



Decoupling of local and regional dominance in trilobite assemblages from northwestern Argentina: new insights into Cambro-Ordovician ecological changes

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Components of biodiversity are strongly scale dependent, but the relative importance of the patterns that operate at different scales and the links between them have been overlooked. To disentangle the ecological structure of Cambro-Ordovician trilobite assemblages from the Argentine Cordillera Oriental at different scales, we explore patterns of abundance, dominance and occupancy across the onshore-offshore profile, and through three time intervals: Furongian, earliest Late Tremadocian (Tr2), latest Middle Floian-earliest Late Floian (Fl2-Fl3). At the regional scale, single taxa are overwhelming dominant in the Furongian (*Parabolina*) and in the earliest Late Tremadocian (*Leptoplastides*). Several dominants occur in the Floian, but just one (*Famatinolithus*) attains high occupancy and, rarely, high dominance. In contrast, only the Furongian records highly dominated local assemblages, whereas dominance distinctly decreases among Tr2 and Fl2-Fl3 ones. Thus, when both scales of analysis are combined, an unexpected scenario becomes evident: Tr2 assemblages resemble those of the Furongian at the regional scale, but mirror those of the Floian at the local scale. These results highlight a decoupling in local versus regional structures triggered by an earlier switch in dominance in local communities and a delayed change at the regional scale. Interestingly, this decrease in local dominance matches previous analyses accounting for a coeval step-up in local evenness, suggesting that the Tr2 appears as a pivotal interval in the reorganization of communities in the Cordillera Oriental. This scenario emphasizes that biogeographical regions witnessed different regional-scale processes, and suggests that scaling local and regional patterns provides new insights to unravel the history of biodiversity among benthic communities. □ *Argentina, Cambro-Ordovician, dominance, ecological decoupling, trilobites.*

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The ecological structure of benthic marine communities underwent major changes in Cambrian and Ordovician times. Understanding the spatiotemporal patterns of abundance and distribution of organisms is fundamental to unravelling the processes underlying changes across this critical interval. Extensive studies of local trends in richness and evenness have addressed key aspects of the tempo and mode of the ecological changes (e.g. Peters 2004, 2006; Balseiro & Waisfeld 2014). The global signal of the changes in biodiversity has also been tackled by several authors (e.g. Miller 2004, 2012; Alroy *et al.* 2008). However, biodiversity is shaped by multiple scales and, so far, the relative importance of the patterns that take place at different scales and the links between them have received comparatively little attention. In particular, dominance is a key parameter in the analysis of biodiversity (Hillebrand *et al.* 2008), yet, studies addressing the spatiotempo-

ral variation in the dominance structure are few. Thus, the analysis of the scale of dominance represents an unexplored challenge that promises important insights for unravelling the Early Palaeozoic paleoecological scenario.

The particular structure of Cambrian-Early Ordovician communities has been studied from different perspectives. Local, temporal and environmental trends in evenness and richness, either for trilobite-dominated assemblages or for the whole fauna, have been investigated in great detail by different authors (e.g. Westrop & Adrain 1998; Adrain *et al.* 2000; Peters 2004, 2006; Adrain & Westrop 2005). Alpha and beta diversity structures (e.g. Sepkoski 1981, 1988; Adrain *et al.* 2000), onshore-offshore diversity gradients (Westrop & Cuggy 1999; Westrop & Adrain 2001) and analyses of the structure of abundance distributions (Wagner *et al.* 2006) have also been addressed.

There is now a fairly comprehensive view of these local-scale ecological changes for the whole interval. During the Cambro-Ordovician, local diversity and evenness rose diachronically in different regions and this rise was more pronounced in deep marine environments relative to shallow ones (Adrain *et al.* 2004; Peters 2004; Balseiro & Waisfeld 2014).

In a series of recent contributions, Balseiro *et al.* (2011a,b) and Balseiro & Waisfeld (2013, 2014) tackled a wide range of ecological patterns of the Cambro-Ordovician trilobite assemblages from the Cordillera Oriental. These authors analysed, among other aspects, general ecological dynamics from a metacommunity perspective, relative abundance distributions, diversity and biotic gradient structures, as well as patterns of stability and taxonomic turnover rates. In particular, Balseiro & Waisfeld (2014) analysed temporal trends in richness and evenness among Furongian to Floian communities that thrived in different depositional settings. This analysis largely addressed low evenness at the local scale, and a decoupling in the timing of increase in both indexes, with a rise in evenness (earliest Late Tremadocian, Tr2) well ahead that of richness (latest Tremadocian, Tr3). Interestingly, this earlier step-up in evenness was largely unrelated to trilobite composition or richness at the family level.

The present analysis assesses a quantitative documentation of the abundance and occupancy of Late Cambrian–Early Ordovician dominant trilobite taxa that occurred in a variety of shallow marine settings in the Argentine Cordillera Oriental. Our aim was to compare patterns of local and regional dominance along three time intervals: Furongian, earliest Late Tremadocian (Tr2) and Floian (Fl2–Fl3), and to discuss the consequences of the observed patterns in the general structure of the trilobite assemblages. This study supplements and broadens the coverage of the analysis by Balseiro & Waisfeld (2014) both in its regional scope and in the taxon-based perspective of the analysis.

Regional background

The studied successions lie within the Santa Victoria Group, widespread in the Cordillera Oriental of northwestern Argentina (Fig. 1). These siliciclastic deposits represent the southern extension of the Central Andean Basin that extends farther north into

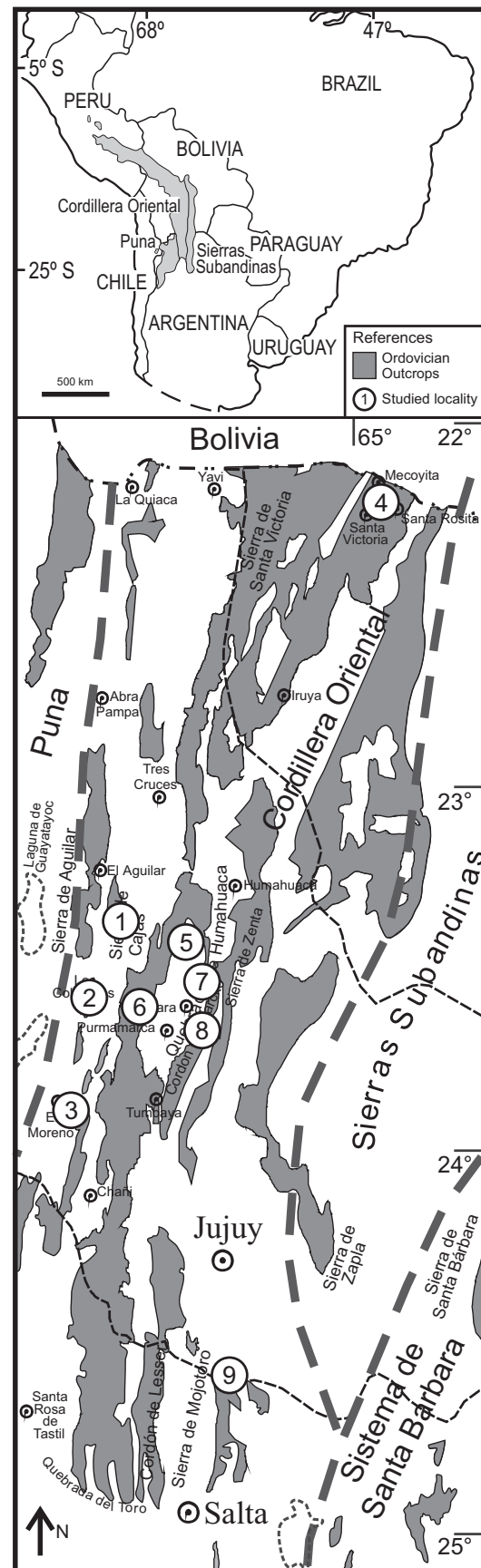


Fig. 1. Map showing location of Central Andean Basin and studied localities in the Argentine Cordillera Oriental. Localities: 1, Sierra de Cajas; 2, Los Colorados; 3, El Moreno; 4, Santa Victoria; 5, Jueya; 6, Quebrada Totora; 7, Arenal; 8, Alfarcito; 9, Ruta Nacional 9. Modified from Astini (2003).

