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Self-regulation of trilobite diversity in Murero (middle Cambrian, Spain) due to compensatory extinction

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| A B S T R A C T |

As species accumulate in a community, competition for available ecospace is expected to prevent the addition of new species and to facilitate species extinction, thus producing a dynamic equilibrium of diversity. This mechanism remains under debate since its empirical support comes mainly from indirect or partial evidence, with very few direct tests at the species level. Here a new method is described to detect the presence of self-regulation feedbacks between species richness and turnover rates. It consists of Monte Carlo simulations which randomize the distribution of species ranges among stratigraphic intervals, providing predictions which allow the detection of genuine self-regulation feedbacks in the real data. Since the simulations include any potential bias due to preservation, sampling, or change in depositional environment, and these biases would also affect the real dataset, they are thus ruled out as explanations for any difference found. This method is applied to one of the best known fossiliferous sequences worldwide, the Rambla de Valdemiedes in Murero (RV1 section, middle Cambrian, Spain), a classic locality that has been studied for more than 150 years and which stands out due to its excellent sampling density, continuous deposition, and homogeneous fossil preservation. The results show that trilobite species richness was self-regulated due to positive feedback with extinction rate, which implies that compensatory extinction regulated this fauna in spite of the on-going Cambrian radiation. The lack of evidence of any origination feedback suggests ecological opportunities were not limiting for new species to colonize this Cambrian community.

KEYWORDS | Extinction rate. Species turnover. Diversification. Macroevolution. Origination rate.

INTRODUCTION

Are there general laws in the evolution of species numbers? This question remains as one of the key subjects in evolutionary ecology and macroevolution (Price, 2015). Current knowledge suggests that species richness may tend to decrease its own increase (species addition rate per species, due to speciation or immigration) and to increase its own decrease (extinction rate per species) over local to regional and ecological to evolutionary timescales. These self-regulatory feedbacks would result in a dynamic equilibrium of species richness (Sepkoski, 1978; Rosenzweig, 1995). However, there is no consensus on this idea, with recent opinions for (Rabosky and Hurlbert, 2015) and against it (Harmon and Harrison, 2015). Self-

regulatory mechanisms would explain the prevalence of diversity steady-states over million years after the initial buildup of species numbers following the colonization of empty ecospace (Rosenzweig, 1995; Brown *et al.*, 2001; Ricklefs, 2010). Views against this equilibrium dynamics argue that there is no compelling evidence that ecology poses any hard limit to species richness at local to regional scales (Harmon and Harrison, 2015).

The stronger arguments to expect diversity-origination and diversity-extinction feedbacks stem on the decrease of survival options with the filling of available ecospace. As species accumulate in the niche hyperspace, negative interspecies interactions (mainly competition) would narrow species niches (denser niche packing, Whittaker,

1972; Ricklefs, 2010). This mechanism is supported by the generality of ecological release on islands (MacArthur and Wilson, 1967; Lack, 1969; Wunderle, 1985; Warren *et al.*, 2015), by the increase of niche segregation (specialization) with diversity (Cox and Ricklefs, 1977; Nürnberg and Aberhan, 2015), and by the resistance to biological invasions provided by local diversity (Elton, 1958; Levine *et al.*, 2004; Lockwood *et al.*, 2013). Narrower niches usually imply a more limited subset of habitats to occupy and so less abundance and smaller geographic ranges, two factors which clearly increase extinction risk (Pimm *et al.*, 1988; Gaston and Spicer, 2009). Thus, as species accumulate, extinction risk per species should rise.

On the other hand, during speciation, incipient species necessarily tend to be scarce and geographically restricted, thus being extremely sensitive to interactive extinction (Stanley, 1979). It is thus not surprising that speciation bursts tend to occur in unusually species-poor situations (Gaston and Spicer, 2009; Yoder *et al.*, 2010), such as after a mass extinction, in the colonization of a new habitat, region or archipelago, or after an adaptive breakthrough which opens an entirely new ecospace realm. In these situations, the lack of interspecies competition allows incipient species to freely cross the adaptive landscape and reach new adaptive peaks, travel which is prevented by species interactions as diversity grows (Wilson, 1992; Rosenzweig, 1995). The result is the origin of many new modes of life during the diversification process (adaptive radiation). In this way, by controlling speciation rates, species interaction may mark the *tempo* of macroevolution (punctuated equilibrium).

