



**QUEEN'S  
UNIVERSITY  
BELFAST**

## First workshop on the Carnian Pluvial Episode (Late Triassic): a report

Dal Corso, J., Benton, M. J., Bernardi, M., Franz, M., Gianolla, P., Hohn, S., Kustatscher, E., Merico, A., Roghi, G., Ruffell, A., Ogg, J. G., Preto, N., Schmidt, A. R., Seyfullah, L. J., Simms, M. J., Shi, Z., & Zhang, Y. (2018). First workshop on the Carnian Pluvial Episode (Late Triassic): a report. *Albertiana*, 44, 49-57. <https://albertiana-sts.org/2018/02/26/meeting-report-first-workshop-on-the-carnian-pluvial-episode-late-triassic/>

**Published in:**  
Albertiana

**Document Version:**  
Publisher's PDF, also known as Version of record

**Queen's University Belfast - Research Portal:**  
[Link to publication record in Queen's University Belfast Research Portal](#)

**Publisher rights**

© 2018 The Authors.

This work is made available online in accordance with the publisher's policies. Please refer to any applicable terms of use of the publisher.

**General rights**

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

**Take down policy**

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact [openaccess@qub.ac.uk](mailto:openaccess@qub.ac.uk).

**Open Access**

This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: <http://go.qub.ac.uk/oa-feedback>

## FIRST WORKSHOP ON THE CARNIAN PLUVIAL EPISODE (LATE TRIASSIC): A REPORT

**Jacopo Dal Corso<sup>1,2,3</sup>, Michael J. Benton<sup>4</sup>, Massimo Bernardi<sup>4,5</sup>, Matthias Franz<sup>6</sup>, Piero Gianolla<sup>7</sup>, Sönke Hohn<sup>2</sup>, Evelyn Kustatscher<sup>8,9</sup>, Agostino Merico<sup>2</sup>, Guido Roghi<sup>10</sup>, Alastair Ruffell<sup>11</sup>, James G. Ogg<sup>12</sup>, Nereo Preto<sup>13</sup>, Alexander R. Schmidt<sup>14</sup>, Leyla J. Seyfullah<sup>14</sup>, Michael J. Simms<sup>15</sup>, Zhiqiang Shi<sup>16</sup>, and Yang Zhang<sup>12</sup>**

<sup>1</sup>Hanse-Wissenschaftskolleg (HWK), Institute for Advanced Study, 27753 Delmenhorst, Germany

<sup>2</sup>Leibniz Centre for Tropical Marine Research (ZMT), 28359 Bremen, Germany

<sup>3</sup>School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK

<sup>4</sup>School of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, UK

<sup>5</sup>MUSE – Science Museum, 38122 Trento, Italy

<sup>6</sup>Department of Applied Geology, Geoscience Center, University of Göttingen, 37077 Göttingen, Germany

<sup>7</sup>Department of Physics and Earth Sciences, University of Ferrara, 44100 Ferrara, Italy

<sup>8</sup>Museum of Nature South Tyrol, 39100 Bozen/Bolzano, Italy

<sup>9</sup>Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität and Bayerische Staatssammlung für Paläontologie und Geologie, 800333 München, Germany

<sup>10</sup>Institute of Geosciences and Earth Resources (IGG-CNR), 35131 Padova, Italy

<sup>11</sup>School of Natural and Built Environment, Queen's University Belfast, BT7 1NN, Northern Ireland, UK

<sup>12</sup>Department of Earth, Atmospheric and Planetary Sciences, Purdue University, West Lafayette, IN 47907, USA

<sup>13</sup>Department of Geosciences, University of Padova, 35131 Padova, Italy

<sup>14</sup>Department of Geobiology, University of Göttingen, 37077 Göttingen, Germany

<sup>15</sup>National Museums Northern Ireland, Cultra, Co. Down, BT18 0EU, UK

<sup>16</sup>Institute of Sedimentary Geology, Chengdu University of Technology, Chengdu 610059, China

**Abstract** – In the late early Carnian (Late Triassic) an important, but yet poorly understood, phase of global climate change occurred. This is roughly coincident with a time of major biological turnover. Many important groups diversified or spread during the Carnian, e.g., dinosaurs, calcareous nannofossils, and modern conifers. Abrupt environmental changes are observed in the geological record worldwide during this interval. These phenomena were roughly synchronous with a carbon-cycle perturbation and could be linked to Large Igneous Province volcanism. Palaeoclimatologists, stratigraphers, geochemists, carbonate sedimentologists, palaeontologists, and modellers met at the Hanse-Wissenschaftskolleg, Institute for Advanced Study in Delmenhorst (Germany), to discuss this intriguing episode of climate change, and the associated effects on the environments and biota. The main aims of the workshop was to summarise the current understanding of the Carnian Pluvial Episode, and discuss future research directions.



Figure 1 – Workshop participants.

## INTRODUCTION

Isotopic records suggest a global carbon cycle perturbation during the Carnian (Late Triassic). This is specifically revealed by a sharp negative carbon-isotope excursion in terrestrial and marine organic matter, and in marine carbonate carbon (Dal Corso et al., 2012, 2015; Mueller et al., 2016a, 2016b; Sun et al., 2016; Miller et al., 2017). In the same time interval, oxygen-isotope analyses of conodont apatite indicate an increase in the sea-surface temperatures (Hornung et al., 2007; Rigo & Joachimski 2010; Trotter et al., 2015; Sun et al., 2016). Carbon cycle disruption and global warming were coincident with complex environmental changes and biotic turnover (e.g., Dal Corso et al., 2015; Sun et al., 2017). This “most distinctive climate change within the Triassic” (Preto et al., 2010), which in the published literature is known by several different names (Ruffell et al., 2015) and here is named the “Carnian Pluvial Episode” (CPE; see discussion below), is recorded in stratigraphic sections worldwide and is often described as a shift from arid to more humid conditions (Simms & Ruffell, 1989). The onset of the CPE is very well constrained in many stratigraphic sections (e.g., in the Southern Alps of Italy, Northern Calcareous Alps of Austria, Transdanubian Range of Hungary, and in the Nanpanjiang Basin of the South China block) and is placed at the Julian 1 – Julian 2 boundary (i.e., *Trachyceras* – *Austrotrachyceras austriacum* ammonoid zones boundary; sensu Gallet et al. 1994). In the marine sedimentary basins of the Tethys realm, the sudden arrival of huge amounts of siliciclastic material, the establishment of anoxic conditions in the restricted basins, and an abrupt change of carbonate factories mark the beginning of the climate change (e.g., Simms and Ruffell 1989; Hornung et al., 2007a,b; Rigo et al., 2007; Preto et al., 2010; Dal Corso et al., 2015; Gattolin et al., 2015; Mueller et al., 2016; Sun et al., 2016; Shi et al., 2017). On the continents and at different latitudes, palaeobotanical evidence shows a shift of floral associations towards elements more adapted to humid conditions (e.g., Roghi et al., 2010; Preto et al., 2010; Mueller

