Ecological uniformitarianism
— help or hindrance to palaeoecology, palaeoclimatology and conservation biology?

Online meeting
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ABSTRACTS

Arranged in order of first author, presenting author underlined

The image on the front cover is of a ring-necked (or rose-ringed) parakeet (*Psittacula krameri*) in its native habitat, the Indo-Gangetic Plain. The species now occurs almost worldwide, including in much colder climatic settings, thus exemplifying a major expansion of realised niche. The frequency of such changes, and how this relates to taxonomic group, mode of life etc., is a topic of importance to palaeontologists and neontologists alike. With what confidence can the environments of fossil organisms be inferred from the ecology of modern counterparts, and to what extent may species be able to adapt to modern (anthropogenic) environmental change? These topics will be addressed in the diverse set of talks—delivered by scientists from a wide range of backgrounds—whose abstracts are contained in this document. The convenors of the meeting anticipate that you will be both informed and stimulated, and hope that you will contribute to the interdisciplinary exchanges that are intended.

Dr Andy Johnson, on behalf of the convenors

Dietary niche shifts and body size reduction as a terrestrial mammal response to an early Paleocene hyperthermal event

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The idea that ecological niches remain stable during periods of rapid climate change has long been central to methods used to assess extinction risk. However, evidence to test this assumption, particularly beyond recent timescales, remains scarce. Here, we examine how a terrestrial mammal responded to rapid climate warming during the Latest Danian Event (LDE; ~62.3 Ma) in the early Paleocene. *Tetraclaenodon puercensis* is an archaic ungulate that exhibits a body size reduction during the LDE in the San Juan Basin of New Mexico, USA. The drivers of this phenomenon—hyperthermal dwarfism—remain poorly resolved and are often linked to biogeographic range shifts rather than in situ ecological responses. Using a novel multi-comparator approach to dental microwear texture analysis, we show that *T. puercensis* shifted from frugivorous to folivorous dietary niches during the LDE. Such a shift is often observed among extant forest mammals during times of food scarcity and moisture stress, which are likely during Paleogene hyperthermals. Our results provide the first robust evidence for mammalian ecological responses and adaptation to lower quality resources during a Paleogene hyperthermal. Dietary niche shifts therefore provide a means of dealing with rapid warming without requiring broad changes in biogeographic ranges.

The dawn of the tropical Atlantic invasion into the Mediterranean Sea

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The Mediterranean Sea is a marine biodiversity hotspot with a high level of endemism. During the Last Interglacial (135–116 ka), tropical West African species occurred in the basin but retracted into the tropical belt during the following glaciation. Because the Last Interglacial is a conservative analogue of future climate, we hypothesize that such tropical Atlantic species may re-enter the Mediterranean due to global warming, putting at further risk its fauna already affected by climate-driven biodiversity collapses. Therefore, we combined modern species occurrences with a unique fossil record from the Last Interglacial (135–116 ka) in a correlative species distribution model to predict the future distribution of a subset of tropical West African molluscs, currently separated from the Mediterranean by cold upwelling off north-west Africa. The inclusion of fossil occurrences and of palaeoclimate improved the predictions by allowing a better description of the environmental niche and avoiding unrealistic outputs. Our results suggested that the south-eastern sectors of the Mediterranean Sea are already suitable for the establishment of a tropical fauna, as demonstrated by the success of Indo-Pacific species entering through the Suez Canal. Already by 2050, under an intermediate climate scenario (RCP 4.5), climatic connectivity along north-west Africa may allow tropical species to colonize a by then largely environmentally suitable Mediterranean. The worst-case scenario (RCP 8.5) leads to a fully tropicalized Mediterranean by 2100. The tropical Atlantic invasion will add to the ongoing invasion through the Suez Canal, irreversibly transforming the entire Mediterranean into a novel ecosystem unprecedented in human history.

Evolution of thermal tolerance:

Can historical climate adaptation inform species' vulnerability to future climate change?