Bolivia and south Peru. From a geodynamic viewpoint, the Cordillera Oriental is interpreted to represent the forebulge (or peripheral bulge) depozone of an extended Ordovician back-arc foreland basin system. Cambro-Ordovician platform deposits developed in a low gradient ramp-like setting. Unusually thick successions were deposited under the influence of an active volcanic-arc complex from the west and large-scale prograding deltaic systems from cratonic areas to the east (Bahlburg & Furlong 1996; Astini 2003).

The Santa Victoria Group includes the Santa Rosita Formation (Furongian–Tremadocian) and the Acoite Formation (Floian). Wave-dominated siliciclastic shelf environments with rare extensions into tide-dominated estuarine complexes during lowstands characterize the depositional history of Furongian–Tremadocian successions (Buatois & Mángano 2003; Buatois *et al.* 2006; Astini 2008). Largely storm- and wave-dominated deltaic systems characterize shallow marine Floian deposits (Astini & Waisfeld 1993; Astini *et al.* 2004). Successions of the Santa Victoria Group are biostratigraphically well constrained on the basis of graptolites, conodonts and trilobites (Albanesi *et al.* 2008; Waisfeld & Vaccari 2008; Toro & Maletz 2009, and references therein).

The analysis of faunal abundance and occupancy is restricted to three distinct time intervals: Furongian, earliest Late Tremadocian (Tr2) and latest Middle Floian–earliest Late Floian (Fl2–Fl3) (Fig. 2). Furongian collections derive from the Lampazar Formation and the Casa Colorada Member of the Santa Rosita Formation that crop out in the western and eastern areas of the Cordillera Oriental, respectively (Fig. 1). According to Buatois *et al.* (2006), this interval records one of the most important basin-wide transgressions in the Cordillera Oriental. Shelf to upper offshore environments are recorded in the western area of the Cordillera Oriental, whereas mostly shelf and offshore transition deposits developed in eastern regions. The Tr2 successions are represented by the Rupasca member of the Santa Rosita Formation, and are largely restricted to the eastern area of the Cordillera Oriental (Fig. 1) as the western successions were truncated by a regional unconformity (Tumbaya unconformity, *cf.* Moya 1999; Astini 2003). According to Balseiro *et al.* (2011a,b), depositional environments are interpreted as shelf (from storm wave base to shelf/slope break) to lower shoreface settings (immediately above fair-weather wave base). The Floian collections come from the middle–upper part of the Acoite Formation that crops out in the western and eastern foothills of the Cordillera Oriental (Fig. 1). Deposits encompass

Series	Stages	N. Am. series	Stage slices	Regional Biostratigraphy		
				Trilobites	Conodonts	
Lower Ordovician	Floian	Ibexian	Fl3			
			Fl2	<i>Famatinolithus</i> fauna	" <i>Gothodus</i> "	
			Fl1	<i>Thysanopyge</i> fauna	No record	
			Tr3	No defined biozone	<i>A. deltatus</i> <i>P. proteus</i>	
			Tr2	<i>N. orthometopa</i> No defined biozone <i>B. tetragonalis</i> <i>Kainella teichii</i>	<i>P. deltifer</i> <i>P. deltifer deltifer</i>	
	Tremadocian		Tr1	<i>Kainella meridionalis</i> ? <i>Kainella andina</i> ? <i>Jujuyaspis keideli</i>	<i>C. angulatus</i> <i>lapetognathus</i>	
			Stage 10	<i>Parabolina (N.) frequens</i>	<i>C. proavus</i>	
	Furongian					

Fig. 2. Correlation chart showing international chronostratigraphy, North American series, Ordovician stage slices and local biostratigraphy. Studied intervals are highlighted in grey. Modified from Waisfeld & Vaccari (2008), Albanesi *et al.* (2008) and Bergström *et al.* (2009).

shelf, lower and upper offshore, offshore transition and shoreface settings developed in a largely wave- and storm-dominated deltaic system. Several large-scale upward thickening and coarsening cycles deposited in increasingly shallow shelf setting are indicative of an active shoreline progradation (Astini & Waisfeld 1993; Astini *et al.* 2004).

Data

The data set for this study comprises 102 bed-level samples, collected from shale intervals. Thirty-seven samples from four Furongian localities, 18 samples from three lowest Upper Tremadocian (Tr2) localities and 47 samples from four Floian localities were studied. The analysis is based essentially on data sets previously assembled by Balseiro & Waisfeld (2014) tallying additional samples from Floian successions. The analysis is conducted at the genus level, including all records that could be identified to this taxonomic level with confidence. The minimum number of individuals (MNI) (Gillinsky & Bennington 1994) counting method was used to score the abundance of trilobite genera. This approach provides a conservative estimation of fossil abundances and avoids bias towards differential preservation potential of

trilobite sclerites. Sample sizes are variable among different environments and time intervals, so a minimum sample size cut-off of 30 individuals was imposed for recoding biological meaningful faunal data (e.g. Bush & Brame 2010). Although the analyses were carried out at the genus level, dominants were essentially monospecific.

Counts were made on shale intervals with comparable taphonomic properties. Low levels of post-mortem disturbance and comparable intensities of taphonomic distortion among Furongian and Floian samples are supported by the analyses of Balseiro *et al.* (2011b) and Waisfeld (1997). Estimation of standard taphonomic criteria such as levels of sorting of trilobite sclerites, orientation, degree of articulation and intensity of fragmentation for samples from the Tr2 interval broadly match the taphonomic signals of the other two intervals. Overall, the analysed samples reflect low, largely within-habitat post-mortem disturbance, and probably comparable levels of time-averaging.

Samples were classified among three major environments, namely shallow sub-tidal (above fair-weather wave base), deep sub-tidal (between fair-weather wave base and maximum storm wave base) and offshore (below maximum storm wave base). This approach represents an oversimplification of the gradient of depth and distance from shore, in order to show general trends of the biota.

It is important to note that there are differences in the environmental coverage of the samples due to the uneven preservation of fossiliferous exposures (Fig. 3). Furongian shallow successions (shoreface and offshore transition settings) were not adequate for sampling; hence, collections are otherwise restricted to upper offshore to shelf environments. Samples from the Tr2 and Fl2–Fl3 intervals record nearly the whole environmental profile. Floian successions preserve a well-represented shoreface setting which has been sampled in detail; however, only a single sample is available from the shelf setting due to the overall lack of benthic fauna in the thick black shale packages of the lower part of the Acoite Formation.

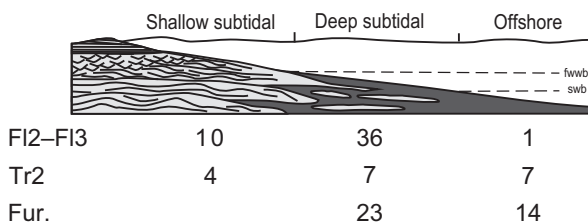


Fig. 3. Environmental distribution of studied samples in each time interval. Abbreviations: Fur., Furongian; fwwb, fair-weather wave base; swb, storm wave base.

Methods

Because neontologists can standardize sampling *a priori*, macroecological studies use absolute numbers of individuals to analyse spatial variation in species abundances. However, the fossil record imposes severe biases regarding the absolute abundance of preserved remains (e.g. Schovsbo 2001). In contrast, fidelity of community-level relative abundance in the sub-fossil record has been addressed quantitatively; thus, this measure has become a valuable tool in palaeoecology (Kidwell 2001; Tomašových & Kidwell 2010).

Therefore, we used relative abundances of taxa in this study. Genera in each sample were ranked according to their abundances, and we defined a dominant taxon as the first-ranked taxon in a sample. Gaston (2011) suggested that common species are those that account for a very high proportion of the total number of individuals in an assemblage and of the total number of locality (or area) occurrences (see also Clapham *et al.* 2006). Therefore, we used two different approaches to characterize ecological dominance at different scales. First, we studied how local dominance is reflected at the regional scale. We analysed dominants' occupancy in each time interval. We also studied their occupancy both as the total number of samples where the taxon was present, and as the total number of samples where the taxon dominated (i.e. it was the most abundant one). A taxon's occupancy is the proportion of available sites that are actually occupied by it (Gaston & He 2011). Occupancy also represents an estimation of the spatial distribution of taxa (Foote *et al.* 2007) and is a proxy for range size (Liow & Stenseth 2007). The breadth of an organism's tolerance is difficult to measure; however, the number and distribution of samples in which it occurs represent a reliable proxy for its environmental tolerance. Thus, taxa with high occupancy are likely to cope with a diverse array of ecological conditions and to have broad environmental tolerance (Bonier *et al.* 2007).

