



Taxonomic sufficiency in a live–dead agreement study in a tropical setting



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ABSTRACT

Community studies in paleontological research often rely on identification at taxonomic levels higher than species (mainly genus or family). Several studies have been conducted on paleo- and modern communities to identify the higher level of taxonomic identification that still depicts ecological patterns: genus- and, to a lesser extent, family-level identification are frequently sufficient. The use of higher taxonomic levels has not yet been explored in the context of studies comparing living and death assemblages (so-called “live–dead agreement studies”), notwithstanding their interest to quantify the fidelity of the fossil record and for environmental assessment. We conducted such exploration in a highly diverse tropical marine setting, targeting shelled molluscs. Our results suggest that the common practice of genus-level identification of paleontological samples allows for a proper reconstruction of the original biological community (e.g., variation in richness, ecological or taxonomic similarity) at the species level because (1) fidelity at the species and genus levels is very similar and (2) genera are sufficient to characterize between-habitat differences in composition and diversity. Live–dead agreement becomes even better at family and higher taxonomic levels for some metrics, but between-habitat differences in composition become weaker above the family level. However, at the genus and family levels, between-habitat differences are equally strong as at the species level. Genus-level identification may provide more robust results when one of the assemblages is dominated by a single species, because differences in abundance can be compensated by co-generic species. Moreover, in death and fossil assemblages, diagnostic characters get lost easily because of taphonomic processes such as abrasion, dissolution, and fragmentation; nonetheless, genus- and family-level identifications can still be reliable because the most conspicuous diagnostic characters which characterize higher taxa are more persistent after the death of the mollusc.

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1. Introduction

Community ecology studies in paleontological research often rely on identification at taxonomic levels higher than species (mainly genus or family) because (1) identification to generic level tends to be more robust when preservation of species-level morphological characters is variable or not optimal, or (2) genera are geologically long-lived and thus allow tracing community types through time (even when species identity changes) (e.g., Patzkowsky, 1995; Holland et al., 2001; Olszewski & Patzkowsky, 2001; Scarponi & Kowalewski, 2004; Redman et al., 2007). This approach has been tested: the differences in patterns between the species and the genus levels tend to have weak effects on paleoecological interpretations (Pandolfi, 2001), while

family-level identification produced results similar to genus-level identification in only approximately 50% of cases (Forcino et al., 2012).

The fidelity of ecological information that can be preserved in fossil assemblages can be quantified by comparing living (LAs) and death assemblages (DAs), i.e. so-called “live–dead (LD) agreement studies”. This approach assumes that DAs are reasonable proxies for fully buried fossil assemblages (Kidwell, 2013). The use of supraspecific taxa has not been explored so far in this context. How does ecological or taxonomic similarity or variation in richness of living assemblages transfer to death assemblages at higher taxonomic levels? And, conversely, if the analysis of death and fossil assemblages is conducted at supraspecific levels, is it possible to assess the extent to which the results faithfully represent the original species-level biological community?

Furthermore, recent evidence suggests that average LD fidelity is significantly poorer in areas of human impact (Kidwell, 2007), opening interesting perspectives for the application of LD agreement studies for environmental assessment and identification of ecological baselines (Kidwell, 2009; Kidwell & Tomašových, 2013; Weber & Zuschin, 2012; Korpanty & Kelley, 2014; Leshno et al., 2015; Zuschin & Ebner, 2015;

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Albano et al., 2015b; Negri et al., 2015). In parallel with studies that addressed the comparability between species and higher taxa in fossil assemblages, multiple ecological studies tested whether higher taxa can detect pollution gradients in living assemblages. Ellis (1985) formalized the concept of “taxonomic sufficiency”: “in any project, organisms must be identified to a level (species, genera, family, etc.) which balances the need to indicate the biology (including for example such matters as diversity) of organisms present with accuracy in making the identifications”. Numerous studies reported that higher taxonomic levels tend to be sufficient to detect natural spatial patterns (e.g., Dethier & Schoch, 2006; Terlizzi et al., 2008; Bevilacqua et al., 2009) and disturbance to ecosystems due to anthropogenic pressures in marine ecosystems (e.g., Warwick, 1988a, 1988b; Ferraro & Cole, 1990, 1992, 1995; Vanderklift et al., 1996; Olsford et al., 1998; Terlizzi et al., 2008). Similar studies assessed sufficiency in freshwater (e.g., Wright et al., 1995; Heino & Soininen, 2007; Jiang et al., 2013; Müller et al., 2013) and terrestrial habitats (e.g., Groc et al., 2010; Rosser & Eggleton, 2012; Timms et al., 2013). In most cases, family-level identification was sufficient, although results may vary among phyla (Heino & Soininen, 2007; Bevilacqua et al., 2009).

