

# Ecological disparity is more susceptible to environmental changes than familial taxonomic richness during the Cretaceous in the Alpstein region (northeastern Switzerland)

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**Abstract** Studies of global palaeoecology through time usually ignore regional details. Such regional studies on palaeoecology are required to better understand both regional- and global-scale palaeoecological changes. We analyzed the palaeoecology of a Cretaceous sedimentary sequence in the Alpstein (cantons of Appenzell Ausser-rhoden, Appenzell Innerrhoden and St. Gallen, northeastern Switzerland), which covers from the Barremian to Cenomanian stage. Two diversity indices of familial taxonomic richness and ecological disparity (ecospace occupation) with the trophic nucleus concept were employed in order to document changes in palaeocommunities through time. Our results illustrate that taxonomic richness did not change dramatically, while distinct changes occurred in ecospace occupation through time. The changes in ecospace utilization likely root in fluctuations in water depth and ocean temperature. In addition to these changes in sea level and temperature, our results suggest that water depth was higher in the eastern part of the Alpstein region. Ecospace occupation was moderately diverse through time, which is likely linked with the favorable conditions such as moderate water depth, which made the region habitable for a range of organisms. Only during the late Barremian, the sea was maybe too shallow, thus preventing highly diverse associations. Statistical tests indicate that the chronological changes of familial taxonomic richness and ecological

disparity are decoupled and that the ecological disparity is more highly variable in response to environmental changes than familial taxonomic richness.

**Keywords** Palaeoecology · Diversity · Ecological disparity · Cretaceous · Switzerland

## Introduction

The ‘Big Five’ mass extinctions (End-Ordovician, Late Devonian, End-Permian, End-Triassic and End-Cretaceous) are known to have severely affected the earth’s ecosystems and ecology (e.g., Murphy et al. 2000; Sheehan 2001; Hesselbo et al. 2007; Knoll et al. 2007; Archibald et al. 2010). Recently, Barnosky et al. (2011) examined fossil and modern biodiversity data to assess whether current extinction rates are as disruptive as those of the previous major mass extinctions. In their article, the authors conclude that we are facing the ‘sixth mass extinction’. It is, thus, of great importance to examine changes in palaeocommunities in relation to palaeoenvironmental changes, although it is often discussed that such palaeoecological analyses tend to suffer from biases of sampling, fossilization potential, taphonomy, taxonomic uncertainties and time averaging (e.g., Bambach 1977; Koch and Sohl 1983; Cherns and Wright 2000; Kidwell 2002; Powell and Kowalewski 2002; Lane and Benton 2003; Bush and Bambach 2004; Kowalewski et al. 2006; Alroy 2010a; Bernard et al. 2010).

Palaeoecological studies on a regional and global scale have been of great interest for paleontologists over the past decades (e.g., Bambach 1977, 1983; Sepkoski 1981; Sepkoski et al. 1981; Sepkoski and Sheehan 1983; Sepkoski 1984, 1988; Bush and Bambach 2004, 2015; Bush et al. 2007; Hofmann et al. 2013; Frey et al. 2014). However, the

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number of large regional data sets of palaeoecology and alpha diversity data, i.e., primary information for a higher resolved picture of the global ecology through the Phanerozoic, is still low. For that purpose, documentation of both taxonomic richness and ecological disparity within communities is necessary. Bambach (1983) introduced the concept of ecological guilds such as body plan, food source and tiering, which permitted to analyze palaeoecological changes through time. This method was further developed by Bush et al. (2007) and adapted to theoretical ecospace use. They also included relative abundance of organisms in their analysis to evaluate what ecological categories are dominant through time. Data resulting from such analyses are also necessary to discuss the link between the external environments and ecologic changes.

The Alpstein (cantons of Appenzell Ausserrhoden, Appenzell Innerrhoden and St. Gallen of northeastern Switzerland) is well known for excellently exposed Cretaceous successions. Although a number of studies have been carried out to examine the geology of this region (Funk 1969; Föllmi and Ouwehand 1987; Ouwehand 1987; Bodin et al. 2006; Sala et al. 2014; Wohlwend et al. 2015), comprehensive overviews of the relatively diverse faunas were published only recently by Sulser et al. (2013) on brachiopods and by Tajika et al. (2017) on cephalopods. Although the palaeoecology was briefly discussed in the latter article, the dataset used therein was much smaller because it lacked detailed systematic information from some fossil groups such as bivalves, corals and gastropods. Also, in this article (Tajika et al. 2017), taxon counts were compiled from raw samples without corrections for variations in sample size and furthermore, taxonomic resolution was much lower (identifications were conducted only at the order level). To accurately document the alpha diversity and palaeoecology in all detail available, we herein use a much refined database. Accordingly, we examine the palaeoecology of the Alpstein in detail to answer the following questions: (1) How did the alpha diversity, i.e., taxonomic richness, change from the early Barremian to the earliest Cenomanian? (2) What main ecologic categories occurred through time? (3) What caused the palaeoecological changes between successive faunas? (4) Is there a correlation between taxonomic richness and ecological disparity through time?

## Locality and geological setting

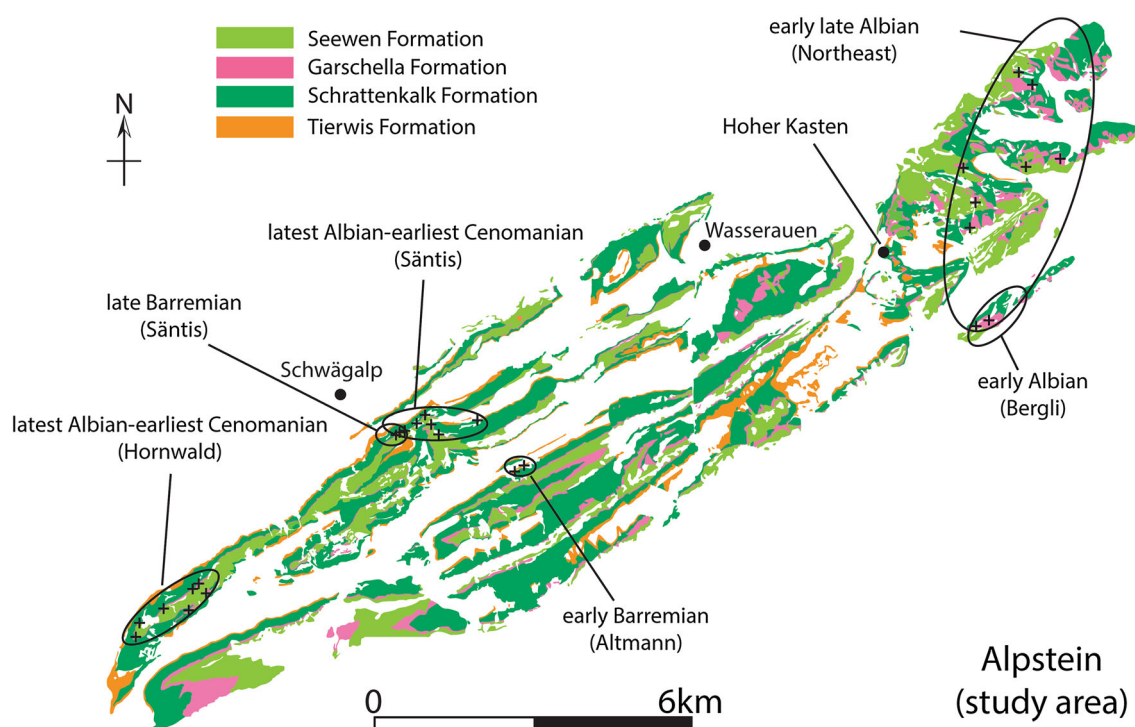
The Alpstein massif is located in the northern part of the Helvetic nappes, which span from southwestern to northeastern Switzerland (Fig. 1 of Tajika et al. 2017; Fig. 1). The study area (Alpstein) includes a part of the Swiss Alps (e.g., Altmann, Hoher Kasten, Wildhuser Schafberg and Säntis), which mainly comprises Cretaceous sediments of the Säntis nappe (Pfiffner 2011). The investigated

stratigraphic sequence and localities are summarized in Fig. 1 and Table 1. Descriptions of each stratigraphic unit are provided in Tajika et al. (2017) and overviews of the corresponding faunas are summarized here:

*Tierwis Formation* (uppermost Hauterivian to upper Barremian; Funk 1969): The Tierwis Formation comprises two subunits, the Altmann Member (carbonates with varying contents of clay and sand) and the younger Drusberg Member (carbonates with varying clay content). The Altmann Member is rich in trace fossils, which are occasionally pyritized. Some condensed and phosphorite-bearing layers contain ammonites and nautiloids in relatively high abundances. Our ecological analyses for the early Barremian were carried out using a fauna from the Altmann Member of Altmann Sattel (Fig. 1). The abundance of fossils in the Drusberg Member is much lower and our sample, therefore, too small to carry out meaningful ecological analyses. These sediments yield ammonites, bivalves, brachiopods and also trace fossils.