At a second step of the analyses, we focused on how much a dominant taxon actually dominated the local community and on ranking the second dominant. In a previous contribution, we tackled a related aspect by studying evenness in local communities (Balseiro & Waisfeld 2014). However, evenness takes into account all the taxa present in a community and not only the dominant one (Magurran 2004). The Berger–Parker index, which is the proportion of the most abundant taxon (Magurran 2004), represents a more suitable approach to explore dominance. Nevertheless, this index is only sensitive to the most

abundant taxon and, it may give misleading ideas of dominance when there are two or three almost-equally subdominants. Thus, the index does not clearly show how *much* the dominant taxon actually dominates the community (i.e. to what extent the relative abundance of the most abundant taxon exceeds that of the second most abundant one). To discriminate these relationships more effectively and to provide a more ecologically meaningful metric, we used a dominance index by modifying the Berger–Parker index. The dominance index is expressed as

$$\text{Dindex} = \log_2(p_1/p_2)$$

where p_1 is the proportion of the first-ranked taxon and p_2 the proportion of the second-ranked taxon. A value of 1 indicates that the dominant species doubles in abundance the second most abundant one, regardless of the actual abundance of both taxa. We coupled the analysis of dominance with the analysis of the abundance of each dominant taxon in the three studied time intervals.

In the case of regional dominance, we are also interested in both the number of dominants and the proportion of local communities that each taxon dominates. Therefore, for the measurement of regional dominance, we used Simpson's lambda, which is expressed as

$$\lambda = \sum p_i^2$$

where p_i is the proportion of local communities dominated by the i th taxon.

Results

The analysis of local dominance at the regional scale indicates an interesting difference in the number of local dominants between the Furongian and Tr2 assemblages, and those of the Floian. Only two different genera dominate local assemblages in both the Furongian and the Tr2, while six genera dominate local ones in the Floian (Fig. 4). The dominants in the Furongian are *Parabolina* (N.) and *Micragnostus*, in the Tr2 are *Leptoplastides* and *Bienvillia*, while in the Fl2–Fl3 are *Famatinolithus*, *Ampyx*, *Hoekaspis*, *Branisaspis*, *Emanuelaspis* and *Ogyginus*.

The threefold change in the number of local dominants is mirrored by the change in dominants' occupancy structure at the metacommunity scale. As can be observed in Figure 5, dominance in the Furongian and Tr2 is not evenly distributed among the two dominants, meaning that only one of them overwhelming dominates most samples (~90%),

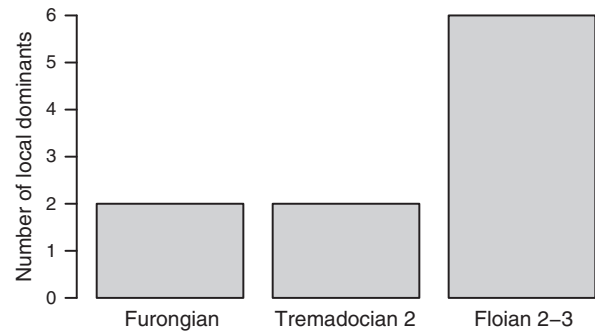


Fig. 4. Number of local dominants in the three studied intervals. Note sharp increase in the number of genera that dominate local assemblages in the Floian. Furongian dominants: *Parabolina* (N.), *Micragnostus*; Tremadocian dominants: *Leptoplastides*, *Bienvillia*. Floian dominants: *Famatinolithus*, *Ampyx*, *Hoekaspis*, *Branisaspis*, *Emanuelaspis*; *Ogyginus*.

whereas the second one actually dominates only a few samples (Fig. 5). Moreover, the most frequent dominant, namely *Parabolina* (N.) in the Furongian and *Leptoplastides* in the Tr2, is also the most frequently recorded taxon at the regional scale in each interval.

In the Floian, however, the frequency of local dominants is more evenly distributed among six different taxa (Fig. 5). *Famatinolithus* attains the highest occupancy, and it is also the most frequent dominant, as it dominates 45% of the samples (Fig. 5). *Ampyx* and *Ogyginus* dominate 25% and 14% of the samples, respectively, while *Hoekaspis*, *Branisaspis* and *Emanuelaspis* are dominant in less than 9% of the samples. Five of six dominants are also the five most frequent taxa in the interval (Fig. 5). *Ogyginus* is the exception as it is present only in a few samples, most of which are dominated by it.

We further studied how such patterns in regional dominance are reflected at the local scale. For this aim, we analysed local dominance among the three intervals. In contrast to what is observed at the regional scale (Fig. 5), dominance at the local scale shows a striking change between the Furongian and the Tr2 (Fig. 6). The Furongian records very highly dominated local assemblages (median Dindex = 3.2), while in the Tr2 and the Floian dominance is lower (Tr2 median Dindex = 1.92; Fl2–Fl3 median Dindex = 1.12). This indicates that while the Tr2 still shows a regional dominance structure similar to the Furongian in having virtually all local assemblages dominated by the same taxon, dominance distinctly decreased at the local scale. Finally, we analysed dominance structure combining two different metrics: Dindex for local dominance and Simpson's lambda for regional dominance. When comparing these indexes, split by environment and