Species addition by immigration could also be depressed by diversity because a high extinction risk is faced by any new immigrant species due to its initial scarcity and restricted range (Pimm *et al.*, 1988). This would explain the generality of the invasion resistance effect provided by diversity (Elton, 1958; Levine *et al.*, 2004; Lockwood *et al.*, 2013). During equilibrium stages, the addition of a new species would increase extinction risk in the assemblage so that the compensatory extinction of another species could easily occur (Darwin, 1859; MacArthur and Wilson, 1967; Rosenzweig, 1995), thus restoring the number of species.

Multiple lines of evidence supports the diversity-speciation (Foote, 2000; Rabosky and Glor, 2010; Rabosky and Adams, 2012; Moen and Morlon, 2014; Price *et al.*, 2014) and diversity-extinction feedbacks (Gause, 1934; Rosenzweig, 1995; Foote, 2000; Alroy, 2008), but see Harmon and Harrison (2015) for the opposite view. However, there are surprisingly few works focusing on how these mechanisms could combine to regulate species numbers at the species level, which is the only realistic taxonomic category to address this subject. Studies at the

family and genus level are abundant (Sepkoski, 1978; Foote, 2000; Alroy, 2008; Gaston and Spicer, 2009) but they do not allow us to reach direct conclusions for species. The objective of this work is to test whether the diversity-speciation and diversity-extinction feedbacks exist and result in local diversity self-regulation at species level and evolutionary timescale using a new method in a case study. I will focus on species data from one of the best known fossiliferous sequences in the world: the trilobite fauna from the Rambla de Valdemiedes in Murero (middle Cambrian, Spain) (Liñán *et al.*, 2013).

Westrop and Adrain (1998) show that local equilibrium of species numbers holds true for Ordovician trilobites occupying different habitats, and so trilobites in general are likely to have experienced self-regulatory feedbacks. Furthermore, trilobites are unusually adequate for macroevolutionary studies because each individual produced during its lifetime a number of *exuviae* which were prone to fossilization, thus multiplying the probability of detection of each individual, and so each species, in the fossil record. The classic fossil site of Murero has been studied for more than 150 years, starting with its discovery by Verneuil (1862) and following the salient contributions of Dereims (1898), Lotze (1969) and Liñán and Gozalo (1986), among more than 100 scientific papers dealing with this fossil site to date. The fossiliferous sequence of Murero covers about 8 million years, from about 511 to 503 million years ago. It has been divided into 14 trilobite biozones, which is the most fine-scale subdivision of this time interval worldwide (Liñán *et al.*, 2013). All these extraordinary features make Murero an optimal choice for the present study. I have focused on the intensely sampled Section 1 of the best known part of Murero, the Rambla de Valdemiedes (RV1; Liñán *et al.*, 2008), which has provided tens of thousands of individual trilobite fossils (Liñán, 2015), as well as other invertebrates including soft-bodied taxa.

METHODS

The stratigraphic ranges of all trilobite species recorded in the section RV1 were retrieved from Liñán *et al.* (2008; their figure 18). This section covers about 150m spanning the Mansilla, Murero and Borobia formations in a continuous record which starts at the Valdemiedes event (the mass extinction at the end of the lower Cambrian) and extends over the upper Leonian and Caesaraugustan (Drumian) stages of the middle Cambrian (Liñán *et al.*, 2008). The fact that the section begins with a mass extinction will improve the observation of biodiversity dynamics by including the subsequent epoch of unusually low diversity. There are no clear differences in depositional environment over the section (Liñán, 2015), which rules out this factor as a relevant source of noise.

In order to estimate diversity and turnover parameters, I followed the Boundary-Crossers (BC) approach described by Foote (2000). The three-timer and gap-filler turnover rates were not adequate in this case study due to the small number of taxa and the almost complete lack of gaps in the species ranges sampled over RV1 (see a discussion of these methods and BC rates in Alroy, 2014). Thus, in practice, these methods provide very similar values compared to BC rates. In this stratigraphic section, the statistical shortages of BC rates (*e.g.* due to uncertainty in range boundaries) are likely to be unimportant because of the extremely intense sampling that has been carried on. In general, the high quality of the paleontological data retrieved from RV1 diminishes the importance of any sampling bias. The same can be said about biases in preservation and depositional environment, since the section seems to represent a quite homogeneous and continuous sequence (Liñán, 2015).