et al., 2016b), and increased resin production (Gianolla et al., 1998; Roghi et al., 2006; Schmidt et al., 2012). This climatic perturbation is also closely associated with biological turnover among many marine groups. One of the most important turnovers in the Triassic ammonoid fauna, with the extinction of the Trachiceratinae and the radiation of the Tropitidae, occurred during the CPE (Balini et al., 2010). Conodonts went through a major crisis (Rigo et al., 2007; Martínez-Pérez et al., 2014). Other groups, like bryozoans and crinoids, show a sharp decline during the Carnian (Simms and Ruffell 1989). On land, key herbivorous groups such as dicynodonts and rhynchosaurs, which had represented 50% or more of faunas, disappeared or dwindled, and their places were taken by dinosaurs, which had been around from the Early-Middle Triassic, but at low abundance and low diversity. Most intriguingly, the CPE seems to be linked to major evolutionary innovations. For example, it acted as the trigger for the diversification of the dinosaurs and the transformation of terrestrial ecosystems for the remainder of the Mesozoic. The beginning of abundant and continuous pelagic calcification is placed during the Carnian (Bown, 1998; Erba, 2004; Preto et al., 2012). The origination and radiation of bona fide modern conifer families and bennettitaleans falls also within this interval (e.g., Willis and McElwain, 2002; Kustatscher et al., 2018, and references therein).

The carbon-cycle disruption, climate change, and biological turnover are roughly coincident with the eruption of the Wrangellia Large Igneous Province (LIP), whose basalts today outcrop in British Columbia, Yukon, and Alaska (Furin et al., 2006; Greene et al., 2010; Dal Corso et al., 2012). Biostratigraphic, radioisotopic, and geochemical data suggest that Wrangellia volcanic activity had a maximum age spanning from the latest Ladinian to the early late Carnian (Tuvanian) (Greene et al., 2010; Xu et al., 2014). Thus, Wrangellia LIP activity, as with other LIPs in the geological record, could have triggered the abrupt phenomena observed during the Carnian. The CPE was also coincident with other substantial volcanic episodes, including the Huglu-Pindos

series in Greece, the Kara Dere basalts in Turkey and the Taimyr Complex in Russia, all or some of which could have enhanced the effects of Wrangellia (Muller et al., 2016; Sun et al., 2016).

In the last years, the interest of the scientific community in the “mysterious” (Ogg, 2015) CPE has increased. Many papers have been published, significantly broadening our knowledge on the phenomena that occurred during the Carnian. Some authors suggested the CPE could be an analogue for today’s climate change, warming, and ocean acidification (e.g., Dal Corso et al., 2012). The study of the CPE is a fast-growing field and, despite the advances of the last years, many aspects of this fascinating time period are still poorly understood. Given the importance of the topic and the knowledge gaps, a first workshop completely focused on the CPE has been organized in 2017 with the aims of outlining the state-of-the-art, understanding the open problems, and identifying future research priorities.

## THE WORKSHOP

The workshop on “The Carnian Pluvial Episode (Late Triassic): Climate Change and Evolutionary Innovations” was organized by Jacopo Dal Corso and Agostino Merico and took place on the 16<sup>th</sup>–17<sup>th</sup> of May, 2017 at the Hanse-Wissenschaftskolleg (HWK), Institute for Advanced Study in Delmenhorst (Germany). A total of 27 scientists from Europe, USA, and China participated in the workshop.

The workshop was structured around two days of oral presentations and discussions, and a final round-table. Invited speakers, who are the authors of this report, gave oral presentations. The talks covered different facets of the CPE, from stratigraphic problems (bio-chronostratigraphic framework, magnetostratigraphy, chemostratigraphy) to siliciclastic and carbonate sedimentology, and palaeontology (marine and terrestrial). All talks raised interesting discussions that also continued during the coffee breaks, the lunches, and the social dinner in the wonderful venue of the HWK.

After the welcome from Doris Meyerdierks, research manager for the area “Earth” at the HWK, Jacopo Dal Corso gave a brief introduction to the CPE, summarizing its main characteristics. He also discussed the carbon-isotope records across the CPE, their correlation, and the links to Wrangellia LIP volcanism. A list of the talks with a brief description of the content follows.

### The History and Palaeogeography of the Carnian Humid Episode

Alastair Ruffell (*Queen’s University, Belfast, UK*) and Michael J. Simms (*Ulster Museum, UK*)

The evolution of theories surrounding palaeoenvironmental changes during the Carnian roughly mirrors the geographic spread (globally) of the broad idea of increased humidity during this time. The initial focus of the theory was the Germanic Keuper basins (Germany, subsurface Low Countries, North Sea, England, Simms & Ruffell, 1989), subsequently extending

to the Italian and Austrian Alps (Roghi, 2004), thence to Iberia and the Eastern Seaboard of North America (Arche & Gomez-Lopez, 2014). Subsequent publications showed evidence of this change in depositional systems in the Himalayas, China, Japan and Svalbard. A recent review by the authors (Ruffell et al., 2016) indicated that the Carnian of southern USA, parts of S America (Argentina), offshore NW Australia and parts of Antarctica may contain evidence of this palaeoenvironmental change. It may be that this humid episode was at least three phases, as evidenced by discrete clastic intervals in successions of the Austrian Alps. Examination of thick deep water successions in the Palaeotethys may resolve this: some of the terrestrial Keuper successions do show more than one grey sandstone interval within the red, evaporitic mudstones. Research on the Southern Hemisphere successions, especially South America, where the link to dinosaur evolution could be resolved, should be a future target for Carnian workers.

