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1 **Contrasting Early Ordovician assembly patterns highlight the** 2 **complex initial stages of the Ordovician Radiation**

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30 **ABSTRACT**

31
32 The Early Ordovician is a key interval for our understanding of the evolution of life on Earth as
33 it lays at the transition between the Cambrian Explosion and the Ordovician Radiation and
34 because the fossil record of the late Cambrian is scarce. In this study, assembly processes (niche
35 vs. dispersal) of Early Ordovician trilobite and echinoderm communities from the Central Anti-
36 Atlas (Morocco), the Montagne Noire (France), and the Cordillera Oriental (Argentina) are
37 explored using the novel Dispersal Niche Continuum Index (DNCI). The results show that
38 during the Early Ordovician, trilobites diachronically increased in dispersal. Dispersal did not
39 increase for echinoderms. Dispersal was most probably triggered by the planktic revolution, the
40 fall in seawater temperatures, and **changes in** oceanic circulation, and was likely controlled by
41 tectonic frameworks and clade inherent features. The diachronous dispersal in the Early
42 Ordovician highlights the complexity of ecosystem structuring during the early stages of the
43 Ordovician Radiation. Considering that selective Early Ordovician regional dispersal was
44 followed by well-documented continental dispersal in the Middle/Late Ordovician, it is possible
45 to consider that alongside a global increase in taxonomic richness, the Ordovician Radiation
46 involved a gradual increase in dispersal.

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KEYWORDS: Ordovician, community assembly, dispersal, niche

INTRODUCTION

The fossil record of the Cambrian Period documents the early diversification of eumetazoans on Earth¹, during which animals developed a wide range of morphological features and characteristics^{2,3}. The ancient ecology of these animals can be reconstructed based on the exceptional fidelity of anatomy preserved in Burgess Shale (BS)-type fossil sites⁴, such as the Burgess Shale, the Chengjiang Biota, and the Qingjiang Biota⁴⁻⁶. The Cambrian Explosion was followed by the Ordovician Radiation². During the Ordovician, diversity significantly increased and was accompanied by structural changes in ecosystems⁷⁻⁹. However, most of the studies focused on the Middle Ordovician onwards; as such, the Early Ordovician remains an understudied interval that is key to understand the transition between the Cambrian Explosion and the Ordovician Radiation particularly that the fossil record of the late Cambrian is scarce (i.e., the Furongian gap)¹⁰.

In order to decipher ecological processes at this critical crosslink in the evolutionary history of Life on Earth, this work investigates the forces that structure community composition (i.e., niche and dispersal) during the Early Ordovician of three regions: The Central Anti-Atlas (CAA; Morocco), Montagne Noire (MN; France), and Cordillera Oriental (CO; Argentina) (Fig. 1). Because not all regions preserve all types of taxa owing to taphonomic biases^{11,12}, this study is **focuses-focusing** on echinoderms and trilobites, because these are readily preserved and are well studied in the three regions (Fig. 2)¹³⁻²³. Moreover, trilobites are the most abundant and diverse group in the three studied regions followed by echinoderms in the CAA and the MN¹³⁻²³.

Communities can be niche-assembled (Fig. 3A) when they are at equilibrium, closed, balanced, and having a stable taxonomic composition maintained by deterministic processes like positive (e.g., mutualism) and negative (e.g., competitive exclusion) interactions between individuals²⁴⁻²⁶. Communities are dispersal-assembled (i.e., non-equilibrium state; Fig. 3B) when they are open, in non-equilibrium state with their compositions depending on continuous dispersion between communities, random originations, and extinctions (i.e., ecological drift)²⁴⁻²⁶. Once seen as incompatible hypotheses, niche- and dispersal-perspectives are now seen as opposite ends of a continuum²⁴⁻²⁶. Within this continuum, the taxonomic composition of an assemblage may result to a greater or lesser extent of each process, or from an equal combination of the two²⁴⁻²⁶.

