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EVOLUTION OF ECOSPACE OCCUPANCY BY MESOZOIC MARINE TETRAPODS

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Abstract: Ecology and morphology are different, and yet in comparative studies of fossil vertebrates the two are often conflated. The macroevolution of Mesozoic marine tetrapods has been explored in terms of morphological disparity, but less commonly using ecological-functional categories. Here we use ecospace modelling to quantify ecological disparity across all Mesozoic marine tetrapods. We document the explosive radiation of marine tetrapod groups in the Triassic and their rapid attainment of high ecological disparity. Late Triassic extinctions led to a marked decline in ecological disparity, and the recovery of ecospace and ecological disparity was sluggish in the Early Jurassic. High levels of ecological disparity were again achieved by the Late Jurassic and maintained through the Cretaceous, when ecospace became saturated by the Late Cretaceous. Sauropterygians, turtles and ichthyosauromorphs were the largest contributors to ecological disparity. Through the Mesozoic, we find that established groups remained ecologically conservative and did not explore occupied or vacant niches. Several parts of ecospace remained vacant for long spans of time. Newly evolved, radiating taxa almost exclusively explored unoccupied ecospace, suggesting that abiotic releases are needed to empty niches and initiate diversification. In the balance of evolutionary drivers in Mesozoic marine tetrapods, abiotic factors were key to initiating diversification events, but biotic factors dominated the subsequent generation of ecological diversity.

Key words: macroevolution, marine tetrapod, plesiosaur, ichthyosaur, ecology, ecospace

UNDERSTANDING the expansion of biodiversity, both in terms of the diversity of species and the diversity of adaptations, are core questions in macroevolution (Simpson 1944; Morlon 2014; Benton 2015). Such questions have often focused on adaptive radiations (Ruta *et al.* 2013; Benson *et al.* 2014), where bursts of diversification coincide with the exploration of new ecological opportunities (niches, or defined portions of ecospace). Simpson (1944) proposed three models for the occupation of new niches: the evolution of key innovations (e.g. wings in birds); the removal of competition through emptying existing niches by extinction; and the generation of new habitats through environmental change (Simpson 1944; Yoder *et al.* 2010). Subsequent debates over which of these three factors is more important in influencing diversity has led to two broad hypotheses, the Red Queen and the Court Jester (Benton 2009). The Red Queen hypothesis (Van Valen 1973) favours intrinsic biotic factors, such as biological innovations or competition, while the Court Jester hypothesis (Barnosky 2001) focuses on abiotic factors, such as mass extinctions or climate change, as the dominant drivers of diversification (Benton 2009).

Mesozoic marine tetrapods make an excellent case study to investigate origins of biodiversity, as they include between 12–18 independent transitions from land to sea (Motani 2009; Benson 2013; Kelley and Pyenson 2015) and their anatomy and ecology are in some cases well documented. Their initial diversification followed the devastating Permian-Triassic mass extinction (PTME), in which >90% of marine species became extinct (Sahney & Benton 2008; Motani 2009; Benton *et al.* 2013; Stubbs & Benton 2016). Through the Mesozoic, marine tetrapods flourished, showing a series of extinctions and clade expansions (Scheyer *et al.* 2014; Kelley & Pyenson 2015; Stubbs & Benton 2016; Foffa *et al.* 2018; Moon & Stubbs 2020) and building complex ecosystems similar to modern marine networks (Fröbisch *et al.* 2013). Triassic marine reptiles ranged from the durophagous placodonts (Rieppel 2000), to the hammer-headed herbivorous *Atopodentatus unicus* (Li *et al.* 2016) and large macrophagous ichthyosaurs such as *Thalattoarchon saurophagis* (Fröbisch *et al.* 2013). The Jurassic saw the rise of Plesiosauria (O’Keefe 2002) the diversification of ‘shark-like’ Neoichthyosauria (Motani 2009; Gutarra *et al.* 2019), and appearance of several clades of marine turtles (Nicholls, 1997; Evers & Benson 2019). New clades arose in the Cretaceous, including predatory mosasaurs, multiple marine snake lineages, chelonoids (the extant group of sea turtles), and Hesperornithidae, penguin-sized diving birds (Pyenson *et al.* 2014; Driscoll *et al.* 2019; Evers & Benson 2019). Most of these clades died out during the Late Cretaceous or at the Cretaceous-Paleogene (K/Pg) mass extinction (Pyenson *et al.* 2014).

Computational studies in macroevolution often focus on taxonomic diversity (species or genus richness) or disparity (morphological diversity). Complex disparity data sets, whether based on discrete or continuous characters, can be represented as morphospaces, summarizing the major axes of variation in form (Raup 1966; Mitteroecker & Huttegger 2009). Morphospaces may be interpreted in ecological-functional terms by incorporating taxa with known lifestyles, but this has to be done with caution because of the ‘many-to-one’ problem (Wainwright *et al.* 2005), whereby one form might have many functions, or many forms might perform the same function. Quantitative ecospace modelling, a variant of morphospace modelling (Bambach 1983; Bambach *et al.* 2007), uses ecological characteristics (prey preference, habitat, body size, environmental preferences, etc.) derived from morphology and sedimentology to create an ecospace (Bush & Novack-Gottshall 2012; Dick & Maxwell 2015). The method makes a link between morphology and ecology, and the resulting ecospace is a reflection of ecospace occupancy within a group and trends in ecological disparity can be assessed.

While Mesozoic marine tetrapod diversity and disparity have been investigated previously, as have the drivers for their diversification (e.g. Benson & Butler 2011; Benson &

Druckenmiller 2014; Pyenson *et al.* 2014; Stubbs & Benton 2016; Foffa *et al.* 2018; Flannery Sutherland *et al.* 2019; Moon & Stubbs 2020), ecospace modelling has only been used in one study of ichthyosaurs (Dick & Maxwell 2015). The aim of this study is to produce the first, holistic, high resolution record of ecospace occupancy and ecological disparity of marine tetrapods through the Mesozoic. The ecospace is defined for marine tetrapod taxa based on a range of ecologically informative characteristics and is then used to test major questions about marine tetrapod evolution: (1) how rapid was the ecological diversification of Mesozoic marine tetrapods in the Triassic? (2) when was maximum ecospace occupancy and disparity seen? (3) what impact did major extinction events have on ecological disparity? (4) what are the relative influences of biotic or abiotic drivers on ecological disparity and evolution?