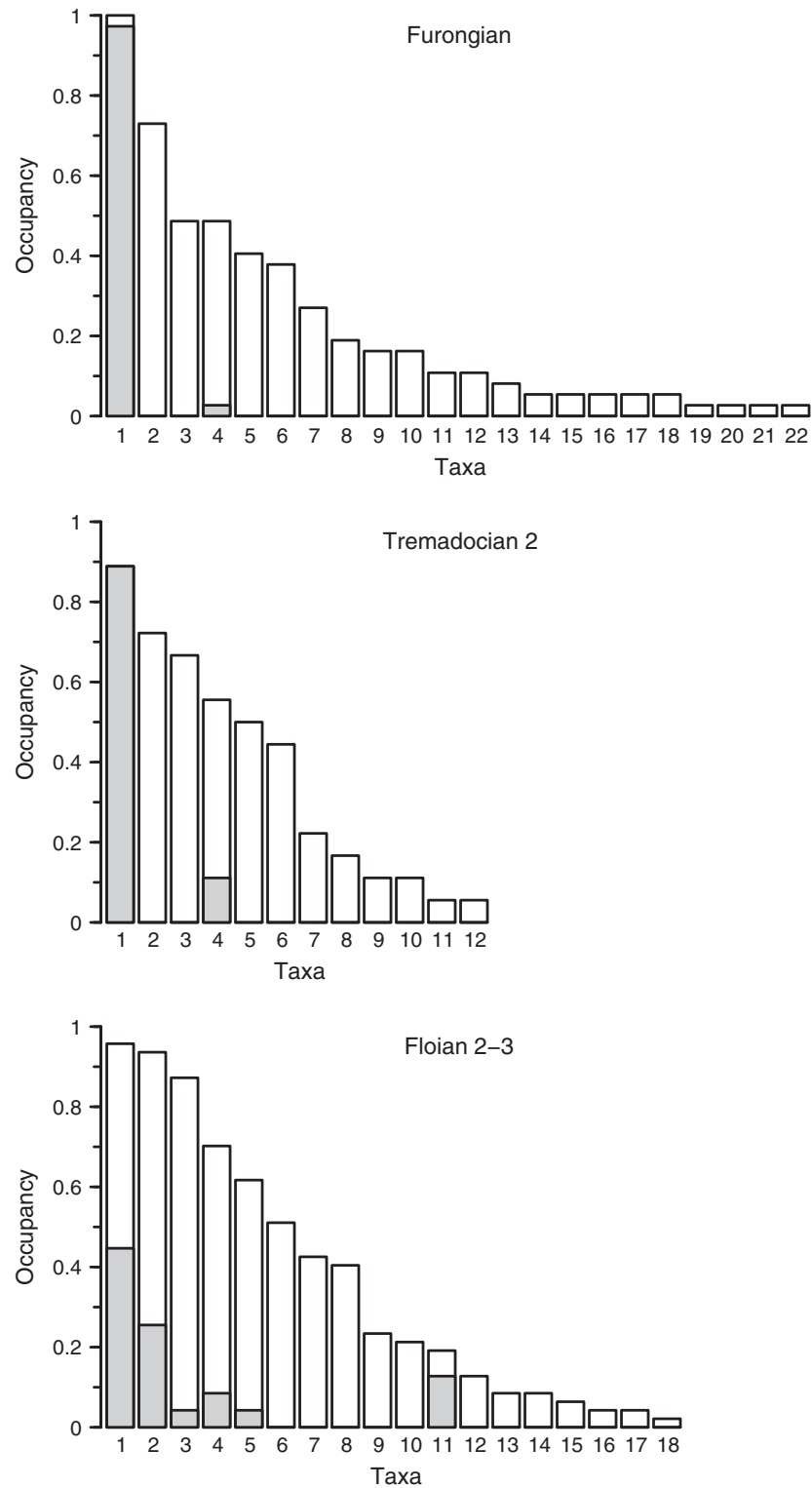


Fig. 5. Occupancy structure in each time interval, measured as the total number of occurrences where a taxon is dominant. Grey bars (proportion of samples where the given taxon dominates) show that a single taxon is highly dominant in most Furongian and Tremadocian samples, while frequency of local dominants is more evenly distributed in Floian ones. Furongian taxa: 1, *Parabolina* (*N.*); 4, *Micrag-nostus*. Tremadocian taxa: 1, *Leptoplastides*; 4, *Bienvillia*. Floian taxa: 1, *Famatinolithus*; 2, *Ampyx*; 3, *Hoekaspis*; 4, *Branisaspis*; 5, *Emanuelaspis*; 11, *Ogyginus*.

through each time interval, it becomes evident that there is a strong drop in local dominance during the Tr2 in all environments, and there are noticeable similarities in regional dominance between the Furongian and the Tr2, for the shallow and deep sub-tidal (Fig. 7). In addition, a trend towards less dominated assemblages at the regional scale can be inferred for the offshore setting as lambda scores for that environment are lower than those of the shallow and deep sub-tidal during both the Furongian and the Tremadocian (Fig. 7).

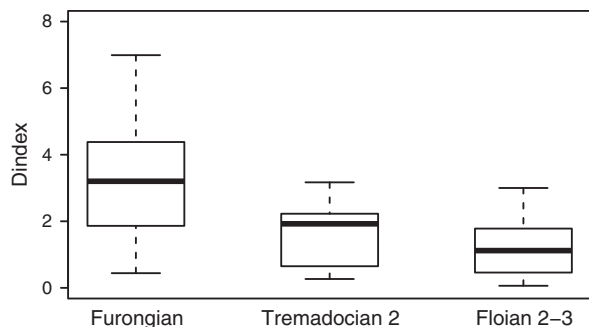


Fig. 6. Boxplot of the variations in local dominance in each time interval. Each box represents two quartiles (50% of the data), the solid horizontal line corresponds to the median values, and the vertical lines show the range (maximum and minimum values). Note significant drop in local dominance between the Furongian and the Tremadocian showing that the dominance structure in the later interval is more similar to that of the Floian.

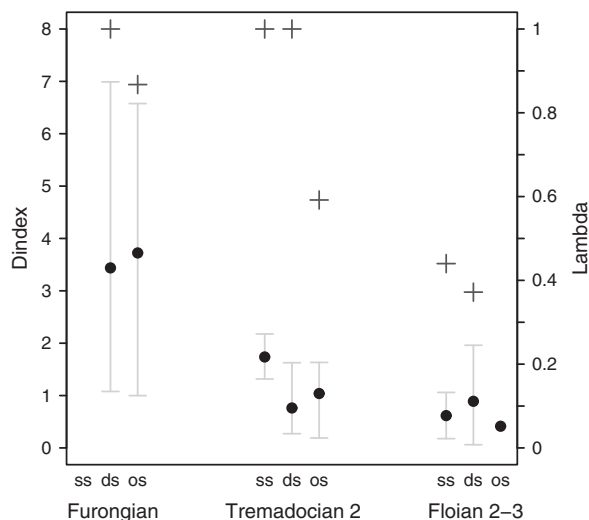


Fig. 7. Boxplot showing regional dominance measured by Simpson's lambda (crosses) and local dominance by Dindex, broken down by environment and time interval. Black circles represent median Dindex in each setting and whiskers correspond to 95% Dindex values. Lambda was not calculated for the Floian offshore because only a single sample is available. Note similar local dominance scores between the Tr2 and the Floian for the whole environmental gradient. Regional dominance values of the Tr2 closely resemble those of the Furongian for the shallow and deep sub-tidal, whereas a trend towards lower dominance in the offshore is evident for both intervals.

As the last step in the analysis, we studied in detail the abundance of each dominant in the three intervals. In the Furongian, *Parabolina* (*N.*) nearly always holds very high abundance, and it frequently achieves abundances between 70% and 100% (median abundance = 86.2%), being rare (<10%) just in one sample (Fig. 8). The opposite is observed for *Micragnostus*, which is most frequently a rare taxon with abundances lower than 10%, reaching 31.5% in the single sample where it dominates (Fig. 8). The analysis of the dominance index reinforces this pattern (Fig. 9), as it shows that *Parabolina* (*N.*) is virtually always double the abundance of the second most abundant taxon (median Dindex = 3.25), frequently reaching very high values of dominance (Dindex >5). The lowest value of dominance that *Parabolina* (*N.*) attains is Dindex = 0.996. However, the single case in which *Micragnostus* dominates corresponds to the lowest value in the interval (Dindex = 0.441). It is also interesting to note that this high dominance is almost invariably attained across the whole sampled depth gradient, regardless of the environmental category (Table 1).

In the Tremadocian (Tr2), *Leptoplastides* is always found in high abundance, between 40% and 90% (median abundance = 68%), and dominates all the samples (Fig. 10). *Bienvillia*, however, is frequently a rare taxon when present, never surpassing 40% (median abundance = 4.6%). It dominates only two samples where its abundance is more than 30% (Fig. 10). Again, this pattern of abundance is reflected in the dominance of local assemblages (Fig. 11). *Leptoplastides*-dominated samples usually have high dominance (median Dindex = 1.98), indicating that this taxon commonly has doubles the abundance of the second most abundant taxon (Fig. 11). Nevertheless, *Leptoplastides* never reaches very high dominance (maximum Dindex = 3.15). The few samples dominated by *Bienvillia*, however, have the lowest values of dominance (Dindex <0.32), indicating that this taxon is almost as abundant as the second most abundant one (Fig. 11). The range of environments sampled for the Tr2 is slightly wider than that of the Furongian. Dominance of *Leptoplastides* covers even the end members of the gradient (Table 2), that is dysoxic black shales of the offshore environment and oxygenated high-energy lower shoreface settings (Balteiro *et al.* 2011a).

The Floian shows a different pattern in the abundance of the dominant taxa, as no one has invariable high abundance (Fig. 12). Only *Famatinolithus* attains a rather regular high abundance (>40%, Fig. 12), but still much lower (median abundance = 27.2%) than the most important dominants in previous intervals. It dominates virtually all the samples

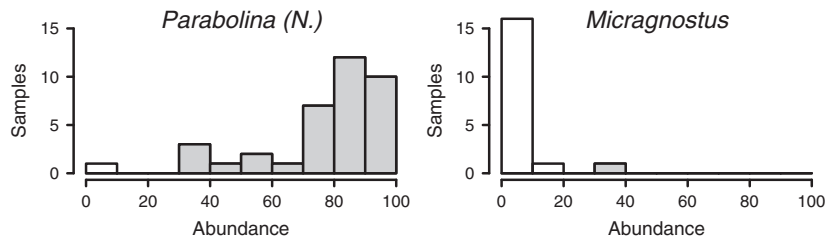


Fig. 8. Histograms of local abundance of dominants in the Furongian. Grey bars indicate samples where the given taxon dominates.