### Tethyan Record of the Carnian Pluvial Episode: The Bio-Chronostratigraphic Framework

Piero Gianolla (*University of Ferrara, Italy*)

The marine and marginal marine sections of Western Tethys records in detail the timing and the effect of the Carnian climate destabilization. The sharp negative carbon-isotope excursion (CIE), which coincides with the onset of CPE, is well defined in the Dolomites (Italy), Northern Calcareous Alps (Austria), and Transdanubian Range (Hungary), and is bio-stratigraphic constrained at the Aonoides/Austriacum boundary interval. The CIE is also coincident with the abrupt demise of high-relief microbial carbonate factories. Sequence stratigraphic analysis of sections from the Dolomites shows that a significant sea level fall followed the onset of the CPE (Gattolin et al., 2015) with a delay not yet resolvable in terms of time. This sea-level fall was probably driven by the formation of vast endorheic basins as a consequence of increasing precipitations. The excellent biostratigraphic control permits to date the different phases of the perturbation, two in the Julian and two in the Tuvialian. The entire CPE is constrained between the Aonoides/Austriacum boundary and the Subbullatus Zone (Tuvialian), but the definition of its absolute duration remains open. Only one radiometric age from Lagonegro Basin is available for this time interval (Furin et al., 2006), and it sets the upper boundary of CPE in Western Tethys at  $230.91 \pm 0.33$  Ma. Cyclostratigraphic analysis of the marine succession of the South China Block (China) and of the continental succession of Devon (UK) suggests the CPE lasted for about 1.2 Myrs (Zhang et al., 2015; Miller et al., 2017).

### Cycle-calibrated magnetostratigraphy of the Carnian and implications for the Global Coincidence of the Carnian Humid Episode

James G. Ogg and Yang Zhang (*Purdue University, USA*)

A cycle-tuned magnetic polarity scale spanning ~2.4 myr was established featured by a relatively long (~1.3 myr) reversed-polarity zone with brief normal-polarity intervals that is consistent with the significant reversed-dominated interval striding the boundary of T. aonoides and A. austriacum ammonoid zones

(late Early Carnian) from three Carnian sections in South China (Zhang et al., 2015). The distinctive upward change from a dominance by reversed to normal polarity just after the onset of clastic-rich influx over the Yangtze Platform is also recorded in magnetostratigraphy of the lower Schilfsandstein in the Germanic Basin and verified by our further sampling in three new Carnian sections in South China and three boreholes in the Germanic Basin. Therefore, we conclude that the termination of the Yangtze Platform is coeval with the Carnian Pluvial Event. The Carnian time scale from South China and our initial work from the Germanic Basin support the “short-Tuvalian/long-Norian” age model of the Late Triassic, implying that the base of the cycle-tuned polarity pattern from the Newark Supergroup of eastern North America lies in Tuvalian.

### **The Schilfsandstein in the North German Basin: Stratigraphy, facies, drainage systems and controls.**

Matthias Franz (*University of Göttingen, Germany*)

Basin-wide re-evaluation of the Schilfsandstein, commonly considered the type-example of the “Carnian Pluvial Episode”, revealed repeated transgressions from Tethyan waters into the Central European Basin (CEB) followed by progradations of fluvio-deltaic environments. The sea-level fluctuations recognised in the CEB are well correlated with contemporaneous NW Tethyan sea-level fluctuations suggesting an eustatic control (Franz et al., 2014). Results of high-resolution subsurface facies mapping and provenance studies point to an endo-rheic drainage pattern of routing systems tributing sediments from surrounding source areas towards the basin centre. This is in strong contrast to the exo-rheic drainage pattern and export of detrital sediment to the Tethyan realm as proposed in earlier works (e.g., Wurster, 1964; Beutler & Häusser, 1984). The very low maturity of the Schilfsandstein, petrographic studies revealed lithic arkoses and feldspathic litharenites, and presence of mature aridisols are not in agreement with a substantial shift towards a more humid climate.

### **Waxing and waning of carbonate production during the Carnian Pluvial Episode: a role for ocean acidification?**

Nereo Preto (*University of Padova, Italy*)

Anisian, Ladinian and lower Carnian carbonate platforms of the Dolomites are mainly microbial, but turn to carbonate ramps with skeletal grains and ooids after the main isotopic excursion of the CPE. Roughly at the same time, calcareous nannofossils become abundant in open marine environments. Microbial carbonate production would return dominant by the Norian, while calcareous nannofossils remained common in hemipelagic periplatform successions until the end of the Triassic. This sequence of events may be explained by ocean acidification at the CPE, but the prolonged duration of the carbonate factory turnover seems to exclude this explanation. It is proposed however that multiple episodes of carbon cycle perturbation may compose the CPE, and it is suggested that the occurrence of calcareous nannofossils and non-microbial carbonate platforms at the CPE should be tested globally.

### **The demise of the sponge mounds along the northwestern margin of the Yangtze Block, South China: links to the Carnian Pluvial Phase.**

Zhiqiang Shi (*Chengdu University of Technology, China*)

Carnian marine sections in the NW margin of Upper Yangtze Region of China show a lithological change from oolitic grey limestone into a sponge-mound limestone to black–grey and dark grey siltstone and sandy shale. Conodonts and ammonoids give a Tuvalian 1 age for the lower part of the black–grey shale above the siliceous sponge mounds. The deposition of the shale may be related to the onset of the Carnian Pluvial Phase. The sponge mounds’ demise in the NW Upper Yangtze Region could have been caused by the combined effect of fresh water input linked to the Carnian Pluvial Phase and a relative sea-level change caused by local tectonism during the Indosinian orogeny.

