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1 EVOLUTION OF ECOSPACE OCCUPANCY BY MESOZOIC MARINE TETRAPODS

2
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13
14 **Abstract:** Ecology and morphology are different, and yet in comparative studies of fossil
15 vertebrates the two are often conflated. The macroevolution of Mesozoic marine tetrapods
16 has been explored in terms of morphological disparity, but less commonly using ecological-
17 functional categories. Here we use ecospace modelling to quantify ecological disparity across
18 all Mesozoic marine tetrapods. We document the explosive radiation of marine tetrapod
19 groups in the Triassic and their rapid attainment of high ecological disparity. Late Triassic
20 extinctions led to a marked decline in ecological disparity, and the recovery of ecospace and
21 ecological disparity was sluggish in the Early Jurassic. High levels of ecological disparity
22 were again achieved by the Late Jurassic and maintained through the Cretaceous, when
23 ecospace became saturated by the Late Cretaceous. Sauropterygians, turtles and
24 ichthyosauromorphs were the largest contributors to ecological disparity. Through the
25 Mesozoic, we find that established groups remained ecologically conservative and did not
26 explore occupied or vacant niches. Several parts of ecospace remained vacant for long spans
27 of time. Newly evolved, radiating taxa almost exclusively explored unoccupied ecospace,
28 suggesting that abiotic releases are needed to empty niches and initiate diversification. In the
29 balance of evolutionary drivers in Mesozoic marine tetrapods, abiotic factors were key to
30 initiating diversification events, but biotic factors dominated the subsequent generation of
31 ecological diversity.

32
33 **Key words:** macroevolution, marine tetrapod, plesiosaur, ichthyosaur, ecology, ecospace

34 UNDERSTANDING the expansion of biodiversity, both in terms of the diversity of species
35 and the diversity of adaptations, are core questions in macroevolution (Simpson 1944;
36 Morlon 2014; Benton 2015). Such questions have often focused on adaptive radiations (Ruta
37 *et al.* 2013; Benson *et al.* 2014), where bursts of diversification coincide with the exploration
38 of new ecological opportunities (niches, or defined portions of ecospace). Simpson (1944)
39 proposed three models for the occupation of new niches: the evolution of key innovations
40 (e.g. wings in birds); the removal of competition through emptying existing niches by
41 extinction; and the generation of new habitats through environmental change (Simpson 1944;
42 Yoder *et al.* 2010). Subsequent debates over which of these three factors is more important in
43 influencing diversity has led to two broad hypotheses, the Red Queen and the Court Jester
44 (Benton 2009). The Red Queen hypothesis (Van Valen 1973) favours intrinsic biotic factors,
45 such as biological innovations or competition, while the Court Jester hypothesis (Barnosky
46 2001) focuses on abiotic factors, such as mass extinctions or climate change, as the dominant
47 drivers of diversification (Benton 2009).

48 Mesozoic marine tetrapods make an excellent case study to investigate origins of
49 biodiversity, as they include between 12–18 independent transitions from land to sea (Motani
50 2009; Benson 2013; Kelley and Pyenson 2015) and their anatomy and ecology are in some
51 cases well documented. Their initial diversification followed the devastating Permian-
52 Triassic mass extinction (PTME), in which >90% of marine species became extinct (Sahney
53 & Benton 2008; Motani 2009; Benton *et al.* 2013; Stubbs & Benton 2016). Through the
54 Mesozoic, marine tetrapods flourished, showing a series of extinctions and clade expansions
55 (Scheyer *et al.* 2014; Kelley & Pyenson 2015; Stubbs & Benton 2016; Foffa *et al.* 2018;
56 Moon & Stubbs 2020) and building complex ecosystems similar to modern marine networks
57 (Fröbisch *et al.* 2013). Triassic marine reptiles ranged from the durophagous placodonts
58 (Rieppel 2000), to the hammer-headed herbivorous *Atopodentatus unicus* (Li *et al.* 2016) and
59 large macrophagous ichthyosaurs such as *Thalattoarchon saurophagis* (Fröbisch *et al.* 2013).
60 The Jurassic saw the rise of Plesiosauria (O’Keefe 2002) the diversification of ‘shark-like’
61 Neoichthyosauria (Motani 2009; Gutarra *et al.* 2019), and appearance of several clades of
62 marine turtles (Nicholls, 1997; Evers & Benson 2019). New clades arose in the Cretaceous,
63 including predatory mosasaurs, multiple marine snake lineages, chelonoids (the extant group
64 of sea turtles), and Hesperornithidae, penguin-sized diving birds (Pyenson *et al.* 2014;
65 Driscoll *et al.* 2019; Evers & Benson 2019). Most of these clades died out during the Late
66 Cretaceous or at the Cretaceous-Paleogene (K/Pg) mass extinction (Pyenson *et al.* 2014).

67 Computational studies in macroevolution often focus on taxonomic diversity (species or
68 genus richness) or disparity (morphological diversity). Complex disparity data sets, whether
69 based on discrete or continuous characters, can be represented as morphospaces,
70 summarizing the major axes of variation in form (Raup 1966; Mitteroecker & Huttegger
71 2009). Morphospaces may be interpreted in ecological-functional terms by incorporating taxa
72 with known lifestyles, but this has to be done with caution because of the ‘many-to-one’
73 problem (Wainwright *et al.* 2005), whereby one form might have many functions, or many
74 forms might perform the same function. Quantitative ecospace modelling, a variant of
75 morphospace modelling (Bambach 1983; Bambach *et al.* 2007), uses ecological
76 characteristics (prey preference, habitat, body size, environmental preferences, etc.) derived
77 from morphology and sedimentology to create an ecospace (Bush & Novack-Gottshall 2012;
78 Dick & Maxwell 2015). The method makes a link between morphology and ecology, and the
79 resulting ecospace is a reflection of ecospace occupancy within a group and trends in
80 ecological disparity can be assessed.

