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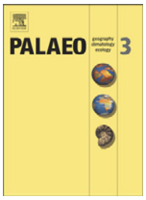

Ecological instability in Upper Cambrian–Lower Ordovician trilobite communities from Northwestern Argentina

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ABSTRACT

Although ecological stability has been widely studied in the fossil record, it has seldom been analyzed in trilobite dominated communities. We test stability in these communities from the Upper Cambrian–Lower Ordovician of the Cordillera Oriental, Northwestern Argentina. The studied interval spans approximately 5 ma. and for this analysis it was divided in four smaller scale informal intervals of approximately 1.5 to 2 ma. Sampling covers a wide geographic area of ~7000 km^2 in each time bin. In order to analyze ecological stability, we tested for patterns predicted from the hypothesis of coordinated stasis and habitat tracking.

For the analysis of coordinated stasis we studied taxonomic turnover. Migrations and evolutionary turnovers based on the regional and global occurrence of taxa were assessed. Results indicate important rates of immigration and emigration, highlighting the relevance of migration in the assembly of the meta-community. The percentage of carryovers and holdovers was variable between intervals and did not show a bimodal pattern, contradicting the coordinated stasis model. In addition, an ordination analysis performed with correspondence analysis suggests that each interval has an idiosyncratic genus composition.

In order to test the model of habitat tracking, an analysis of the stability of biotic gradients and the environmental fidelity of stenotopic taxa was conducted. We carried out a Mantel test to analyze the recurrence of taxa present in different intervals. The results showed that taxa are grouped differently in every interval, indicating instability of biotic gradients. We also performed a gradient analysis for each interval and compared intervals with each other using a Procrustes analysis. Results of this analysis indicate that taxa respond individualistically to environmental changes. Moreover, high Procrustes errors are present in rare taxa. Because rarity is largely related to niche breadth, this result suggests that many stenotopic taxa had little environmental fidelity.

Overall, this study suggests that migration appears to be of great importance in the composition of local and regional communities, and that the biotic gradients formed in each interval had a distinct composition and structure. Such compositional and ecological instability do not show convincing evidence to support coordinated stasis. Finally, the concept of individualistic habitat tracking is more clearly understood in light of metacommunity processes such as dispersal and habitat preferences, rather than as a process by itself.

1. Introduction

Discussions about the (in)stability of communities and the mechanisms underlying community assembly date back a long time. This dispute has persisted for almost 80 yr in the field of ecology since the competing views of Clements (1916) and Gleason (1926) were first published. While Clements (1916) proposed that communities were highly integrated entities, Gleason (1926) stated that communities were aggregated of sp that respond individualistically.

Despite the great deal of ecological research, the importance of random vs. predictable assembly of communities is still a matter of controversy in ecology (Hubbell, 2001; Ricklefs, 2008; Vellend, 2010). Whittaker (1952, 1956) and Bray and Curtis (1957), pointed out that along environmental gradients species abundances varied independently. Later, Ricklefs (1987, 2008) and colleagues (Ricklefs and Schluter, 1993) showed that local communities also depend on regional dynamics and historical processes. Finally, Hanski (1982), Pulliam (1988, 2000), Hubbell (2001), and Leibold et al. (2004) among others, showed how dispersal affects local community composition and interactions among species.

Although this neontological evidence mostly favor a "*Gleasonian*" community dynamic at ecological time scales, it is still difficult to ascertain what happens at evolutionary time scales. The debate about stability of communities in the fossil record also dates back a long time (see reviews of the subject in (Johnson, 1972; Hoffman, 1979; Miller, 1990; Springer and Miller, 1990). The "Gleasonian" view has been supported by several authors such as Hoffman (1979), Miller (1990), Buzas and Culver (1994, 1998), Bambach and Bennington

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(1996); Bennington and Bambach, 1996), Olszewski and Patzkowsky (2001), among others. According to these authors, relative abundances vary continuously along the environmental gradients, with communities representing an epiphenomena caused by the overlap of the ranges of different species (Hoffman, 1979; Olszewski and Patzkowsky, 2001).

Most claims about community stability in the fossil record are in accordance with the "*Clementsian*" idea. Brett and colleagues (Brett and Baird, 1995; Morris et al., 1995; Brett et al., 1996) called attention to a pattern of stability in faunal composition and morphology through several millions years which they termed coordinated stasis. To explain these dynamics of stability and community replacement through time, Morris et al. (1995) proposed the mechanism of ecological locking. This mechanism assumed that interspecific interactions generate the observed stability in relative abundance and morphological evolution. Only when an event was important enough to destabilize communities, did speciation occur in most taxa and a new ecological structure in the composition and relative abundance appeared. The process of ecological locking has been substantially discussed and today it is no longer considered valid (Dimichele et al., 2004; Brett et al., 2007b). However, how general the pattern of coordinated stasis is and why does it pertain in some cases and not in others is still a matter of discussion (Brett et al., 2009; Ivany et al., 2009).