Identifying niche and dispersal processes is a fundamental question in modern ecology and has become a central theme for conservation studies. Lately, novel approaches that can identify assembly-processes within fossil datasets, and observe changes in processes through evolutionary times and their potential link with abiotic and biotic events were developed²⁴. In order to quantify niche and dispersal processes of trilobite and echinoderms assemblages in the three regions, this work applies novel Dispersal and Niche Continuum index (DNCI) analyses to understand changes in community assembly between the Tremadocian and the Floian²⁴, i.e., the two Early Ordovician stratigraphic stages. The DNCI quantifies the relative contribution of niche and dispersal processes to the taxonomic dissimilarity between assemblages, which are defined as statistical clusters of fossiliferous levels in each region²⁴. The DNCI ranges from significantly positive (i.e., niche-assembled community) to significantly negative (i.e., dispersal-assembled community) values. Then, the lower the DNCI, the more important dispersal is in a certain assemblage²⁴. A community is equally both niche- and dispersal-assembled when the mean DNCI and its confidence interval overlap with 0²⁴.

93 From a terminological perspective, we use the generic term “assemblage” to refer to all taxa
94 inhabiting a particular area, regardless of the spatial scale considered (e.g., community, meta-
95 community, bioregions). “Assembly-processes” (i.e., niche and dispersal) are the ecological
96 forces bringing together and maintaining these taxa within assemblages. Niche- and dispersal-
97 assembly should be differentiated from cosmopolitanism and endemism. For instance, within a
98 community model, the dispersal can be the only ecological force considered, and lead to an
99 endemic and/or a cosmopolitan signal. Once niche and dispersal contributions were quantified,
100 they were put in the larger evolutionary framework of trilobites and echinoderms in addition to
101 the geological context of the three localities.

102

103 RESULTS AND DISCUSSION

104 Trilobites in the CAA are assembled equally by both niche- and dispersal-processes during the
105 Early Ordovician (i.e., DNCI and its confidence interval overlap with 0 in the Tremadocian and
106 the Floian; Fig. 4B). Trilobites in the MN are dispersal-assembled in the Tremadocian and the
107 Floian (i.e., DNCI is negative and does not overlap with 0; Fig. 4B). Trilobite assemblages in the
108 CO are equally driven by both niche and dispersal processes in the Tremadocian and mainly
109 driven by dispersal processes in the Floian (Fig. 4B). Trilobites in the MN and CO show little
110 overlap between the Tremadocian and the Floian (Fig. 4B). This indicates a clear difference
111 between the Tremadocian and the Floian records of trilobites in the CO and the MN. This
112 difference is characterized by a transition towards more negative DNCI values (Fig. 4B)
113 associated with a decrease in niche processes, and an increase in dispersal²⁴. The contrasting
114 results for trilobites between the three regions (Fig. 4B) do not reflect a differential sampling
115 effort bias because trilobites in the CAA, the CO, and the MN are equally sampled (i.e., S_{obs}/S_{ex}
116 ~ 0.9 ; Fig. 4A).

117 The increase in trilobite regional dispersal during the Early Ordovician (at least in the MN and
118 the CO) correlates with environmental changes for this time interval. During the Furongian, the
119 planktic revolution started, increasing the availability of a globally distributed food source for
120 animals²⁷. Furthermore, temperatures achieved a global hothouse at the onset of the Furongian
121 also known as the Steptoean Positive Carbon Isotope Excursion (or SPICE event) and started to
122 decrease right afterward in the early/middle Furongian up until the Late Ordovician²⁸. The
123 cooling established a more prominent global oceanic circulation in the Middle/Late Ordovician
124 than in the late Cambrian^{29,30}. This means that at least transitional conditions of oceanic
125 ventilation and circulation existed in the Tremadocian and the Floian (periods of high sea
126 level)³¹. Thus, it is most likely that oceanic circulation, cooling, and the planktic revolution
127 facilitated dispersal because these environmental changes are linked to animals’ specific
128 evolutionary patterns and ecological behavior²⁷. For instance, an increased colonization of deep-
129 sea bottoms, as indicated by ichnologic evidence, took place during the Early Ordovician, and
130 has been attributed to augmented oceanic ventilation³². Moreover, in the Furongian, for the first
131 time, trilobites started to disperse and explore brackish water environments, a trend that
132 continued well into the Middle Ordovician^{20,33}. Additionally, most known early to middle
133 Cambrian trilobite larvae were flat (adult-like protaspides) and have lived on or near the
134 seafloor³⁴⁻³⁷. In the Furongian, some trilobite groups developed bulbous configurations³⁴.
135 Bulbous larvae (non-adult-like protaspides) were adapted to a planktic mode of life³⁸. Although
136 bulbous larvae were originally referred to a low number of Ordovician lineages^{34,38}, Bignon et
137 al.³⁹ argued that this type of larvae must have been more frequent than previously thought. Thus,
138 some of the lineages yielding either bulbous larvae or early instars of this type might explain the

