beyond. These developments included descriptions of novel biodiversity indices (Warwick & Clarke 1995, 1998; Clarke & Warwick 1998a, 2001; Clarke *et al.* 2006), provision of dedicated software (Clarke & Gorley 2015) and a broad range of applied studies that either use or investigate the use of taxonomic surrogates for species (Bayne *et al.* 1988; Gray *et al.* 1990; Warwick & Clarke 1993; Somerfield & Clarke 1995; Olsgard *et al.* 1997, 1998; Olsgard & Somerfield 2000; Tweedley *et al.* 2014). Here, we summarise methods exploiting taxonomic relatedness in applied ecological research, the salient scientific messages arising from their use and innovative applications of these concepts to improve biodiversity monitoring and assessment.

INTEGRATING TAXONOMIC HIERARCHIES INTO DIVERSITY METRICS: TAXONOMIC DISTINCTNESS INDICES

Most classical diversity indices, such as Shannon–Wiener diversity (H') or Pielou's evenness (J'), are designed to measure only two aspects of diversity – the number of species and the distribution of their relative abundances. Generally, the greater the number of species and the more evenly individual abundances are distributed among those species, the higher the value of these classical diversity metrics. However, taxonomic relatedness among species is of basic importance in quantifying the diversity of communities, as it incorporates additional information on the evolutionary diversification of the taxa involved and, potentially, on the ecological coherence of groups of species. For example, a community

comprised of closely related species (e.g. congeners) can be considered less diverse than a community comprised of an equal number of species that are more distantly related (e.g. from different genera or families). To capture and quantify this aspect of diversity, Warwick and Clarke (1995) proposed two new indices, termed *Taxonomic Diversity* (Δ) and *Taxonomic Distinctness* (Δ^*). In addition to information on the presence of taxa in samples, and their abundances, these measures require information on the relative distances among taxa. These distances may be defined in numerous ways, for example using taxonomic, functional-trait, genetic or phylogenetic distances, but for ease of explanation and availability of information Warwick and Clarke (1995) used distances among taxa traced through a tree representing the Linnaean classification. Specifically, Δ measures the average taxonomic distance between all pairs of individuals in the community, whereas Δ^* measures this average taxonomic distance using only individuals belonging to different species.

It is important to note that these measures do not necessarily require a tree for their calculation; they only require values for inter-species distances. In the classical application of these measures, based on Linnaean taxonomic relationships, inter-species distances are calculated as path-lengths linking individuals or species through a Linnaean hierarchical tree, typically with a fixed distance assigned to differences between each taxonomic level (species to genus, genus to family, etc.) scaled so the longest distance is set to 100 (Clarke & Warwick 1999).

When a phylogenetic rather than a taxonomic tree is used, pairwise inter-species distances can be calculated, similarly, as the branch-length through the phylogenetic tree between each pair of species. However, both phylogenetic and taxonomic relationships, as described by a tree structure, may be thought of as rather rough measures of inter-species distance. Indeed, the trees themselves have been constructed typically by applying clustering algorithms or probabilistic evolutionary models to some more direct underlying measure of inter-species relationships. For example, a phylogenetic tree might be built from a genetic distance matrix between every pair of species calculated from nucleotide sequences or allelic structures, while a taxonomic tree might be constructed based on similarities in meristic structures, physiological adaptations or morphological features. Whenever fundamental (and arguably more direct) standardised measures of inter-species distance are available, they can be readily used to calculate distinctness indices (e.g. in PRIMER version 7), thus avoiding the need for any separate tree-building step. Given that a hierarchical tree is often a very poor representation of underlying multivariate distance relationships among objects (Clarke *et al.* 2016), being able to avoid a

'tree-construction' step will reduce this additional source of uncertainty in the resulting biodiversity measures. This feature distinguishes the biodiversity indices proposed by Clarke and Warwick (1998a, 1999, 2001) from other measures that have been designed to account for species' inter-relatedness. For example, phylogenetic diversity (PD; Faith 1992), 'the total branch-length in the tree linking taxa in a sample' is clearly, by definition, a tree-based measure. Furthermore, adding or removing species will also add or remove branches to the tree, so PD is not independent of the number of species in a sample. Warwick & Clarke (1995) successfully sidestepped this issue by using average inter-species distances. Thus, not only do their distinctness indices not necessarily require a tree, *per se*, for their definition or calculation, they are also independent of species richness (Clarke & Warwick 1998a). We hasten to add, however, that phylogenetic models (and the trees arising from them) do focus conceptually and explicitly on proposed evolutionary pathways through time (e.g. typically including both genetic and explicit fossil evidence and validation), whereas taxonomic cladistics may consider a broader array of characteristics (morphological, behavioural, physiological, life-history strategies, etc.), which may or may not reflect tree-like evolutionary pathways.

If the abundances of species are not considered (i.e. if the data set is reduced to presence/absence of individual species), then Δ and Δ^* both converge to the same metric, namely *Average Taxonomic Distinctness* (Δ^+ , Clarke & Warwick 1998a). Average taxonomic distinctness is the average taxonomic distance among all species in the community. Although Δ^+ indicates the taxonomic breadth of a given community, it does not tell us anything about the distribution of path-lengths themselves. Hence, Clarke and Warwick (2001) proposed a further diversity index, *Variation in Taxonomic Distinctness* (Λ^+), which captures the idea of how variable the taxonomic distances are, reflecting the degree of evenness in the distribution of species among higher-level taxa. Interestingly, this measure (Λ^+) is structurally independent of the average taxonomic distance (Δ^+). Higher values of Λ^+ denote uneven taxonomic distances among species within the community (e.g. some very small path-lengths and some very large path-lengths). This can occur in extreme environments (e.g. the deep sea; see Zintzen *et al.* 2011) where there is strong environmental filtering, resulting in 'clusters of specialists' that co-exist with other such clusters that are distantly related. The species within each cluster contribute short path-lengths, while the species belonging to different clusters contribute long path-lengths, yielding a high variance in path lengths overall (Λ^+).