The stratigraphic chart of RV1 was divided into 13 intervals of equal thickness (approximately 12m). For each interval, I counted N_b (number of species crossing the bottom line), N_t (species crossing the top line), and N_{bt} (species crossing both bottom and top). Then I obtained BC turnover rates (Foote, 2000): extinction rate (E) as $-\log(N_{bt}/N_b)$, and origination rate (O) as $-\log(N_{bt}/N_t)$. Diversity per interval was considered as N_b , so that single-interval species are entirely excluded from the analysis, which eliminates a potentially important source of noise due to unequal preservation or sampling. Although this bias is likely irrelevant in RV1, this procedure improves the quality of the statistical analysis. Sampling boundary-crossers means focusing on species assemblages which crossed a geological instant (the interval bottom in a continuous stratigraphic section) instead of a geological interval. Sampling in intervals implies pooling together species which did not necessarily coexist in time – for example, the new species appeared at the end of the interval would be considered to have coexisted with the old species which disappeared at the beginning of the interval – which is not realistic (Foote, 2000).

The comparison between diversity and extinction or origination rate requires detrending the time series data in order to improve the statistical independency of the data points. Detrending was carried on by differencing (values of each band minus values of the previous band).

If biodiversity is self-regulated, then the plot of changes in turnover ratios *vs.* changes in species richness must show that changes in origination rate tend to decrease with diversity (negative Pearson correlation), and the opposite for changes in extinction rate (positive Pearson correlation). The statistical significance of these correlation coefficients was determined by using a Monte Carlo

simulation which generates randomized species-interval distributions. In each simulation, species are treated as blocks with a given length (their observed range in number of intervals) and their first interval is assigned at random, with the only constraint that the species range cannot be reduced by being cut by the top of the last interval. Then the turnover rates are calculated as previously described, and the Pearson correlation coefficients are estimated. One thousand repeats of this simulation served to obtain the probability of observing a Pearson correlation at least as high (for extinction rate) or as low (for origination rate) as that observed in empirical data (*i.e.* one-tailed tests). Considering the many sources of noise which could distort the self-regulatory signal, the significance threshold was set at 0.10.

With this procedure, the simulations include as background noise any conceivable source of bias which may distort the self-regulation signal. The underlying logic is that we are comparing observed *vs.* expected correlations which are subject to the same biases, so that these biases cannot be the explanation for any difference detected. A self-regulation signal in the dataset would reveal a non-random distribution of species ranges among intervals so that the self-regulatory feedbacks are reinforced. If this is the case, then diversity equilibrium due to species interaction will be supported provided that an equilibrium point close to zero (no diversity change) is observed in the plot of change in turnover *vs.* change in species richness.

RESULTS

The distribution of trilobite species among intervals is shown in Table 1. As it is usually seen after mass extinctions, species richness first experiences a relatively fast increase which ends by about the 4th band (Fig. 1). Then the number of species wobbles a lot around a mean value of about 5-6 species per band.

Table 2 shows the corresponding diversity parameters. The relationship between change in turnover rates and change in species richness is exactly in the expected direction for self-regulation to occur (Fig. 2). The regression lines of the changes in origination rate and changes in extinction rate cross at about zero species and so they are interpreted to predict a reasonable equilibrium species number. The Pearson correlations are low for origination rate ($r = -0.119$) and moderate for extinction rate ($r = 0.596$).