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

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

94

95 MATERIALS AND METHODS

96 *Taxon selection*

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

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

115 We excluded genera if their taxonomy is equivocal or the materials are too incomplete to
 116 indicate their ecology. Most Mesozoic marine tetrapods are known from adequate to
 117 excellent specimens, but some have been named from incomplete or fragmentary remains
 118 (Cleary *et al.* 2015; Tutin & Butler 2017; Driscoll *et al.* 2019); we excluded genera for which
 119 we could not code more than five of our nine ecological characteristics. Finally, a few genera
 120 are represented only by juvenile, or suspected juvenile specimens, and these were excluded as
 121 their ecology might have changed through ontogeny. For example, Green turtles (*Chelonia*
 122 *mydas*) shift their diet during ontogeny (Arthur *et al.* 2008), as did the ichthyosaur
 123 *Stenopterygius quadriscissus* (Dick *et al.* 2016). Temnospondyls are reported to have
 124 changed habitat as they matured (Steyer 2003), and some marine reptiles such as ichthyosaurs
 125 may have had ‘nursery’ sites where juveniles lived separately from the adults, as do some
 126 modern sharks (Williams *et al.* 2015). We make one exception to this rule for the Rhaetian
 127 plesiosaur *Rhaeticosaurus*. The only known specimen may be a juvenile, but *Rhaeticosaurus*
 128 is the earliest known plesiosaur, and the only plesiosaur from the Triassic (Wintrich *et al.*
 129 2017). Therefore, excluding this taxon from the Rhaetian time bin would misrepresent
 130 ecological disparity during this interval, where otherwise only placodonts are known. In total,
 131 371 taxa (352 genera) are represented in the matrix (see Reeves *et al.* 2020 for full details).

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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

181 Massare (1988, 1994), we assign categories based on overall body plan: Body Plan I, pursuit;
 182 Body Plan II, ambush; Body Plan III, some pursuit, some ambush (coded as ambush only);
 183 Body Plan IV, foraging. Among axial swimmers, the thunniform mode is related to constant,
 184 fast, powerful motion associated with ‘pursuit’ style predation, and the anguilliform mode
 185 with slow speeds punctuated with sudden bursts of acceleration, so correlating with an
 186 ‘ambush’ style of predation (Massare 1988; Sfakiotakis *et al.* 1999). Paraxial swimmers are
 187 generally considered to be ambush predators, a mode supported by their long neck and
 188 flexible body and agile movements restricted by armour and stiffened limb girdles (Massare
 189 1988). The foraging category, a more passive prey-gathering mode, is identified for taxa that
 190 were less adapted for swimming (with only minor limb and body modifications), and
 191 predominantly associated with paraxial swimming style. Although pliosaurs fit the ambush
 192 body plan, they were considered to have been pursuit predators by Massare (1988) and were
 193 coded as such here.

194
 195 *Food location.* Four categories for food source were recorded (Table 1): pelagic for prey
 196 located in the water column, benthic for prey resting on or near the sea floor, sessile for
 197 stationary or non-active prey and non-sessile for free-moving prey. Most taxa were assumed
 198 to have hunted mobile prey unless the associated literature or prey preference (e.g. herbivory)
 199 indicated otherwise. Placodonts were coded in benthic prey categories following Rieppel
 200 (2002). Benthic feeding was identified by a combination of armour, pachyostosis (Houssaye
 201 2009) and cranial and limb adaptations.

202
 203 *Feeding guilds.* Prey preferences have been established in Mesozoic marine tetrapods through
 204 comparative studies of tooth morphology and prey preference in extant marine predators
 205 (whales) and correlation with gut contents (Massare 1987, 1997). Following these studies,
 206 tooth morphology was used to code prey preference into different feeding guilds (e.g. Foffa *et al.*
 207 2018). Additional guilds were created to incorporate more recently discovered feeding
 208 styles (Table 1). The filter guild was coded from the presence of numerous small thin teeth
 209 and incorporates both herbivorous (e.g. *Atopodentatus*: Li *et al.* 2016) and carnivorous (e.g.
 210 *Morturneria*: O’Keefe *et al.* 2017) lifestyles. The crush-cut guild of Bardet *et al.* (2015)
 211 incorporates the unusual tooth morphology of several mosasaurs. Lunge feeding has been
 212 recognised in several genera and relates to a prey preference and feeding method similar to
 213 baleen whales (Motani *et al.* 2015).

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

225
 226 *Specialist or generalist feeding.* Following Massare (1987), we use the dentition to
 227 distinguish between specialist (homodont) and generalist (heterodont) feeding behaviours.
 228 The assumption is that those tetrapods with identical (homodont) teeth had a more restricted
 229 diet than those with variable (heterodont) tooth shape or size. Size heterodonty, as exhibited

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

233
 234 *Armour*. We coded the amount of armour into four grades (Table 1): absent, rows of
 235 osteoderms or scutes, ‘half’ armour (i.e. either just a carapace or plastron) or a fully encasing
 236 armour. Some clades such as placodonts were often heavily armoured presumably as
 237 protection from predators, whereas in others their lighter armour may also have had functions
 238 in hydrodynamics (Renesto & Tintori 1995) or osmotic regulation (e.g. Rieppel & Reisz
 239 1999).

240
 241 *Aquatic adaptation*. Limb shape was used to approximate aquatic adaptation (Table 1).
 242 Plesio-pedal limbs are associated with the retention of terrestrial abilities, whereas hydro-pedal
 243 limbs indicate a fully aquatic lifestyle and the ability to gather food from more widely
 244 distributed locations (Ross 2009; Kelley *et al.* 2014). We follow Benson & Butler (2011) in
 245 coding these traits.

246
 247 *Ecospace occupancy analysis*
 248 The matrix of ecological traits coded for each taxon was the basis for a multivariate study of
 249 variation and the generation of ‘ecospaces’. The coded ecological character matrix was
 250 converted into a NEXUS file, and a pairwise dissimilarity matrix was calculated based on
 251 Gower’s coefficient (Gower 1971) in the R package Claddis (Lloyd 2016). Dissimilarity is
 252 visualised using non-metric multidimensional scaling (NMDS), with the metaMDS function
 253 in the R package vegan (Oksanen *et al.* 2016). The maximum dimensionality of the ecospace
 254 was set to two axes, and 10,000 random starts were used in the search for a stable solution.
 255 The performance of NMDS was assessed based on stress values (0.136, Reeves *et al.* 2020,
 256 Fig. S1). To explore temporal ecospace trends, taxa were plotted in separate time bins and
 257 convex hulls were used to highlight the overall area of ecospace occupation in each bin.

