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3   # Dinosaur biogeographic structure and Mesozoic

4   # continental fragmentation: a network-based approach

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ABSTRACT

Aim To reconstruct dinosaur macro-biogeographic patterns through the Mesozoic Era using a network-based approach. We test how continental fragmentation affected dinosaur macro-biogeographic structure and evolutionary rates.

Location A global occurrence database of dinosaur families from the Late Triassic to the end-Cretaceous was used for this study.

Methods Biogeographic and geographic network models were constructed. Continental landmasses were linked by direct continental contact and sea level conditioned connections in geographic networks, and by shared dinosaur families in biogeographic networks. Biogeographic networks were run with raw, novel and first-step connections for all dinosaur, ornithischian, theropod, and sauropodomorph taxa.

Results Geographic connectedness declines through time, from peak aggregation in the Triassic-Jurassic to complete separation in the latest Cretaceous. Biogeographic connectedness shows no common trend in the raw and novel connection network models, but decreases through time whilst showing some correlation with continental fragmentation in most of the first-step network models. Despite continental isolation and high sea levels, intercontinental faunal exchange continued right up to the end of the Cretaceous. Continental fragmentation and dinosaurian macro-biogeographic structure do not share a common pattern with dinosaurian evolutionary rates, although there is evidence that increased continental isolation resulted in increased origination rates in some dinosaurian lineages. Spatiotemporal sampling biases and early Mesozoic establishment of family-level distribution patterns are important drivers of apparent dinosaur macro-biogeographic structure.

Main conclusions There is some evidence to suggest that dinosaur macro-biogeographic structure was influenced by continental fragmentation, although intercontinental exchange of dinosaur faunas appears to have continued up to the end of the Cretaceous. Macro-biogeographic patterns are obscured by uneven geographic sampling through time and a residual earlier Mesozoic distribution which is sustained up to the end of the Cretaceous.

Key words biogeography, continental fragmentation, dinosaur, Mesozoic, network analysis ,

INTRODUCTION

The geography of the Earth underwent a series of significant changes throughout the Mesozoic Era (Holtz et al., 2004). The aggregation of the supercontinent Pangaea culminated by the Late Triassic, before subsequently undergoing fragmentation throughout the Jurassic into the northern and southern landmasses Laurasia (North America, Europe, Asia) and Gondwana (South America, Africa, Madagascar, India, Antarctica, Australia). Continental fragmentation continued throughout the Cretaceous (Upchurch, 2008), in tandem with rising sea levels to some 240 m above present day levels (Haq et al., 1987; Miller et al., 2005), resulting in all major landmasses being isolated by the end of the Cretaceous (Smith et al., 1994). The breakup of the supercontinent Pangaea and further fragmentation of Laurasia and Gondwana offers a unique case study for the analysis of macro-biogeographic patterns across terrestrial environments (Sereno, 1999). The dinosaurs arose during the Late Triassic (~230 Ma) and dominated terrestrial ecosystems throughout the Jurassic and Cretaceous following the extinction of major archosaurian competitors at the end-Triassic mass extinction (Sereno, 1999; Brusatte et al., 2008). Continental fragmentation dominated throughout the time of the existence of the non-avian dinosaurs (Holtz et al., 2004; Butler et al., 2011), thus their biogeographic patterns and evolutionary rates should reflect this by increased endemism, regional extinction, and decreased migration between continental landmasses (Sereno, 1999; Turner, 2004).

Previous studies of dinosaur biogeography have used a variety of methods, from early descriptive studies of distributions (Lull, 1910; Nopcsa, 1934), to phenetic (Holtz et al., 2004), cladisitic (Upchurch et al., 2002), and vicariance biogeographic (Sereno, 1997, 1999) methods. Here, we present a novel usage of a network-based approach to analyse dinosaurian biogeographic structure. A network consists of a group of points, commonly referred to as 'nodes', joined together by a series of lines, commonly referred to as 'edges' (Newman, 2010). Nodes are bounded entities defined by the analyst (e.g. a continent, a habitat, a species, an organism); and edges are relations between nodes (e.g. a shared characteristic or interaction) (Cumming et al., 2010; Newman, 2010). Although it is interesting to study the nodes themselves, it is crucial to also understand how they are connected, since the manner in which they are linked can have a large impact on the dynamics and behaviour of the system (Newman, 2003). Although network theory has been known in physics for centuries (Newman, 2003), it has more recently

72   come to the fore in biological (Cumming et al., 2010; Croft et al., 2011; Moalic et al., 2012; Rutz et al.,

73   2012; Boyland et al., 2013; Vilhena & Antonelli, 2015) and palaeobiological (Sidor et al., 2013;

74   Vilhena et al., 2013) systems.

75   Here, we compare geographic and biogeographic network models across the Mesozoic to

76   examine how supercontinent fragmentation affected dinosaur biogeographic structure and whether less

77   connected landmasses resulted in fewer dinosaurian biogeographic connections. In addition, we

78   compare networks constructed from this study with dinosaurian origination and extinction rates to

79   elucidate the influence of biogeography on dinosaur evolution.

80

81   **METHODS**

82   **Data**

83   Fossil occurrence data were downloaded from the Paleobiology Database (PaleoDB)

84   (https:\\paleobiodb.org) on 6 September 2013 (last accessed 15 April 2015) and after pre-processing

85   consisted of 4762 dinosaur occurrences (Carrano et al., 2013). Data were compiled at the family level

86   as few dinosaur genera (or species) are recorded as occurring on more than one major landmass.

87   Families may represent a more robust taxonomic measure than genera or species as, like genera they

88   represent monophyletic clades, and genera (which are dominantly monospecific) and species are

89   frequently revised and renamed in light of new data and taxonomic re-analysis (Benton, 2008; Tschopp

90   et al., 2015). However, it must also be noted that family-level data can produce a number of problems

91   in quantitative studies such as this, brought about by issues with monophyly and disproportionate

92   numbers of species or genera per family caused by different taxonomic practices across clades and

93   across the stratigraphic record.

94   Fossil occurrences were assigned to one of nine continental landmasses (Africa, Antarctica,

95   Asia, Australia, Europe, India, Madagascar, North America, South America) and then binned into ten

96   time intervals constructed in accordance with Geological Timescale 2012 (Gradstein et al., 2012). The

97   ten time bins were: (1) Late Triassic; (2) Early Jurassic; (3) Mid Jurassic; (4) Late Jurassic; (5)

98   Berriasian-Barremian; (6) Aptian-Albian; (7) Cenomanian-Turonian; (8) Coniacian-Santonian; (9)

99   Campanian; (10) Maastrichtian. Chronostratigraphic Stages were amalgamated within time bins to

100 mitigate uneven sampling. Continental landmasses were defined as the isolated major continental

101 landmasses at the end of the time series (end of the Maastrichtian). Although these broad landmass

102 definitions will undoubtedly lead to an oversimplification of biogeographic structure, it would be

103 problematic to subdivide the landmasses further. For example, one could subdivide North America into

104 the western landmasses of Laramidia and the eastern landmass of Appalachia and Asia into a number