*Schrattenkalk Formation* (upper Barremian to middle lower Aptian; Bollinger 1988): The Schrattenkalk Formation is characterized by massive light gray limestones from a shallow carbonate platform environment, which often contain many bioclasts. This formation is abundant in corals, sponges, algae, rudist bivalves and thick-shelled gastropods. The Rawil Member (Schenk 1992; Föllmi et al. 2007), which separates the Schrattenkalk Formation into the Lower and Upper Schrattenkalk Members (Schenk 1992; Föllmi et al. 2007), contains a rich benthic fauna of echinoids (*Heteraster oblongus*, *Leptosalenia prestensis*), abundant forams (*Orbitolina*) and gastropods (*Harpagodes pelagi*), accompanied by wood remains. Our palaeoecological analysis for the late Barremian was conducted in the middle of the Rawil Member. The marly Orbitolina Bed at the top of the Rawil Member marks the boundary between the Barremian and the lowermost Aptian (Bonvallet 2015).

*Garschella Formation* (upper lower Aptian to lowermost Cenomanian; Föllmi and Ouwehand 1987): In the Säntis area, a large part of the Aptian (Grünten and Brisi Members as well as the lower part of the Selun Member) is missing due to erosion, non-deposition and condensation resulting in a 13 m.y. hiatus. The Garschella Formation is rather thin and contains several fossiliferous, phosphatic conglomerates (Durschlägi and Wannenalp Beds; Föllmi and Ouwehand 1987). These are overlain by Aubrig Beds with cephalopods and other invertebrates (Föllmi and Ouwehand 1987). This upper part of the Garschella Formation contains some indications for condensation such as fragmented ammonoids, phosphoritic internal moulds of fossils, and index ammonites from several zones. At the top of the Garschella Fm. (Kamm Bed), there are fossiliferous



**Fig. 1** Geological map of the Alpstein (reproduced from Eugster et al. 1982; Tajika et al. 2017). Localities, where palaeoecological samples were taken, are marked by ellipses

**Table 1** Data of fossil abundance, stratigraphic sequences and localities

	<i>N</i>	Stage	Stratigraphic sequence	Ammonite zones or occurrences	Estimated time range (My) from Scott (2014)	Locality (Fig. 1)
Palaeoecology 1	87	Early Barremian	Altmann Mb. (Tierwis Fm.)	<i>Nicklesia pulchella</i> and <i>Kotetishvilia compressissima</i> zones	2.41–2.90	Altmann Sattel
Palaeoecology 2	96*	Late Barremian	Lower Schrattenkalk Mb. (Schrattenkalk Fm.)	No ammonite record	NA	Säntis
Palaeoecology 3	255	Early Albian	Garschella Fm.	<i>Douvilleiceras mammillatum</i> and <i>Leymeriella tardefurcata</i> zones	2.75	Bergli
Palaeoecology 4	208	Early late Albian	Garschella Fm.	? <i>Mortoniceras inflatum</i> zone and occurrences of <i>Hysteroeras</i>	2.53–?	NE of Alpstein
Palaeoecology 5	132	Latest Albian–earliest Cenomanian	Kamm Bed (Garschella Fm.)	Occurrences of <i>Stoliczkaella</i> and <i>Mantelliceras mantelli</i>	2.53–3.25	Hornwald
Palaeoecology 6	70	Latest Albian–earliest Cenomanian				Säntis

\* Fossils counted on a bedding plane but not extracted

layers with highly diverse ammonoid faunas. We carried out our palaeoecological analyses using faunas from three different stratigraphic parts of the Garschella Fm.: (1) early Albian (*Douvilleiceras mammillatum* and *Leymeriella*

*tardefurcata* zones), (2) early late Albian (with the occurrences of *Mortoniceras*), (3) latest Albian–earliest Cenomanian (Kamm Bed, with *Stoliczkaella* and *Mantelliceras*).

## Materials and methods

### Sampling

We examined fossils from the Alpstein, Switzerland. Part of the examined fossils, which were collected by PK and documented by Tajika et al. (2017), is housed in the Naturmuseum St. Gallen with the numbers NMSG (Coll. PK). Also, this study includes new data on the early Albian fauna in the Alpstein.

We focused on 6 fossiliferous layers to sample macrofossils for palaeoecological analyses. The fossils were either collected ('Palaeoecology 1', '3–6' of Table 1) or determined and counted in situ in the field ('Palaeoecology 2' of Table 1) for quantitative analyses. Note that 'Palaeoecology 5' and '6' of Table 1 were analyzed to examine geographic differences within the more or less identical time range in taxonomic richness and ecological disparity. Due to the varying quality of preservation, the fossils were often determinable only to family level. As such, the taxonomic level family was used to examine taxonomic richness.

### Time averaging

There is a certain degree of stratigraphical faunal mixing in the examined layers: co-occurrence of *Nicklesia pulchella* and *Kotetishvilia compressissima* (early Barremian, Altmann Member), *Leymeriella tardefurcata* and *Douvilleicerias mammillatum*, (early Albian, Garschella Formation), probably *Mortoniceras inflatum* and *Hysterocheras* sp. (early late Albian, Garschella Formation), latest Albian *Stoliczkaiella notha* and *S. clavigera* together with early Cenomanian *Mantelliceras mantelli* and *Hypoturrilites gravesianus* (latest Albian–earliest Cenomanian; Kamm Bed of the Garschella Formation). Such faunal mixing indicates that our analyses do not represent a single association from one environment of one short time interval, and thus some time averaging occurred (Kidwell and Bosence 1991). However, the faunas do not show a mix of neritic organisms (corals, sponges and algae) and pelagic forms (cephalopods), which suggests that the degree of ecological mixing of remains of organisms from extremely different environmental conditions is low. Furthermore, it is a challenge to correctly estimate the timespan included in the sampled layers. To this end, we gathered data on the absolute ages of ammonites, whose ages were radiometrically dated by Scott (2014). Although the preservation sometimes hampers precise taxonomic assignments like in *Hysterocheras* of the early late Albian, we assume that the time ranges of the deposition of each layer are more or less

comparable with a time span of more than 2.5 My (Table 1).

### Alpha diversity (taxonomic richness)

To compare alpha diversities (taxonomic richness at the family level) of faunas from the different geologic units, the abundances of each family were counted per faunal association. Since some fossils were available only as cross sections, and thus not determinable to family level in the late Barremian, the taxonomic richness could not be assessed. Rarefaction analysis (Krebs 1989) was carried out to estimate the effect of sample size and to standardize on a certain sample size (compare Alroy 2010b). This test was performed with the software PAST 3.15 (Hammer et al. 2001).

### Ecospace utilization

We applied the concept of ecospace utilization introduced by Bush et al. (2007), in which the fossils were classified based on their ecological parameters (tiering, motility and feeding) and plotted into a theoretical ecospace. Each parameter represents *x*, *y* and *z* axes in the theoretical ecospace and after completion of plotting the ecology of organisms within a single community, it provides an overview of the ecologic structure of the community. This method is suitable to document how many life styles existed within a community (compare Novack-Gottshall 2007). We followed the ecological classification illustrated in Table 1 of Tajika et al. (2017) with some corrections and additions (Table 2). The rarefaction analysis was also carried out for ecological disparity to correct for sampling biases. To detect which taxa and modes of life were dominant in each fauna, the 'nucleus of a biocoenosis' concept (Neyman 1967; later referred to as 'trophic nucleus' by some researchers) was applied. Accordingly, ecologies of organisms (as number of ecologies calculated using the ecospace above), which constitute 80% of a fauna, were regarded as being ecologically prevalent.