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Understanding the mechanisms that have driven evolutionary change in species' physiological tolerances to temperature is central to predicting their responses to climate change. We tested three non-mutually exclusive theories invoked to explain variation in species thermal limits: (1) adaption to current climatic extremes, (2) evolutionary boundaries to thermal tolerance limits, and (3) deep-climate legacies. To test these theories, we used the largest published thermal physiology dataset (GlobTherm), containing 2,000 wild terrestrial and aquatic species representing major metabolic modes, for example plants, cold-blooded (ectotherms), and warm blooded (endotherms) animals. We show that adaptation to current climatic extremes and evolutionary boundaries or optima in physiological thermal limits explains the most variation in thermal tolerance across taxa and metabolic mode. We also revealed that deep-time climate legacies explain some variation in tolerance to cold limits in ectotherms and plants, where orders that originated in cold paleoclimates have lower cold tolerance limits than those that evolved in a warm paleoclimate. Heat tolerance was not related to climate ancestry. Cold tolerance has evolved more quickly than heat tolerance in endothermic and ectothermic animals. If the past tempo of evolution for tolerance to heat endures, adaptive responses in species' physiological thermal limits will not protect the vast majority of species.

Exploring ecological plasticity in Late Pleistocene ungulates using multi-isotope approaches

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Stratified archaeological deposits in karstic caves and rock shelters are often rich in animal skeletal remains due to the subsistence behaviours of early human groups. These materials represent excellent archives of potential information about the behaviours of Palaeolithic people, but also have great potential to provide insights into the palaeoecology of the animals they depended on. Multi-isotope analyses permit the reconstruction of faunal palaeoecology directly from preserved tooth and bone, revealing the movement dietary behaviours of extinct and ancestral taxa, and are increasingly being combined with geospatial and other modelling tools. With a focus on *Rangifer* and on recent methodological developments using modern materials, this presentation will explore the application of multi-isotope techniques to exploring continuity and change in the dietary and ranging behaviour of Late Pleistocene ungulates.

Long-term evolution of *Arctica* thermal niche: from Paleocene to Quaternary

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The ocean quahog *Arctica islandica* is considered to be the longest-lived non-colonial animal, with a maximum recorded lifespan of 507 years. It lives in North Atlantic cold environments, from the eastern coast of the United States to Scandinavia. Due to the sensitivity of these environments toward global changes and this exceptional lifespan, the species is now widely used as a paleoenvironmental archive, the carbonate of its shell recording accurately the temperature of ambient seawater. *A. islandica* is the only living representative of the genus *Arctica* (and of the Arcticidae family) but other species are known as far back as the Paleocene epoch. In this study, we used oxygen stable isotope ($\delta^{18}O$ and Δ_{47}) data from the shells of European Oligocene, Miocene, Pliocene and Pleistocene *A. islandica* and *A. rotundata,* alongside other bivalves (carditids, glycymerids and pectinids), to reconstruct the seasonal temperatures experienced by each species, comparing these with the thermal niche of living counterparts.

This study aims to establish the long-term ecological history of *Arctica* in terms of temperature and hence if its cold-environment affinity constitutes a persistent trait or has been recently acquired. The outcome of this approach will determine whether the genus can be widely used as a marker of Cenozoic cold-environments. The sclerochronological methodology will also allow us to determine other life-history traits, such as growth rates and the timing of growth interruptions, helping us to test whether the association of slow growth rates, long lifespan and cold environments observed amongst modern bivalves applies over geological time, including warmer epochs.

Ecological Uniformitarianism and Conservation Palaeobiology

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A key assumption of many studies in conservation palaeobiology is that species had the same ecological tolerances in the past as they do today. This assumption, based on the principle of ecological uniformitarianism, introduces inherent uncertainty into palaeoecological reconstructions. Here, I evaluate how epistemic uncertainty stemming from incomplete knowledge or understanding about past species' ecological tolerances has been considered and communicated in the conservation palaeobiology literature. Using selected examples, I demonstrate how relying solely on the assumption of stable ecological tolerances of species can lead to misguided conservation decisions. Transparently reporting the uncertainty surrounding ecological tolerances of fossil species is essential for developing reliable and adaptive conservation strategies that make use of data and insights from the past.