139 observed increase in trilobite dispersal. However, this evolutionary trait only explains the
140 increase in dispersal but it does not explain why trilobite dispersal was non-uniform between
141 regions. The non-uniform dispersal pattern might be resulting from the limited temporal
142 sampling in the CAA (Fig. 1A), which represents a significantly more restricted window in
143 comparison to the CO, and the MN (Fig. 1A). It can also result from differences in regional
144 settings (e.g., geodynamic framework). During the Early Ordovician, the CAA was a restricted
145 area^{40,41}, with limited connection to the global ocean, which may explain why trilobites did not
146 disperse within this area as early as trilobites in other regions (Fig. 4B). Moreover, the CO was
147 partially protected by a volcanic arc to the west, which might explain why the composition of the
148 assemblages of this area remained equally niche- and dispersal-assembled in the Tremadocian in
149 comparison to the dispersal-assembled MN⁴².

150 Another aspect of our data is that echinoderms in the CAA and the MN are assembled equally by
151 both niche- and dispersal-processes during the Early Ordovician, without showing a change in
152 community assembly processes (Fig. 4B). Due to sampling biases, trilobite and echinoderm data
153 cannot be directly compared [i.e., $S_{obs}/S_{ex}(\text{echinoderm}) \sim 0.6 < S_{obs}/S_{ex}(\text{trilobite}) \sim 0.9$; Fig. 4A].
154 However, the similarity between echinoderms in the CAA and the MN is not biased by sampling
155 (i.e., $S_{obs}/S_{ex} \sim 0.6$ for both regions; Fig. 4A). This essentially means that echinoderm assembly
156 patterns were uniform between regions and were not differentially affected by the environmental
157 changes happening at the global scale. Unfortunately, it is impossible to further discuss this
158 finding due to the ~~rarity-absence~~ of fossilized echinoderm larvae. It is assumed that the
159 possession of planktotrophic larvae is a plesiomorphic condition in the five extant classes⁴³,
160 which appeared and diversified either in the Early Ordovician (asteroids, crinoids, ophiuroids) or
161 in the Darriwilian (echinoids, holothuroids)⁴⁴. However, confirming that echinoderm
162 planktotrophic larvae were acquired by the Early Ordovician, is not possible⁴⁵.

163 A corollary of these findings is that it is now possible to better contextualize the transition
164 between the Cambrian Explosion and the Ordovician Radiation. The Cambrian Explosion is
165 primarily linked with increased niche packing, and partitioning⁴⁶. Previous studies made at a
166 global scale suggested that niche-processes remained high during the first two Ordovician
167 stages⁴⁶, indicating that remarkable decrease in niche-assembly were only acquired later starting
168 the Middle Ordovician⁴⁷. The overlap of the DNCI with 0 in the Tremadocian, and to some
169 extent in the Floian, indicates that both niche and dispersive regimes are equally detected in the
170 analyses, highlighting that the Early Ordovician was a transitional period between the Cambrian
171 Explosion and the Ordovician Radiation. This study provides a new perspective complementing
172 previously described dynamics by showing that changes in community assembly (i.e., increase in
173 dispersal in comparison to the Cambrian) can already be observed in the Early Ordovician,
174 especially at a regional scale. This increase in dispersal resulting for example from the
175 development of new morphologies (i.e., bulbous larvae) can be augmented by transient taxa⁴⁸ as
176 new dispersive morphologies enable the development of new demographics (i.e., source/sink)⁴⁹
177 and evolutionary (increased taxa longevity) dynamics⁵⁰. For instance, non-specialized taxa could
178 survive in remote and hostile environments if they show adequate dispersive morphology leading
179 to a continuous influx of new individuals from their source community (i.e., competition-
180 colonization trade-off) leading to a further increase in dispersal.