MATERIALS AND METHODS

Taxon selection

Taxa were coded at generic level to reduce possible inaccuracies from species misidentification, poor fossil representation, and uneven sampling of the fossil record (Benton 2015). Most Mesozoic marine tetrapod genera are monospecific in any case, and those that comprise multiple species are often disputed. The majority of taxa are sauropsids, but we also include temnospondyls. Primary sources for the taxon compilations are: Temnospondyli from Scheyer *et al.* (2014); Rhynchocephalia, Squamata (not including Mosasauridae), Dryosauridae, Pholidosauridae and Testudinata from Bardet *et al.* (2014); Hesperornithiformes from the Paleobiology Database (PBDB; <https://paleobiodb.org>); and remaining datasets by T.L.S. (Thalattosuchia, Sauropterygia, Mosasauridae and Thalattosauria) and B.C.M. (Ichthyosauromorpha), compiled during their PhD work (Stubbs & Benton 2016; Moon 2018).

Where possible, the holotype of the type species of each genus was used, except in cases where the holotype was poor or incomplete, or where more complete or informative specimens had since been reported. In some cases, it was necessary to combine information from both type and non-type species to code the genus accurately because of incomplete preservation. In rare cases where more than one species within a genus demonstrated different ecological characters (such as great size disparity), each species was coded separately. Full information is given in Reeves *et al.* (2020).

We excluded genera if their taxonomy is equivocal or the materials are too incomplete to indicate their ecology. Most Mesozoic marine tetrapods are known from adequate to excellent specimens, but some have been named from incomplete or fragmentary remains (Cleary *et al.* 2015; Tutin & Butler 2017; Driscoll *et al.* 2019); we excluded genera for which we could not code more than five of our nine ecological characteristics. Finally, a few genera are represented only by juvenile, or suspected juvenile specimens, and these were excluded as their ecology might have changed through ontogeny. For example, Green turtles (*Chelonia mydas*) shift their diet during ontogeny (Arthur *et al.* 2008), as did the ichthyosaur *Stenopterygius quadriscissus* (Dick *et al.* 2016). Temnospondyls are reported to have changed habitat as they matured (Steyer 2003), and some marine reptiles such as ichthyosaurs may have had ‘nursery’ sites where juveniles lived separately from the adults, as do some modern sharks (Williams *et al.* 2015). We make one exception to this rule for the Rhaetian plesiosaur *Rhaeticosaurus*. The only known specimen may be a juvenile, but *Rhaeticosaurus* is the earliest known plesiosaur, and the only plesiosaur from the Triassic (Wintrich *et al.* 2017). Therefore, excluding this taxon from the Rhaetian time bin would misrepresent ecological disparity during this interval, where otherwise only placodonts are known. In total, 371 taxa (352 genera) are represented in the matrix (see Reeves *et al.* 2020 for full details).

Ecospace construction

Ecospace was defined by nine ecological characters (Table 1), with a total of 35 possible character states. Where appropriate, multistate characters were used to reduce the influence of repeat coding. Ecological characters were established from morphological evidence that informs on ecology. For example, a connection between body shape, swimming speed, and hunting ability is well documented (e.g. Massare 1988; Motani *et al.* 1996; Sfakiotakis *et al.* 1999). Not all morphological variation is linked to independent ecological characters; for example, the same prey may be caught and eaten whether the predator shows morphological evidence for either suction or ram feeding.

Ecological traits

Size. Body size is related to prey selection, trophic level and habitat use (Cohen *et al.* 1993) and can be measured in various ways. We considered trying to estimate body mass for each taxon, but methods are debated (Alexander 1998), estimates are fraught with error, and there have been few such efforts to estimate mass or volume for Mesozoic marine tetrapods (Motani 2001; Gutarra *et al.* 2019). In comparison, body length is quick and simple to determine, and we used a standard measurement from rostrum (anterior snout) to tail tip. Body lengths were recorded from the literature, either from the description or size estimates, or measured from published images. We recorded exact lengths, and then assigned these to several size range bins (Table 1). Size-range bins such as these have been used in earlier works, including Dick & Maxwell (2015), because exact measurements can entail debates around whether one uses a range or mean for multiple specimens and whether a measurement on a single specimen is exactly representative of the original population. When total body length could not be measured, we compared measurements from those parts of the anatomy represented, such as the skull, trunk or limb bones, and made comparisons to a nearest relative of the same size for assignment to size bins. Such cases are noted in the supplementary data (Reeves *et al.* 2020).

Habitat. We coded two broad habitat types (Table 1), based on the sedimentology and associated fossils of the formations from which specimens had been found, and largely following Benson & Butler (2011).

Diet. We assigned all taxa to one of two categories, herbivore or carnivore. Herbivory is rare among Mesozoic marine tetrapods (Li *et al.* 2016). Most clades (e.g. ichthyosaurs, mosasaurs, sauropterygians, thalattosuchians) have always been regarded as purely carnivorous, and they are all recorded as such. On the other hand, the diet of most extinct turtles is unclear (Parham & Pyenson 2010) and so modern analogues were used. Among extant Cheloniidae, only the Green turtle is reported as herbivorous (Arthur *et al.* 2008); the rest are either carnivorous (*Dermochelys*) or omnivorous. Therefore, we coded all turtles as carnivorous, unless there is specific evidence for herbivory. An omnivorous diet has been proposed for some extinct turtles, but morphological traits related to this diet are ambiguous in the fossil record (Maniel & de la Fuente, 2016), and this lifestyle is inconsistently reported within the literature. To avoid creating an additional category for only a few taxa, omnivorous turtles were coded as carnivores to distinguish them from more specialised herbivores.

Feeding strategy. We identify three feeding strategies (Table 1), based on body shape and swimming style (e.g. Massare 1988; Motani *et al.* 1996; Sfakiotakis *et al.* 1999). Following

Massare (1988, 1994), we assign categories based on overall body plan: Body Plan I, pursuit; Body Plan II, ambush; Body Plan III, some pursuit, some ambush (coded as ambush only); Body Plan IV, foraging. Among axial swimmers, the thunniform mode is related to constant, fast, powerful motion associated with ‘pursuit’ style predation, and the anguilliform mode with slow speeds punctuated with sudden bursts of acceleration, so correlating with an ‘ambush’ style of predation (Massare 1988; Sfakiotakis *et al.* 1999). Paraxial swimmers are generally considered to be ambush predators, a mode supported by their long neck and flexible body and agile movements restricted by armour and stiffened limb girdles (Massare 1988). The foraging category, a more passive prey-gathering mode, is identified for taxa that were less adapted for swimming (with only minor limb and body modifications), and predominantly associated with paraxial swimming style. Although pliosaurs fit the ambush body plan, they were considered to have been pursuit predators by Massare (1988) and were coded as such here.

Food location. Four categories for food source were recorded (Table 1): pelagic for prey located in the water column, benthic for prey resting on or near the sea floor, sessile for stationary or non-active prey and non-sessile for free-moving prey. Most taxa were assumed to have hunted mobile prey unless the associated literature or prey preference (e.g. herbivory) indicated otherwise. Placodonts were coded in benthic prey categories following Rieppel (2002). Benthic feeding was identified by a combination of armour, pachyostosis (Houssaye 2009) and cranial and limb adaptations.