Beyond the advance of integrating taxonomic relatedness (or other measures of relatedness) into the

calculation of diversity metrics, this family of indices, and especially Δ^+ and Λ^+ , also possess a number of desirable statistical properties, including being independent of sample size and sampling effort (Clarke & Warwick 1998a; Warwick & Clarke 2001; Leonard *et al.* 2006; Bevilacqua *et al.* 2009; Wang *et al.* 2019). They are also applicable in different environmental settings, for different groups of taxa and habitats.

We searched the Web of Science Core collection, from 1995 to the present, for papers including 'taxonomic distinctness' in the *Topic* field and found 823 papers, 504 of them reporting the direct use of taxonomic distinctness indices in ecological research. Although we recognise this set of records cannot be considered an exhaustive collection of the scientific literature on taxonomic distinctness indices, it can serve as a representative sample of their range of application in different research fields. Taxonomic distinctness indices are still primarily used in analyses of marine assemblages, although a number of studies have been carried out in terrestrial and freshwater environments (Fig. 1). Whether on land, in rivers, in lakes, in seas or in oceans, the use of taxonomic distinctness indices has focused predominantly on invertebrate assemblages (e.g. Tweedley *et al.* 2012; Heino *et al.* 2015), followed by vertebrates, including mammals (Munian *et al.* 2020), birds (Guerrero *et al.* 2011), amphibians and reptiles (Leyte-Manrique *et al.* 2019) in terrestrial systems, and mostly fish in aquatic systems (Tolimieri & Anderson 2010; Anderson *et al.* 2013; Smith *et al.* 2014; Fig. 1). In aquatic systems, measures of biodiversity for macroalgae and macrophytes accounted for a relatively small fraction of studies, but on land, plant studies were about a quarter of the total; the application of taxonomic distinctness indices to other groups of organisms (e.g. fungi, protists, microalgae) was fairly limited in all environments (Fig. 1).

In the marine realm, these indices have been applied to case studies in almost all geographic areas (Fig. 1), ranging from the poles (Somerfield *et al.* 2006; Brandt *et al.* 2016) to the tropics (Graham *et al.* 2006) and to explore diversity patterns across a wide range of marine habitats, from estuaries (Tweedley *et al.* 2012) to intertidal areas (Iken *et al.* 2010), continental shelves (Renaud *et al.* 2009; Warwick & Somerfield 2015) to open oceans (Woodd-Walker *et al.* 2002) and in the deep sea (Zintzen *et al.* 2011). Initially, these indices were primarily proposed as new, and more effective, metrics to be applied in environmental impact assessment (Warwick & Clarke 1998, 2001). By comparison with classical diversity indices, taxonomic distinctness indices should be less influenced by sampling effort and natural variability (in the form of seasonal variations, natural perturbations or differing habitat features) and therefore should be more sensitive to human-

