# 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.

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## 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).

recording deep to shallow marine environments, alternating to a lesser extent with the development of estuarine and deltaic systems (Buatois et al., 2006; Egenhoff, 2007). Due to the complex facies mosaic present in this region, the lithostratigraphic nomenclature is extremely diverse. The most widely accepted unit is the Santa Victoria Group (Turner, 1960). The lower part of this group corresponds to the Santa Rosita Formation, which is the main unit studied in this work.

The Santa Rosita Formation is subdivided into six members namely the Tilcara, Casa Colorada, Pico de Halcón, Alfarcito, Rupasca, and Humacha (Buatois et al., 2006). In western localities, where the sequences tend to be somewhat deeper, there are numerous equivalent units (Fig. 2). The interval studied in this contribution, corresponds to the lower five members of the Santa Rosita Formation and their equivalents, and is constrained between the Cordylodus proavus biozone (Late Furongian) and the Paltodus deltifer pristinus subzone (Tr2, Bergström et al., 2009; Fig. 2).

The sequence stratigraphy of this interval is complex and has not yet been definitively resolved. However, recent contributions from Astini (2003, 2008), Buatois et al. (2006); see also Mángano and Buatois, 2003, 2004; Mángano et al., 2005) and Egenhoff (2007) provide a generalized framework for low-order sequences with basinwide signals. The succession begins with deltaic systems to the east (Buatois et al., 2006) and shoreface settings to the west (Buatois et al., 2003), namely the Tilcara Member and Padrioc Formation respectively. A major regional transgression is recorded across the Cordillera Oriental at the base of Member Casa Colorada and its equivalent, the Lampazar Formation (Astini, 2003; Buatois et al., 2006). Above these units there is a forced regression and the consequent shallowing is represented by shoreface environments in the western sections and deltas towards the east (Buatois et al., 2003, 2006).

Another major regional transgression is present at the base of Alfarcito Member and equivalent units (Fig. 2; Astini, 2003; Mángano and Buatois, 2003) and possibly coincides with the Cambrian–Ordovician boundary (Tortello et al., 2002). The Alfarcito Member records at least four depositional sequences (Marengo, 2011) during the whole lower Tremadocian (Tr1 of Bergström et al., 2009).

Finally, a third transgressive event of regional importance is recorded at the base of the Rupasca Member in the eastern sections (Buatois et al., 2006) and the Saladillo Member in the region of Pascha-Incamayo (Tortello and Rao, 2000). The latter event would have taken place during the Middle Tremadocian (Tr2) as it coincides with the Paltodus deltifer pristinus subzone (Zeballo et al., 2005). In its type section the Rupasca Member preserves a stepwise transgression subdivided into three depositional sequences (Buatois et al., 2006). However, in other localities this trend is not evident and shallower environments are recorded (Balseiro et al., 2011a). In the western localities no stratigraphic record younger than early Tr1 is preserved due to development of the Tumbaya Tectophase represented by a major regional unconformity (Moya and Monteros, 2000; Astini, 2003). This implies that the record of late Tr1 and Tr2 is restricted to the central and eastern sections. In certain central locations this interval is represented by shallow marine systems, conglomeratic wedges and even deep marine environment (Astini, 2003, 2005; Tortello and Rao, 2000), evincing a complex paleotopography in the region (Astini, 2008). This contribution is focused on the Cambrian–Ordovician boundary interval. To get a more refined chonostratigraphic framework we considered four intervals based on trilobite, conodont, and graptolite biostratigraphy. The boundaries between these intervals often correspond with major sequence boundaries described in the Cordillera Oriental. These intervals and their correlation with lithostratigraphic units in the study areas are shown in Fig. 2.

## 2.1. Data

### 2.1.1. Dataset

Our dataset is based on presence–absence of trilobite genera. More than one hundred samples were obtained from thirteen different localities along the Cordillera Oriental. All samples were obtained from fair-weather shale intervals not exceeding 20 cm thick. This procedure intended to avoid, as far as possible, distortions due to time averaging or other taphonomic signatures that can alter the biological patterns. In order to obtain as many samples as possible per interval and greater geographic and environmental coverage, we added to our dataset samples obtained from literature sources. We selected contributions, which explicitly indicated that the samples were obtained from shale intervals. The main source used was a monograph by Harrington and Leanza (1957) from which 142 samples were available. In addition another 56 samples were obtained from Tortello et al. (1999), Tortello and Rao (2000), Zeballo and Tortello (2005), and Esteban and Tortello (2007). Because literature sources do not indicate relative abundances, the dataset is based on presence–absence information. The final matrix has 307 samples and 1098 occurrences, 118 samples come from the Furongian, 86 from early Tr1, 49 from late Tr1, and 54 from Tr2.

While relative abundances provide crucial information for paleoecological studies (Ludvigsen et al., 1986), results based on presence–absence are also usually as reliable as those based on abundance (Olszewski and Patzkowsky, 2001; Balseiro et al., 2011a). In turn, recent reviews show that the proportion of occurrences at the regional level (occupancy) is highly correlated with local abundance (Gaston et al., 2000), so the first can be used as a reliable proxy for estimating the second.

| Series | Stages | Stage slices | Intervals used | Biostratigraphy | | | Lithostratigraphy | |
|---|---|---|---|---|---|---|---|---|
| | | | | Trilobites | Conodonts | Graptolites | East | West |
| Ordovician | Tremadocian | Tr2 | Tr2 | *B. tetragonalis* | *P. deltifer* | *Bryograptus* | Rupasca | |
| | | | | *Kainella teiichi* | | | | |
| | | Tr1 | Late Tr1 | *Kainella meridionalis* ? | *C. angulatus* | ? | Alfarcito | Guayoc Chico Gr. |
| | | | | *Kainella andina* ? | | *R. f. anglica* | | |
| | | | Early Tr1 | *J. keideli keideli* | *Iapetognathus* | *A. matanensis* | Pico de Halcón | |
| Cambrian | Stage 10 | | Furongian | *P. (N.) frequens argentina* | *C. proavus* | | Casa Colorada | Lampazar Fm |
| | | | | ? | ? | | Tilcara | Padrioc Fm |

**Fig. 2.** Correlation chart of the intervals used, regional biostratigraphy and lithostratigraphy. Stage slices based on Bergström et al. (2009), lithostratigraphy based on Astini (2003). Modified from Waisfeld and Vaccari (2008) and Vaccari et al. (2010).

Discussions concerning the stability of communities are typically based on species as the taxonomic unit of analysis (Bonuso et al., 2002a,b; Brett et al., 2007a; Ivany et al., 2009), while here we study these patterns at the generic level. Recent studies show that biotic gradients can be studied even at familial level (Terlizzi et al., 2009; Forcino et al., 2010) and contributions using genera instead of species have been very useful for the study of compositional stability in the fossil record (Westrop, 1996; Olszewski and Patzkowsky, 2001; Olszewski and Erwin, 2009). Since we are using genera, our analysis is conservative in favor of stability. This means that we can be sure of our result if we show that there is no stability in biotic gradients. If our results suggest stability, it is still possible that a pattern of instability cloud exist at the species level.

### 2.1.2. Geographic and environmental coverage

Fig. 3 shows the geographical coverage of the dataset. The maximum geographical coverage is for the Furongian (~7750 km$^2$). For the early Tr1 the coverage decreases (~6750 km$^2$), although the overall size of the sampled area is not much smaller than for the Furongian. Most samples from these two intervals come from shelf and offshore environments, while fewer were obtained from the offshore transition and none from the shoreface. During the late Tr1, there is also fairly good geographic coverage (~7000 km$^2$). However, the upper part of this interval is not registered towards the west due to the "Tumbaya Break". Samples from the late Tr1 are concentrated in the offshore, while shelf, offshore transition and shoreface contain few samples. Finally, the Tr2 has a similar geographic coverage (~7000 km$^2$). Although there are a relatively high number of localities, they are concentrated in the central region of the Cordillera Oriental. The environmental coverage of the Tr2 samples ranges from shelf to lower shoreface.

### 3. Analytical methods

We used two different approaches to study faunal stability between intervals. First, we studied the number of taxa surviving and migrating in each time interval. Second, we used multivariate techniques to study the biotic gradients. We performed and compared different ordination analyses and conducted a Mantel test.

### 3.1. Migration and turnover

Using a similar approach to that of Buzas and Culver (1998), we studied the number of taxa immigrating, originating, emigrating and going extinct in each time interval. To calculate these indices we tabulated the worldwide FAD and LAD of each genus. We constructed a genus-level pool using the ranges of all taxa that are present in the basin between the Upper Furongian and the Tr2. Genera pool for each interval was calculated as the percentage of genera from the entire generic pool. Originations, extinctions and migration in this study are defined in the following way. Originating taxa have their regional and global first appearance in the interval. Taxa going extinct have their regional and global last appearance in the interval. Immigrating taxa are those taxa that in a given interval were absent in the basin but present elsewhere worldwide, and occur in the basin in later intervals. Emigrating taxa are present in a given interval, regionally absent in the succeeding interval but present elsewhere in the world.

Carryover taxa are present in the basin in an interval and in the subsequent one (i.e. those taxa that survive locally to the next interval). Holdovers are those taxa present in the basin in an interval and in the previous one (i.e. those taxa that survive from the previous interval). The number of holdovers and carryovers for each interval are calculated using diversity, originations, extinctions, immigrations and emigrations in the following way:

Carryovers  Diversity–Extinctions–Emigrations
Holdovers  Diversity–Originations–Immigrations

Because in the Cordillera Oriental there is no Upper Cambrian stratigraphic record previous to the latest Furongian, we assumed that all taxa in the Furongian were either immigrants or originations, and no surviving taxa are tabulated. Furthermore, emigrating taxa were not calculated for the Tr2 because we did not analyze younger intervals, although the stratigraphic record in the basin continues.