Feeding guilds. Prey preferences have been established in Mesozoic marine tetrapods through comparative studies of tooth morphology and prey preference in extant marine predators (whales) and correlation with gut contents (Massare 1987, 1997). Following these studies, tooth morphology was used to code prey preference into different feeding guilds (e.g. Foffa *et al.* 2018). Additional guilds were created to incorporate more recently discovered feeding styles (Table 1). The filter guild was coded from the presence of numerous small thin teeth and incorporates both herbivorous (e.g. *Atopodentatus*: Li *et al.* 2016) and carnivorous (e.g. *Morturneria*: O’Keefe *et al.* 2017) lifestyles. The crush-cut guild of Bardet *et al.* (2015) incorporates the unusual tooth morphology of several mosasaurs. Lunge feeding has been recognised in several genera and relates to a prey preference and feeding method similar to baleen whales (Motani *et al.* 2015).

As previously discussed, extinct turtle diets are difficult to extrapolate from morphology (Parham & Pyenson 2010, Foth *et al.* 2017). Guilds were assigned from descriptions of prey preference discussed in the literature. Where their prey preference thought to show a wide range of feeding preferences taxa were coded in the general guild. Although this guild represents a preference for fish and softer prey it is in the middle of Massare’s (1987) ‘feeding triangle’ and can express a more generalised diet. Some turtles were described as having a “shearing” technique for eating (Parham & Pyenson 2010, fig. 3). As this did not fit into any coding categories, and we did not wish to create an additional mode for one small clade, we also coded it in the general guild. Turtles proposed to have had a diet primarily of jellyfish were coded in the smash guild to reflect the similarity of prey choice with other members of this guild.

Specialist or generalist feeding. Following Massare (1987), we use the dentition to distinguish between specialist (homodont) and generalist (heterodont) feeding behaviours. The assumption is that those tetrapods with identical (homodont) teeth had a more restricted diet than those with variable (heterodont) tooth shape or size. Size heterodonty, as exhibited

by the “fish trap” fangs of *Nothosaurus* (Rieppel 2002a, p. 52), suggests a specialised prey preference, but the diet cannot be resolved any further than fish in this case, so the diet mode is reported as generalist.

Armour. We coded the amount of armour into four grades (Table 1): absent, rows of osteoderms or scutes, ‘half’ armour (i.e. either just a carapace or plastron) or a fully encasing armour. Some clades such as placodonts were often heavily armoured presumably as protection from predators, whereas in others their lighter armour may also have had functions in hydrodynamics (Renesto & Tintori 1995) or osmotic regulation (e.g. Rieppel & Reisz 1999).

Aquatic adaptation. Limb shape was used to approximate aquatic adaptation (Table 1). Plesio pedal limbs are associated with the retention of terrestrial abilities, whereas hydropedal limbs indicate a fully aquatic lifestyle and the ability to gather food from more widely distributed locations (Ross 2009; Kelley *et al.* 2014). We follow Benson & Butler (2011) in coding these traits.

Ecospace occupancy analysis

The matrix of ecological traits coded for each taxon was the basis for a multivariate study of variation and the generation of ‘ecospaces’. The coded ecological character matrix was converted into a NEXUS file, and a pairwise dissimilarity matrix was calculated based on Gower’s coefficient (Gower 1971) in the R package Claddis (Lloyd 2016). Dissimilarity is visualised using non-metric multidimensional scaling (NMDS), with the metaMDS function in the R package vegan (Oksanen *et al.* 2016). The maximum dimensionality of the ecospace was set to two axes, and 10,000 random starts were used in the search for a stable solution. The performance of NMDS was assessed based on stress values (0.136, Reeves *et al.* 2020, Fig. S1). To explore temporal ecospace trends, taxa were plotted in separate time bins and convex hulls were used to highlight the overall area of ecospace occupation in each bin.

Taxa were placed in 30 stage-level time bins for the Mesozoic (total 186 Myr duration), averaging 6.2 Myr in duration. First (FAD) and last (LAD) appearance dates for each taxon were determined from several sources: Temnospondyli from Schoch & Milner (2014), Ichthyosauromorpha, Mosasauroida, Sauropterygia, Thalattosauria and Thalattosuchia from thesis data of B.C.M. and T.L.S., and the remaining taxa from the literature and PBDB. Geological dates come from the most recent ICS Chart (<http://www.stratigraphy.org/>; Cohen *et al.* 2013). In the temporal analyses, raw generic diversity/bin sampling is plotted.

Disparity statistics were calculated to summarize ecospace occupancy. We compare the ecological diversity of major marine tetrapod clades and also assess trends through time. We calculated disparity directly from the Gower pairwise distances matrix using within-bin weighted mean pairwise disparity (WMPD; Close *et al.* 2015; Strickson *et al.* 2016). In addition, we examine metrics that provide insights into the overall expanse of ecospace. As distances in non-metric ordinations may not be directly Euclidean, we needed to instead use a linear approach when calculating metrics based on absolute distances within ecospace. For this we applied principal coordinate analysis (PCOa) to the Gower pairwise dissimilarity matrix, and then calculated the minimum spanning tree (MST) length metric (Guillerme *et al.* 2019; Benevento *et al.* 2019) from the PCOa axes (Fig. S2), in the R package dispRity (Guillerme 2018). Distances between taxa using NMDS and PCOa methods show a moderately strong, significant and linear correlation (Mantel test, $R = 0.92$, $R^2 = 0.85$, $P = 0.001$, Reeves *et al.* 2020, Fig. S3). Our tests revealed that the MST metric is sensitive to bin sample size. We therefore used partial rarefaction to prevent bins with more taxa having

potentially inflated disparity. Bins with a sample size greater than the median of all 30 bins ($n = 16$) were rarefied to 16 samples, whereas bins with fewer than 16 samples were based on their total sample. Unrarefied MST disparity is presented in the supplement (Fig. S4). To dissect the contribution of major groups to overall ecological disparity through time, we calculated Foote's partial disparity metric from the PCOA and NMDS axes using the MDA package in MATLAB (Foote 1993; Navarro 2003). In all these disparity calculations 95% confidence intervals were created using 500 bootstrap replicates.

We characterize ecospace expansion and 'packing' between successive Mesozoic time bins using the niche packing "flexible" metric (NP flexible) of Pigot *et al.* (2016). This metric reveals the number of taxa in one bin that can be packed within the total morphospace/ecospace area/volume of another bin (irrespective of the location of taxa in ordination space). We applied this metric to successive time bins throughout the Mesozoic, beginning with the Induan/ Olenekian expansion in the earliest Triassic, then the Olenekian/ Anisian, right through to the Campanian/Maastrichtian at the end of the Cretaceous. For each comparison, we examine the proportion of taxa in the second bin that expand the ecospace convex hull area of the preceding bin, thus providing insights into bins with notable high ecospace expansion (Nordén *et al.* 2018). Times with low or no expansion reflect bins defined by ecospace packing. We separately applied this method to both the NMDS ecospace axes and the PCOA axes 1 and 2.