### Comparison between taxonomic richness and ecological disparity

Chronological changes in taxonomic richness and ecological disparity were compared to test if they show a similar trend, i.e., if they are coupled or decoupled. To this end, both Spearman's rank correlation coefficient and Kendall's rank correlation coefficient were applied to examine whether or not results are dependent according to statistical tests. These tests were carried out both for raw data and rarefied data. Since we have two different localities (Hornwald and Sântis) in the latest Albian–the earliest

**Table 2** Ecologic categories of tiering, motility and feeding types Modified from Bush et al. (2007), Tajika et al. (2017)

Ecologic category	Examples
<b>Tiering</b>	
(1) Pelagic	Ammonoids, belemnoids, fish, nautilids
(2) Erect	Crinoids, corals, sponges
(3) Surficial	Echinoids, brachiopods, gastropods, <i>Exogyra</i>
(4) Semi-infaunal	“Normal” bivalves, rudist bivalves, scaphopods
(5) Shallow infaunal	Many clams
(6) Deep infaunal	The clam <i>Panope</i>
<b>Motility level</b>	
(1) Freely, fast	Ammonoids, belemnoids, fish, some arthropods
(2) Freely, slow	Gastropods, echinoids, nautilids, scaphopods
(3) Facultative, unattached	Many clams, polychaetes: <i>Sedentaria</i>
(4) Facultative, attached	Corals, mussels
(5) Non-motile, unattached	Reclining brachiopods, boring bivalves
(6) Non-motile, attached	Rudist bivalves, pedunculated brachiopods, sponges
<b>Feeding mechanism</b>	
(1) Suspension	Boring bivalves, brachiopods, bryozoans, corals, rudists, scaphopods, sponges
(2) Surface deposit	Tellinid bivalves, polychaetes
(3) Mining	Nuculid bivalves
(4) Grazing	Echinoids, gastropods
(5) Predatory	Ammonoids, belemnoids, nautilids, fish
(6) Other	

Cenomanian (‘Palaeoecology 5’ and ‘6’ in Table 1), the comparison was performed separately for data from Hornwald and Sântis. Also, we calculated coefficients of variation of taxonomic richness and ecological disparity (number of ecological occupation) to assess which of the diversity indices is more variable. These statistical analyses were performed with MATLAB (MathWorks).

### Plausibility

Our samples derive from layers, which were formed over timespans of arguable durations, which cannot be determined with great accuracy, and thus were likely not absolutely identical. We think that our results are still meaningful because within single samples, the contained organisms are quite likely to have co-existed at the same place (at least within the same water and sediment column at that very place). Furthermore, our results were compared with published sedimentological data, which also corroborate our results and interpretations. In the absence of contradictions, we suggest that our results reflect the actual fluctuations in ecology.

## Results

### Alpha diversity (taxonomic richness)

Taxonomic richness of each fauna is shown in Table 3. Since the sample sizes of the examined faunas vary, which can lead to biased estimates of taxonomic richness, the original data were rarefied. Raw data of taxonomic richness and rarefied data are plotted in Fig. 2a, b. The results of our rarefaction analyses show that taxonomic richness of faunas with high sample size tends to be overestimated. For instance, the early Albian fauna consists of 255 specimens, which yielded the highest diversity in the raw data. After the sample size was rarefied to 70, the taxonomic richness was then estimated more or less as high as that of the other stratigraphic units. As a result, taxonomic richness stayed at more or less 20 except for the early late Albian (Fig. 2b), although data from the late Barremian are missing due to poor fossil preservation, which hampered taxonomic assignments.

### Ecospace utilization

Changes in the three ecologic categories (tiering, motility and feeding) from the early Barremian to the earliest



**Table 3** Taxonomic richness and ecological category of each fauna and abundance

Early Barremian (Säntis)			Early Albian (Bergli)			Early late Albian (NE)		
Family	Abundance	Ecology	Family	Abundance	Ecology	Family	Abundance	Ecology
Barremitidae	27*	A	Sellithyrididae	64*	I	Desmoceratidae	62*	A
Holcodiscidae	11*	A	Desmoceratidae	46*	A	Inoceramidae	56*	L
Terebrataliidae	9*	I	Douvilleiceratidae	20*	A	Brancoceratidae	34*	A
Ancyloceratidae	7*	A	Trochidae	17*	G	Ancyloceratidae	7*	A
Oxyteuthididae	4*	A	Inoceramidae	16*	L	Hamitidae	7*	A
Pectinoidae	4*	L, N	Anisoceratidae	11*	A	Cymatoceratidae	5*	B
Nuculidae	3*	S	Cymatoceratidae	10*	B	Phylloceratidae	5*	A
Pulchellidae	3*	A	Plicatulidae	9*	L	Pleurotomariidae	4	G
Gryphaeidae	2	H	Dentaliidae	8*	K	Holasteridae	3	G
Sellithyrididae	2	I	Hamitidae	8*	A	Sellithyrididae	3	I
Cyclothyrididae	2	I	Tetragonitidae	7	A	Tetragonitidae	3	A
Toxasteridae	2	G	Buchiidae	4	O	Turrilitidae	3	A
Cymatoceratidae	2	B	Terebrataliidae	4	I	Ichthyodectiformes indet. 1	2	A
Desmoceratidae	1	A	Leymeriellidae	3	A	Sacphitidae	2	A
Ammonite indet. 1	1	A	Turbinidae	3	F	Baculitidae	1	A
Ammonite indet. 2	1	A	Amberleyidae	2	F	Buchiidae	1	O
Arcidae	1	H	Aporrhaidae	2	F	Cephalaspida	1	G
Seaurchin indet. 1	1	G	Cerithiidae	2	F	Dentaliidae	1	K
Holactypidae	1	J	Cirsotrema	2	G	Ficidae	1	G
Pleurotomariidae	1	G	Gadilidae	2	P	Haplaraeidae	1	D
Sponge indet. 1	1	E	Hoplitidae	2	A	Laqueidae	1	I
Serpulidae	1	I	Metacerithiidae	2	F	Norellidae	1	I
No. of family	22		Phylloceratidae	2	A	Plicatulidae	1	M
Rarefied ( $N = 70$ )	19.95		Vanikoroidea	2	G	Ringiculidae	1	G
			Burrirhynchia	1	I	Terebrataliidae	1	I
			Clypeidae	1	G	Turbinidae	1	G
			Cyclothyrididae	1	G	No. of family	26	
Late Barremian (Säntis)			Lytoceratidae	1	A	Rarefied ( $N = 70$ )	15.45	
Taxon	Abundance	Ecol.	Pholadomyidae	1	S			
Bivalves (rudists)	56*	O	Ringiculidae	1	G			
Corals	33*	C	Toxasteridae	1	G			
Boring bivalves	7	R	No. of family	31				
No. of family	NA		Rarefied ( $N = 70$ )	19.50				
Rarefied ( $N = 70$ )	NA							
Latest Albian–earliest Cenomanian (Hornwald)			Latest Albian–earliest Cenomanian (Säntis)					
Family	Abundance	Ecology	Family	Abundance	Ecology			
Turrilitidae	27*	A	Turrilitidae	18*	A			
Inoceramidae	15*	L	Desmoceratidae	8*	A			
Acanthoceratidae	14*	A	Inoceramidae	8*	L			
Lyelliceratidae	10*	A	Anisoceratidae	6*	A			
Cymatoceratidae	8*	B	Brancoceratidae	5*	A			
Desmoceratidae	8*	A	Discoididae	3*	G			
Baculitidae	7*	A	Pleurotomariidae	3*	G			
Sellithyrididae	7*	I	Tetragonitidae	3*	A			
Hamitidae	6*	A	Baculitidae	2	A			
Discoididae	4*	G	Cymatoceratidae	2	B			

**Table 3** continued

Latest Albian–earliest Cenomanian (Hornwald)			Latest Albian–earliest Cenomanian (Sântis)		
Family	Abundance	Ecology	Family	Abundance	Ecology
Holasteridae	4*	G	Lyelliceratidae	2	A
Brancoceratidae	3	A	Sellithyrididae	2	I
Pleurotomariidae	3	G	Ampullinidae	1	G
Scaphitidae	3	A	Aporrhaidae	1	G
Tetragonitidae	3	A	Archaeolamnidae	1	A
Ampullinidae	1	G	Holasteridae	1	G
Anisoceratidae	1	A	Hoplitidae	1	A
Archaeolamnidae	1	A	Mesohibolitidae	1	A
Basiliolidae	1	I	Scaphitidae	1	A
Forbesiceratidae	1	A	Turbinidae	1	G
Glycymerididae	1	Q	No. of family	20	
Lamniformes indet. 1	1	A	Rarefied ( $N = 70$ )	20	
Mesohibolitidae	1	A			
Phylloceratidae	1	A			
No. of family	25				
Rarefied ( $N = 70$ )	19.79				

Groups in the trophic nucleus are indicated by asterisks

A pelagic, freely fast, predatory; B, pelagic, freely slow, predatory; C erect, facultative attached, suspension; D erect, facultative attached, other; E erect, non-motile attached, suspension; F surficial, freely slow, suspension; G surficial, freely slow, grazing; H surficial, non-motile unattached, suspension; I surficial, non-motile attached, suspension; J semi-infaunal, freely fast, grazing; K semi-infaunal, freely slow, suspension; L semi-infaunal, facultative unattached, suspension; M semi-infaunal, facultative attached, suspension; N semi-infaunal, non-motile unattached, suspension; O semi-infaunal, non-motile unattached, suspension; P shallow infaunal, freely slow, suspension; Q shallow infaunal, facultative unattached, suspension; R shallow infaunal, non-motile attached, suspension; S deep infaunal, facultative attached, suspension

Cenomanian are shown in Figs. 2 and 3. Original and rarefied data show a similar trend shown in Fig. 2a, b. A big change occurred in the late Barremian with the disappearance of pelagic elements (ammonites, belemnites, nautiloids and fish). Feeding modes of the late Barremian include only suspension feeding, while several other feeding modes are prevalent in the other examined stratigraphic units. The late Barremian is also characterized by the dominance of facultatively and non-motile ‘attached’ animals. Although for the latest Albian, the analysis was carried out using samples from the two localities Hornwald and Sântis, our analyses from these two samples showed a more or less identical ecospace utilization (Fig. 3).