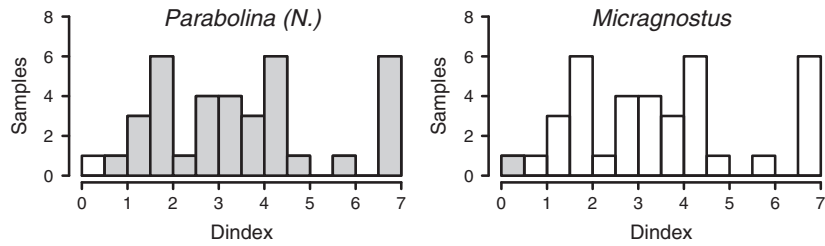


Fig. 9. Histograms of local dominance in the Furongian. Grey bars indicate samples where the given taxon dominates.

Table 1. Abundance and occupancy of dominant taxon in each environment during the Furongian.

	Shallow Sub-tidal			Deep Sub-tidal			Offshore		
	Abundance	Dominant	Occupancy	Abundance	Dominant	Occupancy	Abundance	Dominant	Occupancy
<i>Parabolina (N.)</i>	–	–	–	80	1	1	89	0.93	1
<i>Micragnostus</i>	–	–	–	6.3	0	0.52	2.1	0.07	0.43

Abundance: mean abundance of samples where the taxon is present. Dominant: proportion of samples where the taxon dominates. Occupancy: proportion of samples where the taxon is present.

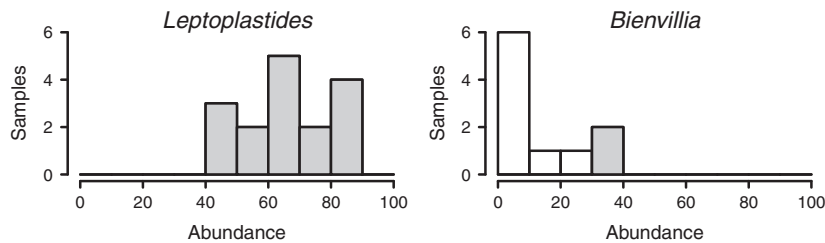


Fig. 10. Histograms of local abundance of dominants in the Tremadocian 2. Grey bars indicate samples where the given taxon dominates.

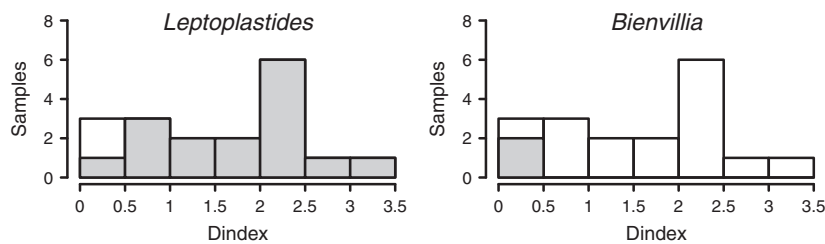


Fig. 11. Histograms of local dominance in the Tremadocian 2. Grey bars indicate samples where the given taxon dominates.

Table 2. Abundance and occupancy of dominant taxon in each environment during the Tr2.

	Shallow Sub-tidal			Deep Sub-tidal			Offshore		
	Abundance	Dominant	Occupancy	Abundance	Dominant	Occupancy	Abundance	Dominant	Occupancy
<i>Leptoplastides</i>	87.5	1	1	52.1	1	1	68	0.71	0.71
<i>Bienvillia</i>	–	0	0	2.5	0	0.57	17.85	0.29	0.86

See Table 1 for further explanation.

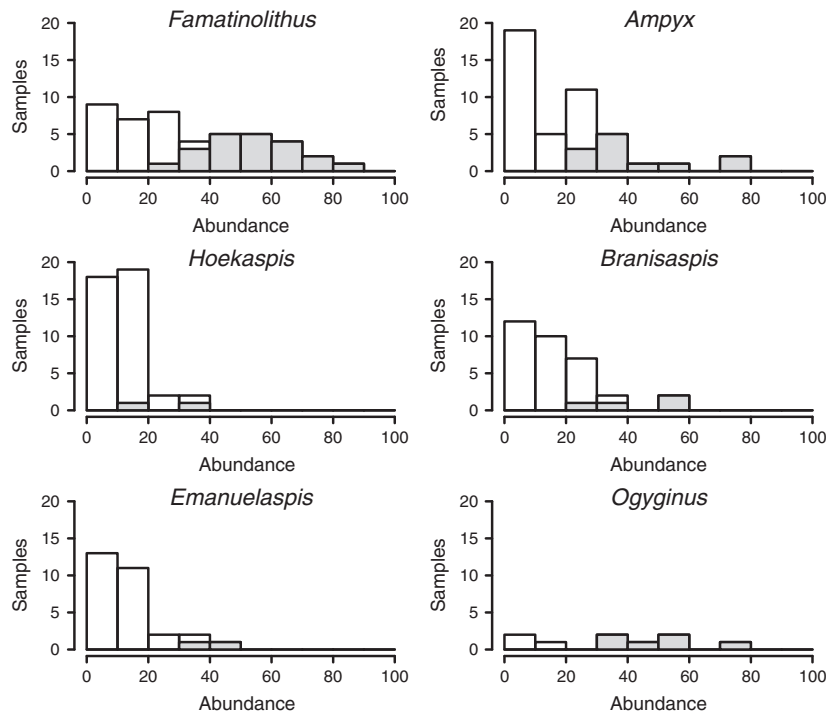


Fig. 12. Histograms of local abundance of dominants in the Floian 2-3. Grey bars indicate samples where the given taxon dominates.

where it attains 30% or more relative abundance. *Ampyx*, *Hoekaspis*, *Branisaspis* and *Emanuelaspis* have a common pattern of right skewed abundance distribution, having low abundance in most samples and relatively high abundance in just a few ones (Fig. 12). In the few cases where any of these four taxa reaches high abundance (>30%), it becomes the dominant taxon in the local assemblage. In contrast, *Ogyginus* achieves high abundance (median = 39.5%) but in a limited set of samples. *Ogyginus* also dominates local assemblages whenever it has more than 30% relative abundance, which constitutes the majority of the samples where it is present (Fig. 12). On the other hand, the pattern of dominance holds some similarities with previous intervals, mostly with the Tr2. *Famatinolithus* is the only taxon that usually dominates assemblages with high dominance (Dindex >1), while the other five taxa rarely dominate in this kind of assemblages (Fig. 13). Moreover, although *Famatinolithus* usually doubles the abundance of the second most

abundant taxon, it never reaches very high dominance (maximum Dindex = 3).

Remarkably, *Famatinolithus* is consistently abundant along the whole onshore–offshore gradient, with the highest scores in the shallow sub-tidal setting (offshore transition) and the lowest ones at the extremes of the gradient (Table 3). The pattern of occupancy exhibited by *Ampyx* resembles that of *Famatinolithus*; however, the former seldom attains high abundance scores. In contrast, *Ogyginus* dominates local assemblages in a limited set of samples, restricted to the shoreface setting, whereas it is absent in the rest of the onshore–offshore profile.

Discussion

Nature of the assemblages

Our results show a particular signal from the perspective of the structure of the assemblages from the

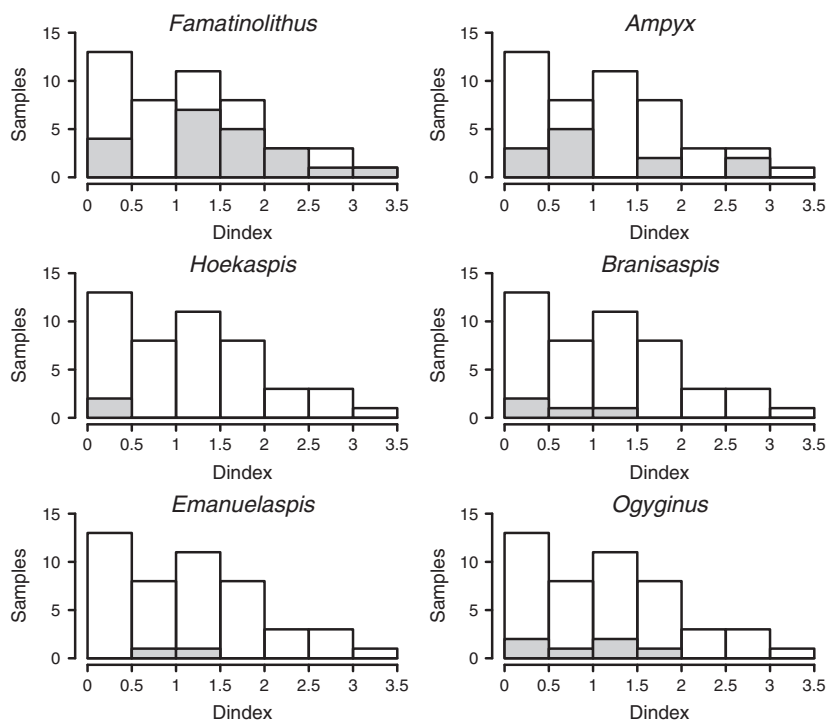


Fig. 13. Histograms of local dominance in the Floian 2-3. Grey bars indicate samples where the given taxon dominates.