### 3.2. Analysis and comparison of ordinations

To display the spatio-temporal turnovers among intervals we carried out an ordination analysis using a Correspondence Analysis (CA) (Legendre and Legendre, 1998). Other ordination methods (namely NMDS and DCA) are also commonly used in paleoecological literature (Jackson et al., 1996; Holland and Patzkowsky, 2007). In our case we prefer to use CA because it has the fundamental advantage of superimposing a priori species and samples in the same multidimensional space allowing a direct comparison between them (Fall and Olszewski, 2010). In any case, performing the same analyses using NMDS or DCA yielded qualitatively very similar results. A preliminary ordination analysis indicated that the sample S.Ros12–P13 was an outlier, hence it was removed from all ordination analyses. For this study we analyzed the dataset in two different ways. First, we conducted a CA with all samples from all intervals to observe the relationship between temporal and spatial turnovers at a large scale.

Second, we carried out an ordination analysis of each interval alone. To analyze the stability in the structure of biotic gradients between intervals, we compared ordinations using a Procrustes analysis (Legendre and Legendre, 1998). This analysis is typically used in geometric morphometric studies (Zelditch et al., 2004), but has also been implemented to compare ecological ordinations (Legendre and Legendre, 1998; Peres-Neto and Jackson, 2001). The Procrustes analysis consists of finding a configuration where a given ordination has the minimum difference to another one. To do this, one of the ordinations is rotated, moved and scaled in relation to the other one which is used as the reference (Legendre and Legendre, 1998). Both ordinations must be composed of the same elements, since the differences between ordinations are measured as the square of the distances between the homologous elements. Such differences between elements are known as Procrustes errors. Comparisons should be performed with the same number of axes in each ordination, because transformations can not be carried out if one space has more dimensions than the other. This analysis was conducted comparing ordinations of successive intervals. Each ordination was performed using all samples and taxa for each interval separately. We compared the position in the multidimensional space of the genera surviving from one interval to the other. Only the first 12 axes of the ordinations were used in the analysis, which accumulated 85% of total inertia. The Procrustes analysis is not symmetrical and the results differ when one or the other ordination is used as the reference (Legendre and Legendre, 1998). Therefore, we performed each comparison twice with either ordination as the reference and the Procrustes errors were calculated as the geometric mean. For the sake of clarity, and because superimposition plots between both analyses did not differ much, only those using the younger interval as the reference are shown in the results. To study the relationship between abundance and instability along the gradient, we examined association of each genus' Procrustes error with its occupancy. The occupancy is the proportion of the total samples where a given taxon is present (McGeoch and Gaston, 2002) and it is a good proxy for estimating abundance (Gaston et al., 2000). We calculated occupancy in each temporal interval. Because taxon occupancy changes between intervals, we used the geometric mean of occupancy in both intervals being compared.

Prior to the analysis all singleton taxa and monospecific samples were removed. Preliminary analysis showed that different outlier taxa were present in each interval, obscuring the results of the ordinations. These were removed prior to the analysis. In the Furongian
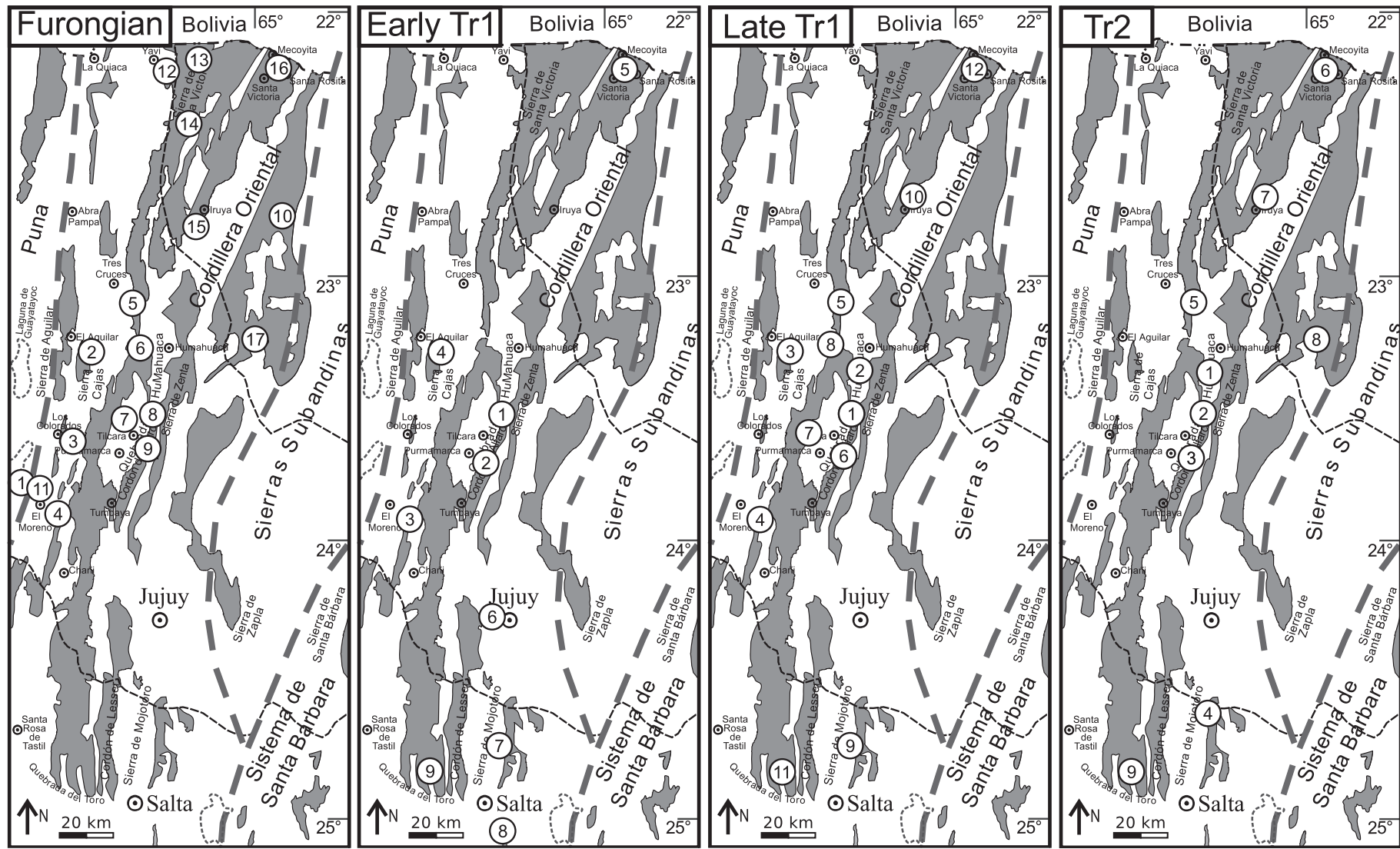
**Fig. 3.** Maps of Cordillera Oriental indicating localities studied in this contribution. Furongiano: (1) Taique, (2) Quebrada Vizcacha, Quebrada Azul, and Quebrada Llama, (3) Quebrada Totora, (4) El Moreno, (5) Azul Pampa, (6) Quebrada de Yacoraite, (7) Jueya, (8) Quebrada de Arenal-Trancas, (9) Quebrada Casa Colorada and Quebrada San Gregorio, (10) Matancillas, (11) Cangrejillos, (12) Yavi, (13) Río Tres Lagunas, (14) Quebrada Colorada de Fundición, (15) Iruya, (16) Río Mesón, (17) Rio Santa Cruz, Quebrada la Escalera, and Río Negrito. Early Tr1: (1) Quebrada de Arenal-Trancas, (2) Quebrada del Salto, (3) El Moreno, (4) Quebrada Amarilla, (5) Quebrada Río Santa Victoria, (6) Cerro Lozano, and Río de Reyes, (7) Finca San José and Yacones, (8) Quebrada de la Cruz, and Quebrada del Pingüiyal, (9) Quebrada de Lampazar. Late Tr1: (1) Quebrada de Arenal-Trancas, (2) Quebrada de Moya, (3) Quebrada Amarilla, (4) El Moreno, (5) Azul Pampa, (6) Quebrada Rupasca, and Quebrada San Gregorio, (7) Quebrada de Huichaira-Pocoy, (8) Quebrada de Yacoraite, (9) La Caldera, and Quebrada Los Canchos, (10) Río Nazareno, (11) Pascha-Incamayo, (12) Quebrada Río Mesón, and Quebrada Río Santa Victoria. Tr2: (1) Angosto de la Chucalezna, (2) Quebrada de Arenal-Trancas, (3) Quebrada de Casa Colorada, Quebrada Rupasca, and Quebrada San Gregorio, (4) Ruta 9, (5) Azul Pampa, (6) Quebrada Río Santa Victoria, (7) Río Nazareno, (8) Quebrada de Parani, (9) Pascha-Incamayo.

the genera Leiostegium, Hapalopleura and Leiagnostus were eliminated from the analysis while *Geragnostus* was eliminated in the early Tr1. In the early Tr2 a group of taxa present in a few samples were also eliminated from the analysis, namely *Pyrometopus*?, *Ceratopyge*, *Dichelepyge*, *Illaenopsis*, and *Niobia*. All analyses were performed in R (R Development Core Team, 2011). We used the functions cca() for the CA and Procrustes() for the Procrustes analysis both in the vegan package (Oksanen et al., 2012).

### 3.3. Mantel test

We also carried out a Mantel test (Legendre and Legendre, 1998) to analyze the stability in the structure of the gradients between time intervals. The Mantel test is designed to test the correlation between two similarity matrices using a permutation method. Here we used 5000 permutations and the Spearman correlation because it is nonparametric and avoids problems related to non-linearity of the data (Dietz, 1983; Sokal and Rohlf, 1995). Because matrices must be composed of homologous data, we used only genera common to both intervals being compared. We ran each test twice, once with and once without singleton taxa. The similarity matrix was made using the Jaccard similarity (Legendre and Legendre, 1998), other distances such as the Morisita–Horn yielded identical results. The distance matrix was created with vegdist() function and the Mantel test was performed using the mantel() function, both available in the vegan package (Oksanen et al., 2012) for R (R Development Core Team, 2011).