105 of sub-continental landmasses. However, most of these landmasses are governed by changing coastlines

106 which are very difficult to identify through geological time. The time bins were produced as such to

107 meet two criteria; (i) to keep fossil occurrence sample size fairly even (to within an order of magnitude),

108 and (ii) to align time bin boundaries with major continental splitting/collision events. Continental

109 arrangement and geographic connection data were obtained from Smith et al. (1994) and sea level data

110 from Haq et al. (1987). Although this study does not consider palaeocoastline and climatic barriers as

111 these are poorly known in contrast to the well constrained continental positions (Upchurch, 2008),

112 effects of changing coastlines across entire networks are accounted for by incorporating sea level into

113 the models. Climatic barriers almost certainly would have limited dispersal of certain dinosaurian taxa,

114 both within and between continental landmasses, and evidence for climatic control on terrestrial

115 tetrapod diversity has been detected in Permo-Triassic Pangaean (Sidor et al., 2005; Ezcurra, 2010;

116 Whiteside et al., 2011; Whiteside et al., 2015) and Cretaceous Gondwanan (Benson et al., 2012; Amiot

117 et al., 2015) communities. However, climatic barriers were most likely far less pronounced than in the

118 present day as through much of the Mesozoic pole-equator gradients were as low as at any other point

119 in the entire Phanerozoic (Huber et al., 2002; Holtz et al., 2004; Mannion et al., 2012; Mannion et al.,

120 2014) and dinosaurs appear to have been able to migrate large distances and transcend climate belts in

121 order to colonize new environments (Longrich, 2014).

122

123 **Network models**

124 Network analysis is employed to capture the dynamic aspect of biogeographic and geographic (tectonic)

125 systems through the Mesozoic. Each of the nine continental landmasses was assigned to a separate node

126 in each network model. The edges between nodes were; (i) continental connections for the geographic

127 networks; and (ii) number of shared dinosaurian families for the biogeographic networks. Two

128 geographic networks were developed. The first is a simple geographic network (GEO) model which

129 only considered direct, continuous continental connections where continents are considered connected

130 if they are not separated by a seaway (unweighted network of 0 or 1 whether land masses were

131 connected or not). For example, direct connections between North America and Europe and Europe and

132 Asia would also result in a further connection between North America and Asia, via Europe, even if

133 there is no direct contact between North American and Asian landmasses. A second model conditions

134 connections on sea level (SL), where shallow-shelf seas retained a probability of containing 'land-

135 bridges' with respect to the average sea level of that time bin (probability network of 0-1 for edge

136 weight). Sea level conditioning was calculated to obtain a probability of land-bridge (P_{LB}) occurrence:

137
$$P_{LB} = 1 - \frac{mean_{SL}}{max_{SL}}$$

138 where the mean relative sea level ($mean_{SL}$) of each time bin was divided by a value slightly higher than

139 the maximum sea level (max_{SL}) of the entire time series (300 m), with the result then subtracted from

140 1. The highest mean sea level of 262.22 m in the Campanian therefore returned a probability of land

141 bridge formation across shallow seaways of 0.13, whereas the lowest mean sea level of 54.68 m during

142 the Early Jurassic returned a probability of 0.82. The method here assumes the relationship between sea

143 level and land bridge emergence to be linear. Although this is almost certainly a simplification of a real

144 world system where shallow shelf seas were of variable area and depth, it does provide a simple

145 calculation by which the effects of changing sea levels in the order of hundreds of metres can be

146 incorporated in to our network models.

147   Biogeographic networks models were developed for; (i) all dinosaur taxa; (ii) ornithischian

148 taxa; (iii) theropod taxa; and (iv) sauropodomorph taxa (weighted networks of 0-n for the number of

149 shared dinosaur families). The first, raw model, considered all dinosaurian family connections for each

150 select group in each time bin. However, the raw model is prone to spatio-temporal sampling error and

151 cumulative connectivity, where family-level distributions are established early in the time series and

152 persist through subsequent time bins. Therefore, only extinction (regional or global) can cause

153 permanent reductions in network connectivity in the raw model. A second, novel connections model,

154 only considered new dinosaurian family connections, i.e. only the first established connection of a

155   particular taxon between specific landmasses were recorded, and did not include the same connections

156   in subsequent time bins. The novel connections model thus eliminates the cumulative connectivity

157   problem by only considering connections that occur within a single time bin, but is still vulnerable to

158   spatio-temporal sampling error. A third, first-step model, only considered the first connection between

159   two landmasses made by a particular taxon and ignored all connections involving that particular taxon

160   in subsequent time bins irrelevant of continental landmass. The first-step model therefore avoids the

161   cumulative connectivity problem and reduces geographic sampling error across the entire network but

162   cannot account for subsequent range expansions following the "first step" between two or more

163   continental landmasses. See Fig. S1 in Appendix S1 for biogeographic network model schematic.

164   We also apply the novel and first-step models to a standardized data set where edge weights are

165   controlled for bias associated with wide and narrow-ranging families. Edge weights are controlled so

166   the individual edge weight for a particular dinosaur family in any one time bin equals the number of

167   newly colonized continents divided by the number of possible edges. For example, a dinosaur family

168   expanding from an existing range of four continents to a single new continent would contribute 4 to the

169   total edge weight in the original data analysis, and is thus biased towards already wide-ranging families.

170   In contrast, this would only contribute a value of 1 in the standardized analysis (0.25 per edge). We also

171   carry out a directed network analysis on the standardized novel and first-step models where we record

172   the direction of movement from the existing range to new continents in each time bin to decipher which

173   landmasses were most important for dinosaur migration events throughout the Mesozoic.

174   We use two metrics to quantify the connectedness of the geographic and biogeographic network

175   models, Link Density (LD) and Average Link Weight (ALW) (Newman, 2010):

176
$$LD = \frac{E}{n(n-1)}$$

177
$$ALW = \frac{\Sigma ij}{E}$$

178   where E = number of edges, n = number of potential edges, and Σij = the weight of the edge between

179   nodes i and j. LD calculates the density of the network (i.e. how close any network is to being completely

180   connected) and ALW records the connection strength of a weighted network (i.e. the mean value of all

181   edge weights within a network). The importance of each node in each biogeographic network was

182   calculated to determine how biogeographically connected each continental landmass was using degree

183   centrality (C_D) (Nieminen, 1974; Freeman, 1978) where a given node, P_k, can at most be adjacent to the

184   value of n - 1 other nodes in a network. The maximum of $C_D(P_k)$, therefore, is the value of n – 1, then

185   the proportion of other points that are adjacent to P_k is:

186
$$C_D(P_k) = \frac{\sum_{i=1}^{k} E_{ik}}{n-1}$$

187   where E_{ik} is the value of a weighted edge between nodes i and k, if i and k are connected by an edge,

188   and 0 otherwise (Freeman, 1978).