RESULTS

Ecospace occupation

Marine tetrapod ecospace is characterized by islands of clustering in densely populated regions. We identified six groupings according to their distinct occupation of ecospace (Fig. 1A). These groupings were identified visually and are characterised by a distinctive combination of character state scores within the ecospace (Fig. 2). As a consequence, some groups have much larger ecospace variance than others. For instance, group 6 has large variance and contains two sub-groups visually separated by a gap in ecospace occupancy, but these sub-groups cannot be explained by the distribution of ecological character states and have thus been retained as a single group. Conversely, groups 1 and 2 have substantially overlapping values along both ecospace axes and low variance (particularly along axis 2), but can be clearly distinguished by a single ecological character, feeding strategy, justifying their separation into two distinct groups. According to this informal grouping scheme, there is evidence for both ecological differentiation by major clades and several instances of convergence (Fig. 1A, Fig. S5). Examining the distribution of ecological character coding reveals that foraging mode, habitat, prey location, armour type and limb shape greatly impact the distribution of taxa in ecospace. The remaining four characters, size, diet, dental guild, and tooth heterodonty have more mixed distributions (Fig. 2).

There are six notable groupings in ecospace, containing taxa sharing ecological characteristics (Fig. 2). Taxa in group 1 (1, Fig. 1A) were pursuit carnivores that hunted pelagic prey in deep ocean environments and had hydropedal limbs (Fig. 2). They showed diverse body sizes, ranging from size category 1–2 m to 8–15 m, and occupied the pierce, crunch, cut and general dental guilds (Fig. 2). This grouping contains derived ichthyosaurs, a small number of pliosaurs and the mosasaur *Plotosaurus* (Fig. 1B). Group 2 (2, Fig. 1A) shares most ecological characteristics with group 1, but taxa in this grouping were instead ambush predators, and represented by plesiosaurian sauropterygians and a few ichthyosaurs (Fig. 1B, 2). Group 3 (3, Fig. 1A) also represents ambush carnivores that fed on pelagic prey and had hydropedal limbs, but this time in shallow water environments (Fig. 2). Once again there is a diverse range of body sizes in this grouping, including both small forms (1–2 m)

and large taxa (categories ranging through 2–15 m total body length). This grouping includes some Triassic ichthyosaurs, most mosasaurs and thalattosuchian crocodylomorphs (Fig. 1B). Group 4 (4, Fig. 1A), located at the high positive region of ecospace axis 2, is a diverse assemblage of shallow water, ambush, pelagic feeders, but which retained plesiopodal limbs (Fig. 2). Taxa at the positive extreme of axis 2 in this assemblage also had body armour in the form rows of osteoderms or scutes (Fig. 2). Many size categories are seen in group 4, but there is a greater proportion of smaller forms with total lengths of less than 1m, and even less than 50 cm. This group includes basal ichthyosauromorphs and hupehsuchians, teleosaurid and pholidosaurid crocodylomorphs, hesperornithiform birds, Triassic eosauropterygians (nothosaurs and pachypleurosaurus), some basal mosasaurs, all lizards and snakes, thalattosaurs and temnospondyls (Fig. 1B).

The extreme positive regions of ecospace axis 1 are more sparsely occupied, as are the extreme negative-value regions of axis 2. These ecospace regions contain two groups of taxa (5 and 6), primarily representing placodont sauropterygians and turtles (Fig. 1). Group 5 (5, Fig. 1A) comprises unarmoured, partially armoured and fully armoured taxa with plesiopodal limbs that existed in shallow water environments. They were foragers that fed on benthic prey and belonged to the crush or filter guilds and often had heterodont dentition (Fig. 2). This region is primarily occupied by placodont sauropterygians, enigmatic taxa such as the herbivore *Atopodentatus* and *Paludidraco*, and some turtles (Fig. 1B). The remaining turtles occupy group 6 (6, Fig. 1A, B) which covers a broad range of ecospace, reflecting varied niches and lifestyles. All turtles in group 6 were armoured, edentulous foragers with hydropedal limbs. This grouping includes both shallow and deep ocean forms, forming two subgroups, that fed on either pelagic or benthic prey, and both carnivores and herbivores (Fig. 2).

Temporal trends in ecospace occupation

Time-slicing marine tetrapod ecospace reveals many notable trends (Fig. 3, Fig. S6). The Triassic (Fig. 3A) is characterised by expanding ecospace, because of the initial increase in species richness of multiple marine tetrapod clades. Ecospace expansion happens quickly, most of it between the Induan and Anisian (e.g. Benton *et al.* 2013, Stubbs & Benton 2016). The Triassic is also notable for the widespread overlap of taxa in ecospace, particularly in group 4 (Fig. 1A). Placodonts are distinct and expand the Triassic ecospace to high positive regions of ecospace axis 1. Ichthyosauromorphs display a clear and dramatic movement through the Triassic ecospace, from group 4 to group 1 (Fig. 1A, 3A). The overall bounds of ecospace realized within the Triassic are not substantially expanded for the remainder of the Mesozoic (Fig. 3B, C).

The Jurassic begins with a notable contraction of ecospace (Fig. 3B), caused by Late Triassic extinctions and the bottleneck in marine reptile evolution previously noted (e.g. Thorne *et al.* 2011; Stubbs & Benton 2016; Moon & Stubbs 2020). This contraction between the Triassic and Jurassic reflects the loss of placodonts, non-plesiosaurian eosauropterygians, thalattosaurs and other Triassic taxa. Only a few lineages of ichthyosaurs and sauropterygians crossed the system boundary, and re-expansion of ecospace was led by these two clades for the first three stages of the Jurassic, but they occupied a limited, and unchanging ecospace for 19 Myr. Then, thalattosuchian crocodylomorphs emerged in the Pliensbachian and Toarcian, expanding the ecospace substantially. Through the remainder of the Jurassic, ichthyosaurs and sauropterygians (plesiosaurs, pliosaurs) remained remarkably static in ecospace occupation, and thalattosuchians (first teleosaurids, then metriorhynchids) also held steady in their separate region of ecospace. Turtles further expanded ecospace to increasingly positive

values along ecospace axis 1 in the Late Jurassic, partially occupying ecospace vacated some 40 Myr earlier, by placodont extinctions at the end of the Triassic (Fig. 3A, B).