## 4. Results

### 4.1. Migration and turnover

Table 1 shows the values of diversity, immigration, originations, emigrations, and extinctions in each interval. In every interval the percentage of taxa from the genera-pool that are present in the basin is rather low. The mean percentage of taxa regionally present is 65%, ranging from ~78% in the Furongian to ~45% in the early Tr1 (Table 1).

Survivorship between intervals is not very high. The mean percentage of holdovers is 63%, ranging from 64% to 40%. Carryovers show a similar pattern, ranging from 60% to 40%. No relationship between carryovers and holdovers is seen (Fig. 4). The absolute values depend on the diversity of the interval, while relative show a different pattern. For example, the Furongian records low percentage of carryovers (~40%) while the early Tr1 shows high percentage of holdovers (~63%) when in both cases the absolute value is 12 genera (Fig. 4). This is because diversity in the Furongian (30 genera) is higher than in the early Tr1 (19 genera).

**Table 1**
Absolute and relative values of diversity of the interval (Div). diversity of the genera-pool (Pool). Immigration (Imm), origination (Ori), emigration (Emi), and extinction (Ext).

| | | Absolute | | | | |
|---|---|---|---|---|---|---|
| | Div | Pool | Imm | Ori | Emi | Ext |
| Fur | 30 | 38 | 17 | 13 | 14 | 4 |
| E.Tr1 | 19 | 41 | 4 | 3 | 5 | 3 |
| L.Tr1 | 27 | 40 | 10 | 6 | 6 | 5 |
| Tr2 | 25 | 37 | 6 | 3 | NA | 8 |
| | | Relative | | | | |
| Fur | 30 | 0.79 | 0.57 | 0.43 | 0.47 | 0.13 |
| E.Tr1 | 19 | 0.47 | 0.21 | 0.16 | 0.26 | 0.158 |
| L.Tr1 | 27 | 0.67 | 0.37 | 0.22 | 0.22 | 0.18 |
| Tr2 | 25 | 0.68 | 0.24 | 0.12 | NA | 0.32 |

Although immigration and emigration are usually low (Table 1), they are always higher than origination and extinction respectively. It is particularly interesting that immigrants are always at least 1/3 relative to survivors, and equal in the late Tr1. These results highlight the importance of migration in the dynamics of regional diversity in the basin.

There are 23 taxa common to all four genera-pools, of which only 7 are present in the Cordillera Oriental in all intervals. Only three genera immigrate and/or emigrate several times, and they do not immigrate or emigrate in groups. *Pharostomina* immigrates in the early Tr1 and Tr2, and *Plicatolina* in the Furongian and Tr2. *Leiagnostus* is the only genus both immigrating and emigrating more than once, it does so in the Furongian and late Tr1.

### 4.2. Correspondence analysis of all intervals

The result of the CA is shown in Fig. 5. We can observe that time seems to be the main factor affecting the pattern of organization in the multidimensional space. The CA1 vs. CA2 plot (Fig. 5A) shows a clear segregation into three groups, each one corresponding a different time interval. A first group is composed of Furongian samples, which group at high values of the CA1 and low values of CA2. The early Tr1 samples determine a second group with intermediate CA1 scores and high CA2 scores. Finally, late Tr1 and Tr2 samples define a third group at low values of both the CA1 and CA2. This clustering of late Tr1 and Tr2, however, does not hold when analyzing the CA3 axis (Fig. 5B). On this axis all Tremadocian samples are distributed in a temporal arrangement. Along CA3, early Tr1 samples exhibit low scores, late Tr1 intermediate scores and Tr2 high scores.

These ordination results indicate that compositional differences between the intervals are more important than their similarities. Hence, we can characterize these four groups compositionally using occupancies of taxa. The Furongian is dominated by *Parabolina* (*Neoparabolina*), *Parabolinella* and *Angelina* with occupancies of 0.98, 0.44, and 0.35 respectively. The early Tr1 is dominated by *Jujuyaspis* with an occupancy of 0.91 followed by *Parabolinella* with 0.54. The late Tr1 is characterized by *Kainella* with 0.89, while both *Asaphellus* and *Leptoplastides* have occupancies of 0.54. Finally, the Tr2 is clearly dominated by *Leptoplastides* with 0.89 while three other taxa have occupancies higher than 0.5, namely *Asaphellus* with 0.61, *Parabolinella* with 0.59 and *Bienvillia* with 0.55.

### 4.3. Environmental and biotic gradients in each time interval

As mentioned above, boundaries of temporal intervals coincide with major sequence stratigraphic surfaces and the internal stratigraphic pattern of each interval is similar. Moreover, there is not any major environmental change that modified the structure of the siliciclastic ramp developed in Cordillera Oriental during the Cambrian–Ordovician (Astini, 2003), and intervals record very similar facies and depositional environments (Astini, 2003, 2008; Buatois et al., 2006). Therefore, environmental gradients controlling the development of biotic gradients, were very similar in all time bins. The latter is an important variable for the analysis of community stability, because if the structure of the environmental gradient changes, then we cannot expect to have community stability.

The structure of biotic gradients has been previously described and discussed by Balseiro and Marengo (2008) and Balseiro et al. (2011a,b). These contributions indicate that gradients are structured mostly along bathymetry. It should be noted, however, that ordinations performed here are not identical to those discussed in previous contributions. The main reason is that current results are based on a larger and revised dataset and time intervals are not exactly equivalent to those previously analyzed.
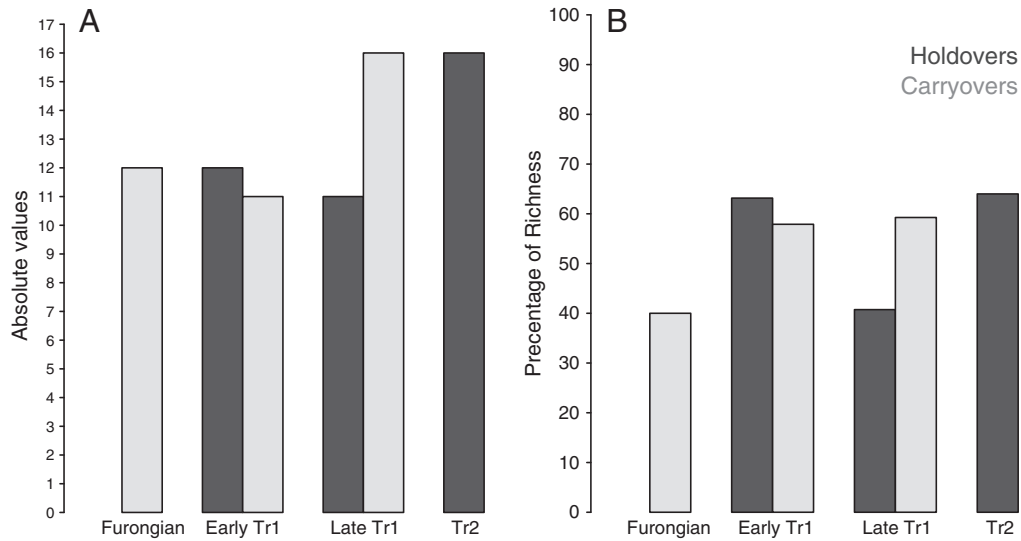
**Fig. 4.** Barplots showing the amount of carryovers and holdovers in each interval. A) Absolute values. B) Percentage relative to the interval's richness.

### 4.4. Procrustes analysis between intervals

The results of Procrustes analysis indicate rather similar patterns of change between all comparisons. In most comparisons there is a wide range of values of Procrustes errors. However, in some comparisons within the Tremadocian, namely early Tr1–Tr2 and late Tr1–Tr2, the range of Procrustes errors are smaller. Nevertheless, the magnitude of Procrustes errors in all six comparisons is similar (Fig. 6).

Regarding the genera individually, it is interesting that each one has a particular pattern of Procrustes errors between comparisons. Some genera (e.g., *Micragnostus*) usually have high errors, others (e.g., *Parabolinella*) have low errors, others (e.g., *Parakainella*) intermediate errors, and finally others (e.g., *Onychopyge*, *Hapalopleura*) have very variable magnitude of Procrustes errors (Fig. 6). In the

case of the agnostid *Micragnostus*, high Procrustes errors are expected based on hypothesis of its ecology as being planktonic and present in a wide range of sedimentary environments (Robison, 1972). However, this pattern should be also expected for other agnostids, as Geragnostus and Gymagnostus, that typically have low Procrustes errors indicating rather stable positions in the gradients. The opposite pattern is seen in Hapalopleura. Although some authors have proposed its restriction to deep environments (Fortey and Cocks, 2003), in our results it may show high Procrustes errors indicating important changes in its position along biotic gradients.

