

# Linking taphonomy to community-level abundance: Insights into compositional fidelity of the Upper Triassic shell concentrations (Eastern Alps)

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## Abstract

Although actualistic live/dead comparisons lead to robust estimates of fidelity of modern death assemblages, quantitative evaluation of fidelity of fossil assemblage remains uncertain. In this paper, effects of storm reworking on compositional fidelity of the Upper Triassic shell concentrations (Eastern Alps, Austria) are evaluated. An exploratory approach is based on comparison of reworked and non-reworked assemblages in ordination analyses. Non-reworked assemblages of one or more communities provide a baseline for evaluation of fidelity of reworked assemblages. In siliciclastic-rich intervals of the Kössen Formation, shell concentrations are represented by (1) packstones with small, shallow infaunal bivalves, (2) floatstones and pavements with large semi-infaunal bivalves, and (3) bioclastic marlstones. In carbonate-rich intervals, bioclastic floatstones with bivalves and brachiopods occur. Analyzing all shell concentrations, eight sample groups sharing similar species composition are discriminated. Limited effect of storm reworking on composition of shell concentrations is indicated by (1) a general persistence of six sample groups when only non-reworked assemblages are analyzed, (2) similarity in composition between reworked and non-reworked assemblages within sample groups, and (3) compositional segregation between non-reworked assemblages of distinctive sample groups, mostly without any reworked assemblages of intermediate composition.

Depth-related variations in dead-shell production, shell destruction and body size governed preservation and distribution of the shell concentrations along onshore-offshore gradient in the Kössen Basin. First, at times when environmental conditions were unfavorable for shell producers, coupled with high background shell destruction rates, limestone beds formed during storm events were shell-poor. Second, less common shell concentrations in upper than in lower parts of siliciclastic intervals can be related to higher environmental stress in shallower habitats. Third, the difference between shell concentrations dominated by small and large bivalves is driven by between-habitat differences in body size and is not due to a differential sorting of small and large shells. Combining community analysis based on species abundances with taphonomic analysis can thus be helpful in tracking fidelity of fossil assemblages. © 2005 Elsevier B.V. All rights reserved.

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## 1. Introduction

Taphonomic analyses are either used for (1) interpreting environmental gradients (Brett and Baird, 1986; Davies et al., 1989; Feige and Fürsich, 1991; Kowa-

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lewski et al., 1994; Nebelsick, 1999; Dominici, 2004; Parsons-Hubbard, 2005), or (2) as a tool for addressing questions related to fidelity of the fossil record (Kidwell and Flessa, 1995; Behrensmeyer et al., 2000). The latter point leads to a choice of which fossil assemblages are minimally affected by compositional bias. Such assemblages can be suitable for further ecologic and environmental analyses. However, in spite of a large amount of research (Johnson, 1960; Miller, 1988; Powell et al., 1989; Kidwell and Bosence, 1991; Kidwell, 2001; Zuschin et al., 2004), quantitative estimation of effects of reworking on fidelity of fossil assemblages still remains uncertain because the original biologic pattern of interest is not controlled (in contrast to actualistic fidelity studies).

If fossil assemblages that show some evidence of reworking are excluded (see Johnson, 1960; Kidwell, 1998), the analyzed patterns in biotic composition should not be artifacts of sorting and mixing. However, some shallow, high-energy habitats are preferentially affected by higher physical destruction rates and transport. If such habitats harbor unique benthic communities, they will be excluded from the analyses due to their poor preservation. Some parts of the environmental gradient will not be analyzed due to such exclusion. High destruction rates can also be typical of some low energy habitats where chemical or biologic destructive processes are very rapid. Episodic short-term reworking events, associated with rapid burial, can lead to better preservation potential in such habitats. Paradoxically, such reworking can produce signs of sorting and transport, possibly also leading to the exclusion of such assemblages from paleoecologic analyses. Clearly, the ability to estimate what and how much of original information was lost during reworking events is crucial in paleoecologic analyses.

The compositional fidelity (i.e., the quantitative faithfulness of the population- and community-level fossil/subfossil data to the original biologic record, Behrensmeyer et al., 2000) can be explicitly assessed in actualistic live–dead studies where original biologic record is available (Schopf, 1978; Nebelsick, 1992; Greenstein, 1993; Murray and Alve, 1999; Hadly, 1999; Zuschin et al., 2000; Kidwell, 2001, 2002; Alin and Cohen, 2004; Tomašových, 2004). However, the direct live/dead comparison is not possible in fossil assemblages. Several indirect measures can be used when the compositional fidelity of fossil assemblages is evaluated. These measures are based mostly on an overall degree of fossil damage and/or sedimentologic evidence for reworking, transport or condensation (Kidwell and Bosence, 1991; Jiménez and Braga, 1993;

Olszewski and West, 1997; Yesares-García and Aguirre, 2005; Cózar, 2002). However, sedimentologic and taphonomic evidence indicating reworking does not tell if and to what degree an original biotic pattern of interest (e.g., species composition, abundances or diversity) is preserved in the fossil assemblage affected by the reworking. For example, Rasser and Nebelsick (2003) showed that Oligocene foraminiferal assemblages preserved in debris flows may well reflect composition of their autochthonous counterparts.

One of the few attempts to quantitatively analyze compositional fidelity which would be applicable to fossil assemblages is an evaluation of within-community transport (Cummins et al., 1986; Miller and Cummins, 1990). Based on the comparisons of observed number of co-occurring species pairs based on field data and predicted number of co-occurring species pairs based on simulation, Cummins et al. (1986) and Miller and Cummins (1990) showed that Spearman rank correlation coefficient can be a viable measure for discerning transport within habitats.

In this paper, an explorative approach is proposed for assessment of the compositional fidelity of fossil assemblages. This method is based on a simple comparison of the composition of reworked and non-reworked assemblages, assuming that they are derived from comparable habitats and time intervals (e.g., are assemblages affected by higher reworking different in composition compared to non-disturbed assemblages?). The relationship of reworked and non-reworked assemblages in Q-mode ordination space should permit inferences on the role of sorting or mixing processes in biasing the composition of fossil assemblages. The main goal of this paper is to apply this explorative approach to the Upper Triassic shell concentrations of the Kössen Formation (Eastern Alps, Austria, Fig. 1). As an initial hypothesis, Golebiowski (1990) assumed that a difference in composition between assemblages dominated by small and large bivalves in the Kössen Formation is due to storm sorting. This hypothesis will be tested and the genesis of shell concentrations from the Kössen Formation will be addressed in general. Although spatial fidelity is also of ecologic importance (e.g., Fürsich and Flessa, 1987; Miller, 1988), the focus in this paper is on the fidelity of taxonomic composition. Effects of time-averaging as another potential biasing factor on community-level properties (Meldahl et al., 1997; Kowalewski et al., 1998) are minimized as the focus is mostly on single-event shell concentrations.

In the first section, shell concentrations are described and interpreted. In the second section, their compositional fidelity is evaluated in multivariate analyses via

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