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

265 Disparity statistics were calculated to summarize ecospace occupancy. We compare the
 266 ecological diversity of major marine tetrapod clades and also assess trends through time. We
 267 calculated disparity directly from the Gower pairwise distances matrix using within-bin
 268 weighted mean pairwise disparity (WMPD; Close *et al.* 2015; Strickson *et al.* 2016). In
 269 addition, we examine metrics that provide insights into the overall expanse of ecospace. As
 270 distances in non-metric ordinations may not be directly Euclidean, we needed to instead use a
 271 linear approach when calculating metrics based on absolute distances within ecospace. For
 272 this we applied principal coordinate analysis (PCOa) to the Gower pairwise dissimilarity
 273 matrix, and then calculated the minimum spanning tree (MST) length metric (Guillerme *et al.*
 274 2019; Benevento *et al.* 2019) from the PCOa axes (Fig. S2), in the R package dispRity
 275 (Guillerme 2018). Distances between taxa using NMDS and PCOa methods show a
 276 moderately strong, significant and linear correlation (Mantel test, $R = 0.92$, $R^2 = 0.85$, $P =$
 277 0.001 , Reeves *et al.* 2020, Fig. S3). Our tests revealed that the MST metric is sensitive to bin
 278 sample size. We therefore used partial rarefaction to prevent bins with more taxa having

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

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

298

299 RESULTS

300 *Ecospace occupation*

301 Marine tetrapod ecospace is characterized by islands of clustering in densely populated
 302 regions. We identified six groupings according to their distinct occupation of ecospace (Fig.
 303 1A). These groupings were identified visually and are characterised by a distinctive
 304 combination of character state scores within the ecospace (Fig. 2). As a consequence, some
 305 groups have much larger ecospace variance than others. For instance, group 6 has large
 306 variance and contains two sub-groups visually separated by a gap in ecospace occupancy, but
 307 these sub-groups cannot be explained by the distribution of ecological character states and
 308 have thus been retained as a single group. Conversely, groups 1 and 2 have substantially
 309 overlapping values along both ecospace axes and low variance (particularly along axis 2), but
 310 can be clearly distinguished by a single ecological character, feeding strategy, justifying their
 311 separation into two distinct groups. According to this informal grouping scheme, there is
 312 evidence for both ecological differentiation by major clades and several instances of
 313 convergence (Fig. 1A, Fig. S5). Examining the distribution of ecological character coding
 314 reveals that foraging mode, habitat, prey location, armour type and limb shape greatly impact
 315 the distribution of taxa in ecospace. The remaining four characters, size, diet, dental guild,
 316 and tooth heterodonty have more mixed distributions (Fig. 2).

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

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

339 The extreme positive regions of ecospace axis 1 are more sparsely occupied, as are the
 340 extreme negative-value regions of axis 2. These ecospace regions contain two groups of taxa
 341 (5 and 6), primarily representing placodont sauropterygians and turtles (Fig. 1). Group 5 (5,
 342 Fig. 1A) comprises unarmoured, partially armoured and fully armoured taxa with plesiopodal
 343 limbs that existed in shallow water environments. They were foragers that fed on benthic
 344 prey and belonged to the crush or filter guilds and often had heterodont dentition (Fig. 2).
 345 This region is primarily occupied by placodont sauropterygians, enigmatic taxa such as the
 346 herbivore *Atopodentatus* and *Paludidraco*, and some turtles (Fig. 1B). The remaining turtles
 347 occupy group 6 (6, Fig. 1A, B) which covers a broad range of ecospace, reflecting varied
 348 niches and lifestyles. All turtles in group 6 were armoured, edentulous foragers with
 349 hydropedal limbs. This grouping includes both shallow and deep ocean forms, forming two
 350 subgroups, that fed on either pelagic or benthic prey, and both carnivores and herbivores (Fig.
 351 2).

353 *Temporal trends in ecospace occupation*

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

364 The Jurassic begins with a notable contraction of ecospace (Fig. 3B), caused by Late
 365 Triassic extinctions and the bottleneck in marine reptile evolution previously noted (e.g.
 366 Thorne *et al.* 2011; Stubbs & Benton 2016; Moon & Stubbs 2020). This contraction between
 367 the Triassic and Jurassic reflects the loss of placodonts, non-plesiosaurian eosauroptrygians,
 368 thalattosaurs and other Triassic taxa. Only a few lineages of ichthyosaurs and sauropterygians
 369 crossed the system boundary, and re-expansion of ecospace was led by these two clades for
 370 the first three stages of the Jurassic, but they occupied a limited, and unchanging ecospace for
 371 19 Myr. Then, thalattosuchian crocodylomorphs emerged in the Pliensbachian and Toarcian,
 372 expanding the ecospace substantially. Through the remainder of the Jurassic, ichthyosaurs
 373 and sauropterygians (plesiosaurs, pliosaurs) remained remarkably static in ecospace
 374 occupation, and thalattosuchians (first teleosaurids, then metriorhynchids) also held steady in
 375 their separate region of ecospace. Turtles further expanded ecospace to increasingly positive

376 values along ecospace axis 1 in the Late Jurassic, partially occupying ecospace vacated some
377 40 Myr earlier, by placodont extinctions at the end of the Triassic (Fig. 3A, B).