189   Network analyses were carried out in R 3.1.1 (R Core Team, 2014) using the packages "igraph"

190   1.0.1 (Csardi & Nepusz, 2006), "network" 1.11.3 (Butts et al., 2014), "MASS" 7.3-42 (Venables &

191   Ripley, 2002), "Matrix" 1.1-5 (Bates & Maechler, 2015), "sna" 2.3-2 (Butts, 2014), "NetIndices" 1.4.4

192   (Kones et al., 2009), and "tnet" 3.0.11 (Opsahl, 2009).

193

194   Origination and extinction rates of dinosaur families

195   Origination (O_r) and extinction (E_r) rates were calculated for the entire dinosaurian clade as well as for

196   the subclades of Ornithischia, Theropoda, and Sauropodomorpha. The methodology introduced by

197   Foote (2000) and modified by Foote (2003) was used:

198
$$O_r = -\ln\frac{N_{bt}}{N_{ft} + N_{bt}}$$

199
$$E_r = -\ln\frac{N_{bt}}{N_{bL} + N_{bt}}$$

200   where N_{bt} is the number of taxa crossing both the bottom and top boundaries of a time bin, N_{Ft} is the

201   number of taxa first appearing in a time bin and crossing the top boundary of that particular time bin,

202   and N_{bL} is the number of taxa crossing the bottom boundary of the time bin but having their last

203   appearance in that particular time bin. Rates are not normalized with time bin duration, so although this

204   may cause underestimation of rates in shorter time bins relative to longer time bins, Foote (2005)

205   demonstrated that both extinction and origination are pulsed rather than spread throughout time

206   intervals.

207

208 **Statistical tests**

209 Geographic and biogeographic network LDs and ALWs and evolutionary rates were detrended using

210 generalised differencing (script obtained from Graeme Lloyd:

211 http://www.graemetlloyd.com/methgd.html). Network model LDs and ALWs and evolutionary rates

212 were compared using Spearman rank correlation tests, both for the raw and generalised differenced

213 data, with false discovery rate corrections applied using the method of Benjamini and Hochberg (1995).

214 All statistical analyses were carried out using R 3.1.1.

215

216 **RESULTS**

217 **Geographic networks**

218 The geographic network models show significant trends of decreasing density (LD) and connection

219 strength (ALW) through time (Fig. 1 and Fig S2 in Appendix S1; see Table S1 in Appendix S1 for

220 network trends). The SL model allows for higher density and connection strength in the Late Triassic

221 and Early Jurassic and also facilitates greater connection strength throughout the Early and early Late

222 Cretaceous (Fig. 1). However, from the late Early Cretaceous onwards continental fragmentation is well

223 advanced so the SL network is relatively isolated (i.e. low density); despite the connection strength

224 score remaining fairly high until the Campanian. Although GEO and SL models correlate closely in the

225 raw data, they do not correlate significantly after detrending, suggesting although both models depict

226 a long-term trend of increased fragmentation, sea-level induced differences in bin-to-bin changes

227 during the Late Jurassic-earliest Cretaceous obscures this relationship over shorter timescales (see

228 Tables S2-S9 in Appendix S1 for network correlation coefficients).

229

230 **Biogeographic networks**

231 The raw biogeographic models for all dinosaur, ornithischian, and theropod taxa display a significant

232 trend of increased density through time (Fig. 2a) with raw ornithischian network density correlating

233 negatively with the geographic networks. The Maastrichtian is the most densely connected in all of the

234 raw biogeographic network models despite being the least geographically connected (Fig. 2a; Figs. S3-

235 S6 in Appendix S1). Low network density in the Middle Jurassic is a phenomenon seen across all groups

236 along with a second commonly observed dip in network density in the early-mid Late Cretaceous (Fig.

237 2a). Connection strength (ALW) is initially low before rising to a high plateau through the Late Jurassic

238 to Aptian-Albian, before a dip into the Late Cretaceous (Fig. 3a). The dinosaur sub-clades show variable

239 patterns with theropod connection strength showing a significant increasing trend to a peak in the Late

240 Cretaceous and correlating negatively with the geographic network models (Fig. 3a). In contrast,

241 ornithischian and sauropodomorph connection strength peaks in the Late Jurassic before falling through

242 the rest of the Mesozoic, albeit with a significant rise in the latest Cretaceous in the ornithischian data

243 set (Fig. 3a). In all data sets, the Laurasian (Asia, Europe, North America) and Samafrican (Africa,

244 South America; Upchurch (2008)) continents display the highest degree of connectivity, with East

245 Gondwanan (Antarctica, Australia, India, Madagascar; Upchurch (2008)) landmasses only assuming a

246 more connected role from the Aptian-Albian onwards (Figs. S7a-S10a in Appendix S1).

247 The novel biogeographic models for all dinosaur and theropod taxa show no discernible trend

248 in density through time and do not correlate with the geographic network models (Fig. 2b). Novel model

249 density is highest amongst all dinosaurs and theropods during the Early Jurassic, Aptian-Albian and the

250 Maastrichtian, with lows that match those in the raw networks in the Middle Jurassic and early-mid

251 Late Cretaceous (Fig. 2b; Figs. S11-S14 in Appendix S1). Ornithischians display low network density

252 until the Late Jurassic before a significant increasing trend through the rest of the Mesozoic which

253 correlates negatively with the geographic networks. Sauropodomorph network density peaks in the Late

254 Triassic-Early Jurassic before significantly decreasing through the Middle Jurassic-Cretaceous (Fig.

255 2b). Novel connection strength starts low before a sharp increase into the Late Jurassic, where we see

256 the highest number of connections across all dinosaurs, ornithischians, and sauropodomorphs, with

257 theropod connection strength peaking slightly later in the Berriasian-Barremian (Fig. 3b). Connection

258 strength then decreases through the Cretaceous before a universal increase in the Campanian-

259 Maastrichtian (Fig. 3b). Standardized connection strength largely reflects the unstandardized data, but

260 with a more pronounced peak in the Late Jurassic and by relatively reduced connectivity in the Early

261 Jurassic, Aptian-Albian, and Maastrichtian (Fig 3c). Standardized connection strength correlates

262 positively with geographic network density in the all dinosaur and sauropodomorph data. The novel

263 biogeographic data sets are similar to the raw data sets with regard to the connectivity of individual

264 nodes with Laurasian and Samafrican landmasses dominating, and East Gondwanan continents not

265 featuring significantly until the Aptian-Albian (Figs. S7b-S10b in Appendix S1). The majority of

266 Jurassic-Early Cretaceous connections are routed into African and Laurasian landmasses with most of

267 these connections occurring out of Europe (Figs. 4ab). In the Late Cretaceous the highest proportions

268 of connections originate from North America, Asia and South America and there are a higher proportion

269 of East Gondwanan destinations (Figs. 4ab). One striking pattern is that although Europe shows a high

270 degree of outward connectivity in the Jurassic-Early Cretaceous, there are no inward connections to

271 Europe in the Early-Mid Jurassic or the Aptian-Albian (Fig. 4c).

272   All dinosaur, theropod, and sauropodomorph first-step biogeographic network densities peak

273 in the Early Jurassic whilst ornithischians peak in the Late Jurassic (Fig. 2c and Fig. 5; Figs. S15-S17

274 in Appendix S1). All clades exhibit a declining trend (which is statistically significant in all dinosaurs