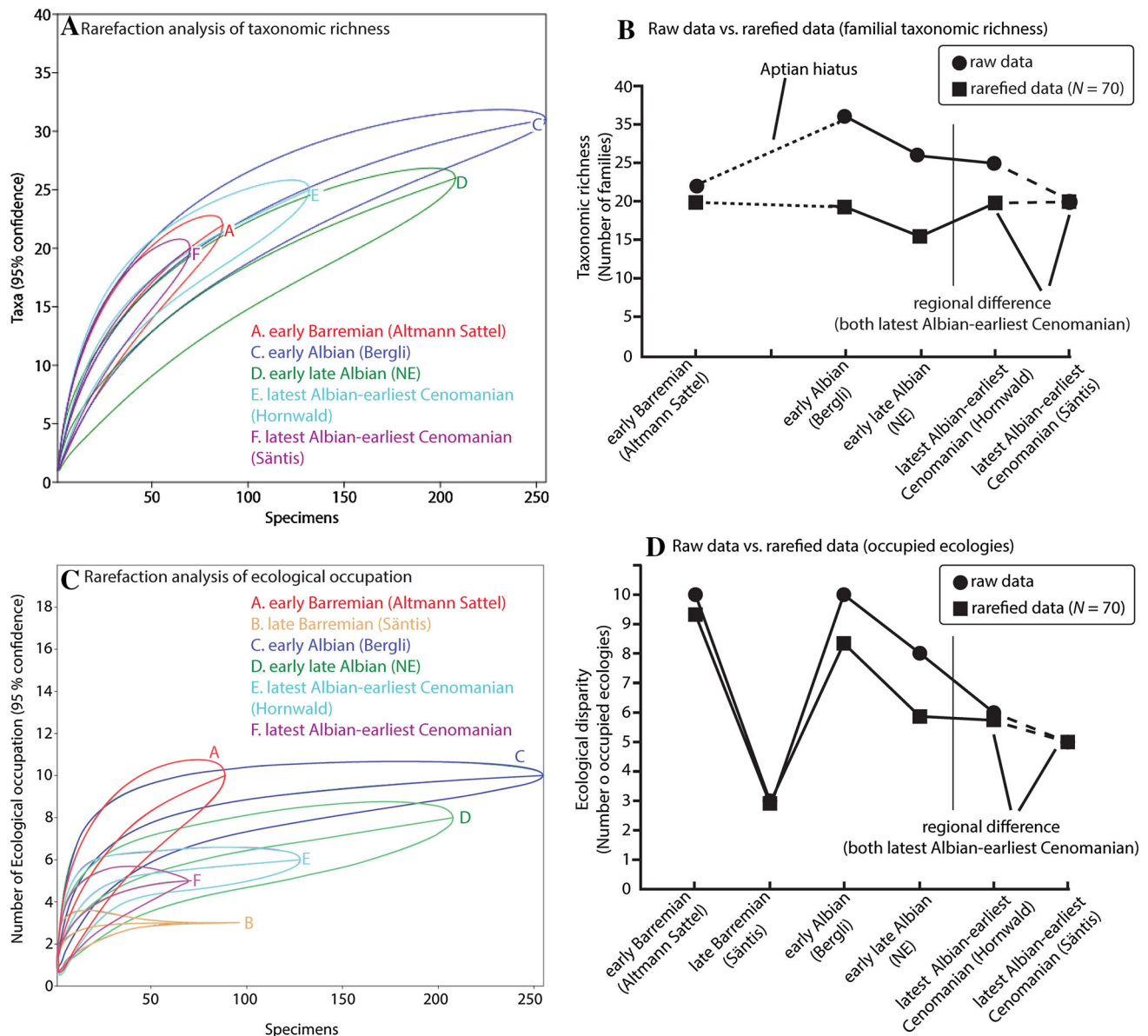
Ecologic changes in three dimensional theoretical ecospace are depicted in the left column of Fig. 4. The trophic nucleus was also determined in order to illustrate the ecology of prevalent organisms in each stratigraphic unit (right column of Fig. 4). It appears that the most extensive ecospace utilization lies either in the early Barremian, early Albian or early late Albian. But when the trophic nucleus is taken into consideration, the early Albian is probably the time, in which the organisms with the most diverse ecologies were present. By contrast, the late Barremian is the time where the lowest diversity of ecospace utilization

was present; however, this partially roots in the sampling mode, because in this case, we counted specimens on a weathered bedding plane using cross sections of fossils. The results demonstrate that only a small number of groups are ecologically dominant within each fauna (right column of Fig. 4), even though sometimes, ecospace occupation appears to be more or less elevated such as in the early Barremian, early late Albian and latest Albian–earliest Cenomanian of the Sântis (left column of Fig. 4). Comparisons between taxonomic richness and ecological disparity are displayed in Fig. 5.

## Discussion

### Environmental and palaeoecological changes through time

A big shift in ecology happened between the late Barremian and the early Aptian; the latter unit was the only time period where pelagic elements were not found. This corresponds to facies changes from glauconite-rich marls and sandy limestones (early Barremian) to massive light gray limestones (late Barremian). Also, we correlated the



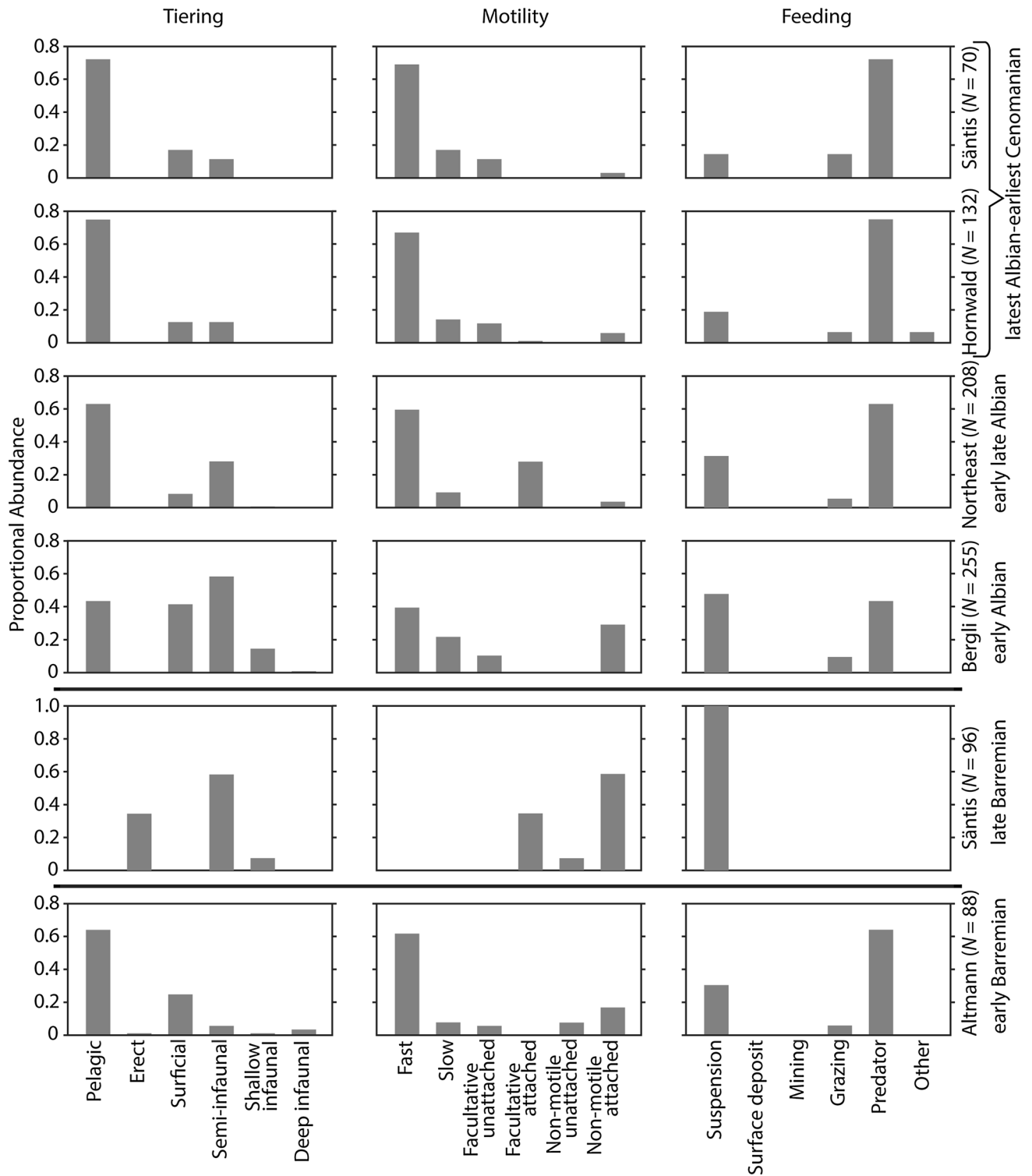
**Fig. 2** Rarefaction analyses of taxonomic richness and ecological disparity in studied geologic times. **a** Rarefaction analysis of raw data of taxonomic richness. **b** Raw and rarefied data of taxonomic