Stability of Planktic Foraminiferal Temperature Preferences

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Stationarity of species' ecological tolerances is a first-order assumption of paleoenvironmental reconstruction based upon analog methods. To test the hypothesis that planktic foraminifer species temperature preferences did not change between the Late Pliocene and present, we previously determined mid-Piacenzian relative abundances of nine taxa in 341 samples from 18 North Atlantic sites. Abundances were compared to SST estimates of the same age derived using alkenone unsaturation ratio ($U_{37}^{K\prime}$) sea surface temperature (SST) estimates. Core-top abundances of the same taxa were compared to pre-industrial SSTs. The results from these initial comparisons were mostly encouraging, suggesting the taxa tested did not change thermal preferences over the past 3 million years. Currently, we are analyzing assemblages from eight additional sites, six of which are outside the North Atlantic region. Initial results suggest that SST preferences from the same species at these new sites are also similar to present day preferences, supporting the North Atlantic findings and the hypothesis that temperature preferences of planktic foraminifera have been stable since the Late Pliocene. This information can be used to evaluate paleoenvironments and, in conjunction with other proxy methods, can be used to identify situations where environmental variables other than temperature may be exhibiting a first-order control on faunal assemblages.

Evolution of benthic foraminifera in the 'stable' environment of the chalk facies

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The chalk succession of N.W. Europe provides a unique record of the evolution of benthic foraminifera over a time span of ~ 30 Myr. While the chalk environment cannot be portrayed as uniform over this interval, it was remarkably constant. Indeed, the clay-rich lower part of the Cenomanian succession is transitional from the underlying Gault Clay Formation (of Middle and Late Albian age), extending still further the range of this environmental uniformity. It is not surprising, therefore, that the benthic foraminifera give us a wonderful example of gradualistic evolution through this interval, punctuated by occasional 'events'. While the lineages of almost every genus recorded in the Late Cretaceous can be traced through the chalk succession, a number have provided quite detailed examples of well-documented evolutionary lineages. The most striking are the lineages of *Arenobulimina*, *Gavelinella* (and related taxa), *Stensiöina,* and *Bolivinoides*. All these taxa have been used in every published zonation of the European Cretaceous based on benthic foraminifera.

The easily accessible coastal sections around Kent and Sussex and cored boreholes in the lower Thames allow systematic, metre by metre, sampling thereby providing semi-continuous representation of these lineages. They have also been used extensively in applied stratigraphy. *Arenobulimina* and *Gavelinella* were used in the micropaleontological work (both site-investigation phase and construction phase) for the Channel Tunnel, while *Gavelinella* and *Stensiöina* were used in the site-investigation work for the Thames Barrier and the Thames Tideway using cored boreholes. In recent years *Stensiöina*, *Bolivinoides,* and many of the gavelinellids have been used in the creation of zonal schemes used in directional drilling of the chalk reservoirs in the North Sea Basin.

Detailed calibration of the benthic foraminifera in parallel with the calcareous nannoplankton zonation has resulted in tight chronostratigraphic control of the evolutionary changes recognised in the former. Subtle morphological changes in the *Stensiöina* lineage suggest possible linkage to water depth changes during the Late Cretaceous succession, implying that some subspecies may be ecophenotypes, rather than defining long-term evolutionary changes.

Quaternary–Recent ostracod niche stability

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Proxy-based palaeoclimatic reconstructions of British early hominin occurrences assume ecological stability of taxa over the past 0.8 million years. This ecological uniformitarian approach, routinely applied to proxies such as beetles and ostracods, should be considered critically. If present ecological lability (niche shifting) of species can be demonstrated, then it almost certainly occurred in the past. Studies of invasive species suggest lability in various organisms including ostracods, not only facilitating invasions but also enabling native taxa to mitigate impacts of invasive competition. Small niche expansions can result in large geographical range shifts. Rice field ostracod studies show species-rich communities are less prone to invasion than those with low diversity. Examples of potentially invasive non-marine ostracods in Europe raise questions about anthropogenic vs "natural" range changes. Holarctic *Ilyocypris salebrosa*, once considered extinct in NW Europe despite Pleistocene fossil records, is now known to inhabit southern European areas with warmer summers. If found living in Britain, would it be considered invasive, or a sentinel of global warming? The European rarity of *Potamocypris humilis* might suggest it is an invasive introduced from southern Africa where it was first described, but the hypothesis that its occurrences (linked by bird migration routes) are "natural" is supported by a British Pleistocene fossil record. Fundamental ecological niches (the full range of conditions in which a species can exist) are rarely seen in single populations, but something approaching them may be represented by metapopulations of lacustrine ostracod species with Holarctic distributions. The realised ecological niche of a species may change in response to variation in (e.g.) dispersal success, habitat availability, competition, and heterogeneity of realised environmental space (which is geographically patchy for non-marine ostracods). The lacustrine species *Cytherissa lacustris* is a test case for ecological stability in Quaternary Ostracoda. Originating in the Pliocene, it achieved Holarctic distribution in the Pleistocene. Following the last glaciation, it dispersed into newly available waterbodies as ice sheets retreated. Although regarded as a cold palaeoclimate indicator, its Nearctic and Palaearctic metapopulations have different climatic niches. Does this indicate a degree of ecological lability, or is it simply a manifestation of variation in realised niche?