275 and sauropodomorphs) through the Cretaceous with short-lived peaks in the Campanian (Fig. 2c). All

276 dinosaur and sauropodomorph first-step network density correlates significantly with the geographic

277 network models. First-step connection strength is initially low before a sharp rise to a peak in the Late

278 Jurassic-earliest Cretaceous followed by a decline through the late Early-Late Cretaceous before a rise

279 in the latest Cretaceous in all groups apart from the sauropodomorphs (Fig. 3d and Fig. 5), which display

280 a significant declining trend through the Mesozoic and correlate positively with the geographic network

281 models. Standardized connection strength differs from the unstandardized data, with relatively higher

282 connection strength in the Middle Jurassic and early Late Cretaceous-Campanian and by relatively

283 reduced connection strength in the Early Jurassic and Maastrichtian (Fig 3e). We see positive

284 correlations between standardized connection strength and geographic network density and connection

285 strength in the sauropodomorph and theropod data sets. As expected, the first-step models show more

286 sporadic node connectivity than the raw and novel biogeographic connection models, with an even

287 lower prevalence of East Gondwanan connectivity (Figs. S7c-S10c in Appendix S1) as most dinosaur

288 families occur on Laurasian and Samafrican landmasses before their first East Gondwanan occurrences.

289 The majority of Jurassic-Early Cretaceous "first steps" are routed into North America and Asia with

290 most of these connections occurring out of South America and Europe (Figs. 4de). In the Late

291 Cretaceous, almost all of the "first steps" occur between Laurasian landmasses with a small proportion

292   of inward "first steps" to South America and outward "first steps" to Australia and South America (Figs.

293   4de). The pattern of European high outward but low inward connectivity in the Jurassic-Early

294   Cretaceous persists in the first-step model.

295

296   **Origination and extinction rates of dinosaur families**

297   All dinosaur clades show initially high origination rates in the Early-Middle Jurassic before

298   rates decline through the Late Jurassic and Cretaceous (Fig. S18a in Appendix S1). Dinosaur origination

299   rates correlate significantly with the GEO and SL geographic models, with higher origination rates

300   corresponding to a higher density and connection strength of continental connection. These significant

301   results are repeated in all the dinosaur subclades. However, almost all the significant correlations are

302   lost after detrending the data. Sauropodomorph origination rates correlate significantly with first-step

303   biogeographic network density and novel and first-step network connection strength (original and

304   standardized data); suggesting high sauropodomorph origination rates are contemporaneous with

305   continental aggregation and a greater density of intercontinental "first steps". Dinosaur origination rates

306   correlate negatively with novel (original and standardized data), and first-step connection strength after

307   generalised differencing (Fig. 6a), suggesting reductions in the biogeographic connectivity result in

308   increases origination rates. Similar negative correlations are observed, after generalised differencing,

309   between ornithischian origination rates and first-step biogeographic network density and connection

310   strength and between sauropodomorph raw and novel biogeographic network density and origination

311   rates (Fig. 6bc).

312   Extinction rate trajectories vary amongst dinosaur clades. Dinosauria as a whole display high

313   initial extinction rates early in the Mesozoic which decline through the Jurassic before rising in the

314   Early Cretaceous and fall into the Late Cretaceous (Fig. S18b in Appendix S1). Theropod and

315   ornithischian extinction rates are lower in the Early-Middle Jurassic and peak during the Late Jurassic-

316   Early Cretaceous whilst sauropodomorph extinction rates are highest in the Early Jurassic and Late

317   Cretaceous. Dinosaur extinction rates correlate positively with SL network density. Ornithischian

318   extinction rates correlate negatively with the GEO network density after detrending, suggesting that

319   increases in continental connectivity result in reductions in extinction rates. Theropod extinction rates

320　correlate positively with novel connection strength, suggesting that a greater number of novel

321　connections lead to higher extinction rates. Sauropodomorph extinction rates correlate positively with

322　SL connection strength after detrending, suggesting that increases in geographic connectivity

323　correspond to increases in sauropodomorph extinction rates.

324

325　**DISCUSSION**

326　The geographic network models display the sequence of continental fragmentation observed throughout

327　the Mesozoic, from total aggregation in the early Mesozoic to complete continental isolation by the end

328　of the Cretaceous. The conditioning of connectivity on sea level allows for possible inter-continental

329　connectivity between all major landmasses up until the Berriasian-Barremian, whereas the Middle

330　Jurassic represents the minimum time period when all continents are connected by direct continental

331　aggregation. Sea level conditioning has little effect on connectivity in the latest Cretaceous, as sea level

332　is so high that the probability of land bridge formation is very low with possible links persisting only

333　between Europe and Asia.

334　　　There is little correlation between continental fragmentation and raw or novel dinosaur

335　biogeographic connectivity through the Mesozoic. In fact, the raw and novel ornithischian and raw

336　theropod biogeographic models correlate negatively with the geographic models, suggesting the

337　movement of dinosaur families increased as continental fragmentation occurred. Patterns observed in

338　the raw and novel biogeographic connection networks can thus be explained by two processes; (i) a

339　residual function of taxonomic rank, where long-lived dinosaurian families have become established in

340　their biogeographic distributions earlier in the Mesozoic before sustaining this pattern through to the

341　end of the Cretaceous (Ali & Krause, 2011; Benson et al., 2012; Ezcurra & Agnolin, 2012b, a); and (ii)

342　a spatiotemporal sampling effect where the latter stages of the Cretaceous (i.e. Campanian-

343　Maastrichtian) are the best sampled time bins (Lloyd et al., 2008; Barrett et al., 2009; Starrfelt & Liow,

344　2015), which contain many biogeographic connections that were established earlier in the Mesozoic,

345　but are not recovered from previous, more poorly sampled time bins (e.g. Cenomanian-Santonian)

346　(Barrett et al., 2009; Mannion & Upchurch, 2011; Benson et al., 2013; Starrfelt & Liow, 2015). This is

347　particularly true amongst the Gondwanan landmasses.

348   The residual distribution effect is mitigated by the novel biogeographic connection model, but

349   the sampling effects are still problematic, particularly in the East Gondwanan landmasses where

350   sampling is known to be particularly poor (Smith et al., 2008; Ali & Krause, 2011; Benson et al., 2013).

351   For example, we see limited biogeographic connectivity between the East Gondwanan landmasses until

352   the later Cretaceous, when sampling of Gondwanan taxa is known to improve (Benson et al., 2013).