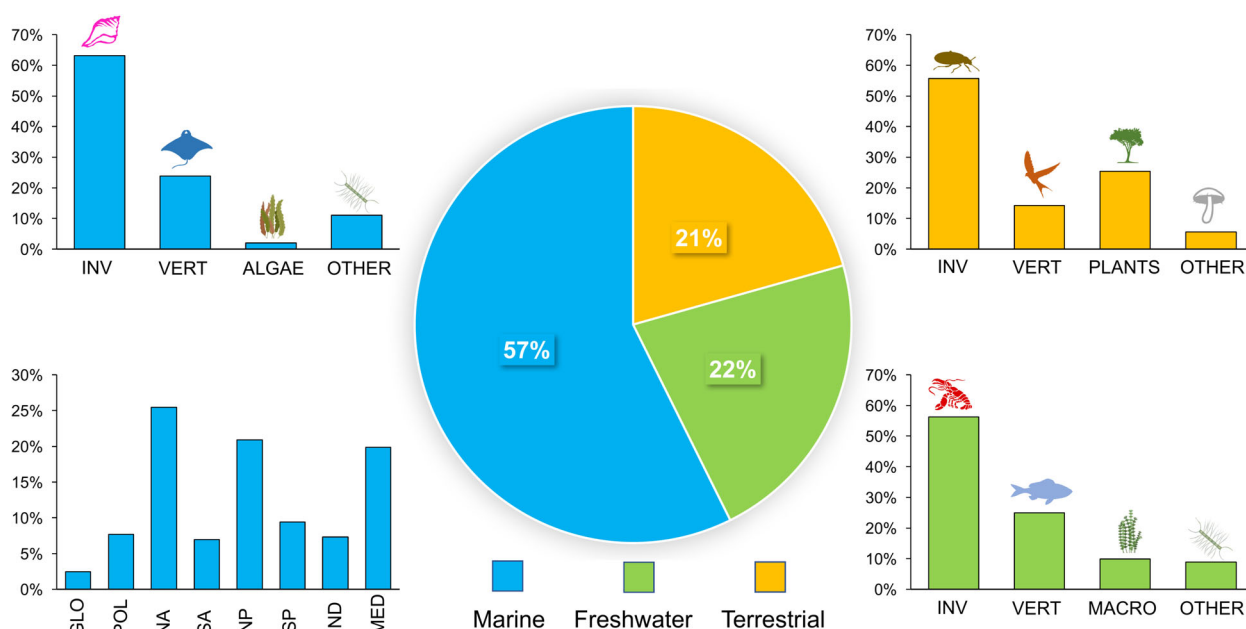


Fig. 1. Percentage of studies on taxonomic distinctness indices for terrestrial, marine and freshwater ecosystems. Bar plots show the application of indices on different organisms, expressed as % of studies on the total of each realm. For marine studies, the % of studies is also reported for five main geographic areas. GLO, global scale; IND, Indian Ocean; INV, invertebrates; MACRO, macrophytes; MED, Mediterranean and Black Sea; NA, North Atlantic; NP, North Pacific; OTHER, protists, bacteria, microalgae, fungi; POL, polar regions; SA, South Atlantic; SP, South Pacific; VERT, vertebrates.

driven impacts on diversity (Warwick & Clarke 1998). The assumption underlying the effectiveness of taxonomic distinctness in impact assessment is that the effects of human disturbance could well manifest at taxonomic levels higher than species by favouring closely related hardy or pollution-tolerant taxa, while removing more sensitive groups (Warwick & Clarke 2001; Helmus *et al.* 2009). In contrast, natural variations mostly occur as replacements of species within taxa that can perform similar ecological roles within the community (Ferraro & Cole 1990; Warwick 1993). Furthermore, the non-dependence of Δ^+ and Λ^+ on sample size means that one can test the null hypothesis (a neutral model) that a given site has a community (a list of species) possessing a taxonomic structure that is consistent with regional (or broad-scale) expectations. This can be done by comparing observed values of Δ^+ (and/or Λ^+) with the distribution of values obtained by taking random draws of species from a regional species pool, either selecting species with equal probability (Clarke & Warwick 1998a) or conditioning the probability of selection of species on their frequency of occurrence (Somerfield *et al.* 2008).

Building on previous work, Warwick *et al.* (2002) considered decreases in Δ^+ and increases in Λ^+ as evidence of deleterious changes in community condition, so assemblages at impacted sites should be composed of species that are more closely related to

one another (i.e. having lower Δ^+) than expected (Clarke & Warwick 1998a) and which could occur in isolated, uneven clusters (i.e. having higher Moreno *et al.* 2009; Xu *et al.* 2012) than would be expected given the regional species list. Research indicates a higher sensitivity of taxonomic distinctness indices to anthropogenic disturbance compared to classical diversity indices (Somerfield *et al.* 1997; Leonard *et al.* 2006; Victorsson & Jonsell 2016; Li *et al.* 2020), although several studies have shown conflicting results (Munari *et al.* 2009; Ware *et al.* 2009; Bevilacqua *et al.* 2012a).

There are many potential reasons for contrasting outcomes. First, the assumption that human impacts result in the persistence of closely related species implies that taxonomic (or phylogenetic) relationships underlie consistent ecological responses to environmental perturbations of species within taxa. This may not be true or may be true only for some lineages (Losos 2008; Crisp & Cook 2012). Second, perhaps some types of human disturbance do not result in drastic changes to taxonomic structures of communities; taxonomic distinctness indices might be less sensitive than classical univariate abundance measures of individual species for more moderate or subtle impacts (Salas *et al.* 2006). Third, some types of disturbance effectively remove species at random, which would clearly affect species richness but would have no appreciable effect on taxonomic distinctness

(Birkhofer *et al.* 2015). Finally, natural environmental variation or perturbations could lead to increases or decreases in taxonomic distinctness, which would reduce the effectiveness of these indices to detect anthropogenic impacts (Yang *et al.* 2016; Ronowicz *et al.* 2018).

Another critical issue here is the reference taxonomic list used in hypothesis tests in which the taxonomic distances among species is calculated under neutral models (Warwick & Somerfield 2008; Somerfield *et al.* 2009). The reference list forms part of the hypothesis being tested. If the list is too narrow, the ability of the indices to discriminate impacted conditions will be hampered, as the reference list may not adequately represent the taxonomic breadth of the broader community of interest (Warwick & Clarke 1998; Bates *et al.* 2005). This could occur, for example, when the study has low spatio-temporal replication and the reference list is built only upon the list of species found within the study itself. Under these circumstances, a test based on taxonomic distinctness indices may not be informative, unless additional species inventories are available for the study area and community of interest. However, the reference list should be carefully calibrated according to the target of the study. A single group of organisms (e.g. a single phylum), or even whole communities, may exhibit values of taxonomic distinctness which are naturally lower than random expectations in specific geographic regions or habitats, irrespective of potential effects of human disturbance (Somerfield *et al.* 2009; Bevilacqua *et al.* 2011). If the reference list includes species from areas outside the region or habitat of interest, then there is a risk that observed departures from expectations may be caused by biogeographic or habitat specificity of samples rather than being caused by anthropogenic impacts. Furthermore, it is possible that a test based on a single group of organisms (e.g. a single phylum) may be more sensitive to, or deliver different results than, one using all the taxa in samples, combining many phyla (Somerfield *et al.* 2009). Of course, if the test is based on frequencies of occurrence in a reference set of samples (Somerfield *et al.* 2008), then whether or not species in the reference list contribute to the hypothesis is more constrained, and the hypothesis more focused.