378 The Cretaceous begins with similar ecospace occupancy to the end of the Jurassic (Fig.
379 3C). Plesiosaur and ichthyosaur ecospace remained stable throughout the Cretaceous, but
380 ichthyosaurs went extinct in the Cenomanian. Mosasaurs and other squamates invaded the
381 oceans after this point but occupied different ecospace to both Jurassic/Cretaceous
382 ichthyosaurs and plesiosaurs, in groups 3 and 4 (Fig. 1A); a zone that was largely empty
383 through the Early Cretaceous. This region was previously occupied by sauropterygians and
384 thalattosaurs in the Triassic and some thalattosuchian crocodylomorphs in the Late Jurassic.
385 In the last three stages of the Cretaceous (Fig. 3C), ecospace filled up until nearly every
386 sector was occupied. The diversifications of mosasaurs, turtles, hesperornithiform birds,
387 marine crocodiles and elasmosaurid plesiosaurs saturated ecospace but did not notably
388 expand overall ecospace when compared with the mid-Cretaceous, or even the Late Jurassic.

389

390 *Disparity Analysis*

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

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

410 Major changes occur in the Late Cretaceous (Fig. 4). Ichthyosaurs became extinct and
411 thalattosuchian crocodylomorphs had already gone. Turtles increase their relative disparity
412 substantially, to ~50%. New marine clades such as mosasaurs, marine lizards and snakes,
413 hesperornithiform birds, and new crocodylomorph groups make modest contributions to total
414 disparity. Sauropterygians continued through all these vicissitudes but contributing only 10–
415 15% of disparity.

416

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

425 to very low levels in the first three stages of the Early Jurassic (Fig. 5B, C). Ecological
 426 disparity then progressively increases to a second high point in the Late Jurassic, which is
 427 characterized by both high pairwise dissimilarity and expansive ecospace occupation (Figs
 428 3B, 5B, C). High levels of ecological disparity are maintained throughout the Early and Late
 429 Cretaceous. WMPD remains stable, with a very minor reduction in the Late Cretaceous due
 430 to ecospace saturation and increasing diversity (Figs 3C, 5A, B). MST disparity documents
 431 reduced disparity during the early stages of the Cretaceous, potentially due to reduced
 432 diversity and sampling (Figs 5A, C). Overall, the rarefied MST metric closely mirrors generic
 433 diversity, but does not show such high peaks in the Middle Triassic and Late Cretaceous.

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

446

447 **DISCUSSION**

448 *Ecospace occupation*

449 All our analyses confirm that the Triassic was distinct from the Jurassic–Cretaceous interval,
 450 documenting an explosive radiation of marine tetrapod groups, most of which disappeared
 451 during the latter half of the Late Triassic. These staggered Late Triassic extinctions massively
 452 perturbed marine tetrapod ecological disparity. Diversity, disparity and ecospace occupation
 453 all remained at low levels through the first 19 Myr of the Jurassic, even though ichthyosaurs
 454 and plesiosaurs were abundant and richly represented in some parts of the world (Cleary *et al.*
 455 2015; Tutin & Butler 2017). It took until the Late Jurassic for marine tetrapods to recover
 456 levels of ecological disparity comparable to the Triassic, and until the Late Cretaceous for
 457 tetrapods to fully reinvade ecospace that had formerly been occupied by placodonts and other
 458 Triassic clades (Fig. 3).

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

468 Placodonts stand out in the Triassic as occupying their own patch of ecospace, reflecting
 469 their unique adaptations to snatching and crushing molluscs (Rieppel 2002a). While
 470 placodonts are often described as having had a superficial resemblance to turtles (e.g. Rieppel
 471 2002b; Fröbisch *et al.* 2013) the, only partial, ecospace overlap between these groups shows
 472 they were not fully ecologically convergent, and that turtles expanded into different areas of
 473 ecospace, such as open ocean environments (Figs. 1, 2).

474 The explosive radiation of marine tetrapods in the first 10 Myr of the Triassic was not
 475 repeated in the Mesozoic, even after the near annihilation of many clades in the Late Triassic.
 476 In the aftermath of this crisis, ichthyosaurs and sauropterygians did not expand into the empty
 477 ecospace (Fig. 3B), nor did they expand their ecospace occupancy again – somehow the
 478 trauma of the Early Jurassic bottleneck and the loss of lineage diversity prevented both clades
 479 from expanding their ecological disparity, even though species richness expanded and
 480 fluctuated for the remaining 134 Myr of the Mesozoic (Benson & Butler 2011). It was
 481 thalattosuchian crocodylomorphs and later turtles that expanded ecospace in the Jurassic
 482 (Figs. 3B, 4, 5), with the thalattosuchians potentially benefiting from the sluggish recovery of
 483 ichthyosaurs and sauropterygians in the Jurassic. Of course, we did not consider other marine
 484 predators such as sharks or cephalopods in our study. For example, neoselachian sharks
 485 diversified in the Jurassic and Cretaceous (Underwood 2006) and may have occupied some of
 486 these ‘empty’ areas of the ecospace, restricting the opportunities for tetrapods. Durophagous
 487 roles occupied by placodonts in the Triassic were to some extent taken over by fishes such as
 488 *Dapedium* in the Late Triassic and Early Jurassic (Smithwick 2015; Smithwick and Stubbs
 489 2018).

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

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

517

518 *Ecospace occupation by Ichthyosauromorpha*

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

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

529 According to our data, in the Triassic (Fig. 3A, Fig. 6C), ichthyosauromorphs began by
 530 occupying groups 3 and 4 (Fig. 1), and reverted mainly to 3, and then added 2 in the
 531 Rhaetian. They then shifted to group 1 for the Jurassic and Cretaceous (Fig. 3B, C, Fig. 6C).
 532 This pattern is inconsistent with the migration model and, instead, corresponds more to the
 533 ‘negative feedback’ model of Bush & Novack-Gottshall (2012), which describes a
 534 combination of contraction and expansion driven by biotic interactions (Fig. 6B). The
 535 ‘negative feedback’ model was rejected by Dick & Maxwell (2015) because they found no
 536 evidence for biotic interactions. However, by incorporating other genera, we find that
 537 Ichthyosauromorpha and Eosauroptrygia shared some ecospace during the Triassic (Figs.
 538 1B, 3A), demonstrating the potential for interaction between members of the two clades.