The Monte Carlo simulations consisted on the random placement of the 34 species among the 13 bands according to their ranges in RV1 (Table 1). The probability distributions

TABLE 1. Distribution of trilobite species among intervals in Rambla de Valdemiedes 1 (RV1), after Liñán *et al.* 2008

Species	Intervals													Number of intervals
	1	2	3	4	5	6	7	8	9	10	11	12	13	
<i>Eccaparadoxides asturianus</i>	X	X	X											4
<i>Bailiella</i> sp.		X												1
<i>Badulesia tenera</i>		X												1
<i>Eccaparadoxides sulcatus</i>		X	X											2
<i>Badulesia granieri</i>		X	X											2
<i>Conocoryphe (Parabailiella) languedociensis</i>		X	X	X										4
<i>Badulesia paschi</i>			X											1
<i>Condylopyge aff. regia</i>			X											1
<i>Ctenocephalus (Hartella) antiquus</i>			X	X	X	X								5
<i>Pardailhanian hispida</i>			X	X										2
<i>Eccaparadoxides rouvillei</i>			X	X										3
<i>Eccaparadoxides sequeirosi</i>			X	X	X	X	X							5
<i>Agraulos longicephalus</i>			X	X										3
<i>Pardailhanian multispinosa</i>				X										1
<i>Bailiaspis aff. meridiana</i>				X										1
<i>Conocoryphe (C.) heberti sampelayosi</i>				X										1
<i>Pardailhanian sdzuy</i>				X	X									1
<i>Solenopleuropsis ribeiroi</i>				X	X	X	X							3
<i>Conocoryphe (C.) heberti snajdri</i>						X								1
<i>Peronopsis acadica</i>						X	X	X	X	X		X		4
<i>Hydrocephalus donairei</i>						X	X	X						3
<i>Conocoryphe (C.) heberti heberti</i>							X	X	X	X		X		4
<i>Solenopleuropsis verdiagana</i>							X	X						2
<i>Solenopleuropsis rubra</i>							X	X	X					1
<i>Solenopleuropsis simula</i>							X	X	X	X		X		2
<i>Eccaparadoxides brachyrhachis</i>							X	X	X	X		X		2
<i>Conocoryphe (C.) sdzuy courtessolei</i>							X	X	X	X	X	X	X	3
<i>Solenopleuropsis marginata</i>								X	X	X	X	X	X	2
<i>Eccaparadoxides pradoanus</i>									X	X	X			1
<i>Condylopyge rex hispanica</i>										X	X			1
<i>Peronopsis ferox</i>											X	X	X	2
<i>Solenopleuropsis thoralii</i>													X	1
<i>Eccaparadoxides melaguesensis</i>													X	1
<i>Ctenocephalus (C.) coronatus</i>													X	1

obtained for the Pearson correlations after 1,000 repeats are shown in Figure 3. As can be seen, the simulations show that there is a very low probability of obtaining the observed correlation for the extinction feedback, but not for origination. The results are significant for the extinction feedback only (p-value = 0.039), but there is no evidence of any origination feedback (p-value = 0.878). Thus the results reveal that the diversity of this trilobite fauna was regulated by compensatory extinction. Species richness increased extinction risk per species, but it seems that new species invaded the community with the same success regardless of whether its diversity was low or high.

The same qualitative result was obtained after some methodological variations, namely a simple permutation test with the detrended parameters, and the Monte Carlo approach but using total species richness Sampled In Bin

(SIB) instead of N_b . These variations yield statistically significant evidence for the extinction feedback but not for the origination one. Thus the results seem to be relatively robust against methodological details.

DISCUSSION

The results show that the observed ranges of trilobite species are distributed so that the extinction feedback is reinforced: as species accumulate in the community, their individual extinction risk increases. This mechanism is enough to create diversity equilibrium despite the fact that no significant origination feedback has been detected. Here the key to diversity equilibrium seems to be the oldest self-regulation mechanism proposed: compensatory extinction (Darwin, 1859).