The Cretaceous begins with similar ecospace occupancy to the end of the Jurassic (Fig. 3C). Plesiosaur and ichthyosaur ecospace remained stable throughout the Cretaceous, but ichthyosaurs went extinct in the Cenomanian. Mosasaurs and other squamates invaded the oceans after this point but occupied different ecospace to both Jurassic/Cretaceous ichthyosaurs and plesiosaurs, in groups 3 and 4 (Fig. 1A); a zone that was largely empty through the Early Cretaceous. This region was previously occupied by sauropterygians and thalattosaurs in the Triassic and some thalattosuchian crocodylomorphs in the Late Jurassic. In the last three stages of the Cretaceous (Fig. 3C), ecospace filled up until nearly every sector was occupied. The diversifications of mosasaurs, turtles, hesperornithiform birds, marine crocodiles and elasmosaurid plesiosaurs saturated ecospace but did not notably expand overall ecospace when compared with the mid-Cretaceous, or even the Late Jurassic.

Disparity Analysis

Partial disparity. Partial disparity (Figs. 4, S7) shows some rapid shifts in dominance and turnovers in the Early Triassic, Early Jurassic, and Late Cretaceous, but stability throughout much of the Jurassic and Early Cretaceous. Initially, all disparity was provided by temnospondyls in the Induan, but their influence was rapidly reduced by the diversification of ichthyosauromorphs in the Olenekian, whose contribution to ecospace was in turn overtaken by sauropterygians in the Anisian as the main contributors to ecological disparity for the remainder of the Triassic - although much of the Triassic sauropterygian disparity is contributed by placodonts. Dramatic changes in the Late Triassic are evidence of the previously reported extinction and bottleneck (Thorne *et al.* 2011; Stubbs & Benton 2016; Moon & Stubbs 2020).

Ichthyosaurs and plesiosaurian sauropterygians make equal contributions to disparity in the earliest Jurassic (Fig. 4). The declining contribution of both clades during the Toarcian and Middle Jurassic corresponds to the substantial expansion of thalattosuchian crocodylomorphs. The Early Cretaceous shows little change from the Late Jurassic, with the exception of the diminishing contribution of crocodylomorphs. A major shift during this interval is the rapid expansion of marine turtles to dominate ecospace in the second half of the Mesozoic, making a steady, high contribution to disparity throughout the Late Jurassic and Cretaceous. Turtles clearly adapted to a broad swathe of ecospace occupancy and were successful in retaining this ecological position through the Cretaceous.

Major changes occur in the Late Cretaceous (Fig. 4). Ichthyosaurs became extinct and thalattosuchian crocodylomorphs had already gone. Turtles increase their relative disparity substantially, to ~50%. New marine clades such as mosasaurs, marine lizards and snakes, hesperornithiform birds, and new crocodylomorph groups make modest contributions to total disparity. Sauropterygians continued through all these vicissitudes but contributing only 10–15% of disparity.

Temporal disparity trends and ecospace expansion. Both disparity metrics (WMPD and MST) show that high ecological disparity was rapidly attained by the Middle Triassic (Fig. 5). WMPD then marginally increased through to the Norian (Fig. 5B), but the MST metric shows a decline between the Carnian and Norian (Fig. 5C). Increasing disparity in the WMPD metric between the Middle Triassic and Norian is linked to a reduction in diversity/sampling (Fig. 5A), leading to ecospace ‘thinning-out’ and increasing the pairwise dissimilarity between taxa - but the overall expanse of ecospace remained stable or was reduced (Figs 3A, 5C). Both metrics show a reduction in disparity through the latest Triassic

to very low levels in the first three stages of the Early Jurassic (Fig. 5B, C). Ecological disparity then progressively increases to a second high point in the Late Jurassic, which is characterized by both high pairwise dissimilarity and expansive ecospace occupation (Figs 3B, 5B, C). High levels of ecological disparity are maintained throughout the Early and Late Cretaceous. WMPD remains stable, with a very minor reduction in the Late Cretaceous due to ecospace saturation and increasing diversity (Figs 3C, 5A, B). MST disparity documents reduced disparity during the early stages of the Cretaceous, potentially due to reduced diversity and sampling (Figs 5A, C). Overall, the rarefied MST metric closely mirrors generic diversity, but does not show such high peaks in the Middle Triassic and Late Cretaceous.

Proportional ecospace expansion was greatest during the Early Triassic, Toarcian, Middle–early Late Jurassic and the mid Cretaceous (Fig. 5D). High levels of expansion in the Early Triassic reflect the initial massive expansion of marine tetrapod ecospace between the Induan and Anisian (Fig. 3A), establishing relatively high disparity by this interval (Figs 5B, C). Toarcian expansion is linked to the emergence of thalattosuchians, which expand ecospace compared to the very low ecological disparity in the preceding three Early Jurassic bins. Expansions during the Middle Jurassic reflect successive contractions and expansion of ecospace during this interval, potentially reflecting low sample sizes, not continued ecospace expansion (Figs 3B, 5A). The Late Jurassic expansion marks the emergence of turtles and ecospace expansion along axis 1 (Figs. 3B, 5D). Finally, ecospace expansion in the mid Cretaceous is caused by the increasing diversity of ecologically disparate turtles in ecospace groups 5 and 6 (Figs. 1, 3B, 5D).

DISCUSSION

Ecospace occupation

All our analyses confirm that the Triassic was distinct from the Jurassic–Cretaceous interval, documenting an explosive radiation of marine tetrapod groups, most of which disappeared during the latter half of the Late Triassic. These staggered Late Triassic extinctions massively perturbed marine tetrapod ecological disparity. Diversity, disparity and ecospace occupation all remained at low levels through the first 19 Myr of the Jurassic, even though ichthyosaurs and plesiosaurs were abundant and richly represented in some parts of the world (Cleary *et al.* 2015; Tutin & Butler 2017). It took until the Late Jurassic for marine tetrapods to recover levels of ecological disparity comparable to the Triassic, and until the Late Cretaceous for tetrapods to fully reinvade ecospace that had formerly been occupied by placodonts and other Triassic clades (Fig. 3).

The initial expansion of marine reptiles in the Early and early Middle Triassic could be interpreted as an example of an ‘early burst’ radiation as empty ecospace was filled rapidly by new taxa (Simpson 1944; Schluter 2000; Stubbs & Benton 2016; Moon & Stubbs 2020). The rapid rise of diversity, and especially disparity and ecospace occupancy, documents how Triassic taxa explored and adapted to newly vacant niches that were emptied by the PTME, as well as to previously unoccupied ecospace (Benton *et al.* 2013; Stubbs & Benton 2016). Saturation of ecospace by the Anisian is a measure of the rapidity of diversification and probably indicates intense competition between marine predators in Middle Triassic seas (Fig. 3).

Placodonts stand out in the Triassic as occupying their own patch of ecospace, reflecting their unique adaptations to snatching and crushing molluscs (Rieppel 2002a). While placodonts are often described as having had a superficial resemblance to turtles (e.g. Rieppel 2002b; Fröbisch *et al.* 2013) the, only partial, ecospace overlap between these groups shows they were not fully ecologically convergent, and that turtles expanded into different areas of ecospace, such as open ocean environments (Figs. 1, 2).