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

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

563 564 *Limitations of ecospace modelling*

565 The main limitation of ecospace modelling among fossils is the crudity of the ecospace
 566 categories. Clades that overlap in ecospace occupancy may have, in reality, been
 567 differentiated, but the traits that separated them are not preserved in the fossil record. While
 568 general prey preference can be established from morphology (Massare 1987; Foffa *et al.*
 569 2018), it is harder to identify a preferred prey species or exclusive diet, except by reference to
 570 gut contents or coprolites or detailed functional analysis in comparison to modern analogues.
 571 In any case, at the level of this study, such detail cannot be achieved for all taxa, and we

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

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

595

596 *Influence of sampling bias*

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

619

620 *Disparity trends*

621 Our study of ecospace evolution confirms some earlier findings and conflicts with others. The
 622 apparently rapid diversification of marine tetrapods in the Early to Middle Triassic seems
 623 clear (Bardet 1994; Benson & Butler 2011; Benton *et al.* 2013; Stubbs & Benton 2016). The
 624 rapid rise of both diversity and ecospace occupation through the evolution of new feeding
 625 guilds and lifestyles supports the finding in Stubbs and Benton (2016) that the Mesozoic
 626 Marine Revolution may have originated in the Triassic and not the Jurassic as previously
 627 thought (Vermeij 1977). Stubbs & Benton (2016) showed highest marine reptile
 628 ecomorphological disparity in the Middle–early Late Triassic and Late Cretaceous,
 629 suggesting it took over 100 million years to recover similar levels of disparity following the
 630 Late Triassic extinctions. Here we also find high disparity in the Middle–early Late Triassic,
 631 but instead show that this level was again attained in the Late Jurassic and maintained, or
 632 even exceeded, during the Cretaceous (Figs 3 and 5). This may reflect the different trait types
 633 used in each study and the differences between morphology and ecology. Stubbs & Benton
 634 (2016) assessed functional ecomorphology of the jaws and dentition, using morphological
 635 disparity as a proxy for ecospace occupancy. Here similar functional morphology (for prey
 636 capture) was incorporated into the prey preference ecological character, condensing different
 637 morphologies into a smaller number of ecological categories. By reducing the range of
 638 morphologies documented by Stubbs & Benton (2016), variations between taxa and total
 639 disparity were reduced. Further, where Stubbs & Benton (2016) used body size variation as
 640 another morphological proxy, here we have used postcranial morphology to inform on
 641 several additional character traits, including habitat and aquatic adaptation. Nevertheless,
 642 there are many shared patterns between the metrics of morphological disparity and ecospace
 643 occupancy, suggesting that our measures of ecospace occupancy capture some of the same
 644 macroecological phenomena as documented by Stubbs & Benton (2016).

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

654
 655 *What drives diversity and disparity in the marine tetrapods?*

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

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

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

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

678

679 CONCLUSIONS

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

693

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700

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703 authors contributed to drafting the manuscript.

704

705 DATA ARCHIVING STATEMENT

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

707 <https://doi.org/10.5061/dryad.XXX>

708

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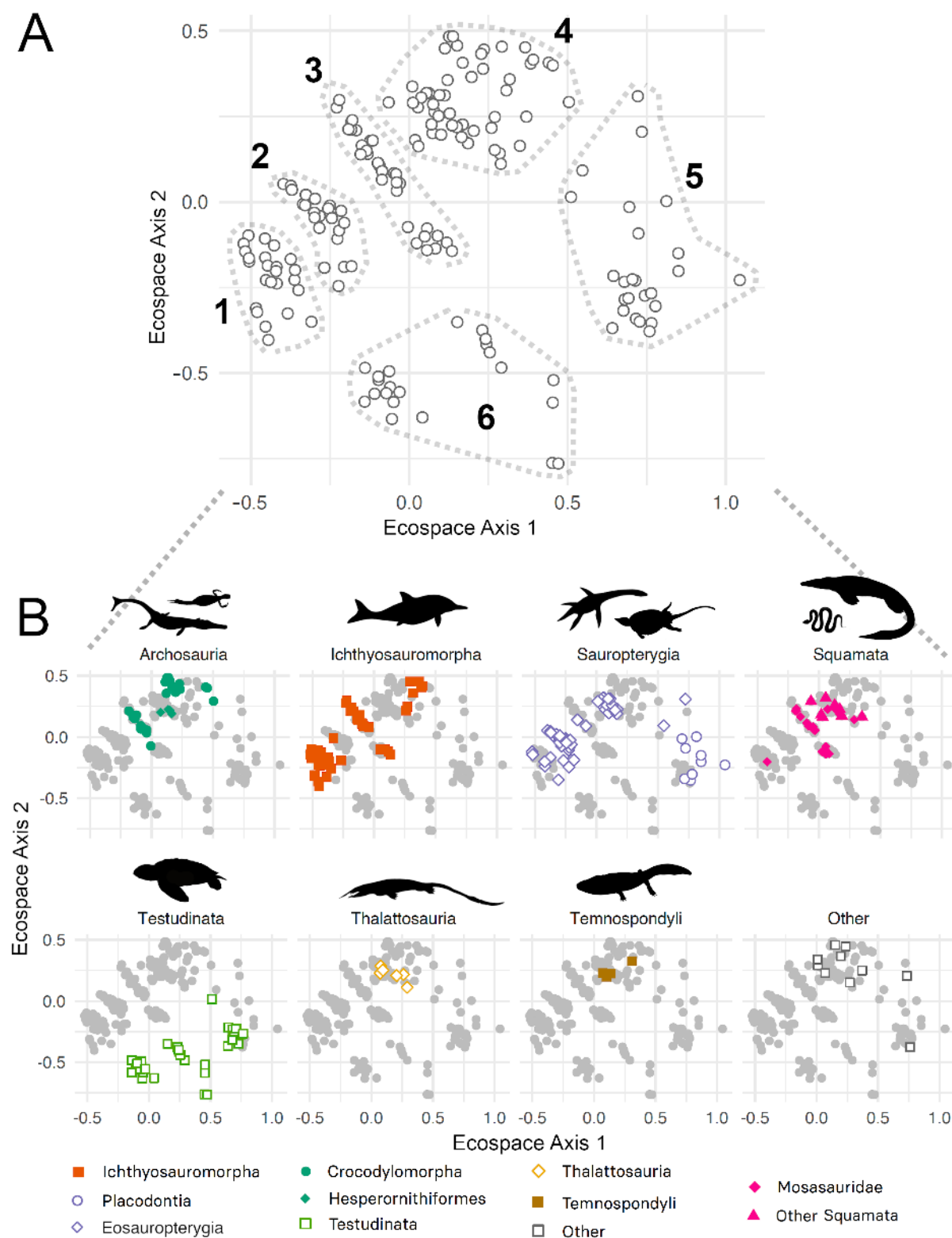
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968