### **The Carnian pluvial party event for plants**

Evelyn Kustatscher (*Museum of Nature South Tyrol, Bozen/Bolzano, Italy & Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, München, Germany*)

The Carnian successions yield one of the most abundant and diverse floras of the Triassic. Typical hygrophytic elements such as ferns and sphenophytes, are often the most abundant groups in the flora, bennettitaleans become more and more abundant in the fossil record. Paralic and lagoonal environments permit an exceptional preservation of the plant fossils as well as findings of amber, megaspores and charcoal associated with the macroremains. Conifer remains become more abundant in allochthonous assemblages of marine sediments and reflect a high transport bias. Several families and orders make their first appearance or start at least their first radiation during the Carnian. This includes bennettitaleans, modern fern (e.g., Dipteridaceae) and conifer families (Pinaceae, Araucariaceae, Cheirolepidaceae) as well as putative angiosperms (e.g., *Furcula*, *Sanmiguelia*) although angiosperm-like pollen have been described already from Middle Triassic successions (Kustatscher et al., 2018).

### **Amber inclusions in deep time: arthropods, plant remains and microorganisms preserved during the Carnian Pluvial Episode**

Alexander R. Schmidt (*University of Göttingen, Germany*)

The oldest biological inclusions found preserved in amber come from the Carnian. The amber containing these preserved organisms is found as thousands of small (2–6 mm) droplets from a well-preserved palaeosol in the Italian Dolomites. The amber contains a diverse microcosm of organisms: arthropods, plant remains, microorganisms including bacteria, fungi, algae, ciliates, and testate amoebae together with spores and pollen grains (Schmidt et al., 2006, 2012). Most of tiny arthropods are diverse representatives of the Triasacaroida, a new superfamily of highly specialized, four-legged, phytophagous mites (Sidorchuk et al., 2015).

### **Palynological indication of upper Carnian hygrophytic associations in European and extra-European Areas**

Guido Roghi (*Institute of Geosciences and Earth Resources, IGG - CNR, Italy*)

Palynological study of the CPE reveals humid pulses characterized by qualitative and quantitative increase of hygrophytic associations recognized not only in Tethysian successions but also in many succession of the Laurasia and Gondwana. This global palynological change is thus interpreted as having climatic origin. Moreover, humid climatic pulses are evidenced by southwards shifting of the hygrophytic associations during the CPE, when palaeoenvironmental conditions became favourable for its proliferation in the Tethys realm. The occurrence of four palynological assemblages within the Carnian represents a potential tool for worldwide Upper Triassic correlation.

### **Testing today's resin-rich plants to try to understand Triassic amber deposits**

Leyla J. Seyfullah (*University of Göttingen, Germany*)

Although trace amounts of amber are reported from the Carboniferous onwards, amber in significant amounts in the fossil record appears for the first time during the CPE. The cause(s) of these resin outpourings are not yet known, nor whether they are linked. Using stress tests on today's modern conifers and hunting for specific stress biomarkers should help us unlock the reason(s) for amber deposits during the CPE.

### **Late Triassic and origin of dinosaurs**

Michael J. Benton (*University of Bristol, UK*)

The origin of the dinosaurs marks a major transformation in terrestrial ecosystems, a switch from the rather slow-moving, sprawling tetrapods of the Palaeozoic, to upright, faster-moving, and even warm-blooded tetrapods. Not only did dinosaurs take over and expand rapidly in Late Triassic ecosystems, but all other modern vertebrates appeared about this time, including frogs, lizards, crocodylians, turtles, and even mammals. The dinosaurs had originated in the Early to Middle Triassic, as part of the rebuilding of ecosystems following the Permian-Triassic mass extinction, 252 Ma, but they existed at low abundance and low diversity for 20 myr before diversifying rather explosively after the CPE, as originally suggested by Benton (1983).

### **Multi-proxy constraints to dinosaur first dispersal**

Massimo Bernardi (*MUSE – Science Museum, Trento, Italy; University of Bristol, UK*)

Until recently, it had proved difficult to exactly correlate the expansion of dinosaurs with the CPE, but new data from the extremely well dated rock sequences of the Southern Alps (Italy) allowed to identify a significant mid Carnian shift in the composition of archosaur ichnoassociations. A review of all known Late Triassic archosaur body and trace fossil evidence suggests that the first dinosaur dispersal in the eastern Pangaea is synchronous with the CPE and that

dinosaurs became dominant in the ecosystems only after this perturbation (Bernardi et al., submitted). The proposed model is in agreement with a gradual process of ecological replacement of crurotarsans and other tetrapods by early dinosaurs (reviewed in Brusatte et al., 2010), but highlights the importance of a specific, relatively brief, interval in the mid Carnian as buster in the early evolution of dinosaurs (Bernardi et al., submitted).

### **Mathematical modelling of geological events: challenges and opportunities**

Agostino Merico (*Leibniz Centre for Tropical Marine Research, Bremen, Germany*)

A number of mathematical models of varying complexity have been developed in the last decades to study the interaction of complex Earth Systems processes also over geological time scales. All these models provide opportunities and poses challenges. Four of these models have been briefly reviewed: (1) the Long-term Ocean-atmosphere-Sediment Carbon cycle Reservoir model (LOSCAR) by Richard Zeebe, (2) the Grid Enabled Integrated Earth system model (GENIE), by Andrew Price and co-workers and the cGENIE version by Andy Ridgwell, (3) the Global Environmental and Ecological Simulation of Interactive Systems (GENESIS), by David Pollard and co-workers, and (4) a Simple Box model by Merico and co-workers. Agostino Merico argued that intermediate- or high-complexity models (such as GENIE and GENESIS) are difficult to use and maintain, take very long to run (months to years for simulating processes over centennial to thousands of years), generate results that can be huge in size (requires energy and space to store data), but have nonetheless, helped to greatly improve our understanding of the physical processes and feedbacks in the climate system. In contrast, simple models (such as LOSCAR and other box models) are easy to use and maintain, run over short times (for example, a 3-million-year run can take less than 20 hours), generate results that are easily to manage and store, but they consider only a very crude representation of the physical processes.

### **Evolutionary aspects of pelagic calcification**

Sönke Hohn (*Leibniz Centre for Tropical Marine Research, Bremen, Germany*)

The CPE marks the first massive appearance of calcareous nannoplankton that became extremely abundant during the Cretaceous and is still important carbonate producers in today's ocean. Sönke Hohn reviewed the potential reasons why pelagic, intracellular calcification evolved and persisted. He concluded that intracellular calcification represents an energetically cheap mechanism to alleviate calcium cell poisoning (Müller et al., 2015). The same cellular requirements, i.e. to get rid of excess intracellular calcium, cause an indirect predator poisoning when calcified cells are ingested (Harvey et al., 2015).