richness. **c** Rarefaction analysis of raw data of ecological disparity. **d** Raw and rarefied data of ecological disparity

absence or presence of pelagic elements with regional sea level changes, which was previously reported by Föllmi (1986; Fig. 5). The early Barremian of the Altmann Member is characterized by heterozoan, partially hemipelagic marl and marly limestones (Bollinger 1988; Föllmi et al. 2007), which implied moderately deep marine settings. The results of our palaeoecological analyses document relatively diverse modes of life at the time (Figs. 3, 4), although the fauna is dominated by pelagic and freely swimming predators such as ammonoids (Ritterbush et al. 2014; right column of Fig. 4). Facies changes that occurred between the early Barremian and the early late Aptian

(Bollinger 1988) suggest that the massive limestones of the Schratenkalk Formation of late Barremian to early Aptian age was laid down under shallow marine conditions. This is further corroborated by the presence of red algae, scleractinians, rudists and other shallow marine organisms (Föllmi et al. 2007). A shallow marine environment with a temporal emergence is further supported by the abundance of remains of land plants, which occur at the base of the Rawil Member. The examined late Barremian fauna derives from the Rawil member, when the platform was temporarily partially emerged (Bonvallet 2015). These shallow to non-marine environments were not



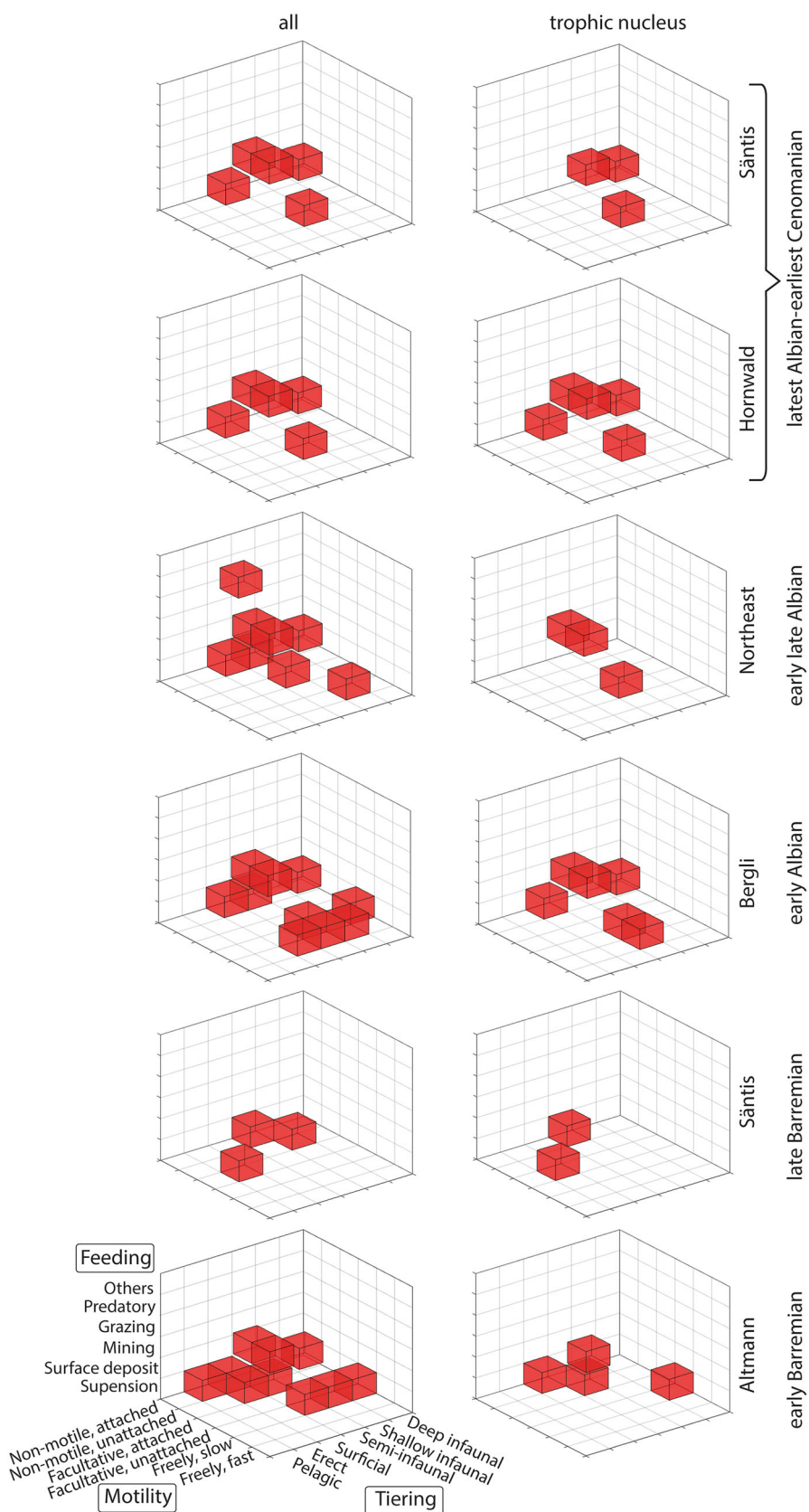


**Fig. 3** Changes in relative abundances of tiering, motility and feeding from the early Barremian to the latest Albian–earliest Cenomanian

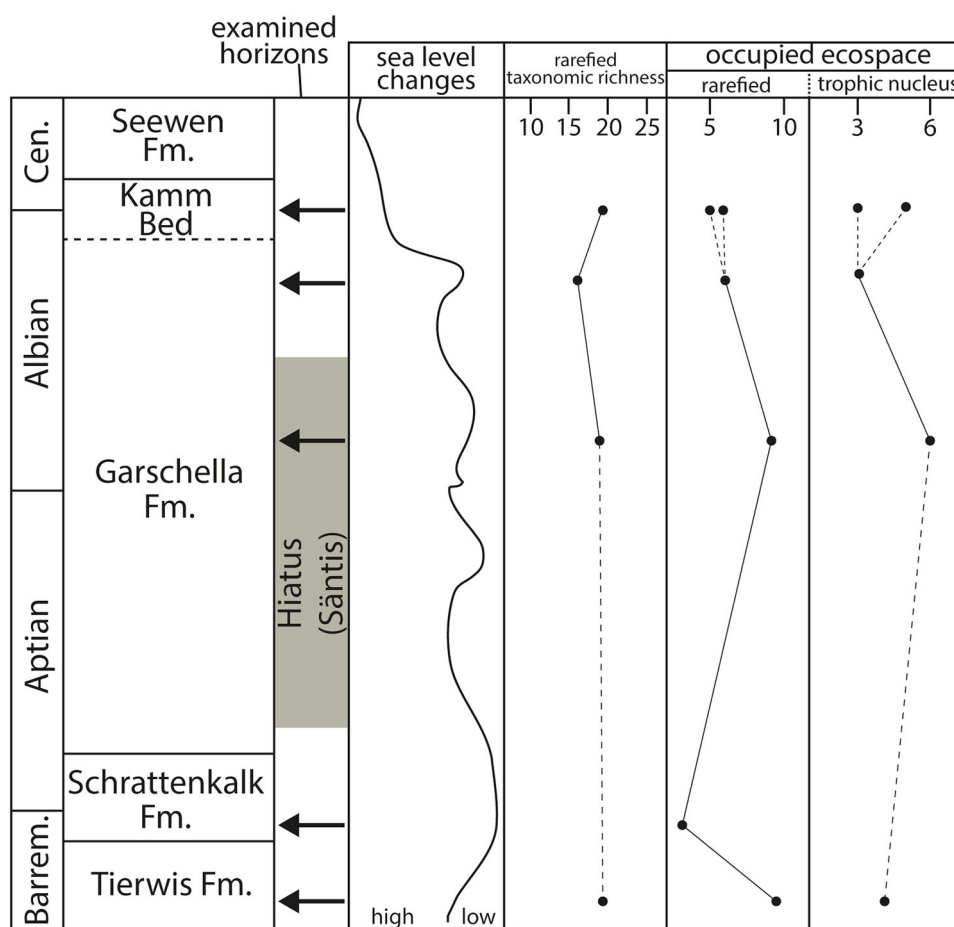
inhabitable by pelagic predators (ammonoids, belemnites and nautiloids). Our results also indicate that there is a distinct change not only in the number of habitats but also in the variation in motility of the animals. This might root in other environmental changes such as temperature

change. Correspondingly, the late Barremian environment with low sea levels fostered the dominance of (facultative and non-motile) attached animals like algae, corals, sponges and rudists (Tajika et al. 2017). The three-dimensional ecospace occupation in the late Barremian is much smaller