In the superimposition plots (Fig. 7) we can observe that in most cases the patterns of change between ordinations are different. It is interesting that the comparisons of Furongian with the late Tr1 and the Tr2 have very similar patterns (Fig. 7). In most superimposition
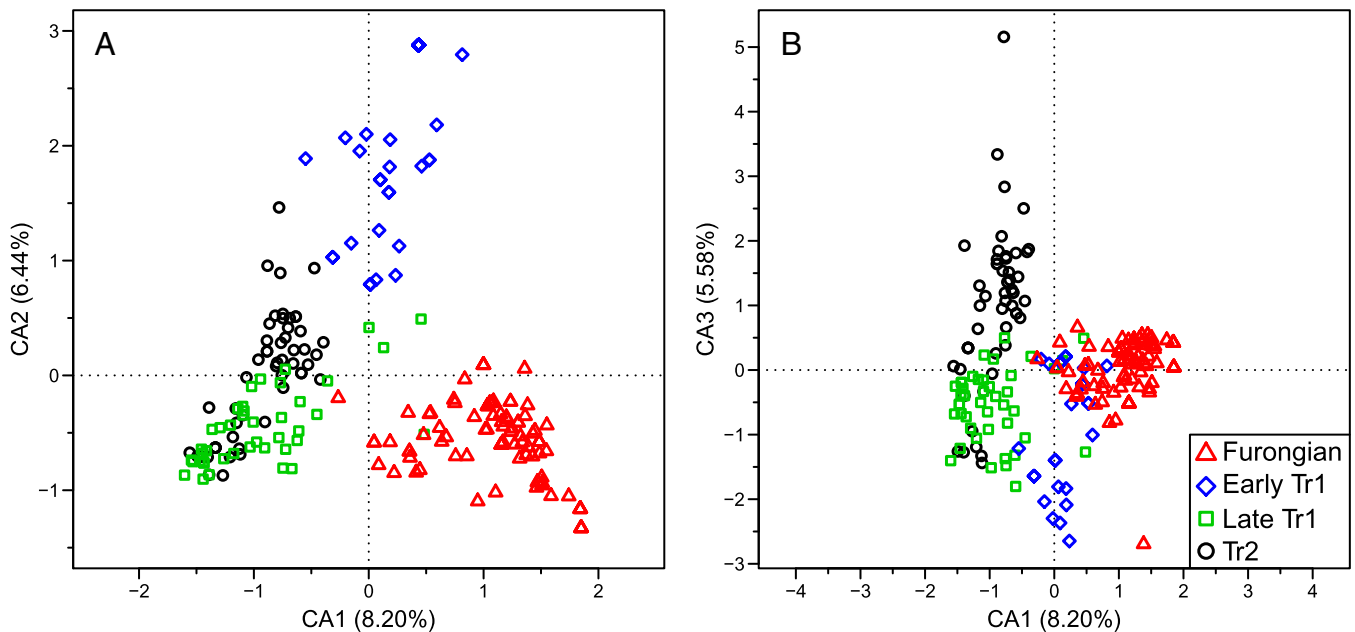


**Fig. 5.** Results of the Correspondance Analysis using all intervals. Note clear separation between groups of samples coming from the same time interval. A) CA1 vs. CA2. B) CA1 vs. CA3.
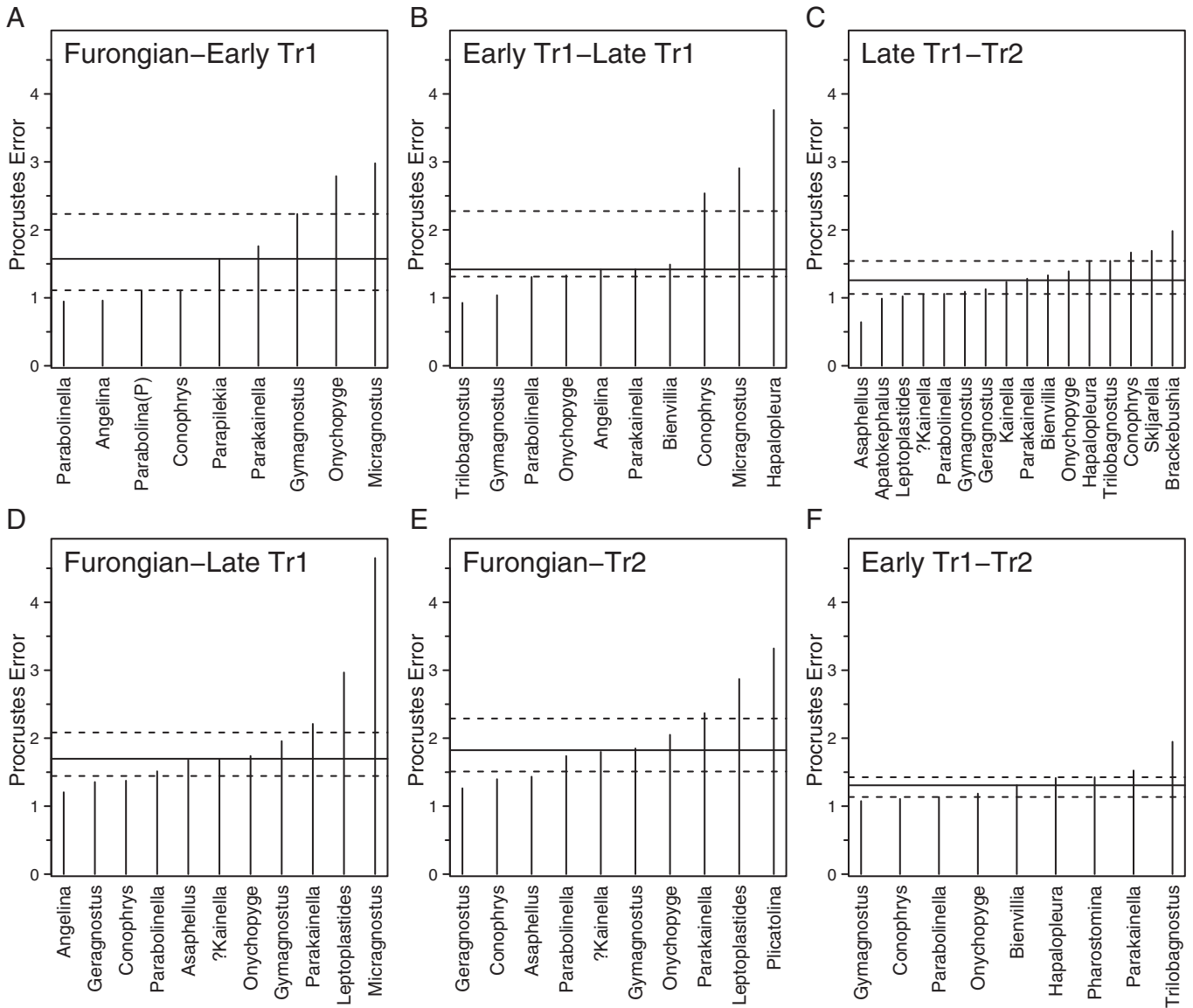
**Fig. 6.** Procrustes errors of each genera in each of the six comparisons. Horizontal solid line indicates median and dashed lines lower and upper quartiles.

plots we can observe that there are variable directions of change. Those taxa with high Procrustes errors tend to have opposite or perpendicular directions, indicating that they do not respond in groups.

All in all, Procrustes analysis shows that taxa in general do not have constant magnitude and directions of Procrustes errors between comparisons and that taxa with high Procrustes errors do not have similar directions of errors. These patterns suggests that (1) taxa do not hold stable patterns of response to environmental changes, and (2) taxa behave individualistically when facing environmental changes.

### 4.5. Procrustes errors and occupancy

Fig. 8 shows the results of the association between Procrustes errors of the genera in each of the six comparisons between time intervals vs. their mean occupancy in the same intervals. No clear correlation is observed (Fig. 8). Several taxa with low occupancy values have very different values of Procrustes errors (Fig. 8A and B). Only in the late Tr1–Tr2, there seems a correlation (Fig. 8C). There is, however, a particular feature shared by all six plots. Taxa having the very high values of Procrustes error always have extremely low occupancies, while those with high occupancies have usually very low

Procrustes errors (Fig. 8). Indeed, no genera plot in the upper right corner of the graphs (Fig. 8).

