The evolution and extinction of the ichthyosaurs from the perspective of quantitative ecospace modelling

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The role of niche specialization and narrowing in the evolution and extinction of the ichthyosaurs has been widely discussed in the literature. However, previous studies have concentrated on a qualitative discussion of these variables only. Here, we use the recently developed approach of quantitative ecospace modelling to provide a high-resolution quantitative examination of the changes in dietary and ecological niche experienced by the ichthyosaurs throughout their evolution in the Mesozoic. In particular, we demonstrate that despite recent discoveries increasing our understanding of taxonomic diversity among the ichthyosaurs in the Cretaceous, when viewed from the perspective of ecospace modelling, a clear trend of ecological contraction is visible as early as the Middle Jurassic. We suggest that this ecospace redundancy, if carried through to the Late Cretaceous, could have contributed to the extinction of the ichthyosaurs. Additionally, our results suggest a novel model to explain ecospace change, termed the ‘migration model’.

1. Introduction

Ecospace modelling is a relatively new technique in which organisms are considered within a hypothetical framework of ecological characters, wherein changes can be visualized and quantified over geological time [1]. A species’ (or some higher taxonomic unit’s) specific multidimensional combination of variables is its ‘ecospace’, a concept analogous to ‘morphospace’: an abstract representation of a number of traits in quantitative space which is then compared with others. Ecospace modelling can be used to recognize convergent behavioural and ecological phenomena that may be missed by standard phylogenetic or morphospace modelling [1]. Here, we demonstrate how applying a novel ecospace framework to the major genera of the Ichthyosauriformes [2] through the Mesozoic allows the degree of ecological diversity, niche narrowing and convergence seen to be placed in an evolutionary framework, and provides insights into the evolutionary history of this clade. We show how continued loss of unique ecotypes, resulting in gradual contraction onto a highly derived and potentially unsustainable ecospace, produced an ecological bottleneck potentially contributing to their eventual extinction in the Late Cretaceous.

While numerous studies have considered ichthyosaur diversity through time, all these studies have concentrated on phylogenetic or morphospace diversity [3,4]. The assumption is that these variables correlate sufficiently with ecological variables such that a qualitative description of ecospace will be sufficient to explain the observed pattern (e.g. dental guild considered in isolation). As a result, this study is significant for a number of reasons; first, for providing a high-resolution quantitative representation of ichthyosaur ecological diversity through time, which can be integrated into future analyses. Second, the results provide evidence of a novel macroevolutionary process by
which ecological evolution can occur, here referred to as the ‘migration model’. Finally, this study contributes to our understanding of the role of ecospace contraction in the extinction of the ichthyosaurs.

2. Material and methods

A multidimensional ecospace matrix was created, wherein 15 ecological categories (electronic supplementary material) were coded for 45 ichthyosaur genera, and grouped across four time bins (following the methodology seen in [3]). The resulting matrix was analysed in Matlab using non-metric multidimensional scaling (non-metric MDS) analysis, rarefaction analysis, disparity analysis (using the package MDA [5]) and Ward’s method cluster analysis (bootstrap \( n = 10000 \)) [3]. The ecospatial data were created by the authors based on descriptions and photographs of the various genera from a number of publications (see electronic supplementary material). Principal coordinate volumes (from the non-metric MDS analysis) for the four different time bins were calculated to examine the pattern of changing ecological disparity against changing taxonomic diversity [3,5,6].

3. Results

Figure 1 shows the results of the non-metric MDS analysis, showing ecospace distribution through time. Ecotype A represents a recently described and unusual basal ichthyosauriform genus, *Cartorhyncus* [2]. *Cartorhyncus* is plotting so far from the rest of the genera due to its unique ecospace; *Cartorhyncus* was a very small and (proposed demersal) suction feeder [2]. This ecotype was attained only once, early in the history of the Ichthyosauriformes, and was lost by the Middle Triassic [2]. Ecotype B, representing the majority of Early–Middle Triassic genera, represents the ecospace occupied by the basal Ichthyopterygia. The species known from these genera inhabited a transitional ecological niche [6,7]. Specifically, these genera are small (less than 2 m), with heterodont dentitions (robust and blunt posterior teeth), possibly implying a facultative durophagous diet [6,7]. Given their small body size and lack of open-water swimming adaptations (i.e. elongate bodies with low-aspect-ratio tail flukes), these genera are suggested to have occupied a circalittoral generalist ecospace (as suggested in reference [8], these species likely had swimming capabilities similar to those of scyliorhinid sharks, which supports the previous suggestion; figure 1).

Ecotype C represents the large hypercarnivorous apex predator ecospace, reached twice in the evolutionary history of the ichthyosaurs; first by *Thalattoarchon* in the Early Triassic, and second by *Temnodontosaurus* in the Early Jurassic. Ecotype D represents the four known large species with reduced dentition, implying a specialized feeding strategy (figures 1 and 2) [9,10]. This ecotype appears to have been lost, and convergently re-evolved by *Temnodontosaurus azerquensis* during the Early Jurassic radiation. Ecotype E represents the four known large species with reduced dentition, implying a specialized feeding strategy (figures 1 and 2). This ecotype appears to be the primary one occupied by the ichthyosaurs through time; in total, 20 genera spanning all four time bins used in the analysis occupied this ecospace; however, this ecospace was not occupied during the Early Triassic. Ecotype F contains *Eurhinosaurus* and *Excalibosaurus*, plotted independently owing to their unusual rostral morphology suggesting a specialized feeding method (here referred to as ‘slash’ owing to previously suggested similarities to swordfishes—see [11]). Ecotype G represents the other consistently occupied ecospace: the large derived Jurassic and Cretaceous ichthyosaurs with robust dentitions for crushing bony fish or hard-bodied cephalopods (figure 1). The robust dentition and highly variable stomach contents seen in representatives of ecotype G imply a potential for generalist/opportunist diets among these genera [12].