181

182 CONCLUSION

183 The Early Ordovician is a complex period in the evolution of life on Earth. Dispersal increase
184 during this time was likely triggered by environmental conditions (e.g., the planktic revolution

185 and oceanic cooling and circulation changes). However, it was not homogenous for all animal
186 groups and regions (Fig. 4B) as it was controlled by a combination of clade inherent features and
187 the tectonic framework of each region. The importance of the results presented herein is that they
188 (i) were obtained using a novel method that is independent of classical taxonomic richness
189 metrics, and (ii) highlight the complexity of the early stages of the Ordovician Radiation.
190 Considering that diachronous regional dispersal in the Early Ordovician was followed by
191 episodes of continental dispersal during the Middle Ordovician⁵¹⁻⁵⁴, it is possible to suggest that
192 the Ordovician Radiation can be envisaged as facilitated by a set of diachronous (i.e., in one
193 region prior to another) increases (i.e., from regional to continental) in dispersal. This increase in
194 dispersal could also represent a transition from fragmented habitat patches separated by non-
195 livable oxygen-depleted zones in the Early Ordovician to a more homogenous ocean that is
196 dominantly cooler and oxygen-rich in the Middle Ordovician⁵⁵. In the future, it is essential to
197 apply DNCI analyses to a wider range of regions in order to investigate whether either latitudinal
198 or longitudinal dispersal gradients exist during this time interval. These future studies will
199 certainly bring remarkable insights on the spreading of regional dispersal during the Early
200 Ordovician, and on how to calibrate the diachronicity of dispersal during this critical time
201 interval.

202

203 **MATERIALS AND METHODS**

204 **Studied fossils and regions**

205 Echinoderm and trilobite data in this study are primarily field-based and result from intensive
206 sampling in the three investigated areas over several decades. Data from the Montagne Noire are
207 based on the public collections of Lyon 1 University, France. The Central Anti-Atlas data was
208 extracted from the public collections of Cadi Ayyad University, Morocco, while data from the
209 Cordillera Oriental is from both the literature and from the public collections at the National
210 University of Córdoba, Argentina. This work comprises more than 300 well-dated levels (Fig.
211 1A). “Levels” represent spatial-temporal limited intervals. For instance, two stratigraphically
212 distinct fossiliferous horizons occurring at the same site were considered as two different levels.
213 Moreover, two coeval fossiliferous layers were considered as distinct “levels”, when they occur
214 in two different sites of a same region. Additional detailed information on the studied fossils is
215 provided in *Supplementary Material 1 (SM1)*.

216 In order to avoid local depositional biases on the analyses, occurrence data within the same range
217 of depositional conditions between the fair-weather wave base and the storm-weather wave base
218 (i.e., offshore) were included in this study. Moreover, there is no dominant oxygen or salinity
219 stress during deposition of most investigated levels and the three regions have a very comparable
220 substrate^{19, 22, 56}. Therefore, levels in which an oxygen stress is evident in the CAA²² were
221 excluded from the analyses. During the Early Ordovician, the CAA was a relatively restricted
222 sea^{40, 41}. The CO was partially protected by a volcanic arc to the west⁴². The MN was an open sea
223 in direct contact with the ocean^{40, 41}. More information on the geological background is provided
224 in the expanded materials and methods section in *SM1*.

225

226 **Statistical and ecological approaches**

227 Incidence matrices reflecting occurrences (absence/presence) in all layers for each region were
228 built (i.e., five datasets; *Supplementary Material 2*). The sampling effort observed as a ratio
229 between observed and extrapolated sampling ($S_{\text{obs}}/S_{\text{ex}}$) was calculated using the iNEXT package
230 on R software⁵⁷ and its confidence interval was obtained using the function “Ratio of counts CI”