Although taxonomic distinctness indices were originally conceived for application in environmental impact assessment, less than one third of the studies in the literature use them in this context. These indices, and especially Δ^+ and Λ^+ , provide extraordinary flexibility to investigate much more general and wide-ranging biodiversity questions across multiple realms and different groups of organisms, allowing formal analysis of diversity patterns even when other routine statistical tools are not applicable. For

example, they can be used on historical presence/absence data, potentially making use of regional species lists from museum records (presence only), or of data collected using different sampling methods and/or efforts (Table 1). The use of these indices also extends well beyond the boundaries of ecology into even very distant research fields, including cancer diagnostics (de Sampaio *et al.* 2018), energy planning (Delgado *et al.* 2013) and media networking (Elejalde *et al.* 2018), showing that their potential and scope for providing novel insights in a wide class of research problems is still far from being fully realised.

TAXONOMIC SURROGATES FOR SPECIES IN ENVIRONMENTAL IMPACT ASSESSMENT AND MONITORING

Clarke and Warwick (1998b) demonstrated a high degree of functional redundancy in marine assemblages. If species within higher-level taxa (e.g. genera and families) are ecologically similar, due to shared evolutionary history, and/or if there is a hierarchical response (from individuals to whole taxa), to increasing levels of anthropogenic disturbance (Warwick 1993; Clarke & Warwick 1998b), one may infer that community-level responses to human impacts can be quantified at taxonomic levels of resolution that are coarser than the species level. Indeed, there are good reasons why effects may be more readily detected at taxonomic levels higher than species (Olsgard *et al.* 1997). This idea is referred to as *taxonomic sufficiency* (Ellis 1985). The essential aim is to identify the level of taxonomic resolution that would be required to detect a given ecological pattern, particularly in the context of studies examining human-driven changes to community structure.

Traditionally, this approach has been used for assessing human impacts on macroinvertebrate assemblages from aquatic environments (e.g. Warwick 1988a,b; Gray *et al.* 1990; Somerfield & Clarke 1995; Olsgard & Somerfield 2000; Terlizzi *et al.* 2003; Anderson *et al.* 2005; Jones 2008), although its application has been attempted in a wide variety of situations where identification of organisms to species level could pose a serious impediment to biodiversity monitoring, including in highly speciose terrestrial ecosystems (Groc *et al.* 2010; Souza *et al.* 2016). A review of the scientific literature, querying the Web of Science Core collection in the last three decades for papers including 'taxonomic sufficiency' or 'taxonomic surrogates' in the *Topic* field, selected 261 papers reporting 367 case studies investigating the effect of reduced taxonomic resolution in replicating ecological patterns. The highest proportion of studies (49%) focused on marine assemblages, followed by freshwater (25%) and terrestrial (26%) ones. One

Table 1. Summary of main fields of application of taxonomic distinctness indices from the scientific literature

Environmental assessment and monitoring	
Local-scale human impacts (Somerfield <i>et al.</i> 1997)	Habitat-dependent changes in biodiversity (Diaz 2012)
Natural disturbance (Ronowicz <i>et al.</i> 2018)	Seasonal changes (Alvarez-Filip <i>et al.</i> 2006)
Indicators of ecological quality (Arvanitidis <i>et al.</i> 2005)	Historical changes in biodiversity (Gravili <i>et al.</i> 2015)
Effect of climate change (Rizvanovic <i>et al.</i> 2019)	Diversity patterns in fossil assemblages (Sun <i>et al.</i> 2020)
Effect of natural extreme events (Sathianandan <i>et al.</i> 2012)	Diversity patterns in death assemblages (Warwick & Light 2002)
Effectiveness of conservation measures (Stobart <i>et al.</i> 2009)	Basic ecology
Assessing restoration success (DeNicola & Stapleton 2016)	Ecological successions (Yang <i>et al.</i> 2016)
Correlating environmental and biological changes (Jiang <i>et al.</i> 2014)	Diet-specificity (Stringell <i>et al.</i> 2016)
Complementing other diversity indices (Barzoki <i>et al.</i> 2020)	Relationships among different aspects of biodiversity (von Eulen & Svesson 2001)
Effects of invasion/extinction (Floerl <i>et al.</i> 2009)	Effects of interspecific interactions (Griffin <i>et al.</i> 2013)
Biodiversity patterns	Biodiversity-productivity relationships (Conlan <i>et al.</i> 2015)
Local to regional patterns of biodiversity (Ellingsen <i>et al.</i> 2005)	Habitat specificity (Bevilacqua <i>et al.</i> 2009)
Spatial-temporal patterns (Barjau-Gonzalez <i>et al.</i> 2012)	Processes of community assembly (Martínez <i>et al.</i> 2019)
Biogeographic patterns of biodiversity (Price <i>et al.</i> 1999)	Parasite–host associations and diversity (Tedesco <i>et al.</i> 2020)
Gradients of biodiversity (Li <i>et al.</i> 2019)	Methods in ecology
Identifying biodiversity hotspots and endemism (Moir <i>et al.</i> 2009)	Effects of sampling procedures (Wang <i>et al.</i> 2019)
Global patterns of biodiversity (Fritz & Rahbek 2012)	Deriving further diversity indices (Somerfield <i>et al.</i> 2008)

reason for the widespread application of this approach is due to the desire for efficiency and cost-savings for long-term routine monitoring programmes. Typically, an initial survey and assessment will be done at the species level with subsequent community assessments being done at a coarser level of taxonomic resolution. This approach helps researchers and practitioners (including citizen scientists) investigate ecological patterns in highly diverse communities or those with organisms that are difficult to identify. By saving time and financial resources, studies can be extended to improve their spatial or temporal replication or extent or to achieve more rapid assessments. Identification of organisms at taxonomic levels that are coarser than species also reduces reliance on taxonomic expertise, which is currently in chronic decline (Wägele *et al.* 2011).