## **ROUND TABLE**

In the afternoon of the last day of the workshop we had a roundtable discussion. We examined the different topics

presented by the speakers during the workshop, with particular emphasis on open problems. The research around the CPE is still relatively “young”. Our understanding of the phenomena that occurred during this time interval is still fragmentary and very limited. Many fundamental questions remain open and need to be addressed. We outlined priorities and future directions.

1) *Nomenclature*. One name used by the entire scientific community is indeed necessary for the Carnian episode, in order to make the literature consistent, to ensure clarity among authors, and to make readers immediately aware of the subject. The published literature shows authors have used many different names for the Carnian Pluvial Episode. It has been called Raibl Event and Reingraben Turnover (Reingrabener Wende; e.g., Schlager and Scöllnberger, 1974; Hornung and Brendner, 2005), Carnian Pluvial Episode (e.g., Simms and Ruffell, 1989), Carnian Pluvial Event (e.g., Visscher et al., 1994; Roghi et al., 2004; Franz et al., 2014; Dal Corso et al., 2015), Carnian Wet Intermezzo (Kozur and Bachmann, 2010), Carnian Humid Episode (e.g., Ruffell et al., 2015; Sun et al., 2016), Carnian Pluvial Phase (e.g., Mueller et al., 2016; Shi et al., 2016), and Mid-Carnian Event (Ogg, 2015). The majority of these names emphasize one aspect of the CPE, i.e. the increase in precipitation. We now know that the CPE wasn't a constant and homogeneous period of higher precipitation. Palynological and sedimentological evidence shows distinct humid pulses interrupted by arid periods (e.g., Roghi et al., 2010; Stefani et al., 2010; Mueller et al., 2016). Moreover, the CPE is not only a time interval of increased humidity, but also a major and complex carbon-cycle perturbation (Dal Corso et al., 2012, 2015; Mueller et al., 2016a, 2016b; Sun et al., 2016; Miller et al., 2017), a time of global warming (e.g., Trotter et al., 2015; Sun et al., 2016), a widespread platform carbonate precipitation crisis and rise of the CCD (Schlager & Scöllnberger, 1974; Hornung et al., 2007a; Rigo et al., 2007; Dal Corso et al., 2012, 2015; Gattolin et al., 2015), a time of reduced oxygen availability in many marginal basins of the Tethys (Hornung & Brandner, 2005; Keim et al., 2006; Hornung et al., 2007a, 2007b; Wang et al., 2008; Rostasi et al., 2011; Souza, 2014; Dal Corso et al., 2015), an interval of increased resin production that yields the oldest significant amber deposits (Gianolla et al., 1998; Roghi et al., 2006), a time of extinctions (Simms & Ruffell, 1989; Benton 1991) but also a time of incredible evolutionary innovation (Benton, 1983, 1991; Preto et al., 2013), and possibly many other still un-described phenomena. Therefore, emphasizing only one aspect of the CPE, i.e. the increase in humidity, could be reductive. However, the main and the first described characteristic of the CPE that it is quickly and widespread recognisable in many geological settings (from continental to deep-water) and at different latitudes is a sedimentological change indicating increased humid conditions (coarse siliciclastic material, laminated shale, clay minerals, etc.). Hence, the use of “Pluvial” or “Humid” is justified. The term “event” can generate confusion. In stratigraphy, an event is assumed to be a short-lived and sudden change (sedimentological, lithological, palaeontological, or geochemical) that is recognisable in the stratigraphic record and used as a marker (e.g., Einsele et al., 1991). Events are thus typically instantaneous or in the order of few thousands of years. We agreed with Ruffell et al. (2015) that

the brief (approx. 41 Kyr; Miller et al., 2017) negative carbon-isotope excursion at the onset of the CPE is an “event”. This is followed by a long interval (approx. 1.2 Myrs; Zhang et al., 2016; Miller et al., 2017) of climatic, geochemical, and biotic changes. For these reasons “Episode” or “Phase” should be preferred. The use of “Mid-Carnian Episode” has been discussed during the workshop and put forward as an option. However, no agreement could be reached, the major concern being the use of “middle Carnian”. In the recent literature the Carnian stage is subdivided in two substages, Lower (or Julian) and Upper (or Tuvallian) (Gradstein et al., 2012), hence, from a chronostratigraphic point of view “Mid-Carnian Episode (or Event)” would be misleading.

2) *Reference sections*. It is necessary to identify reference terrestrial, marginal marine, and deep-sea sections for interdisciplinary studies. Such reference sections should provide information on the effects of the CPE on continents (e.g., palynology, palaeobotany, and vertebrates palaeontology), shallow marine environments (e.g., sea-level changes, platform carbonate production), and oceans (e.g., redox conditions of the water column). Some sort of a “stratotype” and “golden spike” are needed to enable the unambiguous stratigraphic definition of the CPE.

3) *Definition of a pre- and post-CPE “normal Carnian”*. The early Carnian is described in the literature as a climatically arid interval suddenly interrupted by the CPE. The definition of the precursor climatic and oceanographic conditions, and their variability between different geological settings, is necessary to evaluate the extent and rate of the changes occurring during the CPE. Similarly, a deeper understanding of the precursor marine and terrestrial biological community structure is crucial to define the extinction and origination rates during the CPE.

4) *The Structure of the Episode*. Sedimentological and palynological records across the CPE in the Tethys realm show the episode is structured into at least 3–4 discrete humid pulses (e.g., Breda et al., 2009; Roghi et al., 2010). Such sedimentological changes are biostratigraphically constrained in the Dolomites and Northern Calcareous Alps (including Lunz) to the Julian1 – Julian2 boundary, within the Julian2, at the Julian–Tuvallian boundary, and ca. at the Tuvallian1 – Tuvallian2 boundary (e.g., Roghi et al., 2010). A continental carbon-isotope record in southwest England shows multiple carbon-cycle perturbations during the CPE (Miller et al., 2017). However, the lack of biostratigraphic constraints makes it difficult to precisely date these carbon-isotope excursions and to correlate them with the marine marginal sections where multiple climatic changes are documented. Carbon-isotope records across the CPE in different geological settings are thus crucial to understand the structure of the episode and to link carbon-cycle perturbations to environmental changes. Moreover, it is important to understand whether the CPE was preceded by any precursor event/episode. Indeed, current dating of the Wrangellia shows that the LIP activity started already at least at the Ladinian–Carnian boundary.