**Fig. 4** Three-dimensional plot of ecospace utilization through time. Left column includes all analyzed groups. Right column includes only groups of the trophic nucleus



**Fig. 5** Summary of the ecological analysis. The sea level curve was reproduced from Föllmi (1986)



than in the other examined stratigraphic units (Fig. 4). Nevertheless, considering that we only counted fossils from a bedding plane (instead of collecting them as in the other horizons), it is conceivable that the diversity is underestimated in the late Barremian.

Bambach (1977) examined differences in species richness and abundance among bivalves between different habitats through the Phanerozoic. He documented an increasing trend of diversity and abundance from inshore environments with adverse ecological conditions through nearshore to open marine environments. As far as our results are concerned, we lack sufficient data on taxonomic richness of the shallow marine late Barremian to early Aptian environments due to the poor fossil preservation, which impeded even family-level determination. Nevertheless, it appears likely that the late Barremian shallow marine ecology was rather monotonous with moderately narrow ecospace occupation, which may support Bush's observation. Also, Bush and Daley (2008) as well as Bush et al. (2007) reported that the relative abundance of predators was higher offshore than that in the nearshore shallow water zones. This corresponds to our results, in

which the shallow water late Barremian fauna does not contain larger predatory organisms.

According to Föllmi (1986), the sea level began to rise in the early late Aptian and reached a relatively high level during the early Albian (Fig. 5). The most extensive ecospace occupation occurred in the early Albian (Fig. 4), which might suggest that the habitat ('open-ocean zone' of Föllmi (1989a) and upper ocean temperature of 20–25 °C: Pucéat et al. (2003) provided favorable ecological conditions for various organisms including pelagic predators to thrive. The transgressive trend intensified in the latest Albian. This rapid environmental change likely caused condensation, and thus time averaging (Kidwell and Bosence 1991).

In addition, some studies suggest that climate change has a strong influence on species distribution and in turn, ecosystem structure (Pörtner 2001; Pearson and Dawson 2003; Thuiller et al. 2005; Monahan and Tingley 2012; Dixon and Busch 2017). Taking this into account, the dynamic changes in ecological structure (occupation) in the Alpestein also reflect the effect of climate change. When the Cretaceous palaeotemperature curve of the Tethys, which was reconstructed by Pucéat et al. (2003), is compared with

the ecological changes in the Alpstein, there appears to be a certain degree of correlation. This correlation suggests that it is the palaeotemperature change as well as the sea level change that caused such a dynamic ecological shift. Additionally, since temperature fluctuations can have a strong effect on sea level changes such as melting of inland ice and inflation of sea water volume by heat, palaeotemperature probably indirectly caused the changes of ecology in the Alpstein, although this effect would be minimal at the regional scale.

### Environmental differences between the eastern and western Alpstein

The high diversity of the early Albian suggests subtle environmental differences in water depth between the eastern and the western Alpstein region. In contrast to the moderately rich and diverse fauna of the early Albian in the Bergli area, late Aptian to early Albian faunas are absent in the Säntis area. This phenomenon might be linked with phases of temporal subaerial exposure of the carbonate platform of the Säntis area (Bonvallet 2015) and/or increased current intensity, possibly in connection with short term shifts in current direction (Föllmi 1989a), which did not affect the Bergli area strongly. Moreover, the ‘non-motile, attached’ mode is one of the dominant ecologic modes of motility in the Bergli area, thus indicating a moderate water depth, considering the fact that the shallow water late Barremian fauna is dominated by ‘non-motile, attached’ forms (Fig. 3). The same holds true for the feeding modes, where suspension feeding is much more common in the early Albian than in the younger stratigraphic units (Fig. 3), which may also indicate relatively shallow environments.

Similarly, when the roughly contemporary ecospace occupations in the two regions Hornwald and Säntis of the latest Albian to earliest Cenomanian age (‘Palaeoecology 5’ and ‘6’ in Table 1) are compared, there is a difference in ecology of ‘prevalent organisms’ (trophic nucleus): benthic forms were less common in the Säntis than in the Hornwald area (right column of Fig. 4), although the overall ecospace occupation is nearly identical in both areas (Fig. 3). This might have been caused by the greater water depth of the Säntis area compared to the Hornwald region, even though the overall facies as well as taxonomic structure are nearly identical between the two areas. The presence of the Kamm Bed in the Alpstein suggests an inner shelf environment when these sediments were deposited (Föllmi 1989b). Also, Föllmi (1986) found that the inner shelf lied in the western and northern part of the region with its margin running from the southwest (Feldkirch; 10 km east of the Alpstein region) via the northeast (around 1 km south of Ebnit) to the east. Taking this into consideration, it appears

likely that the water depth slightly increased eastwards as well within the inner shelf.

### Taxonomic richness vs. ecological disparity

As far as taxonomic richness is concerned, we found a rather stable diversity in the early Barremian to the earliest Cenomanian samples when they were rarefied to 70 specimens. A relatively low taxonomic richness appears in the early late Albian, although the ecospace occupation of the fauna is relatively diverse (Fig. 4). Taking the effects of time averaging into account, this may root in an unevenness of time range between compared faunas. That is, although we assume that the degree of time range of each examined horizon is similar, more heavily time-averaged faunas may seem artificially more diverse.

We tested if there is a correlation in chronological changes between taxonomic richness and ecological disparity. No significant differences were found in our statistical tests (Spearman’s and Kendall’s rank correlation coefficient). Results suggest that taxonomic richness and ecological disparity are decoupled (Table 4). Also, coefficient of variations of taxonomic richness and ecological occupation were calculated. Results show that taxonomic richness has a higher coefficient of variation (Table 4), which suggests that family-level taxonomic richness is more susceptible to environmental changes (sea level changes).

### Possible biases in palaeoecological analyses

Although we employed the familial taxonomic level for our analyses, the use of different taxonomic levels can lead to different results because different taxonomic levels (species, genus or family) are not standardized, and thus contain a certain degree of biases (Forey et al. 2004). In fact, the use of taxonomic levels has been discussed for many decades (e.g., Raup 1972; Erwin et al. 1987). Generally, the family level has been considered to be more resistant to sampling biases than the lower taxonomic levels, while it can mask subtle diversification patterns (Lane and Benton 2003). In fact, some researchers demonstrated that patterns using species, genus, family and order levels are not congruent (Signor 1985; Lane and Benton 2003). Considering that, it is likely that our results of relatively unvaried familial taxonomic richness have a different pattern compared to those of species and/or genus levels. Nevertheless, we cannot conclude whether the possible difference between the different taxonomic levels roots in variable preservational biases between these levels, lack of taxonomic standardization (taxonomic uncertainty) or a true diversification pattern at this point (Ubukata 2016).

**Table 4** Results of statistical tests

	Spearman's $\rho$			Kendall's $\tau$			Coefficient of variation	
	$\rho$	$p$	Results	$\tau$	$p$	Results	Taxonomic richness	Ecological disparity
Original data (including Palaeoecology 5: Hornwald)	0.1054	1	ns	0.1826	1	ns	0.14	0.23
Rarefied data (including Palaeoecology 5: Hornwald)	0.4	0.75	ns	0.3333	0.75	ns	0.12	0.25
Original data (including Palaeoecology 6: Sántis)	0.6325	0.5	ns	0.5477	0.5	ns	0.20	0.29
Rarefied data (including Palaeoecology 6: Sántis)	− 0.2	0.9167	ns	0	1	ns	0.12	0.30

Both rarefied and original data are separately tested. Null hypothesis for the Spearman's and Kendall's rank correlation coefficients is that there is a significant difference between the two arguments (taxonomic richness and ecological disparity).  $\rho$  and  $\tau$  = correlation coefficient.  $p$  = probability

ns not significant

Bush and Bambach (2004) discussed the preservation potential of aragonitic versus calcitic shell materials because aragonite is more susceptible to dissolution than calcite in sea water and thus, has a lower fossilization potential (Canfield and Raiswell 1991; Smith et al. 1992; Brachert and Dullo 2000; Morse and Arvidson 2002; Kowalewski et al. 2006). Some researchers examined this bias employing different methods (Koch and Sohl 1983; Cherns and Wright 2000). In contrast to the latter authors, Kidwell (2005) argued that these differences in preservability do not have a big impact on studies on macroevolutionary patterns and biodiversity changes in mollusks. Our study covers only a rather short period in geologic time (between ca. 129 and 93 Ma), during which there were no major changes in proportion of mollusks with aragonitic, calcitic or bimineralic shells (Kidwell 2005). Also, assuming that preservation potential is nearly the same within a group with the same shell mineralogy, we consider that this bias does not strongly affect our results. Nevertheless, the late Barremian sediments of the Alpstein lack faunal elements with aragonitic conchs (ammonoids, nautiloids). This might indicate dissolution of aragonitic elements in accordance with sea level fall during the time.