### 4.6. Mantel test

Results of the Mantel test are shown in Table 2. We can see that these results indicate intervals have very low correlation values, all of which are not significant based on a sequential Bonferroni correction (Quinn and Keough, 2002). Even in the case of Late Tr1–Tr2, when survivorship is quite high (Table 2), correlation is insignificant indicating that taxa are not associated equally in successive intervals. This means that each genus tends to occur with a different set of taxa at each interval. We should note that these results do not mean that at each interval a given set of taxa consistently co-occur without variation and that these group(s) change between successive intervals. It is possible that in both intervals the co-occurrences of taxa are random. In such case, Mantel's test would indicate that intervals are uncorrelated. Only a significant correlation would imply a clear interpretation, i.e. that taxa are associated equally in both intervals. The latter pattern is expected by community stability; hence by accepting the null hypothesis we can assume that stability is not the rule here.
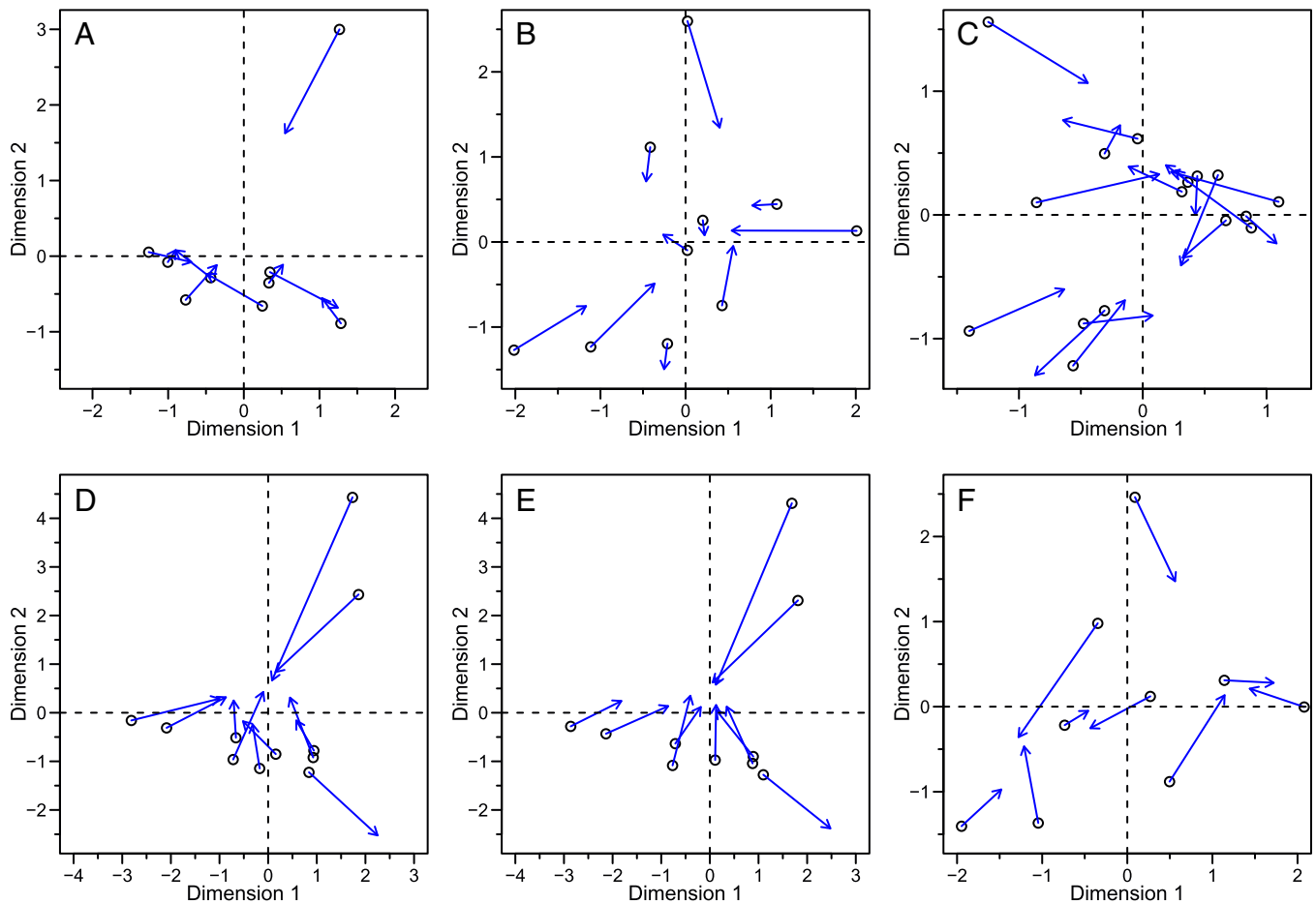
**Fig. 7.** Superimposition plots of each comparison. Points indicate the position of the taxa in the younger interval and arrows in the older interval. The length of the arrow indicates the amount of Procrustes error. Note the variability in the direction and magnitude of Procrustes errors in most comparisons. A) Furongian–Early Tr1. B) Early Tr1–Late Tr1. C) Late Tr1–Tr2. D) Furongian–Late Tr1. E) Furongian–Tr2. F) Early Tr1–Tr2.

## 5. Discussion

As explained above, community stability involves two distinct but related variables. First, the composition between different intervals should not change substantially (Brett and Baird, 1995; Brett et al., 1996). Second, these species should conform to biotic gradients that recur in time accompanying environmental changes (mainly sea level changes) (Morris et al., 1995; Brett et al., 1996, 2007a).

The overall pattern of coordinated stasis is one of time intervals where change is minimal, separated by short times of restructuring and speciation (Brett et al., 1996). Such units, called Ecological Evolutionary Subunits (EESUs), have approximate durations of 5 ma. (Brett et al., 2009; Ivany et al., 2009). The four intervals analyzed in this contribution have together an approximate duration of 5 ma., therefore comparable to a single EESU studied by Brett et al. (1996, 2009), Bonuso et al. (2002a,b), and Ivany et al. (2009) in the Middle Devonian Appalachian Basin, where coordinated stasis was originally defined.

### 5.1. Stability in faunal composition

Brett and colleagues (Brett and Baird, 1995; Brett et al., 1996, 2009; Ivany et al., 2009) argue that in the context of coordinated stasis, the EESUs exhibit very low turnover and are separated by very short intervals of high turnover. Hence, samples coming from similar environmental settings tend to be compositionally very similar during long time intervals (Brett et al., 2007a; Ivany et al., 2009). In

this study the results of the CA using all data suggest, at first glance, that there is a clear differentiation between the intervals relative to their composition.

The analysis of taxonomic turnover indicates a high degree of generic replacement among intervals. Such rates contrast with the predictions of coordinated stasis. The values we found at the boundaries of the four time intervals are of the same magnitude as those at the boundaries of EESUs (Brett et al., 2009). However, as mentioned above, individual intervals are much shorter than most EESUs from the Appalachian Basin. Eventually, we could have expected a single event of high turnover while all other interval boundaries recorded low turnover. However that is not shown in our results because all boundaries have similar amount of turnover. The somewhat high regional turnover observed in our results occurs regardless that many taxa (23 genera) are present in the genera-pool in all four time intervals, indicating the relevance of migration in the assembly of communities. Moreover, our results do not show a pattern of bimodal turnover, which is expected in the scenario of coordinated stasis (Brett and Baird, 1995).

Although this evidence favors compositional instability at time scales of 5 ma., it could be possible that stability is present at a lower temporal resolution. Each of the four ~1.5 to 2 ma. intervals analyzed in this study could be analogous to Middle Devonian EESUs. This could mean that blocks showing compositional stability were shorter for the Cambrian–Lower Ordovician faunas than for the Middle Paleozoic. In fact, some recent results have shown that even a few of the EESUs in the Middle Devonian last for approximately 1 to 2 ma.
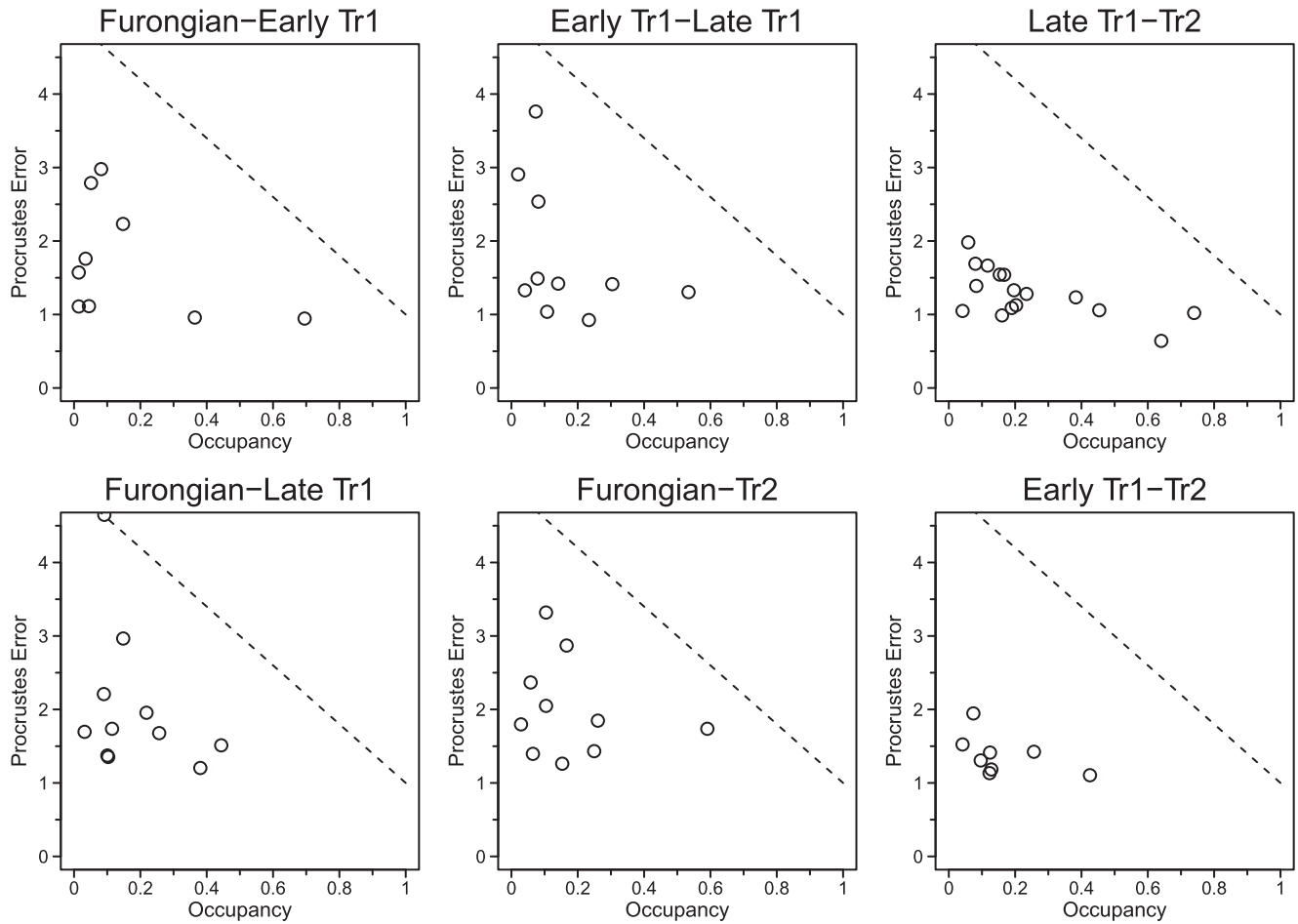
**Fig. 8.** Genera Procrustes errors vs. their occupancy for each of the six comparisons. Note that no genera plot in the upper right corner of the graphs.

(Brett et al., 2009). Unfortunately, the complicated regional stratigraphic framework in the Cordillera Oriental prevents studies at such fine scale. Hence, at this stage, we can only assert that communities in the Cordillera Oriental do not show stability at temporal scales similar to most of the EESUs defined for the Middle Devonian of North America (Brett et al., 2009).

On the other hand, the dynamics of immigration and emigration also indicate instability in the composition of metacommunities. In the context of coordinated stasis and habitat tracking, we might expect that taxa migrate in groups in and out of the basin, following environmental changes (Buzas and Culver, 1998). Our results do not

support such a dynamic, as there is not even one pair of taxa that immigrate and emigrate together. As a consequence of such dynamics of migration, each interval has an idiosyncratic generic composition although most taxa persist in the genera-pool through more than one interval.