Table 3. Abundance and occupancy of dominant taxon in each environment during the FL2–FL3.

	Shallow Sub-tidal			Deep Sub-tidal			Offshore		
	Abundance	Dominant	Occupancy	Abundance	Dominant	Occupancy	Abundance	Dominant	Occupancy
<i>Famatinolithus</i>	25	0.2	0.9	34.3	0.528	0.97	22	0	1
<i>Ampyx</i>	8.835	0.2	0.8	16.2	0.28	0.97	22	0	1
<i>Hoekaspis</i>	15.6	0	0.7	11.9	0.056	0.92	4.5	0	1
<i>Braniaspis</i>	15.7	0	0.5	11.5	0.11	0.78	–	0	0
<i>Emanuelaspis</i>	–	0	0	10.5	0.028	0.78	33.3	1	1
<i>Ogyginus</i>	43.1	0.6	0.8	5.4	0	0.028	–	0	0

See Table 1 for further explanation.

Cordillera Oriental. The patterns of dominance and occupancy suggest unusual ecological conditions during the Furongian, but also during the earliest Late Tremadocian (Tr2), and a distinct change towards a more usual ecological context in the Floian (FL2–FL3).

Furongian and Tremadocian (Tr2) highly dominated communities are distributed with only slight changes across the entire bathymetric gradient with slight abundance shifts among rare taxa. Previous studies from other perspectives also support a pattern of intergrading highly dominated communities with little spatial turnover among different environments, resulting in a largely simple ecosystem dominated by widespread generalists (Balseiro *et al.* 2011a,b; Balseiro & Waisfeld 2014). On the other hand, local and regional equitable communities pre-

sent during the Floian record lower dominance and much higher beta diversity, which is reflected on the number of highly differentiated biofacies (Waisfeld *et al.* 1999, 2003).

Overall, both locally and regionally, highly dominated communities are rarely described in the literature. Interestingly, the peculiar ecological structure of these communities from the Cordillera Oriental recall drops in biofacies differentiation documented through the successive Late Cambrian mass extinctions (biomeres) of Laurentian North America (Ludvigsen & Westrop 1983; Westrop & Ludvigsen 1987; Westrop & Cuggy 1999). For example, Westrop & Cuggy (1999) found a recurrent pattern of a single, low-diversity biofacies occupying nearly the whole environmental spectrum and a broad portion of the shelf

during a brief moment of the earliest recovery phase of each biomere extinction.

These case studies illustrate palaeoecological patterns that arise after major disruptions and collapses of the ecosystems. However, no major perturbation is documented in the Cordillera Oriental or elsewhere along the protracted interval encompassing Furongian to Tremadocian (Tr2) times. Therefore, although community structure resembles the aftermath of mass extinctions in certain aspects, the ecological/environmental context hardly mirrors these events, making it unlikely that they represent a recovery phase.

It is interesting to note that the olenids *Parabolina* (*N.*) and *Leptoplastides* occur along the whole gradient, from shoreface to offshore settings, in either well-oxygenated or dysoxic environments during the Furongian and the Tr2 (respectively). In contrast, among the six dominants occurring in Floian assemblages (involving asaphids, trinucleids and raphi-phorids), only one of them (*Famatinolithus*) attains high occupancy but rarely high dominance. Hence, it seems evident that the peculiar, highly dominated, regional structure appears to be accomplished only among olenid-dominated assemblages. Recently, Balseiro *et al.* (2011a) noted that the Olenidae dominated the whole bathymetric and oxic–dysoxic gradients during the Tr2 in the Cordillera Oriental. The authors emphasized that this pattern was not restricted to that region. Instead, olenid-dominated communities thrived across the whole shelf profile in other palaeogeographical areas accounting for thick, Upper Cambrian–Tremadocian, siliciclastic successions (see references in Balseiro *et al.* 2011a). It is possible that the strong regionally uneven structure and high occupancy among the Furongian and Tr2 assemblages might be linked to the generalist nature of some olenids, able to cope with a wide array of environmental conditions, bringing about a rather unusual ecological scenario. However, this pattern remains to be recognized among olenid-dominated assemblages from coeval successions in other regions.

On the other hand, environmental changes in the basin do not seem to have been influential in the change in dominance structure between the Tremadocian and the Floian, because no significant environmental signal appears to be associated with the shift towards regionally and locally equitable communities. Hence, evidence does not support any suggestion that the decoupled and diachronic increase in local versus regional dominance observed during the Tr2 to Fl2–Fl3 in the Cordillera Oriental might have been triggered by either an important regional environmental change or a mass extinction.

In contrast, this pattern most probably was related to the major ecological changes that communities witnessed during the protracted Cambro-Ordovician interval (Waisfeld *et al.* 2003; Peters 2004, 2006; Harper 2006; Servais *et al.* 2010; Miller 2012; Balseiro & Waisfeld 2014, among others).

Effect of local versus regional signatures

In a study of richness and evenness among Furongian–Early Ordovician trilobite assemblages, Balseiro & Waisfeld (2014) documented a significant rise in both metrics through time. Remarkably, these authors found that richness and evenness trajectories were decoupled, as evenness increased during the earliest Late Tremadocian (Tr2), and the rise in richness was delayed until the latest Tremadocian (Tr3). This early increase in evenness took place when assemblages were still dominated by olenids, and may imply an early increase in resource partitioning prior to the increase in local richness.

Our results based on the analysis of community dominance at different spatial scales shed some light on the way this shift in the dominance structure took place. The regional scenario shows single key taxa being overwhelming dominant in the Furongian and in the Tr2, across the whole bathymetric gradient, while Floian assemblages show a much more even structure with several dominants. However, at the local scale highly dominated communities are indeed restricted to the Furongian (highest Dindex

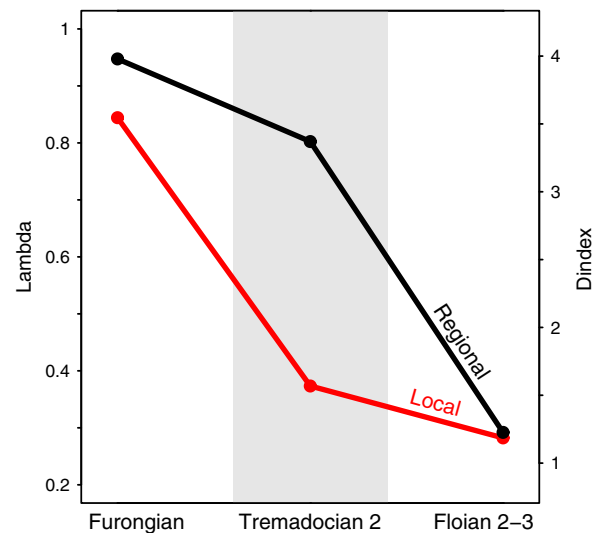


Fig. 14. Trends at different spatial scales through time measured using Dindex for local dominance and Simpson's lambda for regional dominance. Important shifts are represented by a decrease in local dominance in the Tremadocian and in regional dominance in the Floian. Note the decoupling of regional and local dominance during the Tr2.

scores), whereas dominance among Tremadocian local assemblages significantly decreased (Fig. 14). In this sense, dominance of Tr2 assemblages resembles that of the Furongian at the regional scale, but it is more similar to that of the Floian at the local scale. This finding is largely consistent with the local rise in evenness recognized by Balseiro & Waisfeld (2014) during the Tr2. Hence, the earliest Late Tremadocian (Tr2) appears as a pivotal time in the configuration of trilobite communities from the Cordillera Oriental when a dramatic change in dominance structure took place. This switch in dominance was initially manifested in local (more even) communities and became evident later at the regional scale, implying a decoupling in local versus regional dominance structures (Fig. 14).