353   However, it is also noteworthy that direct inter-continental connections between the most southerly

354   landmasses are thought to have remained intact more recently than those between more northerly

355   landmasses; e.g. Antarctica-Australia 84 Ma (Veevers, 2004), Madagascar-India 92.5 Ma (Ali &

356   Krause, 2011), South America-Africa 100 Ma (Gheerbrant & Rage, 2006); Samafrica-East Gondwana

357   138 Ma (Smith et al., 1994); a factor which may partly explain the increased importance of Gondwanan

358   connections from the Aptian-Albian onwards. Whilst most time bins are dominated by the Laurasian

359   and Samafrican landmasses, Australia assumes a more connected role from the Aptian-Albian onwards,

360   Antarctic faunas are sparse throughout the entire sequence but show increased connectivity in the

361   Campanian-Maastrichtian, and Madagascar and India are most connected in the Maastrichtian. All of

362   these connections to East Gondwanan continents are inward and the majority of dinosaurian families

363   (e.g. Abelisauridae, Dromaeosauridae, Dryosauridae, Hadrosauridae and Nodosauridae) behind these

364   connections are already well established in their distributions on Samafrican and Laurasian landmasses

365   (Ezcurra & Agnolin, 2012b, a), as reflected by the absence of East Gondwanan first-step connectivity

366   after the Lower Jurassic. This suggests that this delayed connectivity in the East Gondwanan continents

367   reflects a geographic sampling bias where these landmasses are more poorly sampled than their

368   Samafrican and Laurasian counterparts (Ali & Krause, 2011; Benson et al., 2013).

369   The first-step biogeographic model bypasses the problems of the residual distribution effect

370   and reduces the effect of uneven geographic sampling by only considering a taxon's first inter-

371   continental connection. As a result, we see reductions in connectivity through time in the all dinosaur

372   and sauropodomorph first-step models that correlate well with continental fragmentation. Despite being

373   more robust to sampling error, the first-step model fails to allow the possibility of further range

374   expansion following the initial inter-continental connections of any particular taxon. It is therefore

375   likely that this model underestimates connectivity across the entire network. Lack of correlation

376 between ornithischian and theropod first-step models and the geographic network models may be partly

377 explained by the greater motility of these clades. In comparison with the sauropodomorphs,

378 ornithischians and theropods contain many small genera which may have been more likely to cross

379 narrow seaways via swimming or rafting, a process that is hypothesised to have occurred in other

380 Mesozoic vertebrates (Longrich et al., 2015). This analysis also includes avian theropods (birds), which

381 have increased dispersal capabilities via flight and whose distributions are thus less likely to be

382 exclusively controlled by vicariant processes. This has been shown to be the case for other flying

383 Mesozoic vertebrates (i.e. pterosaurs) (Upchurch et al., 2015).

384   Although the raw biogeographic networks tell us little about the movement of dinosaurian

385 families as patterns are obscured by the residual effects of earlier Mesozoic familial distributions, the

386 novel connection and first-step models should give information about the movement of dinosaur

387 families throughout the Mesozoic. All the novel network models show a cosmopolitan distribution of

388 dinosaurian taxa through the Triassic, Jurassic and Early Cretaceous, albeit one that is obscured by

389 variation in spatiotemporal sampling intensity. The widely accepted poorly sampled Middle Jurassic

390 and early Late Cretaceous (Wang & Dodson, 2006; Barrett et al., 2009; Mannion & Upchurch, 2011;

391 Upchurch et al., 2011; Benson et al., 2013; Stubbs et al., 2013; Dunhill & Wills, 2015; Starrfelt &

392 Liow, 2015) time bins stand out as periods of apparent low biogeographic connectivity in all the network

393 models. The first-step models echo the novel connection network *"cosmopolitanism"* up until the

394 earliest Cretaceous, a result that is consistent with other studies (Ezcurra & Agnolin, 2012a), before we

395 see a sharp decline in the number of "first steps" leading into the Aptian-Albian. These results concur

396 with the patterns observed in the geographic networks, where the possibility of full network

397 connectivity persists up until the Berriasian-Barremian. The novel biogeographic connection networks

398 record decreased connectivity between Europe and the other Laurasian landmasses and Africa during

399 the Aptian-Albian, which is partially concurrent with the isolation of Europe during the Barremian-

400 Aptian detected by Ezcurra and Agnolin (2012a). It also worth noting that all the European connections

401 in this time bin are outgoing, i.e. no new taxa migrating into Europe (Fig. 5c). This may be indicative

402 of a sampling bias where the European record is poor in this interval; however, there are over 100

403 dinosaur occurrences in the Aptian-Albian of Europe. Biogeographic connectivity declines through the

404 more poorly sampled Cenomanian-Santonian before a resurgence of novel and first-step connections in

405 the Campanian between the Laurasian landmasses and South America, despite apparent continental

406 isolation and high sea levels. This could be a sampling artefact where the Campanian is better sampled

407 than the earlier Cenomanian-Santonian (Mannion & Upchurch, 2011; Benson et al., 2013). However,

408 this result is also consistent with the Campanian-Maastrichtian *"Atlantogea"* faunal province of linked

409 Laurasian and Euro-Samafrican-East Gondwanan landmasses proposed by Ezcurra & Agnolin (2012a).

410 The apparent prolonged faunal exchange amongst major landmasses throughout the Late Cretaceous is

411 not consistent with the geographic network models and adds support to the idea that, although

412 continental splitting undoubtedly reduced intercontinental faunal exchange, it did not completely inhibit

413 the migration of terrestrial clades.

414 The high origination rates across all dinosaur clades in their early evolutionary history are

415 consistent with other studies that have identified high levels of diversification in the lower half of the

416 dinosaur tree using phylogenetic methods (Lloyd et al., 2008). Extinction rates vary between major

417 dinosaurian clades with the sauropodomorphs showing a very different pattern to the ornithischians and

418 theropods with Middle Jurassic peaks in extinction rates associated with the demise of the prosauropod

419 lineages (e.g. Yunnanosauridae) and basal sauropods (e.g. Vulcanodontidae) and a Cretaceous peak

420 associated with the demise of characteristic Late Jurassic-Early Cretaceous lineages (e.g.

421 Camarasauridae, Brachiosauridae, Diplodocidae).

422 The close, positive correlations observed between dinosaurian origination rates and the density

423 and connection strength of the geographic network models suggests a greater amount of continental

424 connection results in increased origination rates. We also see positive correlations between the

425 sauropodomorph novel and first-step models and origination rates, suggesting that a greater number of

426 novel and first-step connections resulted in higher origination rates. These results are contrary to the

427 expected pattern that increased continental isolation and decreased intercontinental faunal exchange

428 would lead to increased levels of allopatric speciation via isolation of dinosaur populations on separate

429 landmasses. There are two explanations why this may not be the case: (i) the analyses are carried out at

430 a higher taxonomic rank, i.e. families, across relatively long time bins and, therefore, extinction and

431 origination rates observed at generic or species level may be somewhat different; and (ii) this finding

432   may be the result of autocorrelation where the geographic and first-step biogeographic models and

433   origination rates share a downward trend through time, but where one set of variables is not necessarily

434   driving the other. Indeed, it is likely that these patterns are a result of the fact that origination rates were

435   highest in the early part of dinosaur evolution (Lloyd et al., 2008), which just so happens to coincide

436   with a period of maximum continental aggregation, before the dampening of origination rates through

437   the evolution of the dinosaurian clade and concurrent fragmentation of the Pangaean landmass. This is

438   highlighted by the fact that this correlation is not retained after detrending. Although we still see a

439   significant positive correlation between the GEO model and sauropodomorph origination rates after

440   generalised differencing, we also see a number of strong, negative correlations between the novel and

441   first-step biogeographic models and origination rates after detrending. This suggests that reductions in

442   novel intercontinental exchanges and "first steps" are concurrent with increases in origination rates,

443   supporting a hypothesis that reduced intercontinental migration and increased isolation of dinosaurian

444   populations caused an increase in lineage splitting.