Westrop (1996) discussed the possibility that communities dominated by taxa with high turnover rates show temporal stability, comparable to that of coordinated stasis, at generic but not at specific level. However, our results indicate that even at generic level, regional compositional stability is too low to be comparable to that expected by coordinated stasis at time scales close to 5 ma. Moreover, our results also show that much of the generic turnover between intervals is due to local/regional extinction and immigration and not to evolutionary turnover. Hence, compositional stability is not only dependent on whether taxa have high or low evolutionary turnover, but on the openness of communities to immigration and emigration.

### 5.2. Stability of biotic gradients and habitat tracking

Despite the low recurrence of taxonomic composition between intervals, we could expect that the few taxa surviving in different intervals were arranged similarly along biotic gradients. In other words, surviving taxa could show a pattern of biofacies recurrence similarly to that discussed by Brett (1998; Brett et al., 2007b).

The first issue to be tackled is whether taxa respond in groups or individually. The Mantel test and Procrustes superimposition indicate that the taxa do not respond together to environmental changes, being in conflict with the original conceptual framework of habitat

**Table 2**
Results of the Mantel test. Upper values indicate Spearman's correlation value. Lower values indicate probabilities. All probability values are insignificant based on a sequential Bonferroni correction.

| Without singletons | | | | |
|---|---|---|---|---|
| | Furongian | Early Tr1 | Late Tr1 | Tr2 |
| Furongian | – | 0.1945 | 0.3415 | 0.04172 |
| Early Tr1 | 0.32474 | – | 0.1422 | 0.07387 |
| Late Tr1 | 0.0246 | 0.279 | – | 0.2398 |
| Tr2 | 0.4046 | 0.3582 | 0.014 | – |

| With singletons | | | | |
|---|---|---|---|---|
| Furongian | – | 0.2904 | 0.2012 | 0.1 |
| Early Tr1 | 0.047 | – | 0.1704 | 0.2469 |
| Late Tr1 | 0.0844 | 0.1816 | – | 0.2398 |
| Tr2 | 0.253 | 0.0278 | 0.0152 | – |

tracking (Brett et al., 1990), but taxa respond individualistically as indicated in other studies (Buzas and Culver, 1994, 1998; Jackson and Overpeck, 2000; Olszewski and Patzkowsky, 2001). Once this individualistic response is established, the difficulty arises when trying to decipher the nature of the processes underlying this pattern (Brett et al., 2007b). There seem to be only a few ways to test if habitat tracking is relevant or not (Brett et al., 2007b). Since it necessarily means that the presence or absence of a taxon responds to deterministic processes, Brett et al. (2007b) identified five different fundamental lines of evidence in favor of it. Two of these are essential for our study, namely; (1) the recurrence of similar biotic gradients at different time intervals, and (2) the environmental fidelity of stenotopic taxa.

Relative to the first test, our results indicate that surviving taxa rarely maintain their relationships along biotic gradients. Both Procrustes superimposition and Mantel tests showed that taxa are grouped differently between intervals, not supporting a deterministic response of biotic gradients. Hence, in each case the metacommunity is not only reassembled by a new combination of taxa but also has a different structure of the biotic gradient.

Second, it could be argued that the instability in biotic gradients is caused by eurytopic taxa. Generalists can survive in a wide range of conditions, so they should be prone to change in their positions along the gradients much more frequently than specialists (=stenotopes). Since there is a positive relationship between niche breadth and abundance of both fossil and extant taxa (Brown, 1995; McKinney, 1996; Gaston and Spicer, 2001), we can suppose that rare taxa are the most stenotopic ones. Given this scenario, we should expect that taxa having low occupancies also have little difference in their positions along gradients (i.e. low Procrustes errors). Our results show some variability in the magnitude of Procrustes errors, but in all cases we have found an inverse relationship between their maximum values and occupancy. This relationship is in contrast to expectations for stenotopes in case habitat tracking is an important process.

### 5.3. Metacommunity dynamics and habitat tracking

The observed pattern in the Cordillera Oriental could be explained by different processes. One possibility is that the metacommunities are governed only by strictly stochastic processes. This scenario would match the neutral theory of biogeography and biodiversity put forward by Hubbell (2001). However, Balseiro et al. (2011a,b) showed that the biotic gradients in the Furongian and the Tr2 from Cordillera Oriental were arranged along environmental gradients. Such an arrangement is not expected by the neutral theory, but by models that include some processes related to taxa's habitat preferences (Leibold et al., 2004; Cottenie, 2005; Chase and Bengtsson, 2010). Therefore, the possibility that metacommunities studied herein behave as neutral systems seems unlikely (Balseiro et al., 2011b).

A more probable scenario is one in which different groups of taxa make up the metacommunity in each interval. Which taxa were present or absent would be caused partially by stochastic processes such as migration. The different combinations of taxa, coupled with subtle environmental changes, would yield different results of interspecific interactions. This would modify the structure of the biotic gradients (Jackson and Overpeck, 2000; Vázquez, 2005). Hence, the instability of biotic gradients could be caused by both stochastic (migration) and deterministic (habitat preferences and biotic interactions) processes.

Recent revisions of the concept of habitat tracking propose that this mechanism occurs at the individual level (Brett et al., 2007b), rather than at the community level (Brett et al., 1990; Brett, 1998). However, by redefining this concept in an individualistic way, it loses relevance in discussions about community stability. For example, under such a dynamic it is quite possible that habitat tracking is real but there is little or no recurrence of communities in time due

to small environmental changes unnoticeable in the sedimentary record (Jackson and Overpeck, 2000).

On the other hand, no one would reject the idea that taxa have a preferred habitat and that their distribution will be somehow related to that preference (Brown, 1995; Jackson and Overpeck, 2000; Vázquez, 2005). As mentioned previously, the assembly–disassembly hypothesis argues that migration plays an important role in community composition, but never rules out the existence of deterministic processes (Buzas and Culver, 1998). Hence, assembly–disassembly should be envisioned as a metacommunity model taking into account dispersal and niche related processes (species sorting, Leibold et al., 2004), operating at larger spatial and temporal scales.

As explained by Vellend (2010) most, if not all, patterns in community ecology can be understood in light of four processes; namely, ecological drift, dispersal, ecological selection, and speciation. Following Vellend (2010, and references therein) ecological drift is defined as the random changes in species relative abundances caused by population stochasticity, while dispersal refers to the movement of individuals across space. Ecological selection is the deterministic fitness difference between individuals of different species, e.g. niche processes such as habitat preferences (Vellend, 2010).

Based on this framework, we should be able to understand habitat tracking as a consequence of the interaction of one or more of these four processes. As mentioned by Vellend (2010), the same pattern can be explained by different combinations of these four processes and many other possible explanations can be elucidated. For example, habitat tracking could be a consequence of the interplay of species' dispersal and habitat preferences. If metacommunities were governed by ecological selection and intermediate dispersal (i.e., species sorting sensu Leibold et al., 2004); then with gradual environmental changes (such as small rise and fall of sea level), we should expect at least some species to track their preferred habitats. The latter dynamic would yield as a result individualistic habitat tracking. However, whenever dispersal is limited, the assembly of local communities would not be so deterministic (Hubbell, 2001; Leibold et al., 2004). This could happen, for example, in the case of important regional regressions and transgressions where the whole regional community should be reassembled based on dispersal from the species pool (Miller, 1990; Buzas and Culver, 1998).

Since habitat tracking can be described as a result of a combination of some of the four processes mentioned above, it seems best understood as a pattern rather than as a process. There is no convincing signal to support a dichotomy between individualistic habitat tracking vs. assembly–disassembly (=metacommunity theory) as suggested by Brett et al. (2007b). Finally, we should remark that the pattern of individualistic habitat tracking is definitely present in some taxa, but the question is how frequent it is and how deterministic the assembly of communities is in the fossil record.

### 6. Conclusions

The metacommunities from the Cordillera Oriental show relatively high compositional differences between time intervals. Such a pattern contrasts with the expectations of coordinated stasis for time scales close to 5 ma. Although mechanisms of community assembly are difficult to assess, the composition of the studied communities seems to depend, in a large percentage, on migration. Following the trajectories of community dynamics through time and space it becomes plausible that in each interval many taxa migrate in and out of the basin, reassembling the metacommunity. After such reassembling, biotic gradients formed are unique and surviving taxa do not co-occur in similar ways. In particular, the major differences are found in rare taxa which are in turn the most stenotopic ones.

In a broad sense, the evidence suggests that migration and other non-deterministic processes are of great importance in the composition of local and regional communities. Such a combination of

processes and compositional instability is better understood in the conceptual framework of assembly–disassembly dynamics. Finally, the concept of individualistic habitat tracking is more clearly interpreted as a consequence of metacommunity dynamics than as a process by itself.

## Appendix A. Supplementary information

Supplementary data to this article can be found online at http:// dx.doi.org/10.1016/j.palaeo.2012.11.019.

## Acknowledgments

## References

Astini, R.A., 2003. Sedimentación, Facies, Discordancias y Evolución Paleoambiental durante el Cambrico-Ordovicico. In: Coira, B., Zappettini, E.O. (Eds.), Geologia y Recursos Naturales de Jujuy Relatorio del XVII Congreso Geológico Argentino. Asociación Geológica Argentina, Buenos Aires, Argentina, pp. 50–73.

Astini, R.A., 2005. Las sedimentitas que apoyan en no concordancia sobre el "granito rojo" en el angosto de la Quesera (Cordillera Oriental, Salta): una revisión crítica a más de 60 años de los trabajos pioneros de J. Keidel. Revista de la Asociación Geológica Argentina 60, 513–523.