From the perspective of metacommunity dynamics, such a change in ecological structure at the regional scale can shed light on a previously unexplained pattern observed at the local scale: the diachronic change in evenness and alpha diversity (Balseiro & Waisfeld 2014). Very low turnover of dominant species at the regional scale, coupled with high dominance in local communities, results in a little effect of source–sink dynamics (Hillebrand *et al.* 2008). As most local communities are dominated by the same species, there are fewer places that could act as sources for rare species. One of the main outcomes of this process is the damping of alpha (= local) diversity (Hillebrand *et al.* 2008). Therefore, the delayed change in regional ecological structure could explain why during the Tr2 local communities remained species poor, while having already attained higher evenness values (Balseiro & Waisfeld 2014). As Balseiro & Waisfeld (2014) suggested, evenness and richness were responding to independent, though related, processes. We can now show that while evenness reflected actual ecological changes at the local scale, alpha richness mirrored regional-scale processes. Although an even more complex scenario could be envisaged, the results of this case study highlight the need of studying regional patterns and processes to better understand local ones.

Local–regional dominance and the Cambro-Ordovician ecological changes

The general palaeoecological scenario and the striking regional pattern of dominance that emerges from our study highlight a previously unobserved pattern in the evolutionary palaeoecological context of the Cambro-Ordovician interval. Earlier contributions underscored changes in local evenness or global diversity, while the analysis of regional ecological

patterns was largely neglected. Nevertheless, assumptions of local versus regional dominance trends can be delineated for a few regions based on evenness patterns as a proxy for local dominance and biofacies differentiation for regional dominance.

Peters (2004), for example, documented a distinct increase in local evenness since the latest Cambrian (Sunwaptan) among benthic assemblages from North America. However, a spatial structure of well-differentiated biofacies, implying equitable regional dominance, has been extensively documented as far back as the Middle Cambrian (Marjuman) in this region (Westrop 1986; Pratt 1992; Westrop & Cuggy 1999) or even in the late Early Cambrian–early Middle Cambrian (Tremblay 1996). A similar scenario is observed in the Siberian Platform (Russia), where Pegel (2014) documented late Middle Cambrian–early Late Cambrian reef complexes that account for a set of compositionally different biofacies. All in all, this evidence suggests that, at least in Laurentia – and possibly Siberia – communities were regionally equitable while most local communities were still highly dominated, at least back to the late Early Cambrian. Although it is difficult to trace the palaeoecological structure of Laurentian trilobite communities in earlier times, available data suggest that at the regional scale, communities in Laurentia either (1) were never highly dominated in their early history or (2) exhibited a regional structure of high dominance just in the Early Cambrian, well before the rise in local evenness documented in North America (Peters 2004).

In any of these cases, the pattern in North America appears as exactly opposite to the trend recognized in the Cordillera Oriental. In this region, the change towards less dominated assemblages becomes evident first at the local scale (Tr2) and only later at the regional scale (Fl). Interestingly, the ecological structure of these assemblages displaying an uneven dominance structure and high occupancy matches the old notion put forward by Sepkoski (1981) about the uniqueness of the Cambrian faunas. Notably, that notion was not consistent with the ecological patterns (e.g. high biofacies differentiation) recognized by subsequent workers in Middle and Late Cambrian trilobite assemblages from Laurentian North America (Ludvigsen & Westrop 1983; Westrop 1986; Pratt 1992; Westrop & Cuggy 1999). This inconsistency might now be addressed by considering the second alternative suggested above as more likely. A decoupling in the dominance structure might have also occurred in Laurentia, and thus, the signal of Sepkoski's Cambrian Fauna of local and regional highly dominated communities only applied to the early part of the system.

It is also worthy of note that previous studies have recognized that, although diachronically, Cordillera Oriental and other regions shared a trend of rise in local richness and evenness in all environments (Adrain *et al.* 2004; Balseiro & Waisfeld 2014). This common trend encompassed not only the general increase in both metrics, but also the increase in deep marine relative to shallow marine scores (Balseiro & Waisfeld 2014). The contrasting and decoupled pattern of local and regional dominance between Cordillera Oriental and Laurentia is therefore striking because a shared switch in regional relative to local dominance between regions was expected, with just a simple lag of the changes in the Cordillera Oriental behind those of Laurentia (or other regions). The fact that regional and local processes are somewhat related, and that the delayed decrease in regional dominance can explain the diachronic change in local evenness and richness in Cordillera Oriental, suggests that the whole ecological scenario might have been different between regions, regardless of some similarities.

It is also important to note that the contrasting signals discussed above might eventually reflect the influence of a comparison between a large-scale basin (Cordillera Oriental) and a palaeocontinent (Laurentia). In that sense, a larger geographic area with diverse geodynamic contexts might have favoured a wider array of ecological possibilities.

Overall, the analysis at local–regional scales conducted herein provides a perspective for the understanding of ecological changes that was not tackled before, reinforcing the idea that ecological changes during the Cambro-Ordovician were not caused by a simple common cause. Biogeographical regions that witnessed different regional-scale processes had ecological consequences at least as important as global processes. In addition, our case study further suggests that scaling local and regional patterns within the same region may have significant consequences in the way ecological processes are understood, providing new insights to unravel Early Palaeozoic history of biodiversity among benthic marine communities.

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References

- Adrain, J.M. & Westrop, S.R. 2005: Evenness and diversity of Lower Paleozoic trilobite faunas of Laurentian North America. *Geological Society of America* 461, Abstracts.
- Adrain, J.M., Westrop, S.R., Chatterton, B.D.E. & Ramskold, L. 2000: Silurian trilobite alpha diversity and the end-Ordovician mass extinction. *Paleobiology* 26, 625–646.
- Adrain, J.M., Edgcombe, G.D., Fortey, R.A., Hammer, Ø., Laurie, J.R., McCormick, T., Owen, A.W., Waisfeld, B.G., Webby, B.D., Westrop, S.R. & Zou, Z.-Y. 2004: Trilobites. In Webby, B.D., Paris, F., Droser, M.L. & Percival, I.G. (eds): *The Great Ordovician Biodiversification Event*, 231–254. Columbia University Press, New York.
- Albanesi, G.L., Ortega, G. & Zeballo, F.J. 2008: Faunas de Conodontes y Graptolitos del Paleozoico Inferior de la Cordillera Oriental Argentina. In Coira, B., Zappettini, E.O. (eds): *Geología y Recursos Naturales de Jujuy, Relatorio del 17 Congreso Geológico Argentino*, 98–118. Asociación Geológica Argentina, Buenos Aires.
- Alroy, J., Aberhan, M., Bottjer, D.J. *et al.* 2008: Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321, 97–100.
- Astini, R.A. 2003: The ordovician proto-andean basins. In Benedetto, J.L. (ed.): *Ordovician Fossils of Argentina*, 1–74. Secretaría de Ciencia y Tecnología, Universidad Nacional de Córdoba, Córdoba.
- Astini, R.A. 2008: Sedimentación, Facies, Discordancias y Evolución Paleambiental durante el Cámbrico-Ordovícico. In Coira, B., Zappettini, E.O. (eds): *Geología y Recursos Naturales de Jujuy, Relatorio del 17 Congreso Geológico Argentino*, 50–73. Asociación Geológica Argentina, Buenos Aires.
- Astini, R.A. & Waisfeld, B.G. 1993: Análisis estratigráfico y paleoambiental del Ordovícico inferior (Formaciones Acoite y Sepulturas) al Oeste de Purmamarca, Cordillera Oriental jujeña. *12 Congreso Geológico Argentino Mendoza* 1, 96–106.
- Astini, R.A., Waisfeld, B.G., Toro, B.A. & Benedetto, J.L. 2004: El Paleozoico inferior y medio de la región de Los Colorados, Borde occidental de la Cordillera Oriental (Provincia de Jujuy). *Revista de la Asociación Geológica Argentina* 59, 243–260.
- Bahlburg, H. & Furlong, K.P. 1996: Lithospheric modeling of the Ordovician foreland basin in the Puna of northwestern Argentina: on the influence of arc loading on foreland basin formation. *Tectonophysics* 259, 245–258.
- Balseiro, D. & Waisfeld, B.G. 2013: Ecological instability in Upper Cambrian-Lower Ordovician trilobite communities from Northwestern Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 370, 64–76.
- Balseiro, D. & Waisfeld, B.G. 2014: Evenness and diversity in Upper Cambrian-Lower Ordovician trilobite communities from the Central Andean Basin (Cordillera Oriental, Argentina). *Palaeontology* 57, 1–16.
- 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.
- 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 $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia* 42, 97–107.
- Bonier, F., Martin, P.R. & Wingfield, J.C. 2007: Urban birds have broader environmental tolerance. *Biology Letters* 3, 670–673.
- Buatois, L.A. & Mángano, M.G. 2003: Sedimentary facies, depositional evolution of the Upper Cambrian-Lower Ordovician Santa Rosita formation in northwest Argentina. *Journal of South American Earth Sciences* 16, 343–363.
- Buatois, L.A., Zeballo, F.J., Albanesi, G.L., Ortega, G., Vaccari, N.E. & Mángano, M.G. 2006: Depositional environments 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 stratigraphic framework. *Latin American Journal of Sedimentology and Basin Analysis* 13, 1–29.
- Bush, A.M. & Brame, R.I. 2010: Multiple controls on the composition of marine fossil assemblages from the Frasnian (Late Devonian) of Virginia, with a comparison of ordination methods. *Paleobiology* 36, 573–591.