A high correlation is expected between species-level and supraspecific taxon indices or ordinations in datasets with low species/higher taxon (S/T) ratios. Therefore, datasets, or taxa, dominated by monotypic higher taxa are likely to produce a high level of taxonomic sufficiency (e.g., Olszewski & Patzkowsky, 2001). However, these ratios will tend to increase with the spatial and temporal extent of datasets and will be especially high in the tropics, where rates of evolutionary diversification are high (Krug et al., 2008). The ability of higher taxa to capture compositional and environmental gradients will also depend on whether species belonging to higher taxa respond to gradients similarly (ecological conservatism) and on their taphonomic similarity.

We test the hypothesis that within-phyllum live–dead agreement follows the general patterns already described for paleocommunities and modern living assemblages, i.e., there is a good correlation in community patterns based on species-level and lower supraspecific taxa. Mismatch between LAs and DAs was assessed by measuring similarity in taxonomic composition, rank–order agreement in relative abundance of taxa, taxonomic richness, evenness, and by conducting multivariate analysis. Our case study is a highly diverse subtidal molluscan assemblage in the Persian (Arabian) Gulf. This dataset is characterized by high species richness (ca. 350 species) and by one bivalve species that dominated the DA but was absent from the LA, causing a lower-than-expected fidelity.

2. Materials and methods

2.1. Dataset

Samples containing LAs and DAs were collected in 1999 off the United Arab Emirates, around two oil infrastructures in the Umm Al Dalkh field (UA, 25 km north-west of Abu Dhabi) and Zakum field (ZK, 84 km north-west of Abu Dhabi) (Fig. 1). Sediments showed very low contamination levels in both fields, and the LAs showed little disturbance (Albano et al., 2015a). Moreover, a comparison between LAs and DAs showed no evidence of community shifts (Albano et al., 2015b). Therefore, these samples can be regarded as coming from undisturbed environments. The seafloor at UA is a mixture of sand and shells, lies between 17 and 22 m depth, and is mostly inhabited by a small, sand-dwelling fauna. The seafloor at ZK consists of the so-called cap rock topped by a thin (ca. 1–5 cm) layer of sand, lying between 6 and 17 m depth. The fauna is characterized by less frequent sand-dwelling species and more frequent large-sized organisms, including scattered coral colonies.

At each location, a grid of sampling stations was designed over an area of ca. 45 km² in UA (13 stations) and ca. 240 km² in ZK (16 stations). Sampling for sediments and benthic organisms was carried out by divers with large aluminum scoops used in earlier benthic surveys in the area (Coles & McCain, 1990). The size fraction analyzed here was sieved with minimum 2 mm mesh size and maximum 5 mm mesh size, and then sorted under dissecting microscopes. The minimum mesh size helped avoid the collection of juvenile specimens which would have proved daunting to segregate and identify in this diverse and taxonomically poorly known tropical area. The maximum mesh size helped remove large but patchily distributed individuals which would be undersampled in the DAs due to the limited sampled area. Moreover, the species in this size range are expected to have more comparable “taphonomic half-lives” (Kidwell, 2002) and therefore reduce the effect of differential destruction rates among species.

All living molluscs were extracted from samples, while the extraction of empty shells from DAs was carried out until at least 1000 skeletal elements were collected at each station. In total, the study is based on 523 living individuals and 50,000 skeletal elements. To avoid counting a skeletal element (whole shells for gastropods and scaphopods, valves for bivalves and polyplacophorans) twice, only fragments larger than half a whole skeletal element were considered. Skeletal element counts were divided by the number of skeletal elements of each taxon



Fig. 1. The study area showing the two offshore oilfields (Umm al Dalkh and Zakum) in which the platform structures were sampled.

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