The explosive radiation of marine tetrapods in the first 10 Myr of the Triassic was not repeated in the Mesozoic, even after the near annihilation of many clades in the Late Triassic. In the aftermath of this crisis, ichthyosaurs and sauropterygians did not expand into the empty ecospace (Fig. 3B), nor did they expand their ecospace occupancy again – somehow the trauma of the Early Jurassic bottleneck and the loss of lineage diversity prevented both clades from expanding their ecological disparity, even though species richness expanded and fluctuated for the remaining 134 Myr of the Mesozoic (Benson & Butler 2011). It was thalattosuchian crocodylomorphs and later turtles that expanded ecospace in the Jurassic (Figs. 3B, 4, 5), with the thalattosuchians potentially benefiting from the sluggish recovery of ichthyosaurs and sauropterygians in the Jurassic. Of course, we did not consider other marine predators such as sharks or cephalopods in our study. For example, neoselachian sharks diversified in the Jurassic and Cretaceous (Underwood 2006) and may have occupied some of these ‘empty’ areas of the ecospace, restricting the opportunities for tetrapods. Durophagous roles occupied by placodonts in the Triassic were to some extent taken over by fishes such as *Dapedium* in the Late Triassic and Early Jurassic (Smithwick 2015; Smithwick and Stubbs 2018).

We find that all clades show considerable ecological conservatism. It is well understood that selection pressure from competition can drive a broadening of habitat use (MacArthur *et al.* 1972), and this could be seen as an expansion of occupancy or a movement across ecospace. However, even in times of evidently empty ecospace, such as much of the Jurassic, the incumbent clades such as ichthyosaurs and sauropterygians occupied the same small patches of ecospace throughout. Their conservatism was not caused by competition from other tetrapod clades, as thalattosuchians and turtles had come on the scene well into the Jurassic and entered empty ecospace without apparently impinging on the ichthyosaurs or sauropterygians (Foffa *et al.* 2018). This kind of non-interaction also seems to be a more reasonable explanation of ecospace occupation in the Cretaceous than intra-clade competition. Ichthyosaurs went extinct, and their assumed functional successors, the mosasaurs, diversified later, and into different ecospace (Figs 1–3). Ecological conservatism could relate to morphological constraints, meaning that particular groups could not always expand ecospace opportunistically. The notable exception to this pattern is seen in turtles, which occupied large, diverse, areas of the ecospace. In future, it might be worth testing to what extent their survival through the end-Cretaceous mass extinction related to this wide adaptability.

Mosasauroidea expanded into occupied ecospace in the Late Cretaceous (Fig. 3D), but the primary drivers have been identified as probably abiotic (Bush & Novack-Gottshall 2012; Polcyn *et al.* 2014). Changing environments, most notably rapidly rising sea levels and consequent expansions of the areas of continental shelves, opened new habitats where mosasaurs could hunt newly evolved invertebrates, fishes and reptiles. Overall, our work on marine tetrapod ecospace through the Mesozoic conforms better to the Court Jester than the Red Queen – major environmental changes such as catastrophic extinctions (end-Permian; Late Triassic) triggered losses and expansions, and sea level and climatic changes likely modulated other opportunities for ecospace occupation. However, this refers only to the coarse-scale ecological dynamics, and we cannot comment on interspecies competition.

Ecospace occupation by Ichthyosauromorpha

Ichthyosauromorpha are the only clade that showed clear directional movement through ecospace (Fig. 6C); this matches their well-documented morphological transition from basal ‘eel-like’ forms to derived ‘tuna-like’ forms (Motani 2005; Moon & Stubbs 2020). Dick & Maxwell (2015) described this movement as an ecospace ‘migration’, the complete

evacuation of one ecospace area for a new one, and used this as the basis for a new model of ecospace occupation (Fig. 6A). The data presented here (Fig. 3, Fig. 6C), however, do not fit this migration model, as ichthyosaurs expanded into new ecospace while continuing to occupy a core area of ecospace. Ichthyosauromorph ecospace is characterized by Triassic expansion followed by stasis in the Jurassic and Cretaceous, rather than continually shifting ecospace (Fig. 6C), although our data cannot detect other smaller-scale ecological shifts.

According to our data, in the Triassic (Fig. 3A, Fig. 6C), ichthyosauromorphs began by occupying groups 3 and 4 (Fig. 1), and reverted mainly to 3, and then added 2 in the Rhaetian. They then shifted to group 1 for the Jurassic and Cretaceous (Fig. 3B, C, Fig. 6C). This pattern is inconsistent with the migration model and, instead, corresponds more to the ‘negative feedback’ model of Bush & Novack-Gottshall (2012), which describes a combination of contraction and expansion driven by biotic interactions (Fig. 6B). The ‘negative feedback’ model was rejected by Dick & Maxwell (2015) because they found no evidence for biotic interactions. However, by incorporating other genera, we find that Ichthyosauromorpha and Eosauropterygia shared some ecospace during the Triassic (Figs. 1B, 3A), demonstrating the potential for interaction between members of the two clades.

We believe our results differ from those of Dick & Maxwell (2015) because of two problems: these authors (1) did not define ecological attributes appropriately and (2) they used generalised time bins that concealed change. On the first point, Dick & Maxwell (2015, fig. 1) included an ‘ecological’ trait based on temporal appearance in the fossil record, but this trait was not defined from morphology, so it does not conform to the standards for ecospace construction (Bush & Novack-Gottshall 2012). Their use of binary characters for feeding guilds introduced repeat coding of states, in which genera were coded the same simply because they do not occur in several feeding guilds. Guilds are usually mutually exclusive, so binary states are not necessary; the multistate characters used here, alongside use of Gower distances, have removed coding artefacts and show a more realistic and appropriate representation of similarity and ecospace position. In the analysis by Dick & Maxwell (2015, fig. 1B), their time-based character had a dominant effect on the ecospace by grouping coeval genera together more closely than by their ecology; this contracted the ecospace and gave the impression of temporal ‘migration.’

On the second point, the use of broad multi-epoch time bins by Dick & Maxwell (2015) removed the resolution of small-scale patterns of change, which hid the mechanisms by which the movement was created and so made it impossible to distinguish between migration and negative feedback. By using smaller time bins, as we do, differences in the mode of movement through ecospace become more apparent. Overall, we show that expansions and selective extinctions in ichthyosauromorph ecospace evolution do not fit a strict ‘migration’ model and more closely reflect a ‘negative feedback’ model but with a long-term directional shift. Nevertheless, our data cannot fully differentiate between the underlying processes behind the ‘migration’ or ‘negative feedback’ models of macroevolution, and both models may not accurately describe ichthyosauromorph ecospace evolution.