5) *Causation*. The exact temporal relationships between the emplacement of the Wrangellia LIP and the CPE need to be constrained. New radiometric ages of Wrangellia basalts are necessary to correlate the different phases of the LIP eruption with the CPE. The study of the sedimentary successions below, within and above the Wrangellia basaltic floods in different areas

is required to biostratigraphically constrain the LIP volcanism. This will allow to understand the mechanisms of the climate change and extinction in relation to the magnitude and rate of volcanic gas emissions, as in the case of other similar episodes (e.g., end-Triassic mass extinction and CAMP volcanism). The possible contribution of other known Carnian volcanic centres (in Greece, Turkey, and Russia; Sun et al., 2016) to the carbon-cycle perturbation and climate change, i.e. the age of these volcanic eruptions, extent, and timing, must be assessed.

6) *Sea-level changes*. Substantial mid-Carnian sea-level changes of 3<sup>rd</sup>-order and higher order are well recognised from many Tethyan and peri-Tethyan localities and resulted in, for example, karstification of Carnian platforms (Dolomites) and flooding of peri-Tethyan lowlands (CEB). The resulting stratal pattern architectures were translated into sequences (e. g. Gianolla et al., 1998; Gattolin et al., 2013). Preliminary correlations based on sequence-stratigraphic arguments suggest circum-Tethyan eustatic cycles and thus, have demonstrated the high potential of linking Tethyan and peri-Tethyan sea-level records (Franz et al., 2014). However, these correlations need to be further justified by improved stratigraphic control on reference sections employing bio-, chemo and magnetostratigraphy. Certainly the most challenging question will be the link of 10<sup>6</sup>-year scale cycles to other mid-Carnian environmental perturbations, such as glacioeustatic sea-level changes or the Wrangellia LIP.

7) *Timescale*. Standardized conodont taxonomy, and its calibration to ammonoid biostratigraphy, is necessary to correlate the CPE through different geological settings. More magnetostratigraphic records are required from well-calibrated (ammonoid and conodont) stratigraphic successions. The chemostratigraphic records need to be framed within a firm stratigraphic scheme of the Carnian. Integrated stratigraphy will enable a deeper understanding of the timing and duration of the phenomena (e.g., rate of carbon emissions) related to the CPE.

8) *Extinction and evolutionary innovations*. It is crucial to better estimate the extinction rates among marine and terrestrial taxa, compare them with Mesozoic baseline rates and mass extinctions, and to understand the timing of radiation of major important groups (e.g. dinosaurs, pelagic calcifiers, conifers) and its temporal link with the CPE. This will allow understanding whether extinction and radiation rates during the CPE actually stand out from the Phanerozoic background or not, and if there is any causal relationship between environmental change and evolution. Increasing precision in dating and improved knowledge of fossil records will also improve our understanding of the long-lasting impact of this major perturbation on the rebuilding of new ecosystems in the sea and on land.

9) *Analogies with modern and anthropogenically driven climate change*. A deeper knowledge of the temporal links between volcanism, climate change, and biotic turnover will permit to develop global biogeochemical models to understand the causal relationships and the long-term effects of the climate perturbation on the environments and biota. As other LIP-related episodes, the CPE could be an analogue for today climate change, marked by pCO<sub>2</sub> rise, global warming, and ocean acidification.

## ACKNOWLEDGEMENTS

We thank the rector and all the staff of the Hanse-Wissenschaftskolleg (HWK) Institute for Advance Study in Delmenhorst for hosting this workshop and the financial support. In particular, we would like to thank Dr. Doris Meyerdierks and Marion Wachholz-Logemann for all the administrative and logistic assistance. JDC acknowledges the HWK for a Junior Fellowship (2016–2017), without which this workshop could not have taken place.

## REFERENCES

- Arche, A. & López-Gómez, J.L. 2014. The Carnian Pluvial Event in Western Europe: new data from Iberia and correlation with the Western Neotethys and Eastern North America–NW Africa regions. *Earth-Science Reviews*, 128: 196–231.
- Balini, M., Lucas, S.G., Jenks, J.F & Spielmann, J.A. 2010. Triassic ammonoid biostratigraphy: an overview. *Geological Society, London, Special Publications*, 334:221–262.
- Benton, M.J. 1983. Dinosaurs success in the Triassic: a noncompetitive ecological model. *The Quarterly Review of Biology*, 58: 29–55.
- Benton, M.J. 1991. What really happened in the late Triassic? *Historical Biology*, 5:263–278.
- Bernardi M., Gianolla P., Petti F.M., Mietto P. & Benton M.J. submitted. Dating dinosaur diversification.
- Beutler, G. & Häusser, I. 1982. Über den Schilfsandstein der DDR. *Z. Geol. Wiss.* 10, 511–525.
- Bown, P. R. 1998. *Calcareous Nannofossil Biostratigraphy*, Kluwer Academic, Dordrecht.
- Breda, A., Preto, N., Roghi, G., Furin, S., Meneguolo, R., Ragazzi, E., Fedele, P. & Gianolla, P. 2009. The Carnian Pluvial Event in the Tofane area (Cortina d'Ampezzo, Dolomites, Italy). *Geo.Alp.* 6:80–115.
- Brusatte, S.L., Nesbitt, S.J., Irmis, R.B., Butler, R.J., Benton, M.J. & Norell M.A. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews*, 101:68–100.
- Dal Corso, J., Mietto, P., Newton, R.J., Pancost, R.D., Preto, N., Roghi, G. & Wignall, P.B. 2012. Discovery of a major negative δ<sup>13</sup>C spike in the Carnian (Late Triassic) linked to the eruption of Wrangellia flood basalts. *Geology*, 40:79–82.
- Dal Corso, J., Gianolla, P., Newton, R.J., Franceschi, M., Roghi, G., Caggiati, M., Raucsik, B., Budai, T., Haas, J. & Preto, N. 2015. Carbon isotope records reveal synchronicity between carbon cycle perturbation and the “Carnian Pluvial Event” in the Tethys realm (Late Triassic). *Global and Planetary Change*, 127:79–90.
- Einsele, G., Ricken, W. & Seilacher, A. 1991. *Cycles and events in stratigraphy*. Springer-Verlag New York, Inc., Newark, NJ (United States).
- Erba, E. 2004. Calcareous nannofossils and Mesozoic oceanic anoxic events. *Marine Micropaleontology*, 52:85–106.
- Franz, M., Nowak, K., Berner, U., Haunisch, C., Bandel, K., Rohling, H.G. & Wolfgramm, M. 2014. Eustatic control on epicontinental basins: the example of the Stuttgart Formation in the Central European Basin (Middle Keuper,