Astini, R.A., 2008. Sedimentación, Facies, Discordancias y Evolución Paleoambiental durante el Cambrico-Ordovicico. In: Coira, B., Zappettini, E.O. (Eds.), Geologia y Recursos Naturales de Jujuy Relatorio del XVII Congreso Geológico Argentino. Asociación Geológica Argentina, Buenos Aires, Argentina, pp. 50–73.

Balseiro, D., Marengo, L.F., 2008. Tremadocian Trilobite Assemblages from the Argentine Cordillera Oriental. A preliminary analysis. In: Rabano, I., Gozalo, R., Garcia-Bellido, D. (Eds.), Advances in trilobite research. Instituto Geológico y Minero de España, Madrid, España, pp. 33–40.

Balseiro, D., Waisfeld, B.G., Buatois, L.A., 2011a. Unusual trilobite biofacies from the Lower Ordovician of the Argentine Cordillera Oriental: new insights into olenid palaeoecology. Lethaia 44, 58–75.

Balseiro, D., Waisfeld, B.G., Vaccari, N.E., 2011b. Paleoecological dynamics of Furongian (Late Cambrian) Trilobite-dominated communities from Northwestern Argentina. Palaios 26, 484–499.

Bambach, R.K., 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology 3, 152–167.

Bambach, R.K., Bennington, J.B., 1996. Do communities evolve? A major question in evolutionary paleoecology. In: Jablonski, D., Erwin, D.H., Lipps, J.H. (Eds.), Evolutionary Paleobiology. The University of Chicago Press, Chicago, pp. 123–160.

Bambach, R.K., Bush, A.M., Erwin, D.H., 2007. Autecology and the filling of ecospace: key metazoan radiations. Palaeontology 50, 1–22.

Bennington, J.B., Bambach, R.K., 1996. Statistical testing for paleocommunity recurrence: are similar fossil assemblages ever the same? Palaeogeography, Palaeoclimatology, Palaeoecology 127, 107–133.

Bergström, S.M., Chen, X., Gutiérrez-Marco, J.C., Dronov, A., 2009. The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to δ 13 C chemostratigraphy. Lethaia 42, 97–107.

Bonuso, N., Newton, C., Brower, J., Ivany, L.C., 2002a. Statistical testing of community patterns: uppermost Hamilton Group, Middle Devonian (New York State: USA). Palaeogeography, Palaeoclimatology, Palaeoecology 185, 1–24.

Bonuso, N., Newton, C.R., Brower, J.C., Ivany, L.C., 2002b. Does coordinated stasis yield taxonomic and ecologic stability?: Middle Devonian Hamilton Group of central New York. Geology 30, 1055–1058.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27, 325–349.

Brett, C.E., 1998. Sequence stratigraphy, paleoecology, and evolution; biotic clues and responses to sea-level fluctuations. Palaios 13, 241–262.

Brett, C.E., Baird, G.C., 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. In: Erwin, D.H., Anstey, R.L. (Eds.), New approaches to speciation in the fossil record. Columbia University Press, New York, pp. 285–315.

Brett, C.E., Miller, K.B., Baird, G.C., 1990. A temporal hierarchy of paleoecologic processes within a Middle Devonian epeiric sea. In: Miller, W. (Ed.), Paleocommunity Temporal Dynamics: The Long-term Development of Multispecies Assemblage. The Paleontological Society, Knoxville, Tennessee, pp. 178–209.

Brett, C.E., Ivany, L.C., Schopf, K.M., 1996. Coordinated stasis: an overview. Palaeogeography, Palaeoclimatology, Palaeoecology 127, 1–20.

Brett, C.E., Hendy, A.J.W., Bartholomew, A.J., Bonelli, J.R.J., McLaughlin, P.I., 2007a. Response of shallow marine biotas to sea-level fluctuations: a review of faunal replacement and the process of habitat tracking. Palaios 22, 228–244.

Brett, C.E., Bartholomew, A.J., Baird, G.C., 2007b. Biofacies recurrence in the Middle Devonian of New York State: an example with implications for evolutionary paleoecology. Palaios 22, 306–324.

Brett, C.E., Ivany, L.C., Bartholomew, A.J., DeSantis, M.K., Baird, G.C., 2009. Devonian ecological-evolutionary subunits in the Appalachian Basin: a revision and a test of persistence and discreteness. Geological Society, London, Special Publications 314, 7–36.

Brown, J.H., 1995. Macroecology. University of Chicago Press, p. 269.

Buatois, L.A., Moya, M.C., Mángano, M.G., Malanca, S., 2003. Paleoenvironmental and sequence stratigraphy framework of the Cambrian–Ordovician transition in the Angosto del Moreno Area, Northwest Argentina. In: Albanesi, G.L., Beresi, M.S., Peralta, S.H. (Eds.), Ordovician from the Andes. INSUGEO, Tucumán, pp. 397–401.

Buatois, L.A., Zeballo, F.J., Albanesi, G.L., Ortega, G., Vaccari, N.E., Mángano, M.G., 2006. Depositional environmets and stratigraphy of the Upper Cambrian–Lower Ordovician Santa Rosita Formation at the Alfarcito area, Cordillera Oriental, Argentina: integration of biostratigraphic data within a sequence stratigrafic framework. Latin American Journal of Sedimentology and Basin Analysis 13, 1–29.

Buatois, L.A., Mángano, M.G., Brussa, E.D., Benedetto, J.L., Pompei, J.F., 2009. The changing face of the deep: colonization of the Early Ordovician deep-sea floor, Puna, northwest Argentina. Palaeogeography, Palaeoclimatology, Palaeoecology 280, 291–299.

Buzas, M.A., Culver, S.J., 1994. Species pool and dynamics of marine paleocommunities. Science 264, 1439–1441.

Buzas, M.A., Culver, S.J., 1998. Assembly, disassembly, and balance in marine paleocommunities. Palaios 13, 263–275.

Chase, J.M., Bengtsson, J., 2010. Increasing Spatio-temporal Scales: Metacommunity Ecology. In: Verhoef, H.A., Morin, P.J. (Eds.), Community Ecology: Processes, Models and Applications. Oxford University Press Inc., New York, pp. 57–69.

Clements, F.E., 1916. Plant Succession: an Analysis of the Development of Vegetation, 242. Carnegie Institute Washington Publication, pp. 1–512.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8, 1175–1182.

Dietz, E.J., 1983. Permutation tests for association between two distance matrices. Systematic Zoology 32, 21–26.

Dimichele, W.A., Behrensmeyer, A.K., Olszewski, T.D., Labandeira, C.C., Pandolfi, J.M., Wing, S.L., Bobe, R., 2004. Long-term stasis in ecological assemblages: evidence from the Fossil Record. Annual Review of Ecology, Evolution, and Systematics 35, 285–322.

Egenhoff, S.O., 2007. Life and death of a Cambrian–Ordovician basin: an Andean three-act play featuring Gondwana and the Arequipa–Antofalla terrane. Geological Society of America Special Papers 423, 511–524.

Esteban, S.B., Tortello, M.F., 2007. Latest Cambrian sedimentary settings and trilobite faunas from the western Cordillera Oriental, Argentina. Memoirs. Association of Australasian Palaeontologists 34, 431–460.

Fall, L.M., Olszewski, T.D., 2010. Environmental disruptions influence taxonomic composition of brachiopod paleocommunities in the Middle Permian Bell Canyon Formation (Delaware basin, west Texas). Palaios 25, 247–259.

Foote, M., 1988. Survivorship analysis of Cambrian and Ordovician trilobites. Paleobiology 14, 258–271.

Forcino, F.L., Stafford, E.S., Warner, J.J., Webb, A.E., Leighton, L.R., Schneider, C.L., Michlin, T.S., Palazzolo, L.M., Morrow, J.R., Schellenberg, S.A., 2010. Effects of data categorization on paleocommunity analysis: a case study from the Pennsylvanian Finis Shale of Texas. Palaios 25, 144–157.

Fortey, R.A., Cocks, L.R.M., 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. Earth-Science Reviews 61, 245–307.

Gaston, K.J., Spicer, J.I., 2001. The relationship between range size and niche breadth: a test using five species of Gammarus (Amphipoda). Global Ecology and Biogeography 10, 179–188.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M., Lawton, J.H., 2000. Abundance-occupancy relationships. Journal of Applied Ecology 37, 39–59.

Gleason, H.A., 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53, 7–26.

Hanski, I., 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38, 210–221.

Harrington, H.J., Leanza, A.F., 1957. Ordovician Trilobites of Argentina. University of Kansas Press, Lawrence, p. 276 (University).

Hoffman, A., 1979. Community paleoecology as an epiphenomenal science. Paleobiology 5, 357–379.

Holland, S.M., Patzkowsky, M.E., 2007. Gradient Ecology of a Biotic Invasion: Biofacies of the Type Cincinnatian Series (Upper Ordovician), Cincinnati, Ohio Region, Usa. Palaios 22, 392–407.

Holterhoff, P.F., 1996. Crinoid biofacies in Upper Carboniferous cyclothems, midcontinent North America: faunal tracking and the role of regional processes in biofacies recurrence. Palaeogeography, Palaeoclimatology, Palaeoecology 127, 47–81.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ, p. 375.

Ivany, L.C., Brett, C.E., Wall, H.L.B., Wall, P.D., Handley, J.C., 2009. Relative taxonomic and ecologic stability in Devonian marine faunas of New York State: a test of coordinated stasis. Paleobiology 35, 499–524.

Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 26, 194–220.

Jackson, J.B.C., Budd, A.F., Pandolfi, J.M., 1996. The shifting balance of natural communities? In: Jablonski, D., Erwin, D.H., Lipps, J.H. (Eds.), Evolutionary Paleobiology. The University of Chicago Press, Chicago, pp. 89–122.

*D. Balseiro, B.G. Waisfeld / Palaeogeography, Palaeoclimatology, Palaeoecology 370 (2013) 64–76*

Johnson, R.G., 1972. Conceptual models of benthic marine communities. In: Schopf, T.J.M. (Ed.), Models in paleobiology. Freeman, Cooper, San Francisco, pp. 148–159.