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

970

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)

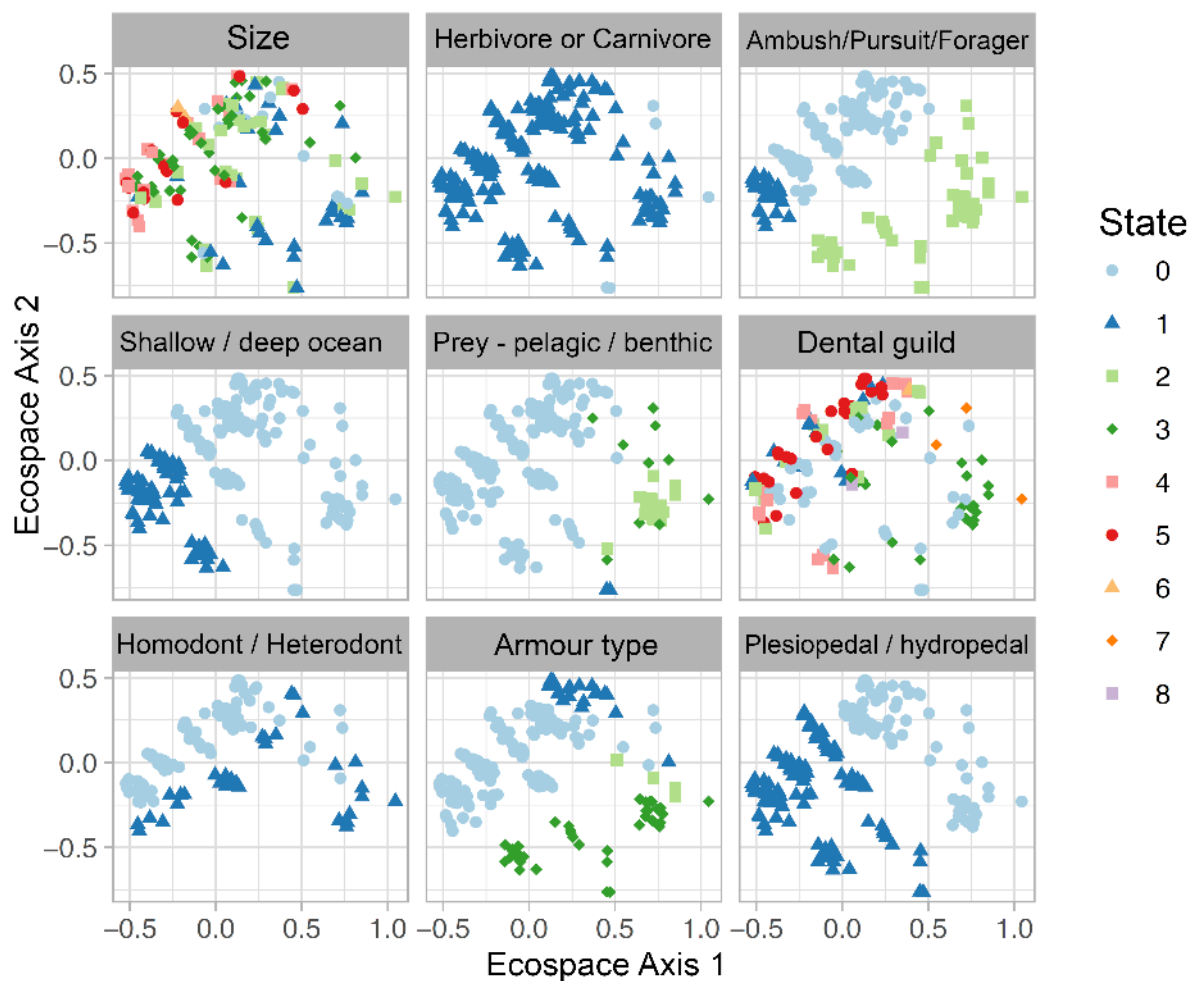
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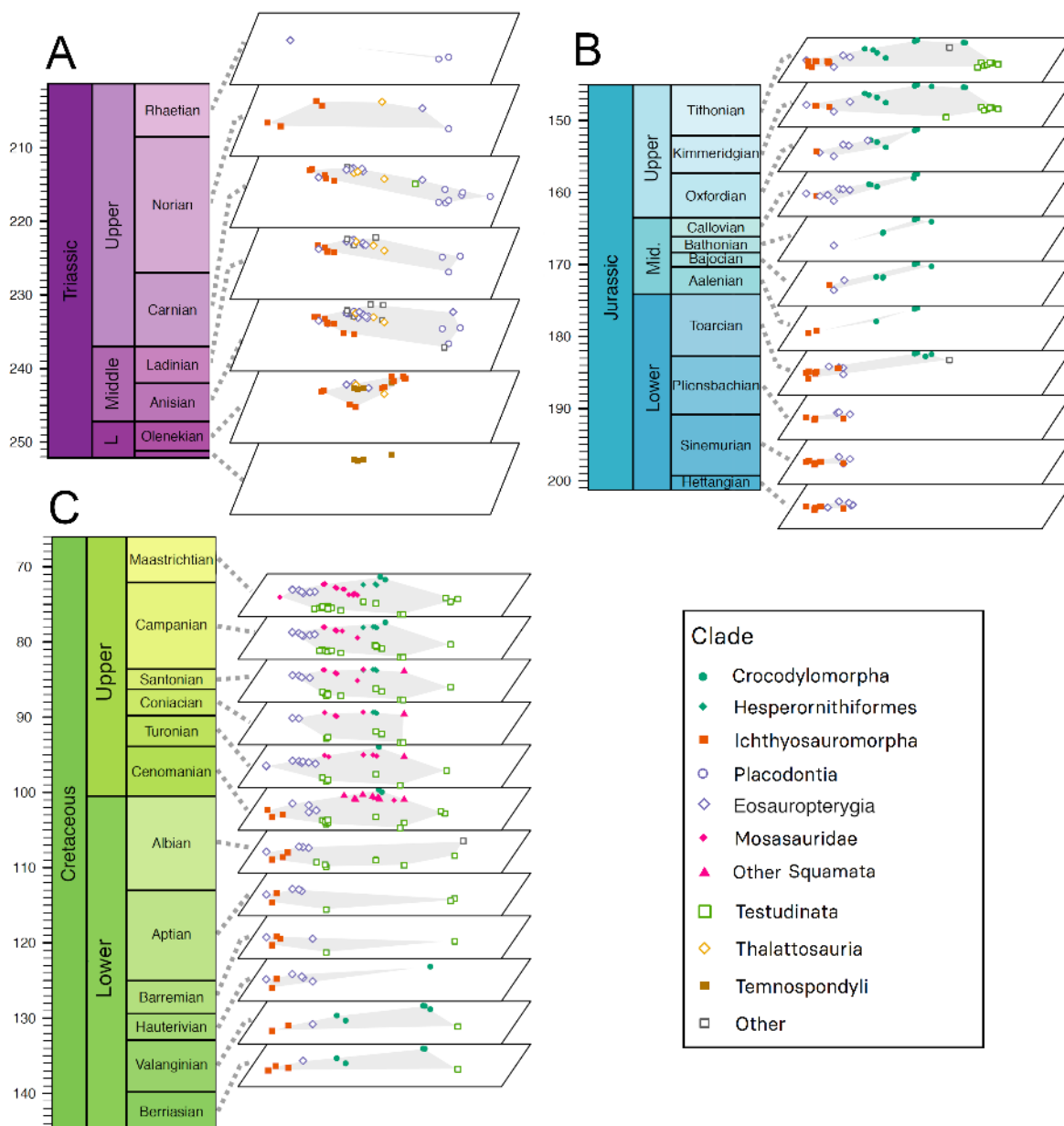
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FIG. 1. Two-dimensional, non-metric