- Late Triassic). *Global and Planetary Change*, 122:305–329.
- Furin, S., Preto, N., Rigo, M., Roghi, G., Gianola, P., Crowley, J.L. & Bowring, S.A. 2006. High-precision U–Pb zircon age from the Triassic of Italy: implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. *Geology*, 34:1009–1012.
- Gallet, Y., Besse, J., Krystyn, L., Thaveniaut, H. & Marcoux, J. 1994. Magnetostratigraphy of the Mayerling section (Austria) and Erenkolu Mezarlik (Turkey) section: Improvement of the Carnian (Late Triassic) magnetic polarity time scale. *Earth and Planetary Science Letters*, 125:173–191.
- Gattolin, G., Preto, N., Breda, A., Franceschi, M., Isotton, M. & Gianolla, P. 2015. Sequence stratigraphy after the demise of a high-relief carbonate platform (Carnian of the Dolomites): Sea-level and climate disentangled. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 423:1–17.
- Gianolla, P., De Zanche, V. & Mietto, P. 1998. Triassic sequence stratigraphy in the Southern Alps (northern Italy): definition of sequences and basin evolution. In: De Graciansky, P.C., Hardenbol, J., Jacquin, T., Vail, P.R. (eds.), *Mesozoic and Cenozoic Sequence Stratigraphy of European Basins*. SEPM Special Publication 60, pp. 719–748.
- Gianolla, P., Roghi, G. & Ragazzi, E. 1998. Upper Triassic amber in the Dolomites (Northern Italy). A paleoclimatic indicator? *Rivista Italiana di Paleontologia e Stratigrafia*, 104:381–390.
- Gradstein, F., Ogg, J., Schmitz, M. & Ogg, G., 2012. *The Geologic Time Scale*. Elsevier, Amsterdam.
- Greene, A.R., Scoates, J.S., Weis, D., Katvala, E.C., Israel, S. & Nixon, G.T. 2010. The architecture of oceanic plateaus revealed by the volcanic stratigraphy of the accreted Wrangellia oceanic plateau. *Geosphere*, 6:47–73.
- Harvey, E.L., Bidle, K.D. & Johnson, M.D. 2015. Consequences of strain variability and calcification in *Emiliania huxleyi* on microzooplankton grazing. *Journal of Plankton Research*, 37:1137–1148.
- Hornung, T. & Brandner, R. 2005. Biochronostratigraphy of the Reingraben Turnover (Hallstatt Facies Belt): local black shale events controlled by regional tectonics, climatic change and plate tectonics. *Facies*, 51:460–479.
- Hornung, T., Krystyn, L. & Brandner, R., 2007a. A Tethys-wide mid-Carnian (Upper Triassic) carbonate productivity crisis: Evidence for the Alpine Reingraben Event from Spiti (Indian Himalaya)? *Journal of Asian Earth Sciences*, 30:285–302.
- Hornung, T., Brandner, R., Krystyn, L., Joachimski, M.M. & Keim, L., 2007b. Multistratigraphic constraints on the NW Tethyan “Carnian Crisis”. *New Mexico Museum of Natural History Bulletins*, 4:9–67.
- Keim, L., Spötl, C. & Brandner, R. 2006. The aftermath of the Carnian carbonate platform demise: a basinal perspective (Dolomites, Southern Alps). *Sedimentology* 53, 361–386.
- Kozur, H.W. & Bachmann, G.H. 2010. The Middle Carnian Wet Intermezzo of the Stuttgart formation (Schilfsandstein), Germanic Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290:107–119.
- Kustatscher, E., Ash, S.R., Karasev, E., Pott, C., Vajda, V., Yu, J. & McLoughlin, S. 2018. Flora of the Late Triassic. In: Tanner, L. (ed.) *The Late Triassic World: Earth in a Time of Transition*. Topics in Geobiology, 46: 545–622, Springer, ISBN 978-3-319-68008-8.
- Martinez-Peréz, C., Cascales-Minana, B., Plasencia, P. & Botella, H., 2014. Exploring the major depletions of conodont diversity during the Triassic. *Historical Biology*, 27:503–507.
- Miller, C.S., Peterse, F., da Silva, A.-C., Baranyi, V., Reichart, G.J. & Kürschner, W. 2017. Astronomical age constraints and extinction mechanisms of the Late Triassic Carnian crisis. *Scientific Reports*, 2557.
- Müller, M.N., Barcelos e Ramos, J., Schulz, K.G., Riebesell, U., Kazmierczak, J., Gallo, F., Mackinder, L., Li, Y., Nesterenko, P.N., Trull, T.W. & Hallegraeff, G.M. 2015. Phytoplankton calcification as an effective mechanism to alleviate cellular calcium poisoning. *Biogeosciences*, 12:6493–6501.
- Mueller, S., Krystyn, L. & Kürschner, W.M. 2016a. Climate variability during the Carnian Pluvial Phase – a quantitative palynological study of the Carnian sedimentary succession at Lunz am See, Northern Calcareous Alps, Austria. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 441:198–211.
- Mueller, S., Hounslow, M.W. & Kürschner, W.M. 2016b. Integrated stratigraphy and palaeoclimate history of the Carnian Pluvial Event in the Boreal realm; new data from the Upper Triassic Kapp Toscana Group in central Spitsbergen (Norway). *Journal of the Geological Society*, 173:186–202.
- Ogg, J.G. 2015. The mysterious Mid-Carnian “Wet Intermezzo” global event. *Journal of Earth Science*, 26:181–191.
- Preto, N., Kustatscher, E. & Wignall, P.B. 2010. Triassic climates—state of the art and perspectives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290:1–10.
- Preto, N., Willems, H., Guaiumi, C., Westphal, H. 2013. Onset of significant pelagic carbonate accumulation after the Carnian Pluvial Event (CPE) in the western Tethys. *Facies*, 59: 891–914.
- Rigo, M. & Joachimski, M.M. 2010. Palaeoecology of Late Triassic conodonts: constraints from oxygen isotopes in biogenic apatite. *Acta Palaeontologica Polonica*, 55:471–478.
- Rigo, M., Preto, N., Roghi, G., Tateo, F. & Mietto, P. 2007. A rise in the Carbonate Compensation Depth of western Tethys in the Carnian (Late Triassic): deep-water evidence for the Carnian Pluvial Event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 246:188–205.
- Roghi, G. 2004. Palynological investigations in the Carnian of Cave del Predil area (once Raibl, Julian Alps). *Review of Palaeobotany and Palynology*, 132:1–35.
- Roghi, G., Gianolla, P., Minarelli, L., Pilati, C. & Preto, N. 2010. Palynological correlation of Carnian humid pulses throughout western Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290:89–106.
- Roghi, G., Ragazzi, E. & Gianolla, P. 2006. Triassic amber of the Southern Alps (Italy). *Palaios*, 21:143–154.
- Rostási, Á., Raucsik, B., Varga, A., 2011. Palaeoenvironmental controls on the clay mineralogy of Carnian sections from the Transdanubian Range (Hungary). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 300:101–112.
- Ruffell, A., Simms, M.J. & Wignall, P.B. 2015. The Carnian Humid Episode of the late Triassic: a review. *Geological Magazine*, 153:271–284.
- Schlager, W. & Schöllnberger, W. 1974. *Das Prinzip*