231 of the software PAST⁵⁸ and is reported on Fig. 4A. Each dataset (e.g., echinoderms in the CAA)
232 was then split into two subsets (e.g., Tremadocian and Floian echinoderms in the CAA;
233 *Supplementary Material 3*). Cluster analyses (UPGMA) were performed on each subset, and
234 results are present in *SM3*. The significance of these clusters was then tested and confirmed as
235 statistically significant with an analysis of similarity (i.e., ANOSIM; *SM3*). These analyses were
236 performed in PAST using the Jaccard index, which is the most commonly used index in
237 paleoecological investigations⁵⁹. DNCI identifies the main assembly process driving species
238 composition between clusters by comparing empirical and null SIMPER profiles⁶⁰. The SIMPER
239 method has been designed to compute and depict the contribution of taxa to the overall
240 taxonomic dissimilarity (OAD) between two clusters/groups of assemblages/communities⁶⁰. The
241 contribution of taxa to OAD depends on the relationship of β -diversity within clusters of
242 assemblages and β -diversity between clusters of assemblages (*Supplementary Material 1*). In
243 other words, SIMPER considers: (i) taxa that are largely distributed within one cluster, (ii) taxa
244 that are largely and evenly distributed between two clusters; (iii), rare taxa that are evenly
245 distributed and (iv) rare taxa that are only distributed within one cluster. Then an empirical
246 SIMPER profile is produced by ordering the contribution of each taxa to the OAD. This profile
247 is then compared to three null permuted SIMPER (PERSIMPER) profiles (only niche, only
248 dispersal or the equal contribution of niche and dispersal processes). The closer the null profile,
249 the more important is the respective assembly model (*Supplementary Material 1*). In this sense,
250 the taxonomic dissimilarity and the β -diversity are at the core of PER-SIMPER/DNCI. However,
251 there is no correlation between dissimilarity indexes or β -diversity variations and DNCI
252 variations. To perform DNCI analyses, sheets in *SM3* (i.e., 10 in total) were exported as CSV
253 files and are present in a compressed folder (*Supplementary Material 4*). Three levels that do not
254 belong to any cluster (i.e., highlighted in yellow in *SM3*) were removed from *SM4* because a
255 cluster has to have by definition more than one level to be used in the following DNCI
256 analyses²⁴. Clusters also need to be composed of a similar number of levels in order to avoid bias
257 on niche and dispersal processes identification⁶⁰. If the compared clusters are uneven, DNCI will
258 shift toward 0, leading to a false identification of an equal contribution of niche and dispersal
259 processes²⁴. A subsampling procedure can be used to make the clusters of equal size and correct
260 this bias. In this case, when clusters differ in size (e.g., cluster 1 has 40% more levels than cluster
261 2), a subsampling randomly reducing the larger cluster(s) to the size of the smallest cluster was
262 implemented 100 times to minimize the sampling bias effect and produce robust mean DNCI
263 values. DNCI analyses were done using DNCImper⁶¹ R package available on Github
264 (<https://github.com/Coentrin-Gibert-Paleontology/DNCImper>). A customized R Markdown
265 script of DNCI analyses is provided in *Supplementary Material 5*. More details regarding the
266 methods used, the choices made, in addition to explanations on how the DNCI operates are
267 provided in *SM1*.

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443 coauthors.

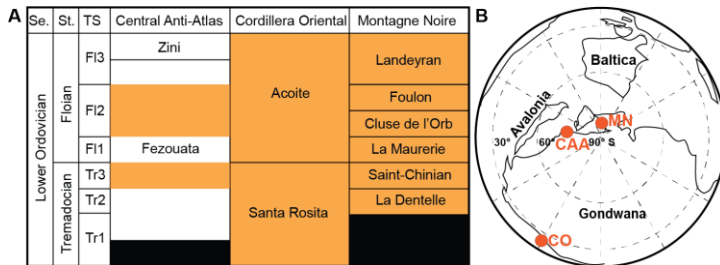
444 **Data availability:** All data needed to evaluate the conclusions in the paper are present in the
445 *Supplementary Materials*. Additional data related to this paper may be requested from the
446 authors.

447 **Competing interests:** The authors declare that they have no competing interests.