445   Positive correlations between geographic connectedness and extinction rates were also

446   observed, suggesting increased continental connectivity resulted in increased levels of dinosaurian

447   extinction. Again, this could be an autocorrelative effect where extinction rates were high during the

448   early evolution of dinosaur subclades when continental aggregation was also at its greatest, a hypothesis

449   backed by the fact that these correlations disappear after detrending. Both negative and positive

450   correlations were observed between geographic connectedness and extinction rates after detrending,

451   suggesting that both increasing and decreasing continental isolation resulted in increased regional

452   extinction rates.

453

454   **CONCLUSIONS**

455   Dinosaur macro-biogeographic structure was influenced by continental fragmentation and rising sea

456   levels throughout the Mesozoic, with fewer first-step family-level connections occurring in the later

457   Cretaceous than in the Triassic, Jurassic and earlier Cretaceous when continents were more closely

458   aligned. The lack of a negative trend in connectivity observed throughout the Mesozoic in the raw

459   biogeographic models, despite the reduced geographic connectivity, suggests dinosaurian macro-

460 biogeographic structure, at least at higher taxonomic levels, was established during the Jurassic and

461 earlier Cretaceous and then sustained through to the end of the Cretaceous. The lack of a relationship

462 between geographic and biogeographic connectedness in the raw and novel biogeographic connection

463 networks is likely a result of this residual connectivity and spatiotemporal sampling biases, where East

464 Gondwanan landmasses in particular, have a very poorly recorded fossil record up until the latest

465 Cretaceous. A possible future method of allaying sampling issues of poorly sampled geographic regions

466 such as East Gondwana could be to incorporate phylogeny into the network models by considering

467 ghost ranges on phylogenetic trees coupled with ancestral areas analysis. The discrepancies between

468 the geographic and biogeographic network models, i.e. the reduced but continued intercontinental

469 faunal exchange right up to the end of the Cretaceous, suggests that although continental splitting

470 certainly reduced the exchange of terrestrial clades, it did not completely inhibit it.

471 There is some evidence to suggest that increased continental and biogeographic isolation led to

472 increased origination and extinction rates in some dinosaurian clades. These findings fit with the

473 hypothesis that dinosaurian evolution was influenced by decreased migration between continental

474 landmasses and increased regional extinction throughout the Mesozoic (Sereno 1999), but dinosaurian

475 macroevolutionary and biogeographic patterns were not exclusively the result of uniform vicariant or

476 dispersive processes (Rowe et al., 2011; Xu et al., 2013).

477 A network-based approach offers a simple and elegant method of quantifying complex

478 biogeographic patterns by combining detailed insights into underlying biogeographic structure and

479 easily interpretable reconstructions of biogeographic connectivity. Thus far, network methods have

480 been seldom used in palaeobiological analysis (Sidor et al., 2013; Vilhena et al., 2013) and they offer

481 a multitude of opportunities in the fields of both palaeo- and contemporary biogeography.

482

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680 **Supporting Information**

681 Additional Supporting Information may be found in the online version of this article:

682 **Appendix S1** Supplementary Tables and Supplementary Figures

683 **Appendix S2** Supplementary data sets

684

685 **Biosketch**

686 Alexander Dunhill is a Research Fellow at the University of Leeds. His research topics are large-scale

687 biogeographic patterns and mass extinctions and assessing biasing factors in the fossil record.

688 Author contributions: A.M.D. and J.S. conceived the ideas; A.M.D., J.B., and H.N. collected the data;

689 A.M.D., H.N. and J.S. analysed the data. A.M.D. led the writing.

690

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692

693   Figure Legends

694

695   **Figure 1** Time series of geographic network models through the Mesozoic depicting density (LD) of

696   GEO and SL models and sea level conditioned connection strength (ALW) of SL model. GEO LD =

697   link density of GEO model; SL LD = link density of SL model; SL ALW = average link weight of sea

698   level model. There is no GEO ALW as the GEO model is binary (0 = no connection or 1 = connection).

699

700   **Figure 2** Times series of biogeographic network density (LD) for Dinosauria, Ornithischia, Theropoda,

701   and Sauropodomorpha; (a) raw network model; (b) novel network model; (c) first-step network model.

702   E = Early; M = Middle; L = Late.

703

704   **Figure 3** Times series of biogeographic network connection strength (ALW) for Dinosauria,

705   Ornithischia, Theropoda, and Sauropodomorpha; (a) raw network model; (b) novel network model; (c)

706   standardized novel network model (d) first-step network model (e) standardized first-step network

707   model. E = Early; M = Middle; L = Late.
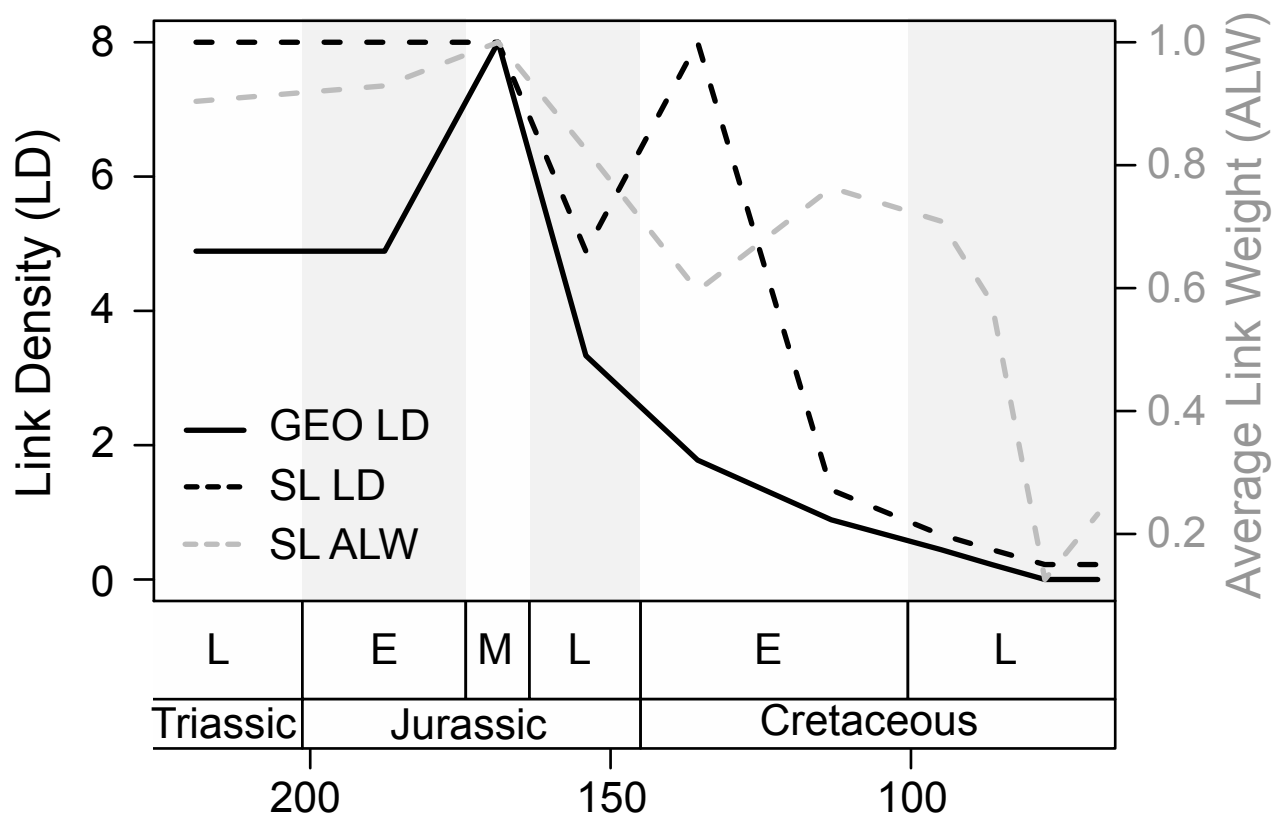
708