The authors defending long-term community stability claim that the *habitat tracking* is a fundamental process (Brett et al., 1990, 2007b; Brett, 1998). This concept has been widely discussed and revised over its history. At the beginning it referred to the tracking of a particular environment by a given biofacies (i.e., a set of taxa) along transgressive–regressive cycles of different orders (Brett et al., 1990; Brett, 1998). Nevertheless, different studies provided a considerable amount of evidence against the persistence of biofacies as homogeneous units (Bennington and Bambach, 1996; Holterhoff, 1996; Olszewski and Patzkowsky, 2001) and highlighted the individualistic response of taxa to environmental changes (Hoffman, 1979; Jackson and Overpeck, 2000).

Brett et al. (2007b) suggested that habitat tracking is an important mechanism that explains biotic replacements in certain shallow marine settings, and drew attention to the confusion between the process of habitat tracking and the pattern of biofacies replacement that such process explains. These authors remarked the notion that some biofacies can recur with considerable fidelity in depositional cycles related to sea-level changes. However, one significant point emerging from the review by Brett et al. (2007b) is the emphasis placed in the individualistic environmental preferences of taxa, with habitat tracking of the biofacies as a whole only a consequence. Upon this criterion, biofaces are not integrated entities that track shifting environments, instead, they result from the grouping of species with closely overlapping habitat preferences.

On the other hand, those authors who favor a more dynamic view of communities over time, emphasize dispersal as a major factor determining the composition of communities (Miller, 1990; Buzas and Culver, 1998). This notion is tied to the concept of metacommunity, recently proposed to explain the ecological dynamics at different scales (Leibold et al., 2004; Chase and Bengtsson, 2010; Vellend, 2010). In this context, interactions among species and their functional attributes play an important role in community assembly, but composition is not necessarily constant because the different taxa become locally extinct and their presence depends on the dispersal from other local communities or from a taxon-pool (Buzas and Culver, 1994, 1998). From now on, we will refer to such idea as assembly–disassembly.

Studies of communities stability in the fossil record are generally concentrated in the post-Middle Ordovician Paleozoic (e.g., Bennington and Bambach, 1996; Patzkowsky and Holland, 1997; Olszewski and Patzkowsky, 2001; Brett et al., 2007a; Ivany et al., 2009), Mesozoic (Tang and Bottjer, 1996), and Cenozoic (e.g., Valentine and Jablonski, 1993; Jackson et al., 1996; Stanton and Dodd, 1997; Buzas and Culver, 1998; Jackson and Overpeck, 2000), while typically Cambrian trilobite dominated communities have received little attention (Westrop, 1996). This is particularly relevant given that these communities differ in many ecological characteristics with respect to post-Cambrian ones. These are, among others, low alpha and beta diversity (Bambach, 1977; Sepkoski, 1981, 1988), the simplicity of their taxon abundance distributions (Wagner et al., 2006), low evenness (Peters, 2004), low ecospace occupation (Bambach et al., 2007) and the high evolutionary turnover rates of trilobites which are the dominant group (Foote, 1988).

This contribution addresses the study of stability in trilobite communities in the Cambrian–Ordovician boundary interval from the Argentinian Cordillera Oriental (Fig. 1) during a time period close to 5 ma. from Late Furongian (Stage 10) to middle Tremadocian (Tr2). This basin has a complex tectosedimentary history (Astini, 2003, 2008; Egenhoff, 2007), where high sedimentation rates and variability in depositional environments represent an interesting challenge to analyze ecological patterns. The advanced taxonomic study of the trilobite faunas (Harrington and Leanza, 1957; Tortello and Esteban, 2003; Waisfeld and Vaccari, 2003) and the recent understanding of ecological patterns at smaller scales (Balseiro et al., 2011a,b) provide an excellent opportunity to study the stability of trilobite dominated communities.

2. Geological setting

The Central Andean Basin corresponds to a retroarc foreland basin located on the western margin of Gondwana during the Paleozoic (Fig. 1; Astini, 2003, 2008; Egenhoff, 2007). It is made up of different depocenters of a foreland basin, in which the Cordillera Oriental corresponds to the peripheral bulge. Regionally the basin shows significant variations in depositional environments along an east–west transect. Towards the western sections exposed in the Puna, volcaniclastic and turbidite systems are recorded (Buatois et al., 2009). In the central belt, corresponding to the Cordillera Oriental, shallow marine systems are present. Finally, towards eastern localities in the Sierras Subandinas, deltas and estuaries become predominant (Astini, 2003, 2008; Egenhoff, 2007).

In particular, in the Cordillera Oriental a siliciclastic platform corresponds to a low angle ramp, with high sedimentation rates

Fig. 1. Map of South America indicating the location of the Central Andean Basin and Cordillera Oriental. Modified from Balseiro et al. (2011a).