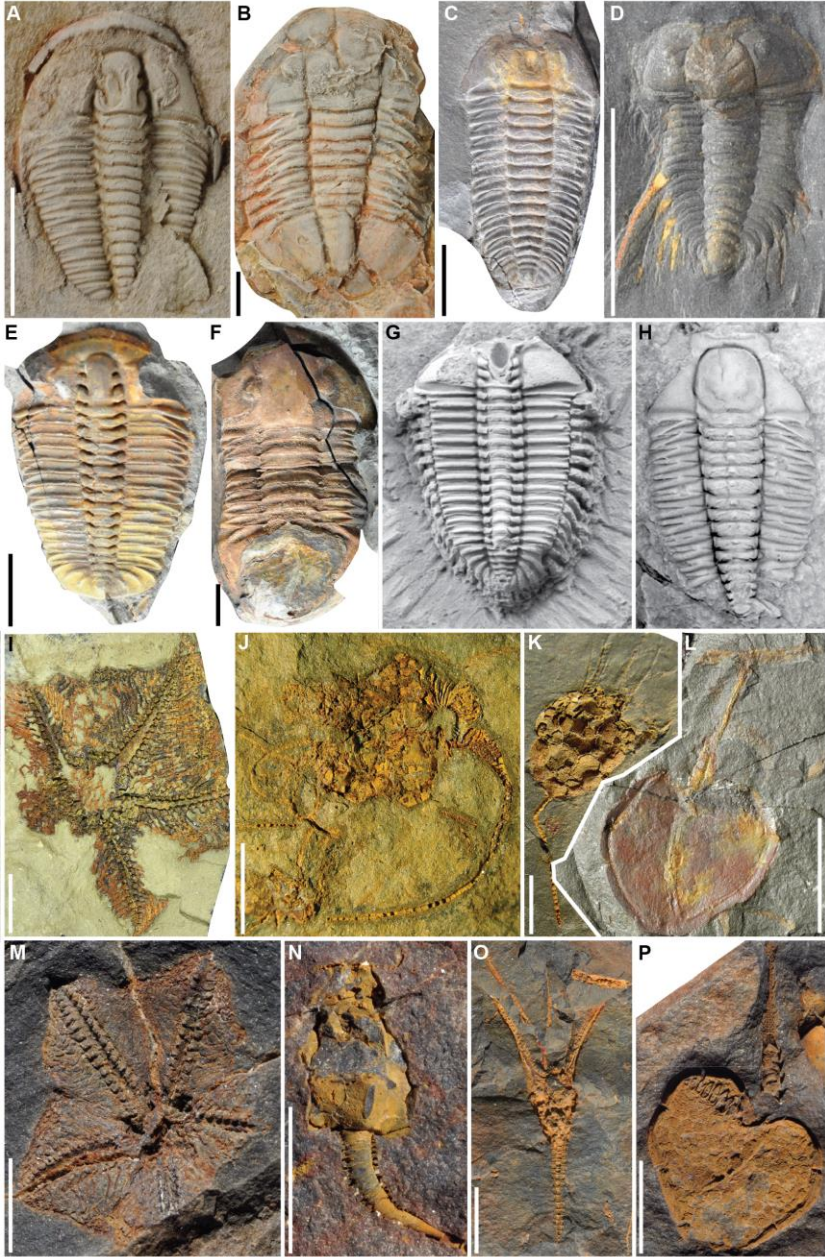
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449 **FIGURE CAPTIONS**

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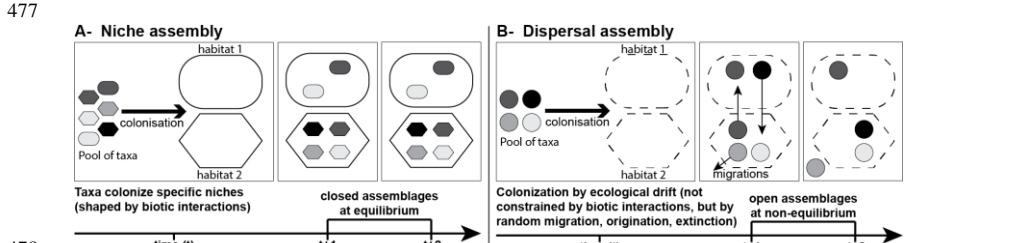


451
 452 **Figure 1.** (A) Stratigraphic correlations between the Central Anti-Atlas (CAA), the Montagne
 453 Noire (MN), and the Cordillera Oriental (CO). The studied intervals within this work are
 454 highlighted in orange. Note that for the Fezouata Shale orange intervals were not selectively
 455 chosen, as those are the only ones yielding echinoderm and trilobite fossils. Se. = Series, St. =
 456 Stage, TS= Time Slices⁶²; Morocco⁶³; Cordillera Oriental¹⁹; Montagne Noire¹⁴. (B)
 457 Paleogeography of the three regions.