709   **Figure 4** Directed connectedness of continental nodes through the Mesozoic for the Dinosauria. (a)

710   standardized novel network model inward connections; (b) standardized novel network model outward

711   connections; (c) directed connections from Europe during the Aptian-Albian; (d) standardized first-step

712   network model inward connections; (e) standardized first-step network model outward connections. EJ

713   = Early Jurassic; MJ = Middle Jurassic; LJ = Late Jurassic; B-B = Berriasian-Barremian; A-A = Aptian-

714   Albian; C-T = Cenomanian-Turonian; C-S = Coniacian-Santonian; Ca = Campanian; Mt =
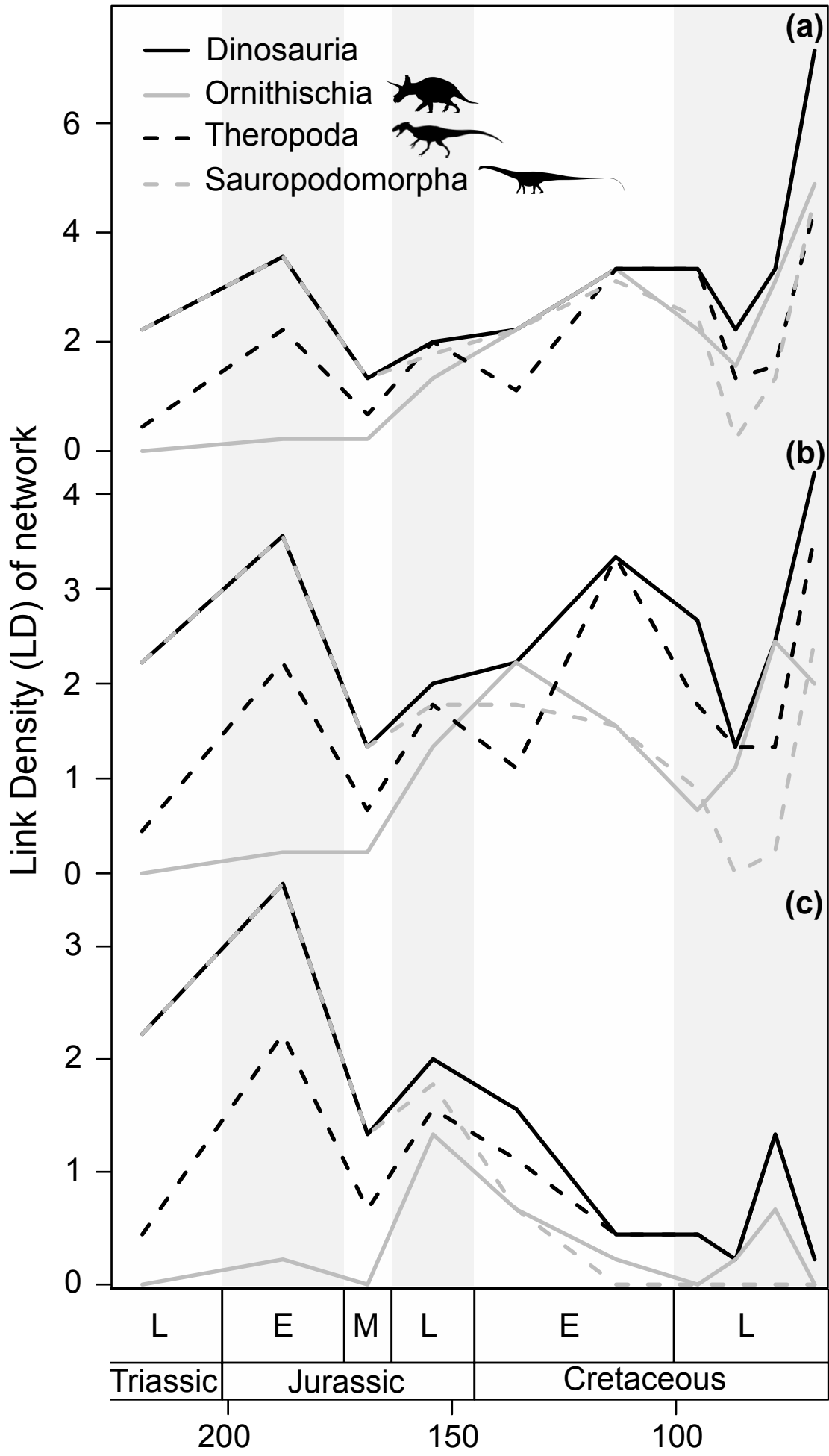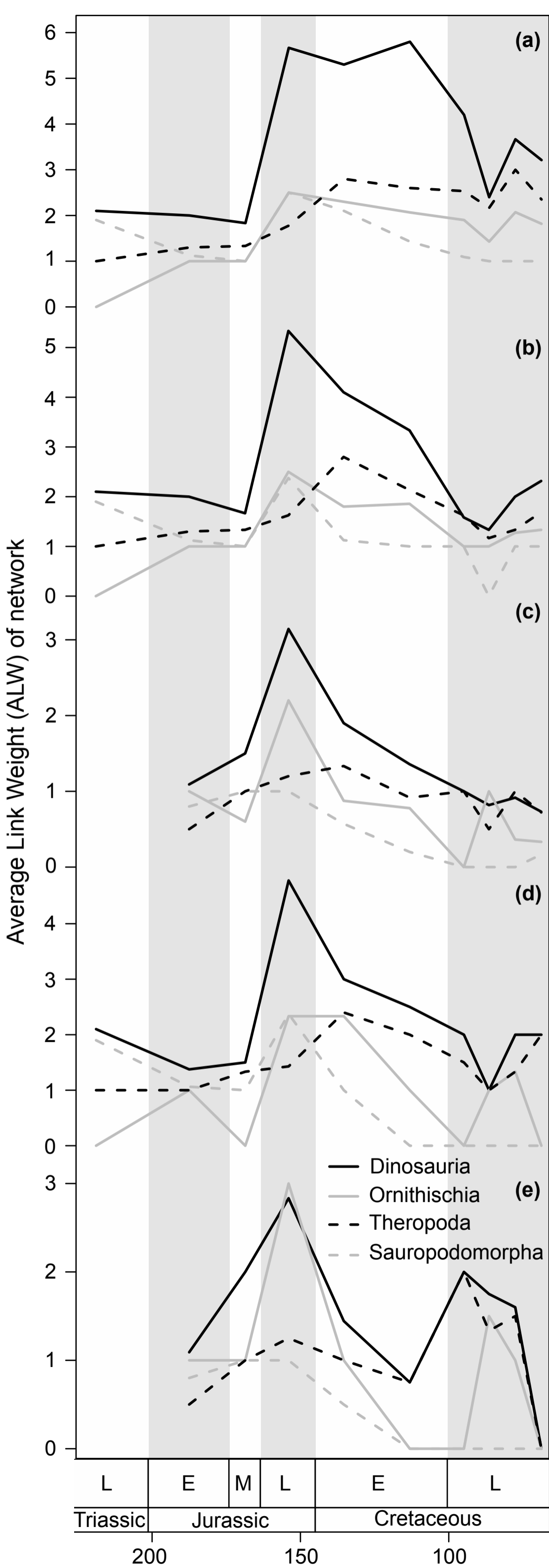
715   Maastrichtian.