- stratigraphischer Wenden in der Schichtfolge der Nördlichen Kalkalpen. *Mitt. Österr. Geol. Ges.* 66–67:165–193.
- Schmidt, A.R., Ragazzi, E., Coppellotti, O. & Roghi, G. 2006. A microworld in Triassic amber. *Nature*, 444:835.
- Schmidt, A.R., Jancke, S., Lindquist, E.E., Ragazzi, E., Roghi, G., Nascimbene, P.C., Schmidt, K., Wappler, T. & Grimaldi, D.A. 2012. Arthropods in amber from the Triassic Period. *Proceedings of the National Academy of Sciences, USA*, 109:14796–14801.
- Shi, Z., Preto, N., Haishui Jiang, H., Krystyn, L., Zhang, Y., Ogg, J.G., Jin, X., Yuan, J., Yang, X. & Du, D. 2017. Demise of Late Triassic sponge mounds along the Northwestern Margin of the Yangtze Block, South China: related to the Carnian Pluvial Phase? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 474:247–263.
- Sidorchuk, E.A., Schmidt, A.R., Ragazzi, E., Roghi, G. & Lindquist, E.E. 2015. Plant-feeding mite diversity in Triassic amber (Acari: Tetrápodili). *Journal of Systematic Palaeontology*, 13:129–151.
- Simms, M.J. & Ruffell, A.H. 1989. Synchronicity of climatic change and extinctions in the Late Triassic. *Geology*, 17:265–268.
- Soua, M. 2014. Early Carnian anoxic event as recorded in the southern Tethyan margin, Tunisia: an overview. *International Geology Review*, 56:1884–1905.
- Stefani, M., Furin, S. & Gianolla, P. 2010. The changing climate framework and depositional dynamics of the Triassic carbonate platforms from the Dolomites. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290:43–57.
- Sun, Y., Wignall, P., Joachimski, M.M., Bond, D.P.G., Grasby, S.E., Lai, X.L., Wang, L.N., Zhang, Z.T. & Sun, S. 2016. Climate warming, euxinia and carbon isotope perturbations during the Carnian (Triassic) Crisis in South China. *Earth and Planetary Science Letters*, 444:88–100.
- Trotter, A.J., Williams, S.I., Nicora, A., Mazza, M. & Rigo, M. 2015. Long-term cycles of Triassic climate change: A new  $\delta^{18}\text{O}$  record from conodont apatite. *Earth and Planetary Science Letters*, 415:165–174.
- Visser, H., Van Houtte, M., Brugman, W. A. & Poort, P. R. 1994. Rejection of a Carnian (Late Triassic) “pluvial event” in Europe. *Review of Palaeobotany and Palynology*, 83:217–226.
- Wang, X., Bachmann, G., Hagdorn, H., Sander, M., Cuny, G., Xiaohong, C., Chuanshang, W., Lide, C., Long, C., Fansong, M. & Guanghong, X. 2008. The Late Triassic black shales of the Guanling area, Guizhou province, south-west China: a unique marine reptile and pelagic crinoid fossil lagerstätte. *Palaeontology*, 51:27–61.
- Willis, K.J. & McElwain, J.C. 2002. *The Evolution of Plants*. Oxford University Press, Oxford, UK, 378 pp.
- Wurster, P. 1964. *Geologie des Schilfsandstein*. *Mitt. Geol. Staatsinstituts Hamburg* 33.
- Xu, G., Hannah, J.L., Stein, H.J., Mørkd, A., Os Vigran, J., Bingen, B., Schutte, D. & Lundschieng, B.A. 2014. Cause of Upper Triassic climate crisis revealed by Re–Os geochemistry of Boreal black shales. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 395:222–232.
- Zhang, Y., Li, M., Ogg, J., Montgomery, P., Huang, C., Chen, Z.-Q., Shi, Z., Enos, P. & Lehmann, D.J. 2015. Cycle-calibrated magnetostratigraphy of middle Carnian from South China: Implications for Late Triassic time scale and termination of the Yangtze Platform. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 436:135–166.