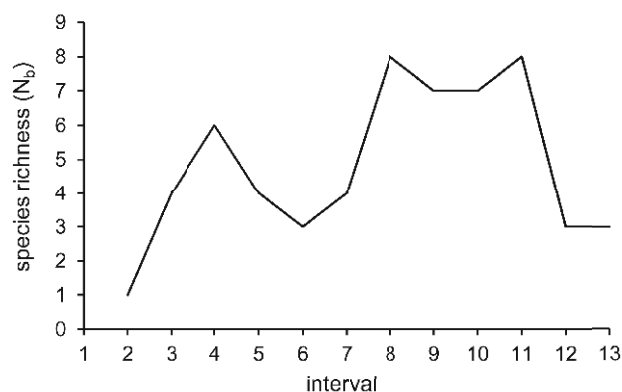


FIGURE 1. Species richness (N_b) over the intervals of Rambla de Valdemiedes 1

At equilibrium diversity, the addition of a new species *statistically* implies the extinction of a preexisting species. Here the term *statistically* means that the steady-state diversity is not a deterministic hard boundary (*sensu* Harmon and Harrison, 2015) but a dynamical state of saturation (“soft saturation”), as demonstrates the noteworthy wobbling in Figure 1. This soft saturation implies that communities are not hermetically closed; they can flexibly accommodate some diversity increase before compensatory extinction starts. In this situation, compensatory extinction is probably triggered by the reduction of available ecospace driven by environmental perturbations that can be seen as random events (Rosenzweig, 1995).

According to the results, trilobite species richness did not make difficult the addition of new species to this assemblage. The lack of evidence for any origination feedback suggests that neither speciation ratio nor immigration controlled the number of species in this trilobite fauna. This fits the idea that Cambrian communities had more available ecospace compared to modern ones (Bambach, 1983; Bambach *et al.*, 2007), where invasion resistance is usually observed at local scale (Elton, 1958; Levine *et al.*, 2004; Lockwood *et al.*, 2013). Relatively unoccupied niches even at relatively high

diversities may have facilitated the colonization of new trilobite species so that invasion resistance or a shortage of ecospace for new species was not common. However, although species addition was not significantly deterred by diversity, as species accumulated their interactions finally facilitated compensatory extinction, probably after abiotic perturbations. This hypothetical dynamics may have prevailed during the Cambrian radiation due to the relative simplicity of animal communities.

No sampling, preservational, or environmental biases can be proposed as explanations to these results because all of them were taken into account in the Monte Carlo simulations for obtaining the null probability distribution of the turnover correlations. A lack of relevant sampling biases must be expected for a classic fossil site with such an enormous fossil record and long history of study (Liñán *et al.*, 2013). These factors improve the adequacy of the equations here applied to calculate turnover rates, because no significant errors in the sampling of the stratigraphic distributions of species can be reasonably expected after tens of thousands of trilobite fossils retrieved from a single section. Furthermore, over RV1 no clear disruptions are observed in stratigraphy, lithology, and fossil record, and so the section probably represents relatively homogeneous and continuous conditions of preservation in a quite uniform depositional environment. Thus it is not likely that the results could be distorted by any of these factors.

Although no clear differences in depositional environment are observed in RV1 (Liñán, 2015; Liñán *et al.*, 2008), possible habitat change within the same depositional environment deserves scrutiny as an alternative explanation to the results, although the Monte Carlo simulation randomizes this factor too. During the deposition of the Murero fossil beds, the sea level first rose, then it remained stable, and finally it rose again (Liñán *et al.*, 2008). Thus progressively deeper habitats are expected to be recorded, in spite that the depositional environment seems to be the same. However, if there is any habitat change towards deeper habitats, it has not been detected in lithology or fauna.

TABLE 2. Data summary of trilobite diversity dynamics in Rambla de Valdemiedes 1. See the methods for details

Interval	1	2	3	4	5	6	7	8	9	10	11	12	13
Species sampled in bin (SIB)	1	6	11	11	4	6	10	9	8	8	9	3	6
Bottom crossers (N_b)		1	4	6	4	3	4	8	7	7	8	3	3
Top crossers (N_t)	1	4	6	4	3	4	8	7	7	8	3	3	
Bottom and top crossers (N_{bt})		1	1	2	3	2	2	6	6	7	2	3	
BC origination rate		0.6	0.778	0.301	0	0.301	0.602	0.067	0.067	0.058	0.176	0	
BC extinction rate		0	0.602	0.477	0.125	0.176	0.301	0.125	0.067	0	0.602	0	
ΔN_b			3	2	-2	-1	1	4	-1	0	1	-5	
Δ BC origination rate			0.176	-0.477	-0.301	0.301	0.301	-0.535	0	-0.009	0.118	-0.176	
Δ BC extinction rate			0.602	-0.125	-0.352	0.051	0.125	-0.176	-0.058	-0.067	0.602	-0.602	