graphical representation of the ecospace occupation of Mesozoic marine tetrapods (A). Groups of taxa are labelled (1–6) based on shared ecological characteristics. In (B) each higher clade is highlighted and plotted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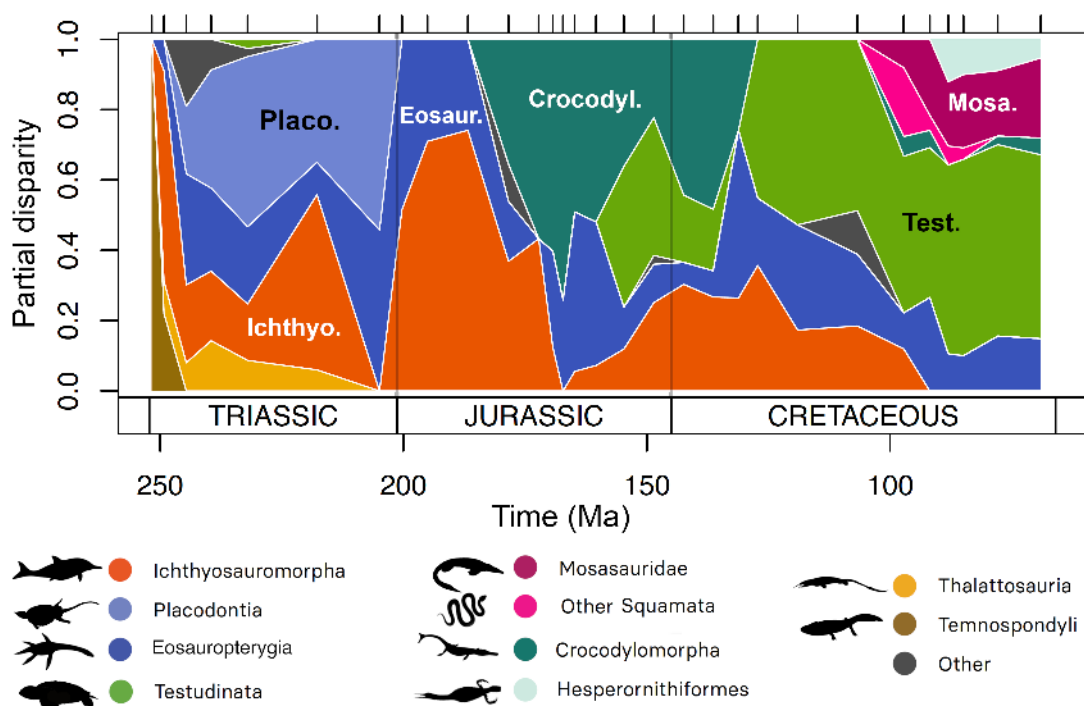