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd English Edition. Elsevier Science, Amsterdam, p. xv + 853.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7, 601–613.

Ludvigsen, R., Westrop, S.R., Pratt, B.R., Tuffnell, P.A., Young, G.A., 1986. Dual biostratigraphy: zones and biofacies. Geoscience Canada 13, 139–154.

Mángano, M.G., Buatois, L.A., 2003. El Paleozoico inferior de la sierra del Campo, provincia de Tucumán: Nuevos datos sobre la prolongación austral de la cuenca eoplaeozoica del noroeste argentino. Revista de la Asociación Geológica Argentina 58, 623–628.

Mángano, M.G., Buatois, L.A., 2004. Integración de estratigrafía secuencial, sedimentología e icnología para un análisis cronoestratigráfico del Paleozoico inferior del noroeste argentino. Revista de la Asociación Geológica Argentina 59, 273–280.

Mángano, M.G., Buatois, L.A., Muniz Guinea, F., 2005. Ichnology of the Alfarcito Member (Santa Rosita Formation) of northwestern Argentina: animal–substrate interactions in a lower Paleozoic wave-dominated shallow sea. Ameghiniana 42, 641–668.

Marengo, L.F., 2011. Análisis tafonómico en los depósitos bioclásticos del Grupo Santa Victoria (Cámbrico Tardío-Ordovícico Temprano), Cordillera Oriental argentina. Doctorado En Ciencas Geológicas, Universidad Nacional de Córdoba, Argentina. PhD Thesis.

McGeoch, M.A., Gaston, K.J., 2002. Occupancy frequency distributions: patterns, artefacts and mechanisms. Biological Reviews 77, 311–331.

McKinney, M.L., 1996. The biology of fossil abundance. Revista Española de Paleontología 11, 125–133.

Miller, W., 1990. Community replacement pathways: what do fossil sequences reveal about marine ecosystem transitions? In: Miller, W. (Ed.), Paleocommunity Temporal Dynamics: The long-term development of multispecies assemblage. The Paleontological Society, Knoxville, Tennessee, pp. 262–272.

Morris, P.J., Ivany, L.C., Schopf, K.M., Brett, C.E., 1995. The Challenge of Paleoecological Stasis: Reassessing Sources of Evolutionary Stability. Proceedings of the National Academy of Sciences of the United States of America 92, 11269–11273.

Moya, M.C., Monteros, J.A., 2000. El Angosto del Moreno (Cordillera Oriental Argentina), un área clave para analizar el límite Cámbrico-Ordovícico y la discordancia Iruya. Actas Congreso Geológico Boliviano 1, 142–147.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2012. R package version 2.0-4. Community Ecology Package, Vegan.

Olszewski, T.D., Erwin, D.H., 2009. Change and stability in Permian brachiopod communities from western Texas. Palaios 24, 27–40.

Olszewski, T.D., Patzkowsky, M.E., 2001. Measuring recurrence of marine biotic gradients: a case study from the Pennsylvanian–Permian midcontinent. Palaios 16, 444–460.

Patzkowsky, M.E., Holland, S.M., 1997. Patterns of turnover in Middle and Upper Ordovician brachiopods of the eastern United States: a test of coordinated stasis. Paleobiology 23, 420–443.

Peres-Neto, P.R., Jackson, D.A., 2001. How well do multivariate data sets match? The advantages of a procrustean superimposition approach over the Mantel test. Oecologia 129, 169–178.

Peters, S.E., 2004. Evenness of Cambrian–Ordovician benthic marine communities in North America. Paleobiology 30, 325–346.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. American Naturalist 132, 652–661.

Pulliam, H.R., 2000. On the relationship between niche and distribution. Ecology Letters 3, 349–361.

Quinn, G., Keough, M., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK, p. 537.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. Vienna, Austria. (http://www.R-project.org/).

Ricklefs, R.E., 1987. Community diversity: relative roles of local regional processes. Science 235, 172–176.

Ricklefs, R.E., 2008. Disintegration of the ecological community. American Naturalist 172, 741–750.

Ricklefs, R.E., Schluter, D., 1993. Species Diversity in Ecological Communities. Historical and Geographical Perspectives. The University of Chicago Press, Chicago, USA, p. 416.

Robison, R.A., 1972. Mode of Life of Agnostid Trilobites. 24th International Geological Congress, 7, pp. 33–40.

Sepkoski, J.J., 1981. The Uniqueness of the Cambrian Fauna. In: Taylor, M.E. (Ed.), Short Papers for the Second International Symposium on the Cambrian System: U.S. Geol. Surv. Open-File Report, 81–743, pp. 203–207.

Sepkoski, J.J., 1988. Alpha, beta, or gamma: where does all the diversity go? Paleobiology 14, 221–234.

Sokal, R.R., Rohlf, F.J., 1995. Biometry: The Principles of Statistics in Biological Research. W.H. Freeman & Company, New York, USA.

Springer, D.A., Miller, A.I., 1990. Levels of Spatial Variability: The "Community" Problem. In: Miller, W. (Ed.), Paleocommunity Temporal Dynamics: The long-term development of multispecies assemblage. The Paleontological Society, Knoxville, Tennessee, pp. 13–30.

Stanton, R.J.J., Dodd, J.R., 1997. Lack of stasis in late Cenozoic marine faunas and communities, central California. Lethaia 30, 239–256.

Tang, C.M., Bottjer, D.J., 1996. Long-term faunal stasis without evolutionary coordination: Jurassic benthic marine paleocommunities, Western Interior, United States. Geology 24, 815–818.

Terlizzi, A., Anderson, M.J., Bevilacqua, S., Fraschetti, S., Włodarska-Kowalczuk, M., Ellingsen, K.E., 2009. Beta diversity and taxonomic sufficiency: do higher-level taxa reflect heterogeneity in species composition? Diversity and Distributions 15, 450–458.

Tortello, M.F., Esteban, S.B., 2003. Trilobites del Cámbrico Tardío de la Formación Lampazar (sierra de Cajas, Jujuy, Argentina). Implicancias bioestratigráficas y paleoambientales. Ameghiniana 40, 323–344.

Tortello, M.F., Rao, R.I., 2000. Trilobites y conodontes de Ordovícico temprano del Angosto de Lampazar (provincia de Salta, Argentina). Boletin Geologico y Minero 111, 61–84.

Tortello, M.F., Rábano, I., Rao, R.I., Aceñolaza, F.G., 1999. Los trilobites de la transicion Cambrico-Ordovicico en la quebrada Amarilla (Sierra de Cajas, Jujuy, Argentina). Boletin Geologico y Minero 110, 3–20.

Tortello, M.F., Esteban, S.B., Aceñolaza, G.F., 2002. Trilobites from the Base of the Ordovician System in Northwestern Argentina. In: Aceñolaza, F.G. (Ed.), Aspects of the Ordovician System in Argentina. INSUGEO, Tucumán, pp. 131–142.

Turner, J.C.M., 1960. Estratigrafía de la Sierra de Santa Victoria. Boletín De La Academia Nacional De Ciencias De Córdoba 41, 163–196.

Vaccari, N.E., Waisfeld, B.G., Marengo, L.F., Smith, L., 2010. Kainella Walcott, 1925 (Trilobita, Ordovícico Temprano) en el noroeste de Argentina y sur de Bolivia. Importancia bioestratigráfica. Ameghiniana 47, 293–305.

Valentine, J.W., Jablonski, D., 1993. Fossil Communities: Compositional Variation at Maney Scales. In: Ricklefs, R.E., Schluter, D. (Eds.), Species diversity in ecological communities. Historical and geographical perspectives. The University of Chicago Press, Chicago, USA, pp. 341–349.

Vázquez, D.P., 2005. Reconsiderando el nicho hutchinsoniano. Ecologia Austral 149–158.

Vellend, M., 2010. Conceptual synthesis in community ecology. The Quarterly Review of Biology 85, 183–206.

Wagner, P.J., Kosnik, M.A., Lidgard, S., 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. Science 314, 1289–1292.

Waisfeld, B.G., Vaccari, N.E., 2003. Trilobites. In: Benedetto, J.L. (Ed.), Ordovician Fossils of Argentina. Secretaria de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba, pp. 295–409.

Waisfeld, B.G., Vaccari, N.E., 2008. Bioestratigrafía de trilobites del Paleozoico Inferior. In: Coira, B., Zappettini, E.O. (Eds.), Geologia y Recursos Naturales de Jujuy Relatorio del XVII Congreso Geológico Argentino. Asociación Geológica Argentina, Buenos Aires, Argentina, pp. 119–127.

Westrop, S.R., 1996. Temporal persistence and stability of Cambrian biofacies: Sunwaptan (Upper Cambrian) trilobite faunas of North America. Palaeogeography, Palaeoclimatology, Palaeoecology 127, 33–46.

Whittaker, R.H., 1952. A study of summer foliage insect communities in the Great Smoky Mountains. Ecological Monographs 22, 2–44.

Whittaker, R.H., 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26, 1–80.

Zeballo, F.J., Tortello, M.F., 2005. Trilobites del Cambrico tardio-Ordovicico temprano del area de Alfarcito, Tilcara, Cordillera Oriental de Jujuy, Argentina. Ameghiniana 42, 127–142.

Zeballo, F.J., Albanesi, G.L., Ortega, G., 2005. Conodontes y graptolitos de las formaciones Alfarcito y Rupasca (Tremadociano) en el area de Alfarcito, Tilcara, Cordillera Oriental de Jujuy, Argentina. Parte 1: Bioestratigrafia. Ameghiniana 42, 39–46.

Zelditch, M.L., Swiderski, D.L., Sheets, H.D., Fink, W.L., 2004. Geometric Morphometrics for Biologists. Academic Press, San Diego, p. 443.