Limitations of ecospace modelling

The main limitation of ecospace modelling among fossils is the crudity of the ecospace categories. Clades that overlap in ecospace occupancy may have, in reality, been differentiated, but the traits that separated them are not preserved in the fossil record. While general prey preference can be established from morphology (Massare 1987; Foffa *et al.* 2018), it is harder to identify a preferred prey species or exclusive diet, except by reference to gut contents or coprolites or detailed functional analysis in comparison to modern analogues. In any case, at the level of this study, such detail cannot be achieved for all taxa, and we

preferred to focus on broad ecological categories. Similarly, behavioural characteristics that can create niche segregation are also lost. Extant marine predators, such as Orcas (*Orcinus orca*), demonstrate subspecies segregation through unique prey and habitat preferences which are not apparent from their morphology (Pitman and Ensor 2003). We cannot say whether the 107 Myr of co-habitation by ichthyosaurs and plesiosaurs is because they were occupying entirely distinct ecospace, or whether some were competing over shared resources. Without an increase of biomechanical and functional morphological studies across Mesozoic marine tetrapods, or the discovery of more ecologically informative fossils, it may be difficult to further refine the ecospace.

It is interesting to note that different body sizes and dental morphologies are scattered throughout ecospace (Fig. 2). These traits have received considerable attention in the literature (e.g. Massare 1986; Polcyn *et al.* 2014; Stubbs & Benton 2016; Foffa *et al.* 2018,), but do not appear to control the distribution of taxa in marine tetrapod ecospace here. This is, in part, because the five dominating characters covary considerably, whereas body sizes and tooth morphologies have more complex distributions. It may also reflect the larger number of character states for body sizes and dental morphologies, whereby extreme trait scores show different distributions, but intermediate states show overlaps (Fig. 2). There may also be some biological implications, particularly for size, where taxa with disparate sizes share ecospace. For example, in modern marine ecosystems, the storm petrel (*Hydrobates pelagicus*) and blue whale (*Balaenoptera musculus*) both feed on krill (Euphausiacea) and engage in some degree of ecological competition and interaction, despite their vastly different body sizes. An important endeavour of future work is to develop new approaches that analyse all these ecological parameters in a holistic and quantitative framework.

Influence of sampling bias

Disparity and diversity are frequently decoupled (Benton 2015), so there is no reason to expect taxonomic palaeodiversity to mirror morphological or ecological disparity. However, it is important to consider that sampling bias is a serious issue in all macroevolutionary studies, and the Mesozoic marine reptile fossil record has been held up for scrutiny. It has been argued that the levels of bias are so great as to make the raw palaeodiversity signal largely misleading (e.g. Benson *et al.* 2010; Benson & Butler 2011), but the methods behind these conclusions are flawed (Sakamoto *et al.* 2017). Other studies of the fossil quality of ichthyosaurs (Cleary *et al.* 2015), plesiosaurs (Tutin & Butler 2017) and mosasaurs (Driscoll *et al.* 2019) show little evidence that fossil number or quality drive palaeodiversity patterns. In addition, a recent study of ichthyosaur morphological disparity showed that patterns are generally consistent even when taxa known only from exceptionally fossiliferous formations are removed (Flannery Sutherland *et al.* 2019). In our study, it is clear that generic diversity is not directly linked with ecological disparity (Fig. 5). For example, disparity is equally high in the Norian ($n = 9$) as in the Anisian ($n = 47$), and in the Berriasian ($n = 10$) and Tithonian ($n = 36$). We also use rarefaction to mitigate against the effects of variable sample sizes on our MST disparity metric (Figs. 5C, S4). Poor sampling may hinder our understanding of the tempo and patterns of marine tetrapod extinctions in the Norian and Rhaetian. The decline in marine tetrapod diversity in these bins could be an artefact of poor sampling or could reflect changing sea levels and a loss of shallow marine habitats (Kelley *et al.* 2014). Nevertheless, it is clear that the faunal turnovers and evolutionary bottleneck during this transition had long-term and drastic impacts on marine tetrapod macroevolution (Figs. 3–5, Fischer *et al.* 2014; Stubbs & Benton 2016; Moon & Stubbs 2020).

Disparity trends

Our study of ecospace evolution confirms some earlier findings and conflicts with others. The apparently rapid diversification of marine tetrapods in the Early to Middle Triassic seems clear (Bardet 1994; Benson & Butler 2011; Benton *et al.* 2013; Stubbs & Benton 2016). The rapid rise of both diversity and ecospace occupation through the evolution of new feeding guilds and lifestyles supports the finding in Stubbs and Benton (2016) that the Mesozoic Marine Revolution may have originated in the Triassic and not the Jurassic as previously thought (Vermeij 1977). Stubbs & Benton (2016) showed highest marine reptile ecomorphological disparity in the Middle–early Late Triassic and Late Cretaceous, suggesting it took over 100 million years to recover similar levels of disparity following the Late Triassic extinctions. Here we also find high disparity in the Middle–early Late Triassic, but instead show that this level was again attained in the Late Jurassic and maintained, or even exceeded, during the Cretaceous (Figs 3 and 5). This may reflect the different trait types used in each study and the differences between morphology and ecology. Stubbs & Benton (2016) assessed functional ecomorphology of the jaws and dentition, using morphological disparity as a proxy for ecospace occupancy. Here similar functional morphology (for prey capture) was incorporated into the prey preference ecological character, condensing different morphologies into a smaller number of ecological categories. By reducing the range of morphologies documented by Stubbs & Benton (2016), variations between taxa and total disparity were reduced. Further, where Stubbs & Benton (2016) used body size variation as another morphological proxy, here we have used postcranial morphology to inform on several additional character traits, including habitat and aquatic adaptation. Nevertheless, there are many shared patterns between the metrics of morphological disparity and ecospace occupancy, suggesting that our measures of ecospace occupancy capture some of the same macroecological phenomena as documented by Stubbs & Benton (2016).

It has been suggested that there was a tetrapod extinction event at the Jurassic–Cretaceous boundary (e.g. Bardet 1994; Benson *et al.* 2010; Benson & Druckenmiller 2014; Tennant *et al.* 2016), but we find no evidence that this event impacted ecospace occupancy and disparity of marine tetrapods; this suggests a turnover and thinning-out of ecospace rather than a major ecological perturbation. The increase of taxonomic diversity and high levels of ecological disparity in the Late Cretaceous suggest that marine tetrapods were not in decline at the end of the Mesozoic, and fossil evidence points to rapid extinction, not a gradual decline, of clades at the K/Pg boundary (Figs 3, 5) (Bardet 1994; Ross 2009; Stubbs & Benton 2016).

What drives diversity and disparity in the marine tetrapods?