4. Discussion

Adjusted for rarefaction, ichthyosaur diversity was relatively constant from the Early Triassic through the Early Jurassic, with a steady decline in mean PCO volume (figures 1 and 2). The Early–Middle Triassic is characterized by transitional ecospecies: generalist ambush feeders with a developing thunniform swimming morphology, likely hunting fish in the circalittoral region, with hard-shelled prey making up a portion of the diet (figure 1) [6,7]. In the unadjusted data (figure 1), at the transition between the Middle and Late Triassic, ecospace disparity changes dramatically, with the loss of the shallow-water generalist forms and the earliest apex-level predator (figure 1). Despite the loss of three distinct ecotypes (two of which (ecotypes A and B) were never re-evolved), disparity remains relatively high in the Late Triassic, owing to the evolution of the large dentally reduced forms (ecotype D) offsetting the loss. The ecospace shift that occurs between the Middle and Late Triassic is effectively a radiation into open water while losing all circalittoral forms. Given that there is little clear evidence of competitive exclusion [6,13] (required for the negative feedback model of [1]), this radiation produces a pattern that cannot be explained using any of the macroevolutionary models described in reference [1]. Here, we propose the name ‘migration model’ for this new model of ecospace diversification, and suggest it be included in the framework of Bush & Novack-Gottshall [1]; species migrate into novel ecospaces while abandoning previously occupied ones (figure 2B).

The end-Triassic extinction event reduced taxonomic diversity, resulting in a bottleneck wherein only the fusiform pelagic ecotypes (the Parvipelvian clade [14]) remained, culminating in a third radiation in the Early Jurassic [3]. The Early Jurassic radiation produced several variants based on the pelagic fusiform morphotype (ecotypes C, E, F and G), resulting in a peak level of pelagic ecospace diversity (figure 1). Despite early stability, by the Middle Jurassic and into the Cretaceous, ichthyosaur ecospace diversity has begun to contract dramatically; the complete loss of specialized feeders like *Eurhinosaurus* and the apex predator ecospace with the extinction of *Temnodontosaurus* resulted in continual occupation of only two ecotypes: E and G (figures 1 and 2). By the Late Cretaceous, ichthyosaurs occupied only two of a possible seven proposed ecospaces (not including theoretical spaces never reached). The large number of taxa aggregated into the Middle Jurassic–Cretaceous time bin (to allow for comparison with the results of [3]) blurs the overlap between ecologically similar taxa throughout this time period (when viewed in figure 2b); however, this is visible in figure 1.

A recent article demonstrating the methodology behind ecospace modelling [1] suggests seven hypothetical models that can be used to explain changes in ecospace utilization through time. Above (figure 2b), we suggested that none of
the models proposed in reference [1] can explain the observed change in ichthyosaur ecospace diversity seen throughout the Mesozoic. For the ichthyosaurs to have followed the negative feedback model, initially fruitful ecological lifestyles would have had to become restricted by lifestyle changes in other taxa resulting from biotic interactions [1]. A modified form of this, here referred to as the ‘migration model’, suggests that a radiating population enters new ecospaces while...
abandoning previously occupied ecospaces. The mechanisms of this process are beyond the scope of this paper, but we speculate that it may occur when constraints from the physical environment steadily force a population to new adaptive peaks. Following this evolutionary migration, the ichthyosaurs appear to follow the contraction model of [1]: continued loss of specialized ecospace reducing the overall disparity (between the Early–Middle Triassic and Late Triassic time bins—figure 1).

We suggest that the pattern seen above can best be understood as demonstrating a combination of two models working in sequence; first, an evolutionary ‘migration’, where the ichthyosaurs ‘abandoned’ the circalittoral ecospaces they inhabited in the Early–Middle Triassic (figure 1). Following this, there was a severe loss of ecospace diversity during the end-Triassic extinction event, creating an ecospatial bottleneck of only fusiform pursuit predators [3,14]. Finally, the ichthyosaurs experienced continued ecospace contraction throughout the Jurassic and Cretaceous owing to continued extinction of more diverse ecotypes (figures 1 and 2; see also cluster analysis in electronic supplementary material). The pattern above contrasts with that seen in reference [3], wherein morphological disparity collapses at the Triassic–Jurassic (Tr–J) boundary. Our results suggest that ichthyosaurs were able to maintain high ecological disparity using only the fusiform morphotype that persisted beyond the Tr–J boundary.

Our results suggest that despite recent discoveries increasing the taxonomic diversity of the Cretaceous ichthyosaurs [15], their ecospace and niche diversity had failed to increase since collapsing in the Middle Jurassic. Where the ichthyosaurs lost a particular ecospace, they appear to have been unable to recolonize it (figures 1 and 2). Whether this pattern of limited ecospace disparity carried through to the extinction of the

Figure 2. (a) Ichthyosauriform ecological disparity and phylogenetic diversity compared using the four time bins from [3]. Error bars represent 90% CIs calculated for the PCO volume metric. (b) Graphic representation of the proposed ‘migration model’, to be added to the framework proposed in [1]. The points represent a unique combination of functional traits, and point proximity indicates similarity [1].
ichthyosaurs in the Late Cretaceous is unclear owing to potential sampling bias. If the pattern is not an artefact of sampling, the high metabolic costs associated with maintaining a large body size and high-energy pursuit feeding strategy may have rendered the remaining ichthyosaur ecospaces unsustainable following the Cenomanian–Turonian boundary event, which greatly reduced available biomass [16]. Further sampling is needed to test this.

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References