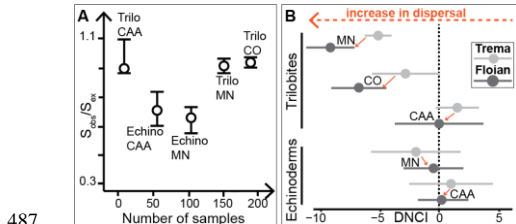


459 **Figure 2.** Trilobites-Early Ordovician trilobites from the Central Anti-Atlas (A-D), the Montagne
 460 Noire (E, F), and the Cordillera Oriental (G, H) in addition to Early Ordovician echinoderms
 461 from the Central Anti-Atlas (I-L), and the Montagne Noire (M-P). (A) *Euloma* sp., late
 462 Tremadocian; AA.TGR1c.OI.232, (B) *Platypeltoides magrebiensis*, late Tremadocian;
 463 AA.TGR0a.OI.132, (C) *Bavarilla spzemmourensis*, late Tremadocian; AA.BIZ15.OI.16, (D)
 464 *Anacheirus adserai*, late Tremadocian; AA.BIZ15.OI.291, (E) *Euloma Filacovi-filacovi*, late
 465 Tremadocian; 4879-03UCBL-FSL 740109, (F) *Paramegalaspis frequens-immarginata*, late
 466 Tremadocian; PS-56UCBL-FSL 740027, (G) *Pliomeridius sulcatus* CEGH-UNC-16311, (H)
 467 *Leptoplastides granulosa* CEGH-UNC-21324, (I) *Villebrunaster* sp., late Tremadocian; FSL 424
 468 961-, (J) *Macrocytella bohémica*, late Tremadocian, MNHM.15690.196, (K) *Eocrinoidea* indet.,
 469 late Tremadocian; MNHM.15690.141, (L) *Cornuta* n. gen. n. sp. cf. "*Phyllocystis*" *jingxiensis*;
 470 FSL.712971, (M), *Villebrunaster thoralis*, late Tremadocian; UCBL-FSL 168673, (N)
 471 *Macrocytella azaisi*, late Tremadocian; MBB-GG50, (O) *Aethocrinus moorei*, late
 472 Tremadocian; MNHN.A49684, (P) *Phyllocystis blayaci*, late Tremadocian; UCBL-FSL 168703.
 473 1cm scale bars (A-F; I-P), xx magnification (G, H); abbreviations (repositories): AA: Cadi-
 474 Ayyad University, Marrakesh (Morocco); MBB: Muséum du Biterrois, Béziers (France); MNHN:
 475 Muséum National d'Histoire Naturelle, Paris (France); UCBL-FSL: palaeontological collections,
 476 Lyon 1 University, Villeurbanne (France).

- Mis en forme : Police :Italique
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478 **Figure 3.** Niche- vs. Dispersal-assembly perspectives. (A) In a niche-assembly scenario,
 479 communities are closed and balanced, built by a limited number of species at equilibrium
 480 (similar assemblages at t+1 and t+2). Niche taxonomic composition is controlled by
 481 deterministic (i.e., non-random) biotic interactions between taxa and their environment. (B)
 482 Dispersal-assembly scenario in which communities are constantly changing (i.e., non-
 483 equilibrium; different assemblages between t+1 and t+2) owing to random processes such as
 484 migrations.
 485
 486



487 **Figure 4.** (A) Estimation of the sampling effort [observed sampling (S_{obs}) over extrapolated
 488 sampling (S_{ex})] of echinoderms (echino) and trilobites (trilo) in the Central Anti-Atlas (CAA),
 489 the Montagne Noire (MN), and the Cordillera Oriental (CO). S_{obs} and S_{ex} were also calculated
 490

491 while separating between the Floian and the Tremadocian of the three regions (*Supplementary*
492 *Material 1*). (B) DNCI analyses for trilobites and echinoderms during the Tremadocian (Trema)
493 and Floian of the Central Anti-Atlas, the Montagne Noire, and the Cordillera Oriental.