The drivers of diversity and disparity in marine tetrapods were both biotic and abiotic. Evidence for the Red Queen, in the form of competition avoidance, is that new marine clades tended to occupy empty ecospace, as seen in the Triassic and in the ichthyosauromorph ecospace expansion. The reinvasion of similar ecospace at different times by basal ichthyosauromorphs, thalattosuchians and mosasaurs indicates that there were a limited number of ecological functions that were accessible to tetrapods, and different clades converged upon them repeatedly. However, filling such empty ecospace often followed a long time gap, so selection to do so may not have been intense.

On the other hand, much of marine tetrapod ecospace evolution reflects abiotic drivers. The process began during ecosystem recovery following the devastation of the PTME, when several clades of tetrapods entered the oceans and evolved fully marine adaptations rapidly. Some of these arguably replaced pre-existing sharks or other fishes that had become extinct, but most occupied ecospace that had been empty before the mass extinction. Detailed studies suggest that sea level change was a major driver of marine tetrapod evolution in the Triassic

(Kelley *et al.* 2014) and Middle-Late Jurassic (Foffa *et al.* 2018), and of mosasaur evolution (Polcyn *et al.* 2014).

Pyenson *et al.* (2014) note that marine shelf and open ocean tetrapods were subject to different environmental controls. On continental shelves, ecosystems are more dependent on minor sea level and climatic fluctuations, whereas pelagic predators in the open oceans depend more on changes in productivity which in turn depend on tectonic and climatic controls on circulation and upwelling. This distinction was highlighted, for example, by Benson & Butler (2011) in their analysis of Mesozoic marine tetrapod palaeodiversity.

CONCLUSIONS

This is the first study of ecospace occupancy by Mesozoic marine tetrapods using ecospace modelling. Ecospace modelling quantifies ecospace occupancy and can be used to describe patterns through time. The explosive radiation of several marine tetrapod groups in the Triassic is highlighted, as well as the disparity crash through the Late Triassic and the sluggish recovery with slow ecospace refilling and expansion through the Jurassic, and then the peak in ecospace occupation in the Late Cretaceous. Through time, sauropterygians, turtles and ichthyosauromorphs were the biggest contributors to ecological disparity. The temporal movement of ichthyosauromorphs through ecospace is more consistent with the negative feedback model, rather than a migration model. Invading new taxa favoured unoccupied ecospace, while most established taxa show minimal ecospace movement and do not exploit empty ecospace. Only minimal evidence for biotic interactions driving diversification is recovered in Triassic ichthyosauromorphs and in the initial Triassic adaptive radiation.

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Author contributions. TLS, BCM and MJB designed and supervised the study, TLS and BCM wrote code and developed the methods, JCR and TLS carried out the analyses, and all authors contributed to drafting the manuscript.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository:

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968

TABLE 1. Ecospace categories and states used in this study.

Category	States
Body size	< 0.5m (0), 0.5–1m (1), 1–2m (2), 2–5m (3), 5–8m (4), 8–15 m (5), and > 15m (6)
Diet	Herbivore (0), carnivore (1)
Hunting style	Ambush (0), pursuit (1), forage (2)
Habitat	Shallow-coastal water (0), deep-open ocean (1)
Food location	pelagic free moving (0), pelagic and sessile (sea grass) (1), benthic and sessile (2), benthic and non-sessile (3)
Feeding guild	General (0), cut (1), crunch (2), crush (3), smash (4), pierce (5), lunge (6), filter (7), crush-cut (8)
Teeth	Homodont (0), heterodont (1)
Armour	None (0), osteoderms and scutes (1), carapace or plastron only (2), carapace and plastron – full armour (3)
Limb shape	Plesiopedal (0), hydropedal (1)

FIG. 1. Two-dimensional, non-metric graphical representation of the ecospace occupation of Mesozoic marine tetrapods (A). Groups of taxa are labelled (1–6) based on shared ecological characteristics. In (B) each higher clade is highlighted and plotted separately to aid visualisation and comparison of ecospace occupancy. Silhouettes are from Stubbs and Benton (2016) except for the hesperonithiform by Michael Keesey and Nobu Tamura (phylopic.org)

978 and the temnospondyl by Dmitry Bogdanov (phylopic.org). Supplementary figure S5 shows
 979 taxa individually labelled (see Reeves *et al.* 2020, Fig. S5).
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981
 982 **FIG. 2.** The distribution of ecological character states in Mesozoic marine tetrapod ecospace.
 983 Each panel illustrates the character scores of individual taxa within ecospace, for each of the
 984 nine ecological characters (Table 1). The key denotes characters scores based on colour. Non-
 985 applicable coding is omitted.

FIG. 3. Temporal patterns in Mesozoic marine tetrapod ecospace. Plots illustrate ecospace occupation in 30 stage level bins through the Triassic (A), Jurassic (B), and Cretaceous (C). Major groups are highlighted with symbols and colours indicated in the key. Convex hulls denote total ecospace area. Supplementary figure S6 shows enlarged plots (see Reeves *et al.* 2020, Fig. S6).

FIG. 4. Partial disparity of marine tetrapod groups through the Mesozoic. Partial disparity is plotted in 30 stage-level time bins, ranging from the Induan to the Maastrichtian. Tick marks denote the temporal occurrence of all sampled bins. Partial disparity calculated from the NMDS ecospace scores, rather than PCOa scores, is plotted in Reeves *et al.* (2020, Fig. S7). Silhouettes are from Stubbs and Benton (2016) except for the hesperornithiform by Michael Keesey and Nobu Tamura (phylopic.org) and the temnospondyl by Dmitry Bogdanov (phylopic.org).

FIG 5. Temporal trends of Mesozoic marine tetrapod ecological disparity. A, generic diversity/sampling in 30 stage-level bins. B–C, disparity in 30 stage-level bins based on weighted mean pairwise disparity (WMPD) (B) and the minimum spanning tree (MST) length metric (C) (MST is from 10 PCOa axes and rarefied to the median sample size for all 30 bins, $n = 16$). In (B) and (C) the 95% confidence intervals (grey envelopes) were created using 500 bootstrap replicates. D, proportional ecospace expansion for 29 stage-level bins. The Induan bin could not be calculated because there is no preceding bin for comparison. Ecospace expansion is always calculated relative to the preceding bin, low or no expansion reflect bins defined by ecospace packing. In (D) the solid line represents expansion derived from the NMDS ecospace ordination and the dashed grey line is expansion based on PCOa axes 1 and 2. Tick marks denote the temporal occurrence of all sampled bins.

FIG. 6. Models for the evolution of ecospace occupation. A, migration model (Dick and Maxwell 2015). B, Negative feedback model (Bush and Novack-Gottshall 2012). C, temporal ecospace evolution in ichthyosauromorphs plotted in six time bins. A and B are redrawn from Bush and Novack-Gottshall (2012) and Dick and Maxwell (2015).