Irrespective of the habitat type, in the majority of cases, family-level identification has been judged as sufficient to discern changes in communities, in response to either natural or human-derived sources of variation, with species-level analysis being strictly necessary in only a few cases (Fig. 2). Notwithstanding evidence supporting the practical effectiveness of taxonomic sufficiency, and its associated advantages, the routine use of coarser levels of taxonomic resolution in ecological studies raises major concerns regarding: (i) the difficulty in attributing ecological meaning to changes observed at high taxonomic levels, (ii) the rigidity of the approach, which presupposes aggregation of species to a specific (coarser) taxonomic level, regardless of their ecological

relevance for the study or their ease of identification, often resulting in an unnecessary loss of detail and (iii) the absence of any formal or transparent procedure for quantifying the probability of failing to detect community patterns when using coarser levels of taxonomic resolution as opposed to using data at the species level (Jones 2008). More importantly, uncertainties remain regarding the mechanisms that may make higher taxonomic levels effective surrogates for species. Ecological similarities among species within higher taxa may be idiosyncratic (e.g. Losos 2008; Carranza *et al.* 2011), so measured responses of a community to anthropogenic stress at different levels of taxonomic resolution may not be correlated (Arvanitidis *et al.* 2009). Instead, closely related species may be no more ecologically coherent than distantly related ones, and the use of higher taxa may simply be equivalent to the use of random groups of species being pooled together that do not necessarily convey consistent ecological signals (Bevilacqua *et al.* 2012b). Indeed, certain evolutionary processes, such as competition or adaptive trait divergence, may lead closely related species to respond in very different ways to environmental change. Thus, grouping species according to a taxonomic hierarchy may not necessarily reflect species-level patterns better than groups of species that might be obtained following some other (any other) proposed aggregation scheme.

We may consider surrogacy from a completely new perspective, abandoning the strict notion of taxonomic sufficiency (Groc *et al.* 2010; Bevilacqua *et al.*

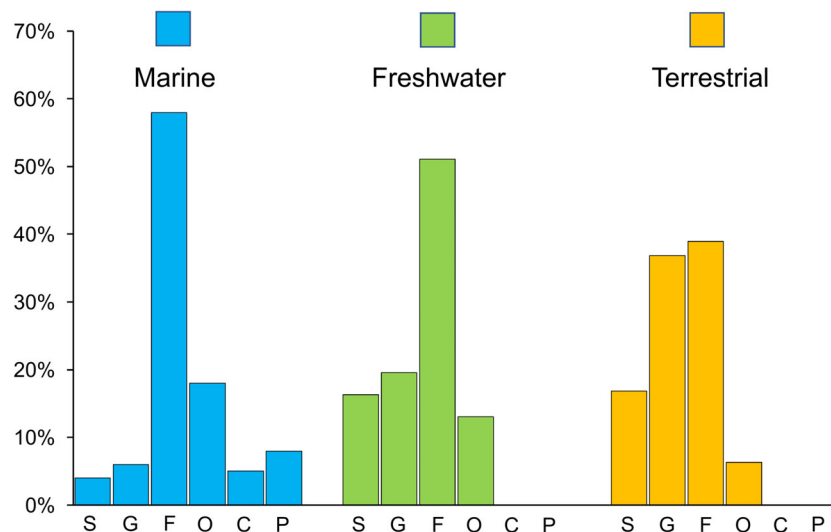


Fig. 2. Percentage of marine, freshwater and terrestrial studies that found a specific taxonomic resolution as sufficient to depict the ecological pattern(s) of interest that were shown at the species level. C, class; F, family; G, genus; O, order; P, phylum; S, species.

2012, 2013; Mueller & Geist 2016). The effectiveness of surrogates in depicting species-level patterns may be understood by considering the nature and the amount of information that is lost when species variables are grouped (and the abundance values within a group summed together) to obtain a smaller number of new aggregate variables. The aggregation (summing) might be done using higher taxa (e.g. genera or families), morphological groups, behavioural groups, functional groups or any other groupings of interest.

We may wish to quantify the degree to which information inherent in the original set of species variables may be lost or ‘compressed’ as a consequence of the aggregation to a smaller set of variables and, therefore, the ability of the new (aggregate) variables to reproduce species-level ecological patterns. The degree of variable compression (or, rather, its inverse) can be expressed as the ratio of the number of aggregate variables to the number of original species variables (ϕ). The greater the compression, the lower this ratio will be. The consistency of retained information post-aggregation may be quantified by Spearman’s rank correlation (ρ) between two similarity matrices: (i) the similarities among samples generated using the full set of original species variables and (ii) the similarities among samples generated using the aggregate variables. As compression increases (i.e. as the ratio value of ϕ decreases), information loss increases and the matrix correlation, ρ , will therefore also decrease, accordingly (Fig. 3). As a consequence, the probability of surrogate variables failing to detect multivariate patterns that may be apparent at the species level will progressively

increase. When the compression of the original variables becomes too great, the information contained in the surrogate matrix will traverse a threshold value (ρ_{\min}) below which the probability of surrogates failing to capture patterns will be higher than a tolerable level, which can be specified *a priori* (β). This threshold (ρ_{\min}) will correspond to the lowest value of ϕ , ϕ_{low} , that may be thought of as the *highest practicable degree of aggregation* of the original variables. This in turn indicates a *minimum* number of surrogates that would be sufficient to reflect species-level patterns consistently under a null model of random aggregate groupings of the species (Fig. 3). The empirical relationship between ϕ and ρ has been documented for real multivariate community datasets, from terrestrial and aquatic ecosystems, and for a variety of types of organisms, including invertebrates, plants, algae and fish (Bevilacqua *et al.* 2012b).