Quaternary altitudinal record for Hermann's Tortoise (*Chersine hermanni*) indicates a wider ecological tolerance

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Hermann's tortoise (*Chersine hermanni*) is a species of medium/small size endemic of Europe. Nowadays, two subspecies are recognized: *Chersine hermanni hermanni* from north-eastern Spain to Italy, and *Chersine hermanni boettgeri* in the Balkan peninsula, from Romania to Greece. The two subspecies differ markedly in their threat level and conservation status. *Chersine hermanni hermanni* has a distribution area formed by small and highly fragmentary populations, whereas *Chersine hermanni boettgeri* presents a more continuous and numerous ones. This is probably the reason why some authors have proposed a higher ecological tolerance in the eastern subspecies. To test the possibility that the ecological niche of the western subspecies was wider in the past, we have build a database comprising the entire testudinid Quaternary fossil record of mainland Europe. This database contains 278 Pleistocene and late Holocene records from sites in which remains attributed to the species or related taxa has been cited. These localities are located in 12 countries, some of them, as Portugal or Hungary, where the species is currently absent. The revision of the overall record allowed us to detect the presence of *Chersine hermanni* at high altitude in the central Spanish area (Central Range) during the Late Pleistocene. All of these records are located at approximately 1,100 metres above sea level. Such an altitudinal record exceeds the current maximum known for the western subspecies (850 metres) and is similar to the one recorded for *Chersine hermanni boettgeri* (1,300 metres). Moreover, the preliminary palaeoclimatic reconstruction based in the palaeoherpetofaunal assemblage recovered from the same sites indicated conditions not recorded in the climatic range of the species in Spain nowadays. These results have high value for the conservation of this highly endangered species and recognized as a flagship species with a high public profile.

When the Modern Analog mentality fails: examples relating to thermal tolerance of freshwater and marine mollusks

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Environmental temperature plays a key role in determining where an organism can live, with each organism having a unique thermal niche, or range of temperatures in which it can survive. Thermal niches are often considered to be conserved through time in related species to the extent that occurrence of a given taxa in a fossil deposit can be used to infer paleoenvironment (aka the “faunal analog” method). The validity of this assumption, that thermal niche is static through time, can be directly tested by comparing quantitative paleotemperature estimates on fossil species to their modern observed thermal niche. In this talk, we present two examples where this thinking outright fails. We present paleoenvironmental reconstructions derived from clumped isotope analysis of fossil mollusks from Last Interglacial coastlines of Bermuda (gastropod *Cittarium pica*) and Late Cretaceous rivers of the Western US (Unionid bivalves). In both cases, reconstructed temperatures are outside of the modern observed thermal range, directly contradicting the idea of a conserved thermal niche. These findings remind us that more factors than just temperature influence where an organism is found today and how and when a mollusk grows its shell, and that modern observed habitats do not always reflect the entire niche an organism is possible of inhabiting.

Fundamental Ecological Niches that Do and Do Not Change and What Happens as a Result in terms of Biological Diversity

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Scientists have focused on the question of conservatism or plasticity in the evolution of fundamental ecological niches. Plasticity has been invoked in ideas about ecological speciation, whereas theoretical examinations have led to an expectation of conservatism. Early studies under the “ecological niche modeling” rubric confirmed the theoretical expectations of ecological niche conservatism. Quite simply, fundamental ecological niches do not evolve frequently or easily, although the literature on the topic is replete with inaccurate conclusions based on incomplete understanding of conceptual frameworks, particularly as regards the difference between fundamental and realized or existing ecological niches (which can and do change more easily and frequently).