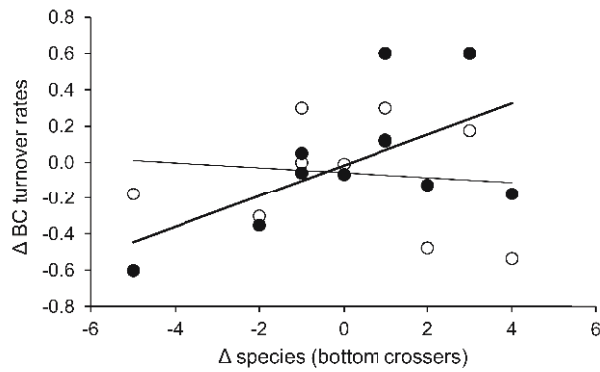


FIGURE 2. Change in origination rate (open circles, thin regression line) and change in extinction rate (closed circles, bold regression line) plotted against change in species richness (N_b).

Furthermore, the analysis here described means that the only habitat change that matters is that occurred between consecutive intervals. Since 13 intervals are here considered, a relatively small habitat change from one interval to the next is expected. This greatly reduces the potential problem posed by this factor.

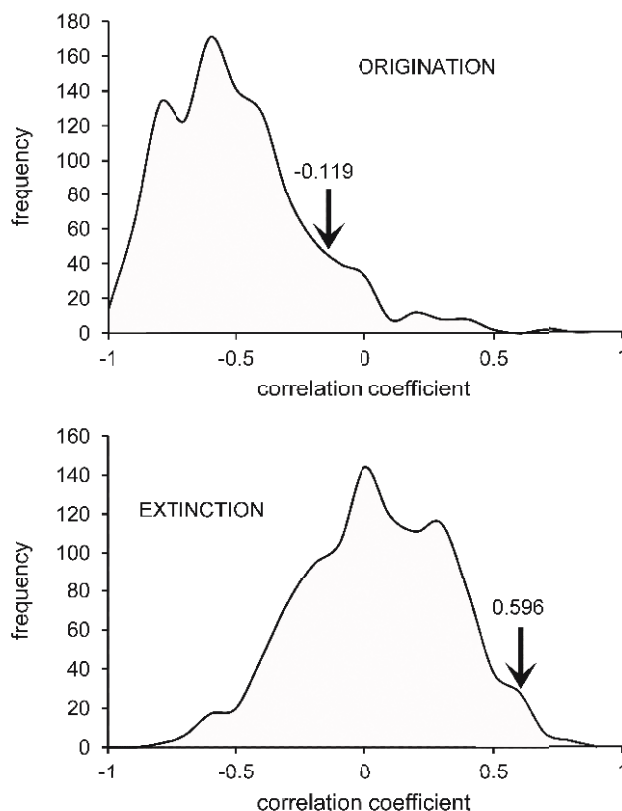


FIGURE 3. Probability distributions of the Pearson correlation coefficient as obtained from the Monte Carlo simulations (1,000 repeats) for A) change in origination rate vs. change in species richness (N_b) and B) change in extinction rate vs. change in species richness (N_b). These plots are smooth histograms with intervals of 0.10.

Considering this factor and the randomization carried on in the simulations, habitat change cannot be seriously considered as an explanation to the results.

CONCLUSIONS

This work demonstrates that there is a genuine self-regulation signal in the diversity record of the trilobite species from Murero RV1, a signal that can be detected more than 500 million years later in spite of the noise caused by preservation, sampling biases and possible habitat change. All these sources of noise are randomized in the Monte Carlo simulation here described and so the results cannot be attributed to them. This case study is an example which suggests that, from the very beginning of the Phanerozoic eon, in the Cambrian fauna, the mechanisms of animal diversity dynamics produced equilibrium of species numbers driven by compensatory extinction due to species interaction. The lack of invasion resistance or diversity-dependent speciation decline may have been typical of animal species assemblages during the Cambrian radiation because their relative simplicity allowed new species to enter the community more easily.

Studies of diversity turnover at the species level, like the present one, are required to determine the generality of these results. A critical step in these analyses would be to focus on a continuous, lithologically homogeneous, and highly fossiliferous sequence starting immediately after a mass extinction and spanning some time after the equilibration of species richness. Different diversity dynamics may be revealed for different organism groups according to the typical strength of their species interactions (Stanley, 1979), a factor which may underlie some of the lack of consensus currently noticed in this field.

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