A new framework for species surrogacy, the *best applicable aggregation of species* (BestAgg, Bevilacqua *et al.* 2013), was developed, based on these concepts and observed relationships. In this framework, community patterns of interest in response to a given source of variation (in time or space, or in response to human impacts, etc.) are first quantified at the species level. Then, species are randomly sampled (without replacement) and assigned into larger and larger-sized groups to yield aggregate variables, from which a null model of decreasing information (ρ) *versus* increasing degree of compression (ϕ) may then be constructed (see Fig. 3). More specifically, the number of aggregate variables (G) is progressively decreased in a step-wise fashion, and 1000 random draws are done, with each draw assigning the list of

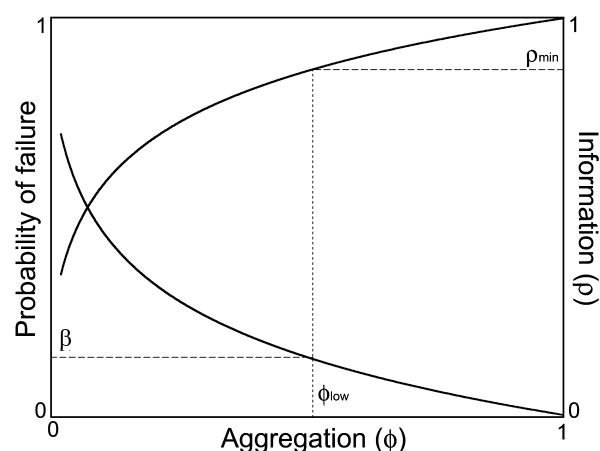


Fig. 3. Theoretical model linking the loss of information (expressed as Spearman's rank correlation, ρ between the original species data matrix and the matrix of aggregate variables) at increasing levels of aggregation (ϕ) to the probability of statistical tests based on aggregate variables (surrogates) failing to detect the effect of a given source of variation (e.g. human impact) that was detected using species-level data (modified from Bevilacqua & Terlizzi 2016)

species (randomly) into the G groups (where also the number of species in each G group is drawn at random) in order to create a random set of G aggregate variables. For each of the 1000 draws performed at a given value of G (which corresponds to a given level of ϕ), the matrix correlation value (ρ) with the original species-level data matrix is calculated. In addition, a dissimilarity-based permutational multivariate analysis of variance (Permanova, Anderson 2001) is performed to test the null hypothesis associated with a term of interest in the study (e.g. the contrast of putatively impacted locations *vs* controls). It is worth noting that the degree of transformation applied to the data prior to calculating resemblance matrices will have a strong influence on the aggregation and final numbers of groups. Assuming the species-level data detects a statistically significant effect for the term of interest, the proportion (out of the 1000 random draws) where the null hypothesis is retained is an empirical measure of the probability surrogacy failure (β). Finally, the maximum allowable degree of compression of the original variables may be set *a priori* as the lowest value of ϕ for which 95% of the statistical tests give results consistent with those obtained using the original dataset at the species level.

The BestAgg procedure aims to identify how far the species-level information can be compressed into a smaller number of (randomly generated) aggregate variables before species-level ecological information of interest is lost. In contrast to taxonomic sufficiency, which only applies to taxonomic groupings,

BestAgg identifies the level of compression that is allowable, regardless of the grouping used. Thus, other types of aggregations (groupings), provided they do not pass this acceptable level of compression, can be utilised by the experimenter (e.g. morphological, functional, taxonomic or even mixtures of different types of groups) that may be appropriate for a particular study. Of course, in any particular context, a researcher may also simply decide *a priori* to use particular surrogate variable(s) according to the particular focus of a given assessment. However, in such cases, (i) the choice of surrogate(s) may be completely subjective, having no particular statistical justification, (ii) the efficacy of the surrogate(s) to detect patterns of interest reliably remains unknown and (iii) the experimenter may not achieve potential gains in cost-effectiveness of assessments. BestAgg can be used to maximise both the ecological relevance and the logistic efficiencies associated with simplified lists of aggregated species groups, while ensuring that genuine species-level information is unlikely to be compromised in the analysis of the community as a whole (Bevilacqua *et al.* 2013).

The approach has been applied in different habitats to different types of organisms in the marine environment (Bevilacqua & Terlizzi 2016), but also in transitional (Bevilacqua *et al.* 2015) and freshwater systems (Milošević *et al.* 2014; Jiang *et al.* 2017). It is more effective than classical taxonomic sufficiency approaches (Jiang *et al.* 2017; Bevilacqua *et al.* 2018a), allowing more information on multivariate patterns to be retained (i.e. yielding a higher value of matrix correlation, ρ), even for a comparable or lower number of surrogate variables (Milošević *et al.* 2014; Bevilacqua & Terlizzi 2016; Jiang *et al.* 2017; Bevilacqua *et al.* 2018a).