Additionally, Bush and Bambach (2004) discussed the effect of latitudes on diversity measurements, since some studies documented a gradient of diversity between temperate and tropical regions (e.g., Roy et al. 1998; Crame 2001, 2002). However, as mentioned before, the studied time interval is too short for significant effects of changes in latitude and thus, the effects of such a biogeographical bias is likely negligible. Therefore, the results of our palaeoecological analyses likely reflect mainly environmental changes with regional causes.

## Conclusions

We analyzed the palaeoecology of the Alpstein region from the early Barremian to the earliest Cenomanian with focuses on the taxonomic richness and ecological disparity (ecospace utilization).

*Alpha diversity of the Alpstein* Our raw data show a fluctuation in taxonomic richness (number of families) through time. After rarefaction of the palaeobiodiversity data, however, it turned out that taxonomic richness did not change dramatically from the early Barremian to the earliest Cenomanian.

*Ecospace utilization* A distinct change in ecospace utilization occurred during the late Barremian, when the fauna was dominated by organisms with monotonous ecological requirements such as non-pelagic, facultative or non-motile and suspension feeding groups. We documented the widest ecospace occupation for the early Albian. Ecospace utilization of prevalent groups (trophic nucleus) is reduced in the early Barremian, early late Albian and latest Albian to earliest Cenomanian in the Sántis area.

*What caused the changes in palaeoecology?* Although there are some biases affecting our palaeoecological analyses, they likely did not significantly alter our results. In contrast, our results most likely reflect actual environmental changes, which are reflected in synchronous facies changes. The differences in ecospace occupation were probably caused by fluctuations regional and global sea level, and ocean temperature. The fact that the more monotonous pelagic-dominated faunas were found eastwards in the latest Albian to the earliest Cenomanian suggests that water depth slightly increased towards the east within the inner shelf.



**Taxonomic richness vs. ecological disparity** Statistical tests show that taxonomic richness and ecological disparity are decoupled. Also, taxonomic richness was relatively stable through time, whereas ecological disparity changed more dramatically. This suggests that ecological disparity is more susceptible to environmental changes than taxonomic richness is.

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## References

- Alroy, J. (2010a). Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. *Quantitative Methods in Paleobiology. Paleontological Society Papers*, 16, 55–80.
- Alroy, J. (2010b). Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology*, 53(6), 1211–1235.
- Archibald, J. D., Clemens, W., Padian, K., Rowe, T., Macleod, N., Barrett, P. M., et al. (2010). Cretaceous extinctions: Multiple causes. *Science*, 328(5981), 973.
- Bambach, R. K. (1977). Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology*, 3(2), 152–167.
- Bambach, R. K. (1983). Ecospace utilization and guilds in marine communities through the Phanerozoic. In M. J. S. Tevesz & P. L. McCall (Eds.), *Biotic interactions in recent and fossil benthic communities* (pp. 719–746). New York: Springer, US.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471(7336), 51–57.
- Bernard, E. L., Ruta, M., Tarver, J. E., & Benton, M. J. (2010). The fossil record of early tetrapods: Worker effort and the end-Permian mass extinction. *Acta Palaeontologica Polonica*, 55(2), 229–239.
- Bodin, S., Godet, A., Vermeulen, J., Linder, P., & Föllmi, K. B. (2006). Biostratigraphy, sedimentology and sequence stratigraphy of the latest Hauterivian–early Barremian drowning episode of the Northern Tethyan margin (Altmann Member, Helvetic Nappes, Switzerland). *Eclogae Geologicae Helveticae*, 99(2), 157–174.
- Bollinger, D. (1988). Die Entwicklung des distalen osthelvetischen Schelfs im Barremian und Früh-Aptian: Drusberg-, Mittagsspitze und Schrattenkalk-Fm. im Vorarlberg und Allgäu. Dissertation. Universität Zürich.
- Bonvallet, L. (2015). Evolution of the Helvetic Shelf (Switzerland) during the Barremian–Early Aptian: Paleoenvironmental, Paleogeographic and Paleooceanographic Controlling Factors. Dissertation. University of Lausanne.
- Brachert, T., & Dullo, W.-C. (2000). Shallow burial diagenesis of skeletal carbonates: Selective loss of aragonite shell material (Miocene to Recent, Queensland Plateau and Queensland Trough, NE Australia)—implications for shallow cool-water carbonates. *Sedimentary Geology*, 136(3), 169–187.
- Bush, A. M., & Bambach, R. K. (2004). Did alpha diversity increase during the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. *The Journal of Geology*, 112(6), 625–642.
- Bush, A. M., & Bambach, R. K. (2015). Sustained Mesozoic–Cenozoic diversification of marine Metazoa: A consistent signal from the fossil record. *Geology*, 43(11), 979–982.
- Bush, A. M., Bambach, R. K., & Daley, G. M. (2007). Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology*, 33(01), 76–97.
- Bush, A. M., & Daley, G. M. (2008). Comparative paleoecology of fossils and fossil assemblages. *The Paleontological Society Papers*, 14, 289–317.
- Canfield, D., & Raiswell, R. (1991). Carbonate precipitation and dissolution: Its relevance to fossil preservation. In P. Alison & D. Briggs (Eds.), *Taphonomy: Releasing the data locked in the fossil record* (pp. 411–453). New York: Plenum.
- Cherns, L., & Wright, V. P. (2000). Missing molluscs as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea. *Geology*, 28(9), 791–794.
- Crame, J. A. (2001). Taxonomic diversity gradients through geological time. *Diversity and Distributions*, 7(4), 175–189.
- Crame, J. (2002). Evolution of taxonomic diversity gradients in the marine realm: A comparison of Late Jurassic and Recent bivalve faunas. *Paleobiology*, 28(2), 184–207.
- Dixon, A. L., & Busch, J. W. (2017). Common garden test of range limits as predicted by a species distribution model in the annual plant *Mimulus bicolor*. *American Journal of Botany*, 104(6), 817–827.
- Erwin, D. H., Valentine, J. W., & Sepkoski, J. J. (1987). A comparative study of diversification events: The early Paleozoic versus the Mesozoic. *Evolution*, 41(6), 1177–1186.
- Eugster, H., Forrer, M., Fröhlicher, H., Kempf, T., Schlatter, L., Blaser, R., Funk, H., Langenegger, H., Spoerri, M., & Habicht, K. (1982). Säntis (map sheet 1115), Geological Atlas of Switzerland 1:25,000, N. 78. Wabern: Federal Office of Topography, Swisstopo.
- Föllmi, K. (1986). Die Garschella- und Seewerkalkformation (Aptian–Santonian) im Voralberger Helvetikum und Ultrahelvetikum. *Mitteilungen aus dem Geologischen Institut der Eidgenössischen Technischen Hochschule und der Universität Zürich, Neue Folge*, 262, 1–391.
- Föllmi, K. (1989a). Mid-Cretaceous platform drowning, current-induced condensation and phosphogenesis, and pelagic sedimentation along the eastern Helvetic shelf (northern Tethys margin). *Cretaceous of the Western Tethys: Stuttgart, E. Schweizerbart'sche Verlagsbuchhandlung* (pp. 585–606). Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.
- Föllmi, K. (1989b). *Evolution of the mid-Cretaceous triad: Platform carbonates, phosphatic sediments, and pelagic carbonates along the northern Tethys margin*. Berlin: Springer.
- Föllmi, K., Bodin, S., Godet, A., Linder, P., & Van De Schootbrugge, B. (2007). Unlocking paleo-environmental information from Early Cretaceous shelf sediments in the Helvetic Alps: Stratigraphy is the key! *Swiss Journal of Geosciences*, 100(3), 349–369.
- Föllmi, K., & Ouwehand, P. (1987). Garschella-Formation und Götzis-Schichten (Aptian–Coniacian): Neue stratigraphische Daten aus dem Helvetikum der Ostschweiz und des Vorarlbergs. *Eclogae Geologicae Helveticae*, 80(1), 141–191.
- Forey, P. L., Fortey, R. A., Kenrick, P., & Smith, A. B. (2004). Taxonomy and fossils: A critical appraisal. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 359(1444), 639–653.
- Frey, L., Naglik, C., Hofmann, R., Schemm-Gregory, M., Frýda, J., Kroeger, B., et al. (2014). Diversity and palaeoecology of Early