716

717   **Figure 5** First-step biogeographic network models for all dinosaur taxa through the Mesozoic.

718   Thickness of lines represents number of families shared between landmasses; (a) Late Triassic; (b)

719   Early Jurassic; (c) Mid Jurassic; (d) Late Jurassic; (e) Berriasian-Barremian; (f) Aptian-Albian; (g)

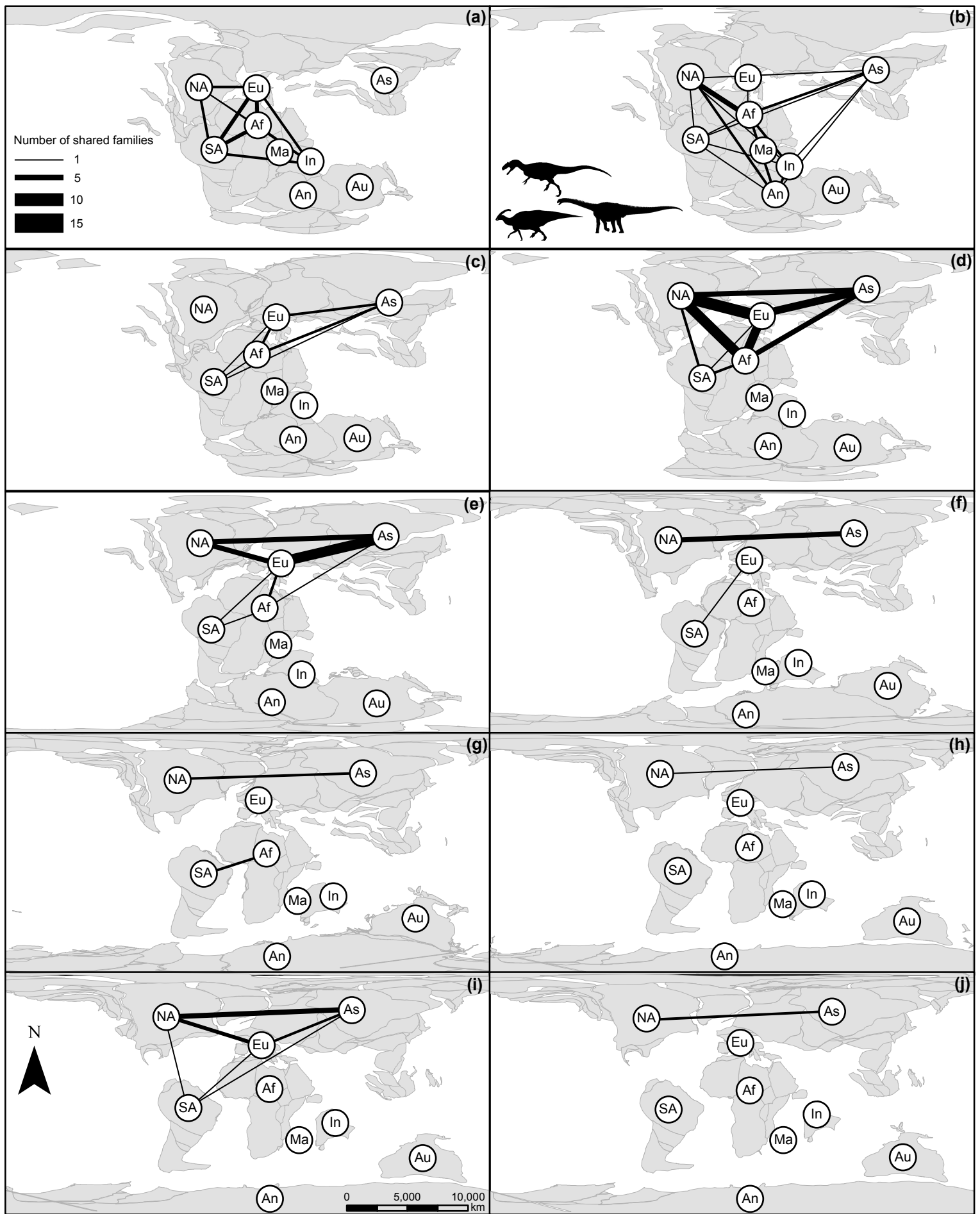720   Cenomanian-Turonian; (h) Coniacian-Santonian; (i) Campanian; (j) Maastrichtian.

721

722   **Figure 6** Scatterplots showing significant negative correlations after detrending between origination

723   rates and (a) standardized novel network connection strength (ALW) across all Dinosauria; (b) novel

724   network density (LD) across the Sauropodomorpha; (c) first-step network density (LD) across the

725   Ornithischia.

Legend:
- Africa
- Antarctica
- Asia
- Australia
- Europe
- India
- Madagascar
- North America
- South America

(a) IN — Degree of centrality (CD) of nodes: EJ, MJ, LJ, B-B, A-A, C-T, C-S, Ca, Mt

(b) OUT: EJ, MJ, LJ, B-B, A-A, C-T, C-S, Ca, Mt

(c) Aptian-Albian

Number of connections
- 0.2
- 1.0
- 2.5

Map labels: NA, As, Eu, Af, SA, Ma, In, Au, An

N

0   5,000   10,000km

(d) IN — Degree of centrality (CD) of nodes: EJ, MJ, LJ, B-B, A-A, C-T, C-S, Ca, Mt

(e) OUT: EJ, MJ, LJ, B-B, A-A, C-T, C-S, Ca, Mt

(a) $r_s = -1$, $p < 0.001$

(b) $r_s = -0.89$, $p = 0.03$

(c) $r_s = -0.93$, $p = 0.007$