981
 982 **FIG. 2.** The distribution of ecological character states in Mesozoic marine tetrapod ecospace.
 983 Each panel illustrates the character scores of individual taxa within ecospace, for each of the
 984 nine ecological characters (Table 1). The key denotes characters scores based on colour. Non-
 985 applicable coding is omitted.



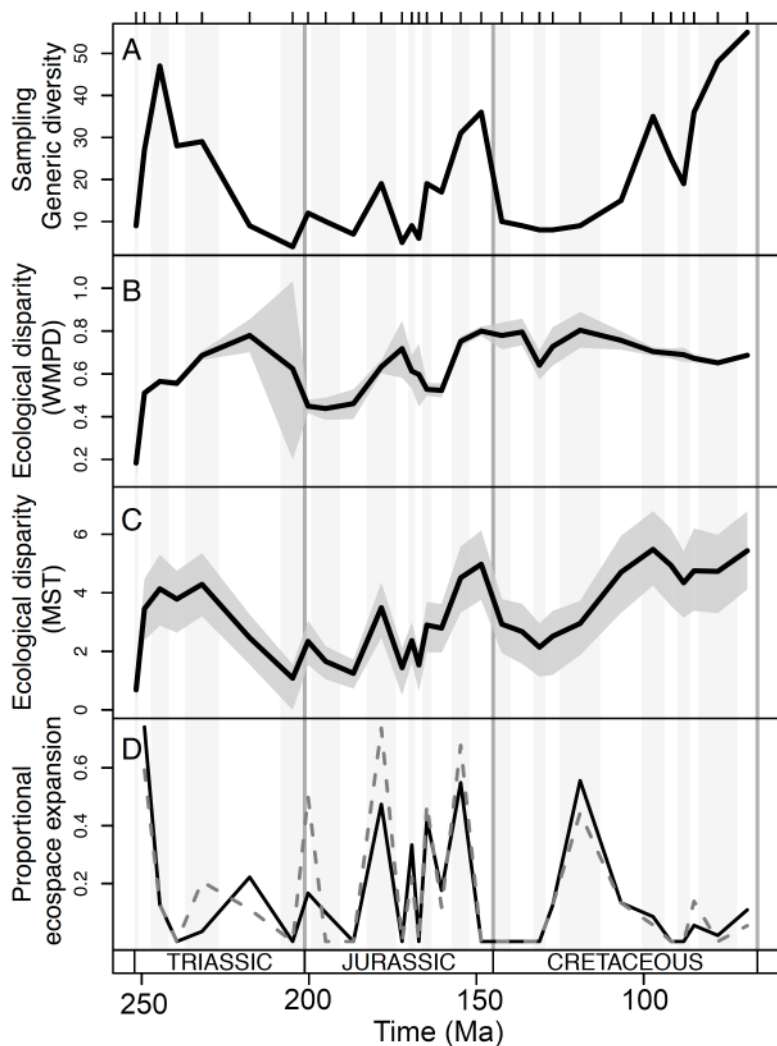
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FIG. 3. Temporal patterns in Mesozoic marine tetrapod ecospace. Plots illustrate ecospace occupation in 30 stage level bins through the Triassic (A), Jurassic (B), and Cretaceous (C). Major groups are highlighted with symbols and colours indicated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



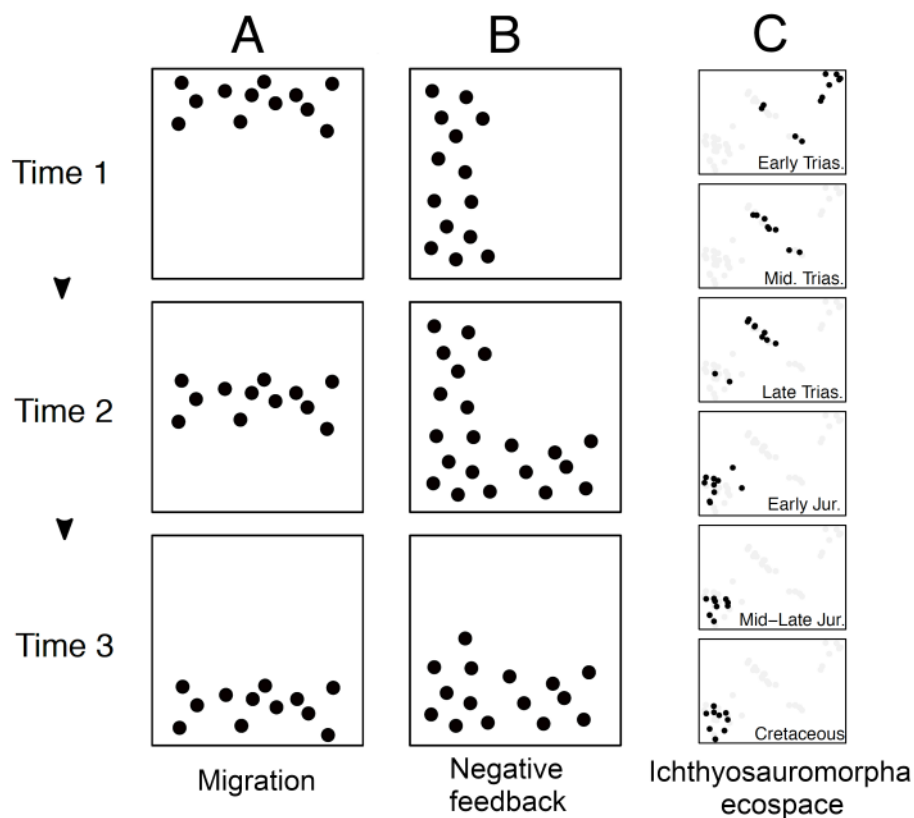
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FIG. 4. Partial disparity of marine tetrapod groups through the Mesozoic. Partial disparity is plotted in 30 stage-level time bins, ranging from the Induan to the Maastrichtian. Tick marks denote the temporal occurrence of all sampled bins. Partial 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).



1000

1001 **FIG 5.** Temporal trends of Mesozoic marine tetrapod ecologically disparity. A, generic
 1002 diversity/sampling in 30 stage-level bins. B–C, disparity in 30 stage-level bins based on
 1003 weighted mean pairwise disparity (WMPD) (B) and the minimum spanning tree (MST)
 1004 length metric (C) (MST is from 10 PCOa axes and rarefied to the median sample size for all
 1005 30 bins, $n = 16$). In (B) and (C) the 95% confidence intervals (grey envelopes) were created
 1006 using 500 bootstrap replicates. D, proportional ecospace expansion for 29 stage-level bins.
 1007 The Induan bin could not be calculated because there is no preceding bin for comparison.
 1008 Ecospace expansion is always calculated relative to the preceding bin, low or no expansion
 1009 reflect bins defined by ecospace packing. In (D) the solid line represents expansion derived
 1010 from the NMDS ecospace ordination and the dashed grey line is expansion based on PCOa
 1011 axes 1 and 2. Tick marks denote the temporal occurrence of all sampled bins.



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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).