Effective and well-designed tools are now in hand that permit quantitative comparisons of fundamental ecological niches. The picture that emerges is one of widespread ecological niche conservatism, but with occasional important exceptions. A fundamental question is whether such conservatism of niche characteristics promotes or retards biological diversification. With colleagues in China, the U.K., and the U.S.A., I have developed virtual world simulation-based assessments of this question, simulating global biodiversity in situations in which fundamental ecological niches do and do not evolve. Ecological niche conservatism emerges as a key force in stimulating biological diversification.

Physiology, Fitness, and Macroevolution: Survival of the Sluggish?

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This talk focuses on metabolism to consider the macroevolution and macroecology of marine molluscs over the last 3 million years. Metabolism is known to be a highly significant property of organisms that influences their resource use as well as their survival. We examine whether the metabolic rate of organisms scales up to also influence long term survival at the species level. We further examine how patterns of inferred energy use change in assemblages. Our specific focus is on 299 well known species of marine gastropods and bivalves known from the fossil record and the extant biota of the West Atlantic region, along the eastern coast of the United States of America. This is a region with an exceptional and intensely sampled fossil record. Furthermore, many species alive today occur back to 3 million years ago. At that time the ocean was relatively warm, and temperature conditions approximated those expected by the next century. Using information from paleoclimate and other variables, along with data from museum collection visits and digital museum records, metabolic rate values were calculated and compared between those species that survived and those that went extinct. A highly statistically significant difference in metabolic rate was found, with survivors having lower metabolic rate values. This indicates that sometimes properties of organisms can be extrapolated upwards to explain the survival of species, which is informative regarding macroevolutionary hierarchies. It further documents that in the face of climate change it will be species containing organisms possessing lower activity levels and using fewer resources that are more likely to survive. However, metabolic rate is not is the only factor associated with survival: geographic range and niche breadth are also implicated. We also examined Basal Metabolic Rate patterns among assemblages through time. Among these data, no significant changes in metabolic rate at the assemblage level through time were found. This suggests that even in the face of substantial extinction, these mollusc communities were energetically stable, pointing to a disconnect between macroevolutionary and macroecological patterns.

Species Responses to Change in South Florida Viewed Over Different Temporal and Spatial Scales

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Everglades National Park, an International Biosphere Reserve in south Florida, has undergone significant changes since the Late Pleistocene. During the last interglacial ~120,000 years before present, much of the Florida platform was underwater, but by ~18,000 years ago at the height of the Wisconsin Glacial stage, sea level dropped, and the land mass of the Florida peninsula was nearly double its current size. To examine the degree of species resiliency in the marine ecosystem to such a wide range of changes, occurrence records of Pleistocene mollusks in south Florida were extracted from the Paleobiology Database. Species names were taxonomically standardized and compared to multiple databases of living mollusks. Of the 304 valid Late Pleistocene mollusk species, 90% occur in south Florida today. These findings suggest that the south Florida mollusk species are relatively stable when examined at the regional scale across geologic timescales. However, when we change our temporal focus to the last 500 years and narrow the spatial focus to the nearshore zones of southernmost Florida, a different picture emerges. The estuarine and nearshore marine areas of south Florida have been naturally shaped by the shallow carbonate platform, sub-tropical climate, and frequent hurricanes that impact the vast underwater seagrass meadows and the mangrove forests on the coast. During the 20th century, anthropogenic alteration of the landscape and hydrology reduced freshwater supply to the estuaries and caused shifts in salinity patterns that are exacerbated by rising sea level. Low salinity molluscan taxa that are abundant in the bottom of nearshore cores that date from 100 to 500 years before present are rare to absent in these areas today. The taxa appear to have shifted their spatial distribution in response to shifting salinity zones. In addition, starting in the late 20th century the estuarine assemblages are dominated by mollusks that can tolerate wide ranges of salinity. The well-preserved late Cenozoic fossil record of south Florida, coupled with a stable carbonate platform and sub-tropical climate, provides an opportunity to focus on factors affecting species survival and resiliency at various spatial and temporal scales.