Despite the advance in methods and theory underlying species surrogacy, it remains an area of debate, due to potential hidden risks, including the spread of taxonomic minimalism (Beattie & Oliver 1994) in ecological studies (Maurer 2000; Jones 2008). Indeed, far from being useless, zoology, botany and all disciplines with inherent taxonomic and systematic underpinnings, are crucial to inform applied ecology and management decisions. Clearly, studies on biodiversity in a broad sense, particularly regarding underlying mechanisms driving biodiversity changes and the ensuing functional consequences to ecosystems, require detailed taxonomic information and autecology of individual species. To date, we are still far from achieving a deep understanding of how different anthropogenic disturbances interact in affecting species and what the consequences might be on communities and ecosystems (Crain *et al.* 2008), especially in relation to future climate scenarios (Gissi *et al.* 2021). However, ecological responses of single species or even whole communities to

specific types of human disturbances, in some cases, are well-known (e.g. Olsgard *et al.*, 1998). Given the current unprecedented and rapidly accelerating human threats to communities and ecosystems, from local to global scales, responsive environmental management must quickly adapt to optimise and enhance rapid and effective assessments in routine monitoring programmes, including through careful and scientifically validated use of species surrogacy.

It is also important to recognise that the idea of surrogacy (where the sole objective of aggregate variables – or possibly sub-sets of variables, so-called ‘indicator species’ – is effectively to reproduce whole-community species-level multivariate results) is quite distinct from the general notion of aggregation, *per se*. Different kinds of aggregate variables may in fact reflect the researchers’ desire to investigate purposefully entirely different types of hypotheses (e.g. regarding guild structures, trophic positions/feeding types, behaviours, morphologies, dispersal methods and life-history strategies), that may not be expected to give similar results to a direct multivariate analysis of species abundance data. Such hypotheses extend community analysis across a broader swathe of ecological concepts and are clearly useful in their own right.

ENHANCEMENT OF SPECIES RICHNESS ESTIMATES USING TAXONOMIC INFORMATION

Quantification of biodiversity and comparisons of estimated species richness values, through time and across large spatial scales globally, is a pressing imperative in our current world, where species are being lost faster than they are being described (Chapin *et al.* 2000; Pennisi 2019).

Numerical relationships across taxonomic hierarchies offer a unique opportunity to improve our ability to derive reliable estimates of species richness over large spatial scales. For instance, a major issue with estimates of species richness is that, unless the true species richness is known, it is difficult to determine if an estimator is under- or overestimating the actual number of species existing in a given area of interest. The completeness of family-level inventories, in contrast, can be often greater than the completeness of species lists for a given region, and the total number of families can serve as a reference to test the ability of estimators to produce reliable extrapolations (Bevilacqua *et al.* 2018b).

Another problem when estimating species richness in a given region is that it requires a massive effort in terms of sampling and identification of collected organisms. To alleviate this issue, higher taxon richness has been proposed as a proxy for species

richness to quantify biodiversity, especially for mega-diverse groups of organisms (Balmford *et al.* 2000). For example, after intensively sampling a given area, with organisms identified at species level, the ratio of species to genera (or families) can be calculated and used to derive values of species richness in areas where identifications of organisms have been done only at genus or family level, thus saving time and resources (Williams & Gaston 1994). However, this shortcut naturally only provides a rough approximation. The ratio of the number of species to the number of genera, or families, can vary strongly from one place to another and also depends heavily on the sample size and sampling effort, thus limiting the utility of this approach (Gotelli & Colwell 2001).

Terlizzi *et al.* (2014) proposed a more refined procedure to estimate species richness over large areas based on estimates of the species-to-family ratio. Here, the ratio is not calculated directly by simply dividing the number of species observed by the number of families. Instead, the ratio is *estimated* by integrating the semi-log species-accumulation model proposed by Ugland *et al.* (2003) with an analogous model of accumulation of families within the same region. First, an initial representative set of samples from the region of interest is obtained, and organisms are identified to species level. From this, the models are constructed and it is then possible to estimate the species-to-family ratio over the whole area. A sample randomisation procedure is used to determine how many samples need to be identified down to species level in order to obtain a reliable estimate of the species-to-family ratio. Subsequent investigations may be done where the identification of organisms down to the species level is needed only for this minimum required number of samples, with the rest only requiring identification at family level, while still allowing reliable estimates of species richness. The approach led to a reduction in the number of samples required to be identified at species level by 35–50% in a series of case studies estimating species richness of marine molluscs across large areas of the North Atlantic Ocean, Mediterranean Sea and Pacific Ocean.

TAXONOMIC RESEMBLANCE

Many key multivariate analyses of change in marine (and other) ecological communities rely on, as a starting point, the distances or dissimilarities among all pairs of sampling units (e.g. Clarke 1993). In their work on structural redundancy, Clarke and Warwick (1998b) described a measure they called a ‘taxonomic mapping coefficient’ to compare the taxonomic composition of samples by quantifying the average taxonomic distance between species in one sample and species in another sample. Izsak and Price (2001) introduced a similar measure, which

they called 'TD', to study β -diversity. These 'taxonomic dissimilarity' measures, allowing the inclusion of taxonomic (or other inter-species) relationships in the definition of a measure of resemblance between samples, were refined and explained by Clarke *et al.* (2006). The TD measure of Izsak and Price (2001), called Γ^+ by Clarke *et al.* (2006), is a variant of the widely used Bray–Curtis resemblance coefficient, while Clarke and Warwick's (1998b) coefficient, called Θ^+ by Clarke *et al.* (2006), is a variant of the well-known Kulczynski coefficient.