- Devonian invertebrate associations in the Tafila (Anti-Atlas, Morocco). *Bulletin of Geosciences*, 89(1), 75–112.
- Funk, H. (1969). Typusprofile der helvetischen Kieselkalk Formation und der Altmann-Schichten. *Eclogae Geologicae Helvetiae*, 62, 191–203.
- Hammer, Ø., Harper, D., & Ryan, P. (2001). Paleontological statistics software: Package for education and data analysis. *Palaeontologia Electronica*, 4(1), 9.
- Hesselbo, S. P., McRoberts, C. A., & Pálffy, J. (2007). Triassic–Jurassic boundary events: Problems, progress, possibilities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 244(1), 1–10.
- Hofmann, R., Hautmann, M., Wasmer, M., & Bucher, H. (2013). Palaeoecology of the Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic recovery. *Acta Palaeontologica Polonica*, 58(1), 149–173.
- Kidwell, S. M. (2002). Time-averaged molluscan death assemblages: Palimpsests of richness, snapshots of abundance. *Geology*, 30(9), 803–806.
- Kidwell, S. M. (2005). Shell composition has no net impact on large-scale evolutionary patterns in mollusks. *Science*, 307(5711), 914–917.
- Kidwell, S. M., & Bosence, D. W. (1991). Taphonomy and time-averaging of marine shelly faunas. In P. A. Allison & D. E. G. Briggs (Eds.), *Taphonomy: Releasing the data locked in the fossil record* (pp. 115–209). New York: Plenum.
- Knoll, A. H., Bambach, R. K., Payne, J. L., Pruss, S., & Fischer, W. W. (2007). Paleophysiology and end-Permian mass extinction. *Earth and Planetary Science Letters*, 256(3), 295–313.
- Koch, C. F., & Sohl, N. F. (1983). Preservational effects in paleoecological studies: Cretaceous mollusc examples. *Paleobiology*, 9(01), 26–34.
- Kowalewski, M., Kiessling, W., Aberhan, M., Fürsich, F. T., Scarponi, D., Wood, S. L. B., et al. (2006). Ecological, taxonomic, and taphonomic components of the post-Paleozoic increase in sample-level species diversity of marine benthos. *Paleobiology*, 32(4), 533–561.
- Krebs, C. J., (1989) *Ecological Methodology*. New York: Harper & Row.
- Lane, A., & Benton, M. J. (2003). Taxonomic level as a determinant of the shape of the Phanerozoic marine biodiversity curve. *The American Naturalist*, 162(3), 265–276.
- Monahan, W. B., & Tingley, M. W. (2012). Niche tracking and rapid establishment of distributional equilibrium in the house sparrow show potential responsiveness of species to climate change. *PLoS One*, 7(7), e42097.
- Morse, J. W., & Arvidson, R. S. (2002). The dissolution kinetics of major sedimentary carbonate minerals. *Earth Science Reviews*, 58(1), 51–84.
- Murphy, A. E., Sageman, B. B., & Hollander, D. J. (2000). Eutrophication by decoupling of the marine biogeochemical cycles of C, N, and P: A mechanism for the Late Devonian mass extinction. *Geology*, 28(5), 427–430.
- Neyman, A. (1967). Limits to the application of the ‘trophic group’ concept in benthic studies. *OCEANOLOGY-Academy of Sciences of the USSR*, 7(2), 149–155.
- Novack-Gottshall, P. M. (2007). Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas. *Paleobiology*, 33(2), 273–294.
- Ouwehand, P. J. (1987). Die Garschella-Formation (“Helvetischer Gault”, Aptian-Cenomanian) der Churfirsten-Alvier Region (Ostschweiz). Dissertation. ETH Zürich.
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12(5), 361–371.
- Pfiffner, O. A. (2011). Structural Map of the Helvetic Zone of the Swiss Alps, including Vorarlberg (Austria) and Haute Savoie (France), 1: 100 000. In: Geological Special Map 128. Explanatory notes. Wabern: Swisstopo.
- Pörtner, H. (2001). Climate change and temperature-dependent biogeography: Oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, 88(4), 137–146.
- Powell, M. G., & Kowalewski, M. (2002). Increase in evenness and sampled alpha diversity through the Phanerozoic: Comparison of early Paleozoic and Cenozoic marine fossil assemblages. *Geology*, 30(4), 331–334.
- Pucéat, E., Lécuyer, C., Sheppard, S. M., Dromart, G., Reboulet, S., & Grandjean, P. (2003). Thermal evolution of Cretaceous Tethyan marine waters inferred from oxygen isotope composition of fish tooth enamels. *Paleoceanography*, 18(2), 1029.
- Raup, D. M. (1972). Taxonomic diversity during the Phanerozoic. *Science*, 177(4054), 1065–1071.
- Ritterbush, K., Hoffmann, R., Lukeneder, A., & De Baets, K. (2014). Pelagic palaeoecology: The importance of recent constraints on ammonoid palaeobiology and life history. *Journal of Zoology*, 292(4), 229–241.
- Roy, K., Jablonski, D., Valentine, J. W., & Rosenberg, G. (1998). Marine latitudinal diversity gradients: Tests of causal hypotheses. *Proceedings of the National Academy of Sciences*, 95(7), 3699–3702.
- Sala, P., Pfiffner, O. A., & Frehner, M. (2014). The Alpstein in three dimensions: Fold-and-thrust belt visualization in the Helvetic zone, eastern Switzerland. *Swiss Journal of Geosciences*, 107(2–3), 177–195.
- Schenk, K. (1992). Die Drusberg- und Schrattenkalk-Formation (Unterkreide) im Helvetikum des Berner Oberlandes (pp. 1–169). Ph.D. thesis. Geological Institute, University of Berne.
- Scott, R. W. (2014). A Cretaceous chronostratigraphic database: construction and applications. *Carnets de Géologie-Notebooks on Geology*, 14(2), 15–37.
- Sepkoski, J. J. (1981). A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, 7(1), 36–53.
- Sepkoski, J. J. (1984). A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology*, 10(02), 246–267.
- Sepkoski, J. J. (1988). Alpha, beta, or gamma: Where does all the diversity go? *Paleobiology*, 14(03), 221–234.
- Sepkoski, J. J., Bambach, R. K., Raup, D. M., & Valentine, J. W. (1981). Phanerozoic marine diversity and the fossil record. *Nature*, 293(5832), 435–437.
- Sepkoski, J. J., & Sheehan, P. M. (1983). Diversification, faunal change, and community replacement during the Ordovician radiations. In M. J. S. Tevesz & P. L. McCall (Eds.), *Biotic interactions in recent and fossil benthic communities* (pp. 673–717). New York: Springer, US.
- Sheehan, P. M. (2001). The Late Ordovician mass extinction. *Annual Review of Earth and Planetary Sciences*, 29(1), 331–364. doi:10.1146/annurev.earth.29.1.331.
- Signor, P. (1985). Real and apparent trends in species richness through time. In J. Valentine (Ed.), *Phanerozoic diversity patterns: Profiles in macroevolution* (pp. 129–150). Princeton: Princeton University Press.
- Smith, A., Nelson, C., & Danaher, P. (1992). Dissolution behaviour of bryozoan sediments: Taphonomic implications for nontropical shelf carbonates. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 93(3), 213–226.
- Sulser, H., Friebe, G., & Kürsteiner, P. (2013). Little-known brachiopods from the Cretaceous of the Helvetic realm of NE Switzerland (Alpstein) and W Austria (Vorarlberg). *Swiss Journal of Geosciences*, 106(2), 397–408.

- Tajika, A., Kürsteiner, P., Pictet, A., Lehmann, J., Tschanz, K., Jattiot, R., et al. (2017). Cephalopod associations and palaeoecology of the Cretaceous (Barremian–Cenomanian) succession of the Alpstein, northeastern Switzerland. *Cretaceous Research*, 70, 15–54.
- Thuiller, W., Lavorel, S., & Araújo, M. B. (2005). Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, 14(4), 347–357.
- Ubukata, T. (2016). Biases in paleontological data and their calibration for paleobiodiversity studies. *Fossils*, 100, 29–43.
- Wohlgend, S., Hart, M., & Weissert, H. (2015). Ocean current intensification during the Cretaceous oceanic anoxic event 2—evidence from the northern Tethys. *Terra Nova*, 27(2), 147–155.