- Clapham, M.E., Bottjer, D.J., Powers, C.M., Bonuso, N., Fraiser, M.L., Marenco, P.J., Dornbos, S.Q. & Pruss, S.B. 2006: Assessing the ecological dominance of Phanerozoic marine invertebrates. *Palaaios* 21, 431–441.
- Foote, M., Crampton, J.S., Beu, A.G., Marshall, B.A., Cooper, R.A., Maxwell, P.A. & Matcham, I. 2007: Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science* 318, 1131–1134.
- Gaston, K.J. 2011: Common ecology. *BioScience* 61, 354–362.
- Gaston, K.J. & He, F. 2011: Species occurrence and occupancy. In Magurran, A.E. & McGill, B.J. (eds): *Biological Diversity: Frontiers in Measurement and Assessment*, 141–151. Oxford University Press, New York.
- Gillinsky, N.L. & Bennington, J.B. 1994: Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record. *Paleobiology* 20, 245–258.
- Harper, D.A.T. 2006: The Ordovician biodiversification: setting an agenda for marine life. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232, 148–166.
- Hillebrand, H., Bennett, D.M. & Cadotte, M.W. 2008: Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89, 1510–1520.
- Kidwell, S.M. 2001: Preservation of species abundance in marine death assemblages. *Science* 294, 1091–1094.
- Liow, H.L. & Stenseth, N.C. 2007: The rise and fall of species: implications for macroevolutionary and macroecological studies. *Proceedings of the Royal Society B* 274, 2745–2752.
- Ludvigsen, R. & Westrop, S.R. 1983: Trilobite biofacies of the Cambrian-Ordovician boundary interval in North America. *Alcheringa* 7, 301–319.
- Magurran, A.E. 2004: *Measuring Ecological Diversity*, 256 pp. Blackwell Science Ltd., Oxford.
- Miller, A.I. 2004: The ordovician radiation: towards a new global synthesis. In Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (eds): *The Great Ordovician Biodiversification Event*, 380–388. Columbia University Press, New York.
- Miller, A.I. 2012: The Ordovician Radiation: Macroevolutionary crossroads of the Phanerozoic. In Talent, J.A. (ed.): *Earth and Life: Global Biodiversity, Extinction Intervals and Biogeographic Perturbations Through Time*, 381–394. Springer Science+Business Media B.V., New York.
- Moya, M.C. 1999: El Ordovícico en los Andes del norte argentino. In González Bonorino, G., Omarini, R., Viramonte, J. (eds): *Relatorio del 14 Congreso Geológico Argentino, Geología del noroeste argentino*, 134–152. Asociación Geológica Argentina, Buenos Aires, Argentina.
- Pegel, T.V. 2014: Biofacies and age of Cambrian trilobites associations of the Diringde reef complex (northern Siberian Platform, Russia). *Bulletin of Geosciences* 89, 335–345.
- Peters, S.E. 2004: Evenness of Cambrian-Ordovician benthic marine communities in North America. *Paleobiology* 30, 325–346.
- Peters, S.E. 2006: Genus richness in Cambrian-Ordovician benthic marine communities in North America. *Palaaios* 21, 580–587.
- Pratt, B.R. 1992: Trilobites of the Marjuman and Steptoean stages (Upper Cambrian), Rabbitkettle Formation, southern Mackenzie Mountains, northwest Canada. *Palaeontographica Canadiana* 9, 1–179.
- Schovsbo, N.H. 2001: Why barren intervals? A taphonomic case study of the Scandinavian Alum Shale and its faunas. *Lethaia* 34, 271–285.
- 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*, 203–207. United States Geological Survey, Open-File Report, Washington.
- Sepkoski, J.J. 1988: Alpha, beta, or gamma: where does all the diversity go? *Paleobiology* 14, 221–234.
- Servais, T., Owen, A., Harper, D.A.T., Kroeger, B. & Munnecke, A. 2010: The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology* 294, 99–119.
- Tomašových, A. & Kidwell, S.M. 2010: Predicting the effects of temporal scale on species composition, diversity, and rank abundance distributions. *Paleobiology* 36, 672–695.
- Toro, B.A. & Maletz, J. 2009: The proximal development in *Cymatograptus* (Graptoloidea) from Argentina and its relevance for the early evolution of the Dichograptacea. *Journal of Paleontology* 82, 974–983.
- Tremblay, J.V. 1996: Trilobites and strata of the Lower and Middle Cambrian Peyto, Mount Whyte, and Naiset formations, Alberta and British Columbia. Unpublished Thesis McMaster University, 343 pp.
- 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. 1997: Concentraciones fosilíferas ordovícicas en las formaciones Acoite y Sepulturas, Cordillera Oriental jujeña. Significado tafonómico y paleoecológico. *Ameghiniana* 34, 317–332.
- Waisfeld, B.G. & Vaccari, N.E. 2008: Bioestratigrafía de trilobites del Paleozoico inferior de la Cordillera Oriental. In Coira, B., Zappettini, E.O. (eds): *Geología y Recursos Naturales de Jujuy, Relatorio del 17 Congreso Geológico Argentino*, 119–127. Asociación Geológica Argentina, Buenos Aires, Argentina.
- Waisfeld, B.G., Sánchez, T.M. & Carrera, M.G. 1999: Biodiversification patterns in the early Ordovician of Argentina. *Palaaios* 14, 198–214.
- Waisfeld, B.G., Sánchez, T.M., Benedetto, J.L. & Carrera, M.G. 2003: Early Ordovician (Arenig) faunal assemblages from western Argentina: biodiversification trends in different geodynamic and palaeogeographic settings. *Palaeogeography, Palaeoclimatology, Palaeoecology* 196, 343–373.
- Westrop, S.R. 1986: Trilobites of the upper Cambrian Sunwaptan stage, southern Canadian rocky mountains, Alberta. *Palaeontographica Canadiana* 3, 1–179.
- Westrop, S.T. & Adrain, J.M. 1998: Trilobite alpha diversity and the reorganization of Ordovician benthic marine communities. *Paleobiology* 24, 1–14.
- Westrop, S.T. & Adrain, J.M. 2001: Sampling at the species level: impact of spatial biases on diversity gradients. *Geology* 29, 903–906.
- Westrop, S.R. & Cuggy, M.B. 1999: Comparative paleoecology of Cambrian trilobite extinctions. *Journal of Paleontology* 73, 337–354.
- Westrop, S.R. & Ludvigsen, R. 1987: Biogeographic control of trilobite mass extinction at an Upper Cambrian 'biomere' boundary. *Paleobiology* 13, 84–99.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Taxa abundance in Furongian samples.

Table S2. Taxa abundance in Tremadocian samples.

Table S3. Taxa abundance in Floian samples.