Other resemblance measures that incorporate inter-variable relationships exist, including the widely used Unifrac coefficient (Lozupone *et al.* 2007) and its variants, which are used particularly in microbial studies where the identities of biological variables in a sample may be unknown, but distances among them may be inferred from their genetic DNA sequence information. These measures, such as the within-sample measure PD (Faith 1992), are explicitly defined using a tree or a hierarchy which, for reasons discussed above in the section on taxonomic distinctness indices, may not be as sensible as simply using the distance information that may be available directly in a species-by-species matrix.

Taxonomic dissimilarity, Γ^+ (gamma+), was defined as the mean of all taxonomic distances between each species in one sample and its closest relation in the other sample and vice versa (Clarke *et al.* 2006). Thus, the dissimilarity between two samples having no (or few) species in common, can not only be calculated using Γ^+ , but will indeed reflect, in a biologically meaningful way, the underlying inter-species relationships captured by taxonomic structures. The Γ^+ measure has also been readily adapted to accommodate phylogenetic or functional inter-relationships among species as well, particularly to study turnover (beta diversity) along environmental gradients (e.g. Swenson *et al.* 2011, 2012; Brandt *et al.* 2016; Myers *et al.* 2021, *this issue*) or between different habitats (Bevilacqua *et al.* 2012c). Other contexts where Γ^+ may be useful include situations where the species names or the level of taxonomic expertise has changed over time within a given study (e.g. Clarke *et al.* 2006). It can also be useful for studies conducted at very large spatial scales, where samples from distant locations may have no species in common at all. In such cases, taxonomic resemblance will still provide a biologically meaningful way of calculating distant inter-sample relationships.

FINAL REMARKS: TAXONOMY AND ECOLOGY UNITED IN FUTURE DIRECTIONS

We conclude by stressing the need for close interactions between taxonomists and ecologists to solve

urgent ecological and environmental issues, with a mutual reciprocal appreciation and valorisation of expertise. The following points may assist researchers from different fields to achieve a unified approach:

- Understanding how the structural patterns of biodiversity of natural systems can change in relation to anthropogenic pressures is an ecological challenge that must be supported by taxonomists (Wheeler *et al.* 2004), who deal most closely with a crucial fundamental element of biodiversity: the species.
- Biodiversity certainly can be measured using units other than species (e.g. higher taxa, DNA profiles, morphospecies and OTUs). Rapid genetic sequencing and environmental DNA (eDNA) methods, in particular, may provide helpful new tools to explore and assess the biological diversity of ecosystems, if implemented with due caution and ground-truthing (e.g. Cristescu & Hebert 2018). Modern approaches should not be seen as a threat to classical taxonomy but, rather, as complementary tools, which may be, in some situations, crucial for ecological assessments.
- Alternative methods for quantifying biodiversity should not be used as a justification for dismissing taxonomy.
- The work of taxonomists, which is not merely to identify and name individual species, but embraces structural morphology, life-history strategies, biological and functional traits, evolutionary relationships, methods of feeding, locomotion, reproduction, development – indeed, the biological organism's entire 'way of life', is indispensable in the study of natural systems.
- The use of instrumental variables necessarily places limits on the ecological relevance of potential hypotheses that can be examined in natural systems, particularly regarding causal mechanisms that may drive changes in biodiversity (Boero 2010). Determining a lower bound on the number of aggregate variables to which species-level variables may be reduced without resulting in an unacceptable loss of information may be a way to ensure efficient surrogacy can still serve a useful purpose in monitoring.
- Performing multivariate analyses of aggregate variables that are *not* designed to be surrogates, but rather emphasise functional, morphological, behavioural, trophic or other types of species groups with interpretable ecological relevance, certainly may not mirror the patterns seen in analyses based on multi-species abundances, but rather can enhance and broaden our overall understanding of community-level responses in ecological systems.
- Analyses of communities in ecological systems should seek to incorporate the greatest amount of

information currently available to practicing scientists. Ongoing development of, and investment in, global online repositories containing accessible data on traits, spatial distributions, biogeographic history and genetic structures at broad scales (such as Dryad, the Ocean Biogeographic Information System (OBIS), and the Global Biodiversity Information Facility (GBIF), to name but a few), must be further enhanced and drawn upon by researchers to advance our collective ecological knowledge of species and their responses to a changing world.

The ground-breaking work of K. Robert Clarke and colleagues, to incorporate and exploit taxonomic (or phylogenetic or functional) relationships among species to advantage in ecological studies (Clarke & Warwick 1998a; Clarke & Warwick 2001; Clarke *et al.* 2006), provides an exemplar for future ongoing innovations through data integration. The past decade, in particular, has seen a steady rise in the development of novel statistical methods and approaches for incorporating not only taxonomic and phylogenetic information, but also functional, trophic and evolutionary relationships among species in ecological data analysis (e.g. Ovaskainen *et al.* 2017; Pavoine *et al.* 2017; ter Braak 2019). An important future challenge will be to follow Bob's lead and establish excellent inter-disciplinary networks among statisticians, ecologists, biologists, geneticists and taxonomists. We consider this to be the best way to ensure that newly proposed statistical methods will have genuine relevance and a grounding in biological and ecological knowledge regarding what species are actually like, what they actually do, how they respond to changes and how they function in natural environments.

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AUTHOR CONTRIBUTIONS

Stanislao Bevilacqua: Conceptualization (equal); Investigation (lead); Writing-original draft (equal); Writing-review & editing (equal). **Marti J. Anderson:** Conceptualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Karl Ugland:** Conceptualization (equal). **Paul J. Somerfield:** Conceptualization (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Antonio Terlizzi:** Conceptualization (equal); Writing-original draft (supporting); Writing-review & editing (supporting).

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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